

**Effects of oil development on habitat quality and its perception by
mixed-grass prairie songbirds**

by

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Abstract

Oil development has altered mixed-grass prairies in south-eastern Alberta, potentially impacting habitat quality and suitability for grassland birds. I tested whether three passerines can accurately assess habitat quality in the presence of this anthropogenic disturbance. I monitored nesting success and stress hormones and tested for differences in settlement patterns at sites impacted by real oil infrastructure, simulated noise, and control sites. Corticosterone levels suggested that habitat quality was reduced in some cases by disturbance. I also found disturbance impacted perceived habitat quality; however, perceived and realized quality were not always affected similarly. Both Chestnut-collared Longspurs and Savannah Sparrows exhibited stress near infrastructure, but higher-quality Longspur females nested near infrastructure while Savannah Sparrows avoided it. This mismatch may help explain why species suffer disproportionately in response to disturbances. Managers should reduce human presence by concentrating above-ground infrastructure using directional drilling, decommissioning old well heads, reclaiming roads, and reducing traffic.

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Dedication

I want to dedicate this thesis to Laura Burns: my wife, field technician, lab technician, editor, project manager, bread winner, confidant, cat mom, therapist, chef, and best friend. Laura, I love you, and I couldn't have done this without you.

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Chapter 1: Introduction

Conservation biology is an interdisciplinary field that directly addresses the impacts of anthropogenic disturbances on landscapes and ecosystems with the maintenance of biodiversity at its forefront (Soulé 1985). This focus on biodiversity leads to a concentration of effort on managing species at risk. To identify species at risk, population declines and range decreases are tracked using species distribution models based on occurrence and abundance data (Guisan and Thuiller 2005, Sinclair et al. 2010, Bland et al. 2015). The weakness of this approach is that it is reactive, and populations can only be deemed at risk once they have already experienced significant declines (Maron et al. 2012). The emerging field of conservation physiology seeks to identify physiological aspects of individuals that could help predict whether there is a risk of future declines for studied populations (Wikelski and Cooke 2006). Measures of organismal condition, disease resistance, toxicant tolerance, or susceptibility to stress may be able to help identify populations or species that are likely to be most negatively affected by human-induced rapid environmental change (Cooke et al. 2013). Changes in these individual physiological measures may be more prevalent in populations at risk of declining, possibly acting as early warning signs of negative responses to human induced environmental change (Martin et al. 2018b). As we refine our ability to apply the approach of conservation physiology to conservation issues, the hope is that conservation biology can shift from a reactive discipline, attempting to mitigate effects on species that have already suffered declines, to a proactive discipline that is better able to predict and prevent future species declines (Ellis et al. 2012).

I applied the paradigm of conservation physiology to examine species-specific responses of songbirds to conventional oil development in the North American mixed-grass prairies. I tested the potential of using measures of physiological stress to identify sensitive species using three

grassland songbirds experiencing unequal rates of range-wide decline (-1.36% to -5.9% per year; Environment and Climate Change Canada 2017). The southeastern area of the province of Alberta has been a stronghold for mixed grass prairie habitat in Canada (Samson et al. 2004). However, this region is experiencing rapid development (Daniel 2015). This makes it the perfect location to test whether species sensitivity to habitat alteration and species at risk status are linked intrinsically. Habitat suitability, defined by both habitat quality and whether species can accurately assess habitat quality, may be affected by oil development, and individual measures of stress may represent physiological responses to these changes in habitat suitability. In this chapter I will introduce the mixed-grass prairie ecosystem and some of the threats facing it. This will include discussions of the realities for migratory grassland songbirds breeding in this dynamic and human influenced landscape, approaches to measuring habitat quality for grassland songbirds, the physiology behind using stress to examine the capacity of birds to cope with the changes in their environment and measuring the perception of habitat quality by grassland songbirds. I will conclude by outlining the research objectives of this thesis.

The State of the Prairies

The prairie region of North America is a high conservation priority as it has historically been heavily impacted by land conversion for annual crops and remains highly threatened by human land-use practices today (Hoekstra et al. 2005, Gage et al. 2016, Comer et al. 2018). Consequently, bird populations within grassland and aridland ecosystems are experiencing the steepest declines among North American bird guilds (Herkert 1995, Brennan and Kuvlesky 2005, North American Bird Conservation Initiative 2016, BirdLife International 2018), and the second steepest declines among Canadian bird guilds (North American Bird Conservation Initiative

Canada 2012). Since the initiation of the North American Breeding Bird Survey (BBS) in 1966, grassland bird species in Canada have declined by 55% on average (World Wildlife Fund 2017). There are now 17 birds with breeding grounds on the prairies listed under the Canadian Species At Risk Act (Table 1). Alarming, 72 - 99% of mixed grass prairie habitat was lost between 50 - 150 years ago (Samson et al. 2004), before the initiation of the BBS. Since much of the habitat loss occurred before baseline population estimates were established for these species, the total declines suffered by some grassland obligates have likely been more drastic than is currently estimated.

Habitat loss, degradation, and fragmentation from agricultural (~21.5 million hectares converted 2009-2016, Gage et al. 2016) and energy development (~1.5 million hectares converted 2000-2012, Allred et al. 2015) continue to be major threats to grassland ecosystems (Brennan and Kuvlesky 2005, Roch and Jaeger 2014, North American Bird Conservation Initiative 2016). The physical footprint of the infrastructure associated with energy development is relatively small and diffuse on the landscape (Allred et al. 2015). However, under current development practices, the ecological footprints of these oil developments may be surprisingly large once fragmentation from roads and transmission lines, noise from infrastructure and service vehicles, and encroachment of invasive vegetation are considered (Sliwinski and Koper 2012, Francis and Barber 2013b, Koper et al. 2014). New technologies, such as horizontal drilling, can help reduce the spatial distribution of well heads. By following and improving on industry best practices many of the consequences of oil development could be circumvented (Finer et al. 2013).

Some species, such as Brown-headed Cowbirds (*Molothrus ater*), may benefit from these habitat changes (Bernath-Plaisted et al. 2017). Brown-headed Cowbirds are attracted to roads and other linear oil-related infrastructure, perhaps because as obligate brood parasites they rely on the

provided vantage points to search for nests to parasitize (Sliwinski and Koper 2012). In contrast, Greater Sage-Grouse (*Centrocercus urophasianus*) have suffered significant reductions in leks (breeding sites), and males displaying in these areas, coinciding with energy development (Walker et al. 2007).

When estimating the impacts of energy development on bird communities using changes in abundance and distribution, some impacts may be overlooked (Ellis et al. 2012, Maron et al. 2012). Demographic shifts in habitat use can result in age-biased reductions in pairing or reproductive success (Habib et al. 2007), habitat modifications could result in increased disease transmission (Walker et al. 2007), noise from infrastructure could impact communication (Francis et al. 2010, Curry et al. 2018), and nesting near energy infrastructure can cause stress and reduce fitness (Kleist et al. 2018). Therefore, habitat degradation from oil development could reduce the fitness of the individuals occupying that habitat and impact the persistence of vulnerable populations (Ellis et al. 2012). Quantifying the quality of the surrounding habitat after alteration by oil development is critical to prioritizing industry standards to minimize these effects and should, therefore, be a priority for future research.

Table 1. Status and declines of birds with breeding ranges in the Canadian prairies.

COMMON NAME	SPECIES NAME	BBS TREND ¹	SARA STATUS ²	IUCN STATUS ³
GREATER SAGE-GROUSE	<i>Centrocercus urophasianus</i>	NA	Endangered	Near Threatened
WHOOPING CRANE	<i>Grus americana</i>	NA	Endangered	Endangered
BURROWING OWL	<i>Athene cunicularia</i>	-3.84	Endangered	Least Concern
SHORT-EARED OWL	<i>Asio flammeus</i>	-4.64	Special Concern	Least Concern
COMMON NIGHTHAWK	<i>Chordeiles minor</i>	-2.48	Threatened	Least Concern
FERRUGINOUS HAWK	<i>Buteo regalis</i>	1.18	Threatened	Least Concern
MOUNTAIN PLOVER	<i>Charadrius montanus</i>	NA	Endangered	Near Threatened
PIPING PLOVER	<i>Charadrius melodus</i>	NA	Endangered	Near Threatened
LONG-BILLED CURLEW	<i>Numenius americanus</i>	-0.78	Special Concern	Least Concern
LOGGERHEAD SHRIKE	<i>Lanius ludovicianus excubitorides</i>	-2.72	Threatened	Near Threatened
RED-HEADED WOODPECKER	<i>Melanerpes erythrocephalus</i>	-2.20	Threatened	Least Concern
BARN SWALLOW	<i>Hirundo rustica</i>	-3.28	Threatened	Least Concern
SAGE THRASHER	<i>Oreoscoptes montanus</i>	NA	Endangered	Least Concern
BOBOLINK	<i>Dolichonyx oryzivorus</i>	-3.23	Threatened	Least Concern
SPRAGUE'S PIPIT	<i>Anthus spragueii</i>	-3.00	Threatened	Vulnerable
BAIRD'S SPARROW	<i>Centronyx bairdii</i>	-1.92	Special Concern	Least Concern
MCCOWN'S LONGSPUR	<i>Rhynchophanes mccownii</i>	-5.81	Special Concern	Least Concern
CHESTNUT-COLLARED LONGSPUR	<i>Calcarius ornatus</i>	-5.90	Threatened	Vulnerable

¹Breeding Birds Survey data 1970-2015 (Environment and Climate Change Canada 2017)

²Species At Risk public registry (Government of Canada 2018)

³IUCN Red List (Nature 2018)

Habitat Quality in Grasslands

Habitat quality is realized as an organism's ability to survive and reproduce, often expressed as productivity (Boulinier and Danchin 1997, Vance et al. 2003, Doligez et al. 2003, Faaborg et al. 2016). The requirements of high-quality habitat for a migratory songbird will be dependent on the life-history stage of an individual and will change seasonally (Sherry and Holmes 1996, Norris and Marra 2007). In the non-breeding season, the requirements for an individual are to stay alive and build energy stores for return migration, as there is no reproductive output (Sherry and Holmes 1996). During the breeding season, occupied habitat must provide the conditions for adults to survive and reproduce, and for young of the year to survive. Therefore, productivity can be thought of as a combination of adult survival, reproductive output per adult, and juvenile survival (Powell et al. 1999). Food availability is often a key component of habitat quality (Madliger et al. 2015, Cutting et al. 2016), as adults must find enough food to keep themselves alive and feed young. However, insectivorous grassland passerines are generally not food-limited (Mcewen et al. 1972, Wiens and Rotenberry 1979), suggesting that food availability is not an important factor in habitat quality for grassland songbirds. Adult survival, and the survival of their altricial young, must therefore be more strongly impacted by mortality due to predation than food availability. During the breeding season, adult survival is generally high for grassland songbirds (Carey and Koper, unpublished data), suggesting that population vital rates are most strongly impacted by nest failure due to predation (Vickery et al. 1992b, Bernath-Plaisted and Koper 2016). Habitat quality for grassland songbirds can therefore be equated to the probability of a successful nesting attempt in that habitat.

Habitat alteration from oil development may reduce habitat quality by lowering nest success in areas near oil wells and roads. Construction, industrial activities, and vehicle traffic can

cause direct mortality of adults or offspring through physical disturbance (Northrup and Wittemyer 2013). Additionally, oil development can increase the risk of predation. Nest predation risk varies spatially (Pietz and Granfors 2000), even within a small area, and may be affected by both habitat features and noise. Modified habitat features, such as increased perch availability and the introduction of exotic vegetation can increase the abundance of predators, or improve the ability of predators to detect prey (Andersson et al. 2009, Campos et al. 2009, Bernath-Plaisted and Koper 2016). Anthropogenic noise may decrease an individual's ability to detect or communicate the presence of predators reducing their ability to avoid predation (Ceradini et al. 2017, Antze and Koper 2018). This increased risk of predation for adults and their offspring can have negative impacts other than nest loss. Adult birds may spend less time foraging or caring for young to increase vigilance behaviour, which may impact their health or that of their offspring (Strasser and Heath 2013, Ng et al. 2018). This additional stressor could also have physiological consequences such as reduced immune function or body condition (Francis and Barber 2013a). While nest success for grassland songbirds may be most strongly influenced by nest predation, individual lifetime reproductive success may also be influenced by carryover effects associated with the demands of breeding under increased predation risk and physical disturbance from human activity and noise (Crino et al. 2011, Done et al. 2011, Harms et al. 2015, Sorenson et al. 2017). The physiological stress from the increased effort of reproducing in oil development-impacted habitat may therefore be a useful metric for measuring habitat quality.

Stress and Corticosterone

Physiological stress can be thought of as the cost of maintaining homeostasis. The maintenance of homeostasis, which is necessary for the survival of an organism, is regulated by

homeostatic mediators, such as glucocorticoids from the hypothalamic-pituitary-adrenal (HPA) axis, catecholamines from the cardiovascular system, and neurotransmitters in the central nervous system that are constantly circulating through the body (McEwen and Wingfield 2003, Romero et al. 2009). Organisms are required to adjust their levels of these homeostatic mediators in response to predictable seasonal and diel variations in the requirements of homeostasis, such as migration, hibernation, and reproduction (Romero et al. 2009). These predictable fluctuations in the requirements for homeostasis are described as allostasis (McEwen and Wingfield 2003). The difference between the energetic demands of maintaining homeostasis compared to the energy available to the organism from the environment is called the “allostatic load” experienced by that organism (McEwen and Wingfield 2003). If the energy required to maintain homeostasis increases, or the energy available from the environment decreases, the organism will experience a higher allostatic load. Unpredictable environmental changes may increase an organism’s allostatic load to a point where coping with the environmental perturbations will necessitate an organism to enter a state of reactive homeostasis (Astheimer et al. 1995). This is characterized by a physiological response resulting in deviation from the basal levels of stress hormones or glucocorticoids, specifically corticosterone in the case of birds (Romero et al. 2009). I will refer to the physiological response associated with an organism entering reactive homeostasis as the ‘stress response’.

Over a short period, a bird exhibiting a stress response is adaptive for coping with environmental perturbations. This is accomplished by increasing available energy to an individual by elevating the heartrate and modifying metabolic pathways as well as promoting behaviours such as foraging and increased vigilance (Wingfield et al. 1998). These mechanisms should allow that individual to reduce its allostatic load out of the range of reactive homeostasis (Romero et al.

2009). In extreme cases, if environmental conditions result in a consistently elevated allostatic load, an individual may be forced past reactive homeostasis into homeostatic overload (Romero et al. 2009). Under conditions of homeostatic overload an individual will initiate the “emergency life history stage” wherein individuals abandon reproductive and territorial behaviours in favour of those that promote self-preservation (Wingfield et al. 1998, Romero et al. 2009). However, frequent or prolonged exposure to minor environmental perturbations that induce reactive homeostasis can result in acclimation in the stress response, which decreases the magnitude of an individual’s stress response (Rich and Romero 2005). The cause of this decreased stress response may be that remaining in reactive homeostasis for extended periods of time puts ‘wear and tear’ on the physiological systems responsible for initiation of the stress response (Romero et al. 2009). This depression of the stress response limits the ability of a bird to cope with environmental challenges by decreasing the intensity of disturbance necessary to force an individual past reactive homeostasis and into homeostatic overload (Romero et al. 2009).

The pathophysiological effects of chronic exposure to a stressor can directly increase the risk of mortality by altering metabolic pathways causing muscle deterioration or suppressed immune function, or have carry over effects, such as suppressed reproduction, and neuronal deterioration that reduce lifetime fitness (Wingfield et al. 1998, McEwen and Wingfield 2003, Romero et al. 2009). Repeated or prolonged increased expression of corticosterone by grassland songbirds in response to disturbances from oil development may cause significant short- or long-term health consequences if the reaction by birds in proximity to the disturbances is strong enough to elicit a response. Corticosterone levels should, therefore, represent the physiological stress from breeding in oil development-impacted habitat. The magnitude of the effect of disturbance on corticosterone may be initially buffered by the act of breeding. Reproductive effort can act to

initially suppress systemic rises in corticosterone to avoid nest abandonment due to mild environmental perturbations (Bókony et al. 2009). Therefore, any effect I am able to detect is likely conservative compared to exposure to a similar disturbance in the non-breeding season.

Habitat Selection in an Altered Environment

Because it is adaptive to avoid higher rates of nest predation and stress, as this should translate to higher lifetime fitness (Norris and Marra 2007, Angelier et al. 2010, Fairhurst et al. 2013), the quality or fitness of an individual should be strongly linked to their ability to accurately assess habitat quality prior to establishing a territory. Each spring, migratory grassland songbirds of the North American Great Plains select territories and nesting sites on the landscape. Oil development, however, may impact an individual's ability to correctly assess breeding habitat quality by altering the perception of cues that individuals use to select a territory. Building new oil infrastructure can change vegetation characteristics (Koper et al. 2014), reduce the ability of birds to communicate with conspecifics (Curry et al. 2018, Antze and Koper 2018), or render social or experiential information from previous years inaccurate (Doligez et al. 2003). Therefore, the habitat alterations resulting from oil development could affect how individuals perceive the potential benefits of occupying impacted habitat relative to the actual reproductive potential afforded by that impacted habitat. This creates the potential for a mismatch between perceived habitat quality and realized habitat quality that could result in lost reproductive potential or increased energetic demands for breeding grassland songbirds (Arlt and Pärt 2007, Gilroy and Sutherland 2007, Robertson and Hutto 2016).

The ideal despotic distribution model (IDD; Fretwell 1972) suggests that high quality, or competitive, birds should choose the best habitat in which to breed and exclude lower quality, or

less competitive, individuals from those breeding sites. The Great Plains are a spatially and temporally heterogeneous landscape due to both human disturbance, such as energy development and agriculture, and natural variation, such as rain, grazing and fire cycles. Philopatry among migrant grassland passerines is generally low (Jones et al. 2007), possibly due to this high temporal unpredictability in grassland patch productivity (Doligez et al. 2003). Thus, this landscape of patchy resource distribution (Samson and Knopf 1994) may necessitate assessment and competition for breeding sites by grassland songbirds resulting in the IDD. Since the consequences of misjudging habitat quality would be reduced reproductive success and therefore fitness (Arlt and Pärt 2007), selection should be particularly strong for these migratory grassland birds to accurately assess habitat quality at breeding sites between years. While the challenge of assessing habitat quality several times annually in areas that are geographically and ecologically distinct may actually select for individuals that are particularly adept at assessing habitat quality, it is unclear how oil development will affect this ability.

Research Objectives

In this thesis, I assessed the effects of oil development in the Canadian prairies on the perceived and realized habitat quality for three grassland songbird species. These species varied in conservation status (no status, Special Concern, Threatened), so species-specific changes in perceived and realized habitat quality can help inform our understanding of how different members of avian communities in the grasslands respond to anthropogenic modifications to their habitat. I used measurements of reproductive success and physiological stress to provide metrics of habitat quality as experienced by individual birds exposed to disturbances associated with oil development. I also examined how oil development changes the way individuals perceived habitat

quality during territory establishment. I quantified the impact of oil development on perceived habitat quality by measuring where high-quality individuals choose to settle on the landscape with respect to disturbances from oil infrastructure as a metric for habitat preference. Finally, I assessed whether anthropogenic noise may be a potential mechanism driving any effects I detected of disturbance from oil development on perceived or realized habitat quality.

Chapter 2: Effects of oil development on perceived and realized habitat quality

Abstract

Habitat suitability is defined by both habitat quality and whether species can accurately assess habitat quality. Oil development has altered mixed-grass prairies in south-eastern Alberta, potentially impacting both habitat quality and how habitat quality is perceived by wildlife. I tested whether three passerines that vary in phylogenetic divergence, life histories, and conservation status can accurately assess habitat quality in the presence of anthropogenic development. I monitored nesting success and stress hormones to measure realized habitat quality and tested for differences in settlement patterns to measure perceived habitat quality at sites impacted by real oil infrastructure, simulated oil well noise, and control sites. Corticosterone levels suggested that habitat quality was reduced in some cases by the presence of oil wells, oil well noise, and/or roads. I also found evidence that these anthropogenic disturbances impacted perceived habitat quality; however, perceived and realized habitat quality were not always affected similarly. Savannah Sparrows exhibited signs of stress near screw pump but also showed a negative preference for nesting near them. Chestnut-collared Longspurs exhibited signs of stress near pumpjacks and simulated oil well noise but selected nest sites near oil infrastructure. Mismatches in perceived and realized habitat quality caused by oil development may help explain why some species suffer disproportionately in response to anthropogenic disturbances. Managers should aim to reduce human presence on the landscape by concentrating above-ground infrastructure using directional drilling, decommissioning old well heads, reclaiming under used roads, and reducing vehicle traffic. To contextualize the non-lethal effects of stress, future research should focus on estimating lifetime fitness of individuals using impacted and unimpacted habitat during the full annual cycle.

Introduction

Since the turn of the century, oil and gas development across the North American Great Plains has reduced net primary productivity of both cropland and native rangeland, and has converted more than 1.5 million hectares of habitat to well pads, roads, and storage facilities (Allred et al. 2015). Additionally, oil and gas development alters the habitat surrounding these structures by disturbing vegetation structure, creating edge habitat, and generating chronic noise (Sliwinski and Koper 2012, Francis and Barber 2013b, Koper et al. 2014). The Great Plains contain numerous imperiled ecosystems and species that are threatened by this habitat loss and alteration (Brennan and Kuvlesky 2005). Grassland songbirds are a particularly vulnerable guild, having suffered range-wide population declines of 55% on average since 1966 (Askins et al. 2007, North American Bird Conservation Initiative 2016, Sauer et al. 2017). While the majority of declines are a result of habitat loss due to agricultural conversion (Gage et al. 2016), oil and gas development poses a significant threat to remaining tracts of intact prairie (Allred et al. 2015). The province of Alberta, Canada has undergone particularly rapid resource development to extract oil and gas (Alberta Energy 2012). Cumulatively, these resource extraction activities impact a vast area in this region via habitat loss and alteration, with obligate grassland songbirds suffering reduced abundance or nest success in an estimated 50% of the available habitat (Daniel 2015). In order for conservation efforts to be effective at reducing the impacts of oil development, we must understand the mechanisms by which oil development affects grassland birds. For example, habitat fragmentation from road construction, noise from oil wells, delayed decommissioning of inactive oil wells, and the drilling of new oil wells may all impact birds differently and require vastly different management solutions (Chalfoun et al. 2002, Francis and Barber 2013a, Roch and Jaeger 2014).

Habitat alteration from oil development may impact vital rates of grassland songbirds, potentially contributing to population declines (Askins et al. 2007, North American Bird Conservation Initiative 2016, Sauer et al. 2017). Construction, industrial activities, and vehicle traffic can cause direct mortality of adults or offspring (Northrup and Wittemyer 2013). Perch availability and the introduction of exotic vegetation can increase the abundance of predators, thereby increasing predation risk (Andersson et al. 2009, Campos et al. 2009). Anthropogenic noise may also increase the perception of predation risk for grassland songbirds by decreasing an individual's ability to detect or communicate the presence of predators (Ng et al. 2018, Antze and Koper 2018). Oil development could also impact an individual's ability to correctly assess breeding habitat quality by altering the perception of cues that individuals use to select a territory, such as vegetation (Lloyd and Martin 2005), or the presence of conspecifics (Ahlering et al. 2009), or by rendering social or experiential information from previous years inaccurate (Doligez et al. 2003, Arlt and Pärt 2007, Maron et al. 2012). Therefore, the habitat alterations resulting from oil development could affect how individuals perceive the potential benefits of occupying impacted habitat relative to the actual reproductive potential afforded by that impacted habitat. This creates the potential for a mismatch between perceived habitat quality and realized habitat quality that could result in lost reproductive potential or increased mortality for breeding songbirds (Arlt and Pärt 2007, Gilroy and Sutherland 2007, Robertson and Hutto 2016).

Noise is one mechanism by which anthropogenic disturbance may decouple perceived and realized habitat quality for grassland songbirds. Birds may fail to completely integrate anthropogenic noise into their territory selection process but suffer negative consequences as a result of occupying noisy habitat. For example, masking of conspecific alarm calls may result in

reduced anti-predator behaviour around nests, possibly increasing the chances of nest predation (Antze and Koper 2018). Additionally, anthropogenic noise may mask cues used by individuals to detect predators, artificially increasing perceived habitat quality during territory establishment, which could also result in higher rates of nest predation (Slabbekoorn and Ripmeester 2008). In these instances, noise could create an ecological trap (Robertson and Hutto 2016). Alternatively, acoustically sensitive species may avoid noisy areas, even if oil development has a neutral or positive impact on realized habitat quality by decreasing predator abundance or activity (Lendrum et al. 2017), or decreasing resource competition (Francis et al. 2012a). This perceptual trap (Gilroy and Sutherland 2007) would result in unnecessary habitat loss, which could have population-level consequences, particularly since the main reason thought to explain declines of grassland songbirds is habitat loss (Vickery and Herkert 2001, Brennan and Kuvlesky 2005, Sauer et al. 2017, World Wildlife Fund 2017).

Where individuals breed in habitat with reduced quality they may suffer direct fitness costs including reduced nesting success (Lloyd and Martin 2005, Bernath-Plaisted and Koper 2016), or reduced nestling quality (Loman 2003, Potvin and MacDougall-Shackleton 2015). Nesting success is a strong predictor of vital rates for grassland songbirds (Vickery et al. 1992b) and is therefore an important index of habitat quality. For grassland songbirds, nesting success is most strongly influenced by nest predation (Vickery et al. 1992b, Bernath-Plaisted and Koper 2016). For example, 89% of Chestnut-collared Longspur nest failures in Alberta were due to predation (O'Grady et al. 1996). If oil development reduces realized habitat quality for grassland songbirds by increasing the efficacy of nest predators, then nesting success should be lower near oil development.

Breeding in poor quality habitat may also carry indirect fitness costs including reduced pairing success (Habib et al. 2007), increased effort necessary to fledge young (Lüdtke et al. 2013, Bernath-Plaisted et al. 2017), higher rates of physical disturbance (Askins et al. 2007), and greater perceived predation risk (Chalfoun et al. 2002). Measurements of physiological stress provide a metric for these indirect effects of breeding in poor quality habitat (McEwen and Wingfield 2003, Busch and Hayward 2009). In birds, the primary hormone involved in mediating the stress response is corticosterone, a glucocorticoid released from the Hypothalamic-Pituitary-Adrenal (HPA) axis (Wingfield et al. 1992, Romero et al. 2009). Baseline stress levels of a bird can be approximated by measuring circulating levels of corticosterone under normal allostatic conditions, and the magnitude of a bird's stress response can be measured as the increase in circulating levels of corticosterone from basal levels in response to a stressor (Wingfield et al. 1998). Predation risk, human disturbance, and habitat degradation have been linked with increased stress in Snowshoe Hares (*Lepus americanus*), Spotted Salamanders (*Ambystoma maculatum*), and Eastern Yellow Robins (*Eopsaltria australis*), respectively (Boonstra et al. 1998, Newcomb Homan et al. 2003, Maron et al. 2012). In combination, the measures of baseline and stress-induced corticosterone can be useful indicators of an individual's ability to cope with its current environmental circumstances and could be used to identify individuals living in sub-optimal conditions (Boonstra et al. 1998, Romero and Wikelski 2002, Maron et al. 2012).

These consequences of breeding in poor-quality habitat mean that congruence, or lack thereof, between perceived and realized habitat quality surrounding oil development may impact fitness of songbirds. This can result in four alternative patterns depending on whether perceived and realized habitat are aligned and the amount of available habitat:

Matched - Density Independent: if habitat quality is perceived accurately, and the availability of suitable habitat is not limited, all birds should reduce the use of the impacted habitat relative to its availability (e.g. Bayne et al. 2008). In this case the habitat loss associated with oil development is substantially larger than the physical footprint of the oil infrastructure itself as the surrounding habitat would be essentially lost as well.

Matched - Density Dependent: if habitat quality is perceived accurately, but the availability of suitable habitat is limited, then the use of impacted habitat by some individuals may be unavoidable. In this case there may be a shift in the local demographic structure (e.g. Habib et al. 2007), such that birds that are subordinate are more likely to settle in the impacted habitat (*Ideal Despotic Distribution*; Fretwell 1972), and will be disproportionately affected by oil development.

Mismatched - Density Independent: if the cue(s) used by an individual to assess habitat quality are misleading (e.g. Maron et al. 2012), then dominant and subordinate individuals may settle in impacted and undisturbed habitat in equal frequencies (*Ideal Free Distribution*; Fretwell and Lucas 1969). This represents a mismatch between perceived and realized habitat quality since high-quality individuals do not preferentially select the highest-quality habitat. This is an example of Non-Ideal Habitat Selection (Arlt and Pärt 2007), which limits population growth since some do not reach their fitness potential.

Mismatched - Density Dependent: in an extreme case of mismatched perceived and realized habitat quality, competitive individuals may perceive impacted habitat as higher quality and may preferentially use the impacted habitat (*Ideal Despotic Distribution*; Fretwell 1972). This would result in an ecological trap (Robertson and Hutto 2016) with potentially severe consequences to vital rates.

To distinguish between the settlement patterns described above, it is first necessary to determine which traits of grassland songbirds are indicative of their competitiveness. Typically, young, naive breeders lack the experience or social status to select or defend high quality breeding sites (Holmes et al. 1996, Habib et al. 2007). Therefore, if there is a high proportion of first-time breeders in an area, that area is likely perceived as low-quality habitat by dominant individuals. Similarly, smaller individuals may lack the competitive ability to defend prime territories or acquire high-quality mates (Linhart and Fuchs 2015). Consequently, the probability of a bird settling in the habitat most highly impacted by oil development should vary with individual age and size, as indices of social status, and should be dependent on how that habitat is perceived among individuals.

Low-quality individuals in a population can also be identified by metrics of reduced productivity, such as smaller clutch sizes or lower nestling quality (Holmes et al. 1996). However, occupants of poor-quality habitat may generally show reduced productivity regardless of the actual intrinsic quality of those individuals (Battin 2004). This creates a problem in that we are unsure if the reduced productivity in impacted habitat is due to habitat quality or individual quality, necessitating the measurement of separate metrics for individual and habitat quality. Assessing characteristics of adults that are correlated with higher productivity (clutch size, nestling size, etc.) while controlling for variation in habitat quality is necessary to separate out traits of individual competitiveness and quality (Vitousek et al. 2014). It is important to distinguish between individual competitiveness and quality since competitiveness may be more important between males during territory establishment (e.g. male-male competition; Kort and Eldermire 2009), but individual quality may be more important during pairing (e.g. mate selection; Horváthová et al. 2011). For example, larger males may be able to establish territories in high-quality habitat due to

their high competitiveness but may provide less parental care in favor of seeking extra pair paternity (Hill et al. 2011, Cleasby and Nakagawa 2012). High-quality females may therefore socially pair with lower-quality males to ensure support in brood rearing (Griffin et al. 2013). Together the distribution of competitive and high-quality individuals should reflect how habitat quality is perceived by songbirds.

The magnitude and proportional impacts of the effects of oil development on perceived and realized habitat quality are likely species-specific (Northrup and Wittemyer 2013), based on habitat requirements, mechanisms of habitat selection, and tolerances to visual and acoustic disturbance (Doligez et al. 2003, Davis 2004, 2005, Arlt and Pärt 2007, Francis et al. 2012b, Sliwinski and Koper 2012, Maron et al. 2012). This may help explain why the responses of individual species to energy development on the landscape are mixed. Within the grassland songbird guild, there are differences in the severity of population declines observed in recent decades (Environment and Climate Change Canada 2017). These differences may be due to differences in tolerance to anthropogenic disturbances among species. I focused on identifying potential mismatches between perceived and realized habitat quality for three species of grassland songbirds in southeastern Alberta: Chestnut-collared Longspur (*Calcarius ornatus*), Baird's Sparrow (*Centronyx bairdii*), and Savannah Sparrow (*Passerculus sandwichensis*). These species co-occur on remaining patches of mixed grass prairie, but variation in sensitivity to disturbance among these species might play a role in driving the disparity in population declines.

Chestnut-collared Longspurs are mixed grass prairie obligates that are federally Threatened (SARA) and provincially listed as At Risk in Alberta (Alberta Environment and Parks). Chestnut-collared Longspurs display area sensitivity (Davis 2004), a negative association with habitat edges (Sliwinski and Koper 2012), and reduced nesting success in the presence of exotic vegetation

(Lloyd and Martin 2005). Nonetheless, recent studies have reported no effect of shallow gas or oil wells on Chestnut-collared Longspur abundance (Hamilton et al. 2011, Rodgers and Koper 2017, Nenninger and Koper 2018) or nest success (Bernath-Plaisted and Koper 2016, Yoo and Koper 2017), despite the presence of exotic vegetation, edge effects, and noise associated with oil development (Sliwinski and Koper 2012, Francis and Barber 2013a, Koper et al. 2014). This is possibly because the construction of oil wells increase local grazing activity by attracting cattle (Koper et al. 2014), creating the preferred nesting habitat for Chestnut-collared Longspurs of short, sparse vegetation (Davis 2005, Bleho et al. 2014).

Baird's Sparrows, a federally listed species of Special Concern (SARA), and provincially listed as Sensitive (Alberta Environment and Parks), show declines in abundance with proximity to oil wells (Nenninger and Koper 2018). However, there is no evidence to suggest that Baird's Sparrow nesting success is lower near oil wells. Baird's Sparrows may simply avoid using habitat close to oil wells since their populations tend to be low density and ephemeral (Ahlering et al. 2009), so it is not necessary for subordinate individuals to use sub-optimal habitat.

Savannah Sparrows are relatively more common (~6 times more abundant) grassland generalists in southeastern Alberta and the presence of oil development does not negatively impact abundance (Nenninger and Koper 2018). However, the presence of oil wells is associated with lower nesting success (Bernath-Plaisted and Koper 2016) and productivity (Ng et al. 2018) of Savannah Sparrows. Perhaps the use of impacted habitat by some individuals is unavoidable due to high breeding densities.

To understand how habitat alteration from oil development impacts perceived versus realized habitat quality, I investigated how oil infrastructure, and the associated noise and service roads, impact nest success, stress, and settlement patterns of Chestnut-collared Longspur, Baird's

Sparrow, and Savannah Sparrow in the mixed-grass prairie in south eastern Alberta. To determine whether anthropogenic noise is the mechanism driving changes in perceived or realized habitat quality, I compared effects of real infrastructure with effects of simulated oil well noise on several metrics. To assess whether oil development reduces habitat quality for each focal species I used nesting success (daily probability of nestling survival prior to fledging) as a proxy for productivity, and corticosterone as a proxy for the physiological response of songbirds to disturbance caused by oil development. To understand the effect of oil development on perceived habitat quality I examined the distribution of competitive and high-quality individuals in relation to oil infrastructure. If oil development reduces realized habitat quality for grassland songbirds, then individuals living near oil development should 1) have lower nesting success than birds living far from oil development and 2) show signs of physiological stress compared to birds living far from oil development. If all individuals perceive habitat quality accurately, then 3) high quality, competitive individuals should settle preferentially in habitat with the highest realized quality and exclude low quality individuals from that habitat. Given that the intensity of habitat change should vary spatially with proximity to oil development, birds in greater proximity to oil infrastructure are expected to experience greater impacts.

Methods

This research was conducted under University of Manitoba animal care protocol F15-005, Canadian bird banding permit 10840, Canadian Wildlife Service permit #11-MB/SKL/AB-SC007, and Alberta Environment and Sustainable Research Development Research Permit #56016 and Collection License #56017.

Study Area

All research occurred within 60 km of Brooks, Alberta, Canada (50°33'51"N 111°53'56"W, 760 MASL), on land owned by the Eastern Irrigation District (EID), a private landowner that primarily uses grasslands for grazing cattle and owns more than 282,800 ha in Alberta. These lands are annually grazed mixed-grass prairie, consisting mainly of native grasses and forbs: needle and thread (*Hesperostipa comata*), porcupine grass (*Hesperostipa spartea*), blue grama (*Bouteloua gracilis*), western wheatgrass (*Pascopyrum smithii*), pasture sagewort (*Artemisia frigida*), and silver sagebrush (*Artemisia cana*); intermixed with a low abundance of invasive grasses and forbs, including goatsbeard (*Tragopogon dubius*), dandelion (*Taraxacum officinale*), crested wheatgrass (*Agropyron cristatum*), and smooth brome (*Bromus inermis*). Brooks receives an average of 252.6 mm of rainfall annually (347.5 mm total precipitation; Environment Canada 2018) and is on the edge of the prairie pothole region. Pastures are divided by three-wire fences into Sections (1.6 x 1.6 km) or larger, which are also often accompanied by range roads (1 by 1 to 2-mile grid). Active lease sites are operated for oil and natural gas on EID lands around Brooks. Lease sites are 1 hectare (100 m x 100 m) and can have up to 3 well heads per lease. Oil infrastructure generally consists of an oil well pad (usually approximately 50 m x 50 m of level gravel), which is connected to the rural road system by a gravel or dirt service road, and

one or more centralized oil wells (~ 2m - 4m high) that generate noise and have pump components that sweep up and down vertically or spin horizontally.

From 2015 to 2017, I studied Chestnut-collared Longspurs, Baird's Sparrows, and Savannah Sparrows at sites that contained either oil well(s), a playback unit producing simulated oil well noise mimicking the noise levels around real oil infrastructure, or control sites containing no oil infrastructure. Sites ranged in size from 800 m x 800 m to 2000 m x 2000 m such that all the birds or nests at a given site were closer to the disturbance at the center of the site (oil well or playback unit) than to any other surrounding disturbance. The spatial arrangement of the site types also ensured no overlap in treatments or other nearby disturbances, such as natural gas compressor stations. Sites with oil wells had one of two types of oil infrastructure at the approximate center of the site: screwpumps ($n=4$) or pumpjacks ($n=3$). These infrastructure types are both commonly implemented in this region yet differ greatly in the physical size of the pump and the noise spectra and power they produce (Rosa et al. 2015). Screwpumps are short (2.7m), have a small horizontal spinning mechanism, and produce higher sound pressure levels than Pumpjacks, which are taller (4.5m), and move up and down in a rhythmic fashion.

All of the oil wells that I studied were generator-powered, meaning that the pump mechanism is powered by a generator and the well is not connected to the power grid via transmission lines, in contrast to grid-powered oil wells which are electric-powered pumps and are connected to the power grid. In 2016 and 2017, I added sites with high fidelity playback units ($n=6$), broadcasting recordings of generator-powered screwpumps (simulated oil well noise) 24 hours a day throughout the breeding season (approx. May 1 to July 31) in order to distinguish the effects of noise from the physical infrastructure. These units were confirmed to mimic the spectral composition, sound pressure levels, and frequencies of actual infrastructure with four cardinal 100-

meter audio transects (see Rosa et al. 2015). The playback units included a solar panel array, small housing unit for batteries, iPod (Apple), two high fidelity speakers facing in opposite directions, and were surrounded by a technical fence to prevent cattle from accessing the equipment. Noise was emitted from ~0.5-1 meter off the ground by the playback unit and between ~0.5-2 meters off the ground from an actual screw pump, so interference from wind should affect sound propagation equally between treatments. I also established silent playback sites ($n=6$) with identical equipment as the playback units, but did not broadcast any noise, to control for the potential impacts of the playback equipment itself on habitat selection or quality.

Control sites ($n=5$) contained neither oil wells nor playback infrastructure and were located such that no bird territory or nest on a control site was within 800 m of an oil well or playback infrastructure. All sites were selected based on the presence of all three of my study species, therefore differences in site scale vegetation characteristics did not differ enough to render any site unsuitable for occupancy by any of my focal species. Additionally, all sites were dominated by a mosaic of mixed native grass species. This is similar to Nenninger and Koper (2018), who found that the inclusion of vegetation characteristics in models testing for an effect of oil infrastructure on abundance did not improve model fit and so were not included in their analysis.

Field Methods

To quantify nesting success, field assistants and I found and monitored nests between May and August 2015-2017. We found nests using behavioural cues and checked nests every 1-5 days until nests failed or fledged. Nests were considered successful if at least one nestling fledged. The youngest nestling ever confirmed to have fledged were day 7 (*personal observation*). Therefore, successful fledging was only considered possible after once the nestlings reached day 7 and was

determined by a combination of signs at the nest, such as fecal sacs outside the nest cup, no scattered feathers, and no disturbances to the nest cup integrity; parental behaviour, such as food carrying, and alarm calling; and the visual confirmation of fledglings. If fledglings or an adult with food were not observed in 30 minutes of observation, then the nest was considered failed, unless the signs at the nest clearly indicated fledging and the adults were present and alarm calling for the full observational period. Productivity of a nest was calculated as the number of young in the nest at day 7 when the nestlings were banded as this is the youngest age at which the nestling are capable of fledging and counting the number of fledglings once they have left the nest is prohibitively time consuming and disruptive to the adults (Jongsomjit et al. 2007). We also measured nestling weight, tarsus length, and the length of the outer primary feather at banding.

We captured and banded territorial adult birds between May and August 2015-2017 using target netting for actively displaying males and walk-in drop traps for nesting pairs when nestlings were 3 - 10 days old. I considered an individual territorial if it was a male that actively responded to, and defended against, a simulated territorial intrusion using conspecific playback, or a male or female was found with a nest. For target netting we used two 6-m mist nets (30 mm mesh) set up in a central displaying location in a “V” formation surrounding a decoy (painted model bird), and speaker. Males were subjected to conspecific songs and calls for 30 minutes or until captured. For walk-in drop traps we used mist netting material over a wire frame (Sutherland et al. 2005), propped up over a nest with a stick tied to a 50m spool of twine. The observer would then wait in a hidden location for up to 30 minutes or until the target adult entered the trap to attend the nest, at which point the twine was pulled to remove the prop and the trap would fall and contain the bird. We assessed age (second year or after second year; Pyle et al. 2008), sex, fat score (0-9), pectoral muscle index (0-3), weight, un-flattened wing-cord, tarsus length, and took blood samples

for all captured birds. All individuals were banded with a unique numbered CWS metal band and a unique combination of two or three coloured plastic bands (Darvic) for subsequent identification in the field. Colour bands were sealed shut in the field with a portable soldering iron to prevent reopening.

Blood Samples

To determine pre-capture circulating corticosterone levels (baseline), 70 uL of blood was taken from the brachial vein within three minutes of capture. Blood plasma levels of corticosterone remain representative of baseline within 2-3 minutes of capture (Romero and Reed 2005). Individuals were then subjected to a standardized 12-minute stress handling protocol (Wingfield et al. 1992) followed by an additional 30-70 uL blood sample to determine the increase in corticosterone in response to handling (stress-induced). To maintain consistency in the protocol among species, I used the same length of stress handling protocol for all three species. I used Chestnut-collared Longspurs, my study species of highest conservation concern, as the benchmark to determine the minimum time required to achieve maximum increase in circulating levels of corticosterone. Peak increase in corticosterone for Chestnut-collared Longspurs occurs after approximately 10 minutes of handling (Lynn et al. 2003). I therefore choose a stress handling protocol of 12 minutes to maximize the observed increase in corticosterone while minimizing total handling time and therefore the potential for adverse effects from capture. Blood samples were collected via brachial venipuncture using a heparinized micro-capillary tube and kept on ice (< 6 hours) until the plasma was separated by centrifuge (10 minutes at 15,000 G) and then frozen at -20°C until extraction.

Assay Procedure

Plasma corticosterone concentrations were determined using a radioimmunoassay (Sheriff et al. 2011; Wingfield et al. 1992; Crossin et al. 2012) from the blood plasma as follows: samples were extracted using absolute ethanol in a 12:1 ratio with the plasma volume, centrifuged at 6000 G for 3 minutes, and the supernatant decanted. This process was repeated, and the supernatants were pooled. This extract was then dried and frozen until assayed. Extraction efficiency of corticosterone from my plasma samples was 113.2%. On the day of the assay procedure, samples were allowed to reconstitute in RIA buffer (phosphate buffer, NaCl, and Bovine serum albumen), to an appropriate dilution such that 100uL of buffer constituted 4-20uL of plasma depending on the species and sample, for one hour after an initial agitation of 5 seconds in an orbital shaker (vortex). Each assay tube contained 100uL each of 1:6000 diluted corticosterone antibody (Antibodies-online, cat no. ABIN343319), 3H-labeled corticosterone, and reconstituted sample or corticosterone standard. After incubation, unbound corticosterone was removed using an activated charcoal separation buffer (RIA buffer, charcoal, dextran), the supernatant was decanted into scintillation vials, and 4mL of scintillation fluid (UltimaGold; PerkinElmer) was added. Vials were counted in a scintillation counter for 5 minutes each. Sample corticosterone values were interpolated from the dose-sigmoidal response curve produced by a serial dilution of corticosterone standards included in each assay using Prism 6 (Graphpad). Inter-assay variability was 14.5%, intra-assay variability was 13.4%, and parallelism was achieved.

The assay specific upper and lower detection limits were 3.0 ng/mL and 0.2 ng/mL of corticosterone respectively. Some samples failed to produce interpretable corticosterone values due to low concentrations of corticosterone in the plasma sample and therefore could not be assigned specific concentrations of corticosterone. Since the concentration of corticosterone is

calculated post-hoc based on the absolute amount of corticosterone in the assay tube and the volume of plasma represented in that tube, it is possible to calculate the minimum concentration of corticosterone necessary in a sample of a given volume to produce an interpretable value on the dose-sigmoidal response curve. If these samples had large enough plasma volumes that I would have been able to detect corticosterone above 1-2 ng/mL in the sample, then those samples were assigned the assay specific minimum detectable corticosterone value based on the sample's plasma volume and included in subsequent analyses. Samples that produced interpretable values above the detectable limit of my assay were similarly assigned the assay specific maximum detectable value corticosterone and were included in subsequent analyses. While I cannot be certain of the concentration of corticosterone in the aforementioned samples, my method of assigning corticosterone values is particularly conservative when assigning low volume samples, which biologically must fall below 0 and the minimum detectable value (1-2 ng/mL). The benefit of assigning these samples a value is that it greatly increases my sample size for Chestnut-collared Longspur in particular, a species at risk from which the data I collected are extremely valuable.

Spatial Analysis

To estimate the distance from which a bird is primarily exposed to disturbances from oil development, I assumed an approximate territory center as one of two locations: 1) for birds that I did not find an associated nest I used the capture location, which represented a location central to a territorial male's display area, or 2) if I captured a bird on a nest, or subsequently discovered a nest for a previously captured bird, I used the nest location. To determine distances from bird locations to anthropogenic disturbances, oil wells, service roads, and rural roads within 1000 m of any bird's location were mapped using handheld GPS units (Garmin etrex 20). I used GIS to

estimate distances to the nearest oil well for any bird location that was greater than 1000m from a ground-truthed oil well using a GIS layer of all active oil lease sites in my study region (Cenovus 2014). For roads, I assumed that all bird locations were no more than 1600 m (1 mile) from a road, as this is generally the dimension of the rural road grid in the area, so I assigned a distance of 1600m to any bird location more than 1000m from a ground-truthed road. Distances to disturbances from each bird location were calculated in R (R Core Team 2017). Shapefile layers were created from Garmin's GPX files using packages *rgdal* (Bivand et al. 2018) and *raster* (Hijmans 2016). Pairwise distance matrices were created using package *rgeos* (Bivand and Rundel 2018) and summarized to calculate the minimum distance from each bird location to each disturbance feature, including site centers for all treatments (screwump, pumpjack, playback, silent playback, and control).

Statistical Analyses

I conducted all statistical analyses in R (R Core Team 2017). Generalized and mixed models were constructed with package *LmerTest* (Kuznetsova et al. 2017), data were visualized using *ggplot2* (Wickham, 2016), tables of model outputs were assembled using *sjPlot* (Lüdecke, 2018). Since Chestnut-collared Longspur and Baird's Sparrow are listed species protected under SARA, I used an alpha level of 0.1 to determine the significance of the effects of oil development on our focal species, which is often used in conservation when the consequences of a type I error outweigh those of a type II error (Taylor and Gerrodette 1993).

Independent Variables – Oil Development

To assess effects of infrastructure on each of my response variables (described in more detail below), I ran two sets of models. (1) To test for the effect of the structures associated with oil development, I included both the minimum distance from each nest or capture location to the nearest oil well and the nearest road as continuous fixed effects as collinearity between these variables was generally low across models. To test for effects of infrastructure type and noise *per se* (2), I modelled treatment type (pumpjack, screw pump, simulated screw pump noise, silent playback infrastructure, and control), distance to that experimental feature (or site center for controls), and their interactions as fixed effects. I excluded any birds or nests outside of 800 m from site center so that all distances to disturbance could be accurately ground-truthed, as no GIS information was available that identified well types and other noise sources. As my experimental playback units were running prior to the earliest nest initiation for any of my study species I am confident that all three species were exposed to comparable levels of simulated oil well noise. In 2015 I established sites around 3 active pumpjack oil wells; however, in 2016 one pumpjack was deactivated by the operators for the duration of the field season and in 2017 the remaining 2 pumpjack sites were abandoned for logistical reasons. Consequently, my sample size for birds around pumpjacks is smaller than for other treatments. Additionally, I tested if the inclusion of year or site as random variables improved model fit for all preliminary models using AIC; in no case did adding year or site as a random variable improve model fit by greater than 2 Δ AIC so they were not included in any final models.

Response Variables - Habitat Quality

I used nest success, defined as fledging at least 1 young, and corticosterone as indices of realized habitat quality for each focal species. These metrics provide a view of both the effort required to make a breeding attempt, and the chances of that attempt being successful for an individual in a specific location. There are other ways that habitat quality could be quantified such as clutch size, total annual productivity, and adult or post-fledging survival. However, since the majority of nest failures are due to predation, nesting success has the largest impact on vital rates (Vickery et al. 1992b, O'Grady et al. 1996) and therefore provides the simplest means to estimate productivity. Since adult survival on the breeding grounds is close to 100% (Carey and Koper, unpublished data), stress hormone levels, representing the physiological response to disturbance, provide a finer metric of the environmental conditions being experienced by the adult.

I estimated nesting success as the daily probability of survival using a logistic exposure analysis (Shaffer 2004). This uses a general linear model fit with a binomial distribution and a modified logit link function that accounts for different time lengths between nest checks. My models included the fixed variables in models (1) and (2) as outlined above. I also assessed whether year or site influenced daily probability of nest survival; however, these variables did not have a significant effect on nesting success for any species, so I did not include those terms in the final model. Additionally, inclusion of the Julian date of the nest check as a fixed effect did not have a significant influence on daily probability of nest survival, and so was not included in subsequent models.

To assess if there was an effect of oil-related disturbances on corticosterone, I first identified biologically important factors that might influence levels of corticosterone in species by sex. I ran two general linear models for each species-sex group; one for basal corticosterone, and

one for the stress response (change in corticosterone during the stress handling protocol). Each model included weight, age, day of season, and time of day as independent variables, and the stress response model also contained basal corticosterone as a predictor variable. All significant factors were retained in subsequent models. For each species-sex group I included these statistically significant variables, as well as fixed variables in models (1) and (2) as outlined above.

Response Variables - Individual Quality

I used morphometric data of adults and nestlings to determine which physical characteristics of adults were indicative of productivity (i.e. producing heavier offspring) and thus high individual quality. I defined productivity as having more or larger nestlings in the nest at fledging. To evaluate individual quality, I tested whether adult age (SY or ASY), weight (g), and size (tarsus length in mm) predicted productivity. I ran two sets of models using two different metrics of productivity as response variables: (1) individual nestling weight, or (2) summed nestling weight per clutch, for each species-sex group. Model (1) included adult age, weight, and size as fixed effects, nestling age as a fixed effect to account for slight differences in sampling times, and nest ID as a random effect. Model (2) included adult age, weight, and size as fixed effects, and the average age of the nestlings as a fixed effect to account for slight differences in sampling times. Additionally, I tested if any male physical characteristics were predictive of attracting a more productive female. These models contained female traits associated with productivity identified above as the dependent variable and male age (SY or ASY), weight (g), and size (tarsus length in mm) as independent variables.

Response Variables - Habitat Selection

To assess if there was an effect of oil-related disturbances on patterns of habitat selection by experienced, competitive, or high-quality individuals, I used adult age (SY or ASY), weight (g), and size (tarsus length in mm) to determine where older, larger, or higher quality (as identified above) individuals preferentially established territories and therefore perceived the habitat to be high quality. To determine the territory location of individuals I used the capture location, which represented a location central to a territorial male's display area, as an approximation of the territory center, unless updated by a subsequent nest discovery. I used adult age, weight, and tarsus length as the response variables in two sets of models to test for evidence of non-random habitat selection. My models included the fixed variables in models (1) and (2) are as outlined above in *Independent Variables – Oil Development*. Additionally, Julian day was included for all weight models to account for possible changes in weight across the breeding season. Body condition (the residuals of a weight by tarsus length regression) yielded the same significant results as uncorrected weight, so I just present results for the simpler metric of weight below. There was not enough variability in fat scores to detect an effect of infrastructure within any species-sex group.

Results

Habitat Quality – Nesting Success

We found 411 nests and performed 2562 nest checks from 2015 to 2017 to monitor for nest success or failure (Table 2). My sample size of 7 Baird's Sparrow nests was too small to analyse. Nest success, calculated as daily probability of nest survival, was not significantly influenced by proximity to wells or roads (Table 3). Noise *per se* also did not impact daily probability of nest survival, and there was no evidence that nesting success varied with type of well (Table 4).

Table 2. Nests found, and nest checks of three grassland passerines performed in Southern Alberta by species and year from 2015-2017.

Year	Chestnut-collared Longspur		Baird's Sparrow		Savannah Sparrow	
	Nests	Checks	Nests	Checks	Nests	Checks
2015	63	350	3	12	26	94
2016	138	989	4	31	43	244
2017	130	834	0	0	4	8
Total	331	2173	7	43	73	346

Table 3. Predicted effects of distance (log(m)) to oil infrastructure and roads on nest survival of Chestnut-collared Longspur and Savannah Sparrow in southern Alberta, 2015 -2017. Model predictions are of the daily probability of survival using a logistic exposure analysis (Shaffer 2004). This uses a general linear model fit with a binomial distribution and a modified logit link function that accounts for different time lengths between nest checks.

<i>Predictors</i>	Chestnut-collared Longspur			Savannah Sparrow		
	<i>Log-Odds</i>	<i>CI</i>	<i>p</i>	<i>Log-Odds</i>	<i>CI</i>	<i>p</i>
(Intercept)	3.15	2.24 – 4.10	<0.001	3.56	1.04 – 6.39	0.009
Distance to oil well	-0.03	-0.18 – 0.12	0.662	-0.17	-0.61 – 0.28	0.468
Distance to Road	0.03	-0.14 – 0.20	0.702	0.10	-0.54 – 0.67	0.744
Observations	1704			253		
Cox & Snell's R ² / Nagelkerke's R ²	0.004 / 0.010			0.002 / 0.004		

Table 4. Predicted effects of distance (log(m)) oil infrastructure types and noise treatments (see footnote) on nest survival of Chestnut-collared Longspur and Savannah Sparrow from 2015 to 2017 in southern Alberta. Model predictions are of the daily probability of survival using a logistic exposure analysis (Shaffer 2004). This uses a general linear model fit with a binomial distribution and a modified logit link function that accounts for different time lengths between nest checks.

Predictors	Chestnut-collared Longspur			Savannah Sparrow		
	Log-Odds	CI	p	Log-Odds	CI	p
(Intercept)	5.34	2.27 – 8.97	0.002	0.56	-4.51 – 5.96	0.832
Distance to Control	-0.35	-0.98 – 0.20	0.235	0.44	-0.49 – 1.36	0.346
Distance to Silent	-0.24	-1.26 – 0.71	0.628	0.49	-1.38 – 2.52	0.623
Distance to Playback	-0.08	-0.88 – 0.72	0.841	-2.07	-8.41 – 2.28	0.412
Distance to Screwump	0.16	-0.57 – 0.92	0.664	2.02	-1.03 – 6.28	0.250
Distance to Pumpjack	0.98	-0.97 – 2.89	0.309	-0.06	-3.57 – 2.91	0.967
Observations	1704			253		
Cox & Snell's R ² / Nagelkerke's R ²	0.011 / 0.025			0.040 / 0.081		

‘Pumpjack’ refers to propane-powered pumpjack oil wells that draw oil from underground using a vertical see-saw motion. ‘Screwump’ refers to propane-powered screwump oil wells, another type of oil well without the associated large movements of a pumpjack.

‘Playback’ is a high-fidelity experiential noise treatment, broadcasting the sound of a screwump oil well 24h a day in field absent of oil infrastructure throughout the breeding season. ‘Silent’ treatments have the same fencing and build as the playback infrastructure, but do not broadcast noise. Controls are field with no infrastructure nor experimental playback manipulations.

Habitat Quality – Corticosterone

I captured 191 adult Chestnut-collared Longspurs, 56 adult Baird's Sparrows, and 130 adult Savannah Sparrows between May and July 2015-2016, from which I collected 801 blood samples (Table 4). Twenty-four plasma volumes were too small to detect corticosterone and 6 samples failed to produce repeatable duplicates, so these samples were omitted from analyses. Samples that contained concentrations of corticosterone that were too low (n=108) or too high (n=2) to be interpretable but had sufficiently large sample volumes that detection should have been possible were assigned the minimum and maximum detectable corticosterone values, respectively.

For all species and both sexes, corticosterone was higher in the 12-minute sample than in the under 3-minute sample (Fig 1). Chestnut-collared Longspurs had much lower basal and stress-induced corticosterone than either sparrow species (Fig 1). Sex was a strong predictor of both basal and stress-induced corticosterone for all species, so for all subsequent analyses I treated male and females separately. Other biologically important variables were included in subsequent models if they were significant in the preliminary model (Table 5-6). While, season day was a significant predictor of basal corticosterone for male Savannah and Baird's Sparrow, I was unable to determine if this was an effect of nesting stage changing as the season progressed as I did not find nests for most of these individuals.

In several instances birds living closer to oil wells, simulated oil well noise, or roads had elevated levels of corticosterone, though the influential stimulus and type of response was not always consistent. Female Chestnut-collared Longspurs had higher basal corticosterone when beside playback infrastructure broadcasting simulated screw pump noise and lower basal corticosterone near pumpjacks (Table 9; Figure 3). Corticosterone levels of male Chestnut-collared Longspurs were independent of distance to oil wells, simulated oil well noise, and roads (Table 7-

10). Males of both sparrow species, by comparison, showed elevated stress-induced corticosterone levels in the presence of disturbances from oil development. Male Savannah Sparrows had higher stress-induced corticosterone when in close proximity to pumpjacks (Table 10; Figure 4), but lower basal corticosterone near silent playback infrastructure. Male Baird's Sparrows had higher stress-induced corticosterone close to roads (Table 8; Figure 2).

Table 5. Total number of blood samples taken, and numbers of samples with subsequent interpretable corticosterone (CORT) values from three grassland songbird species (separated by sex) from 2015 to 2017 in Southern Alberta.

Species	Blood Samples		Recovered CORT	
	< 3 min	12 min	< 3 min	12 min
Male Chestnut-collared Longspur	131	130	115	127
Female Chestnut-collared Longspur	89	85	86	84
Male Baird's Sparrow	53	51	49	50
Female Baird's Sparrow	2	2	2	2
Male Savannah Sparrow	109	109	107	107
Female Savannah Sparrow	21	19	21	19

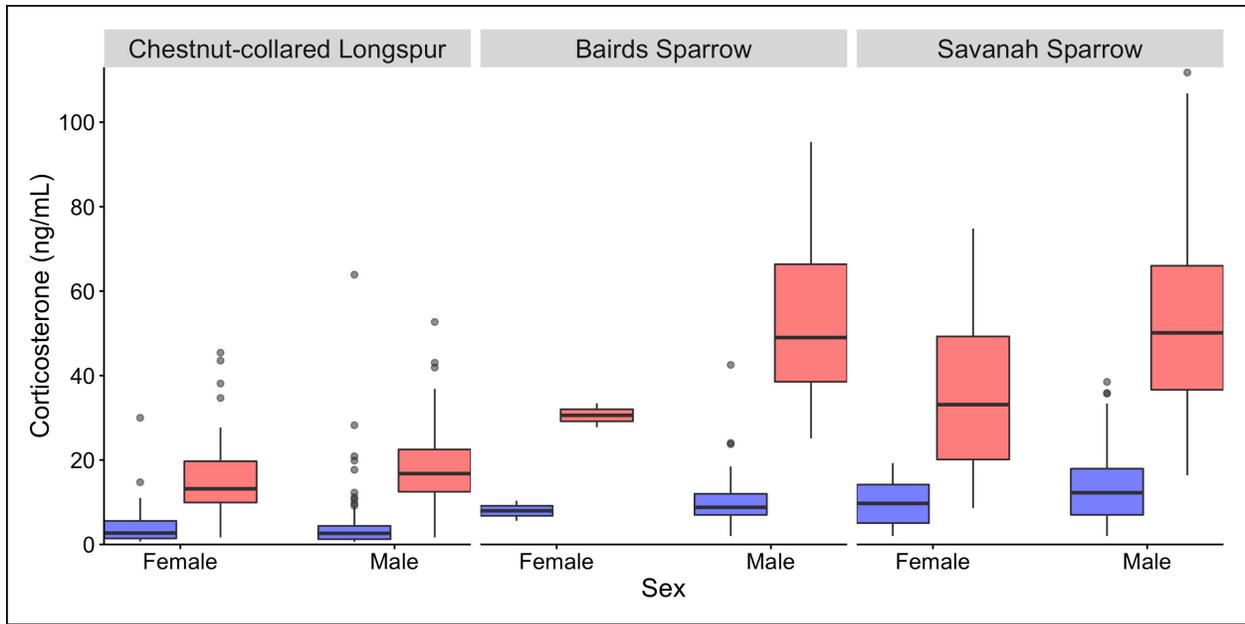


Figure 1. Corticosterone values from the basal (<3min; blue) and stress response (12min; red) sample from southern Alberta, 2015 – 2016.

Table 6. Influence of weight, age (see footer), season, and time of day on basal corticosterone levels (Log (ng/ml)) in female and male Chestnut-collared Longspur, male Baird's Sparrow, and male and female Savannah Sparrow. Samples were obtained during the breeding seasons of 2015 to 2016 in Southern Alberta.

Basal Predictors	Female Chestnut-collared Longspur			Male Chestnut-collared Longspur			Male Baird's Sparrow			Female Savannah Sparrow			Male Savannah Sparrow		
	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p
(Intercept)	1.35	2.15	0.53	1.95	1.74	0.26	10.3	2.24	<0.01	8.79	5.95	0.16	6.64	1.56	<0.01
Weight	-0.07	0.09	0.41	-0.02	0.07	0.80	-0.28	0.10	0.01	-0.32	0.27	0.26	-0.10	0.07	0.18
Age: ASY	0.08	0.21	0.71	0.35	0.21	0.09	0.28	0.17	0.12	-0.05	0.39	0.89	0.31	0.14	0.03
Season Day	0.01	0.01	0.11	0.00	0.00	0.97	-0.01	0.01	0.01	-0.01	0.02	0.47	-0.02	0.00	<0.01
Time of Day	-0.00	0.00	0.42	-0.00	0.00	0.06	-0.00	0.00	0.20	0.00	0.00	0.75	0.00	0.00	0.88
n	82			114			46			20			103		
R ² / adjusted R ²	0.057 / 0.008			0.048 / 0.013			0.297 / 0.228			0.113 / -0.123			0.204 / 0.171		

ASY: After second year bird – a bird in its third calendar year since hatching, indicating a mature adult bird.

Table 7. Influence of weight, age (see footer), season, and time of day on stress response corticosterone levels (ng/ml) from a 12-minute stress handling protocol for female and male Chestnut-collared Longspur, male Baird's Sparrow, and male and female Savannah Sparrow. Samples were obtained during the breeding seasons of 2015 to 2016 in Southern Alberta.

Stress Response Predictor	Female Chestnut-collared Longspur			Male Chestnut-collared Longspur			Male Baird's Sparrow			Female Savannah Sparrow			Male Savannah Sparrow		
	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p
(Intercept)	33.2	21.4	0.12	32.4	15.4	0.04	151	81.0	0.07	28.6	103	0.79	82.8	43.4	0.06
Basal CORT	-0.27	1.13	0.82	0.81	0.87	0.35	-0.19	4.75	0.97	9.30	4.66	0.07	3.34	2.59	0.20
Weight	-0.68	0.91	0.46	-0.32	0.64	0.62	-2.44	3.17	0.45	-3.15	4.54	0.50	-1.21	1.87	0.52
Age: ASY	0.41	2.02	0.84	-2.89	1.86	0.12	7.76	5.30	0.15	12.7	6.53	0.07	-3.53	3.61	0.33
Season Day	0.01	0.05	0.84	-0.05	0.04	0.22	-0.17	0.17	0.33	0.02	0.28	0.95	-0.14	0.11	0.21
Time of Day	-0.02	0.01	0.03	-0.01	0.01	0.61	-0.09	0.03	0.01	0.04	0.05	0.37	-0.01	0.02	0.49
n	79			110			45			19			101		
R ² / adjusted R ²	0.071 / 0.007			0.054 / 0.008			0.239 / 0.141			0.538 / 0.360			0.071 / 0.022		

ASY: After second year bird – a bird in its third calendar year since hatching, indicating a mature adult bird.

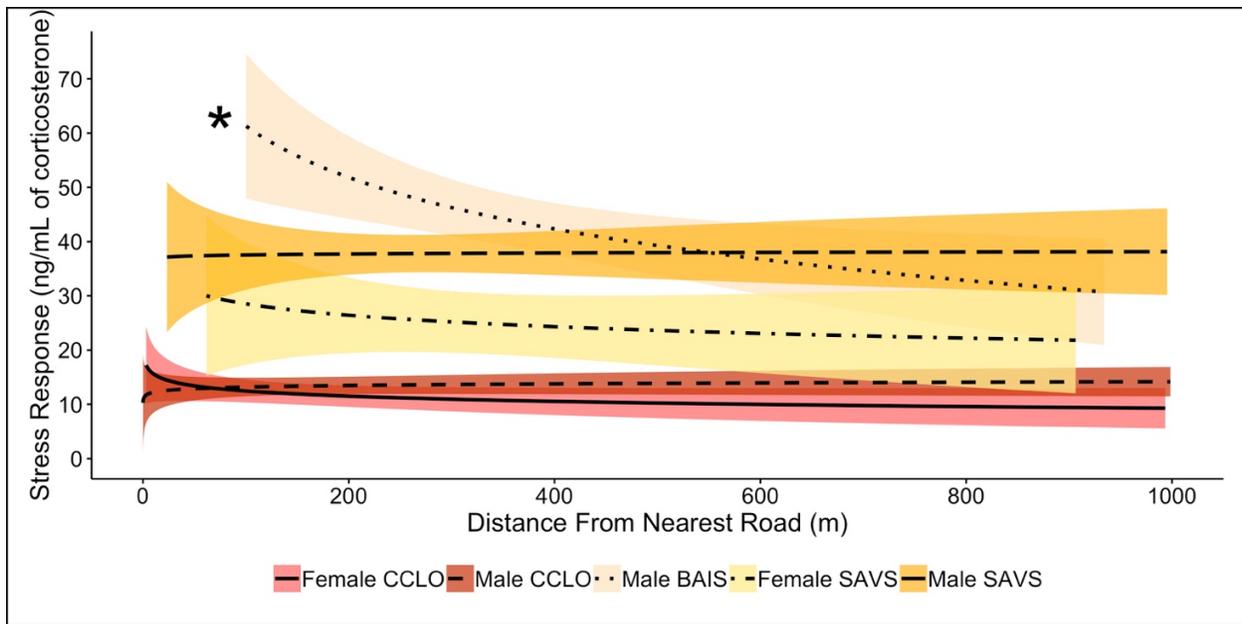


Figure 2. Predicted stress response corticosterone levels relative to proximity to roads (CLO – Chestnut-collared Longspur; BAIS – Baird’s Sparrow; SAVS – Savannah Sparrow).

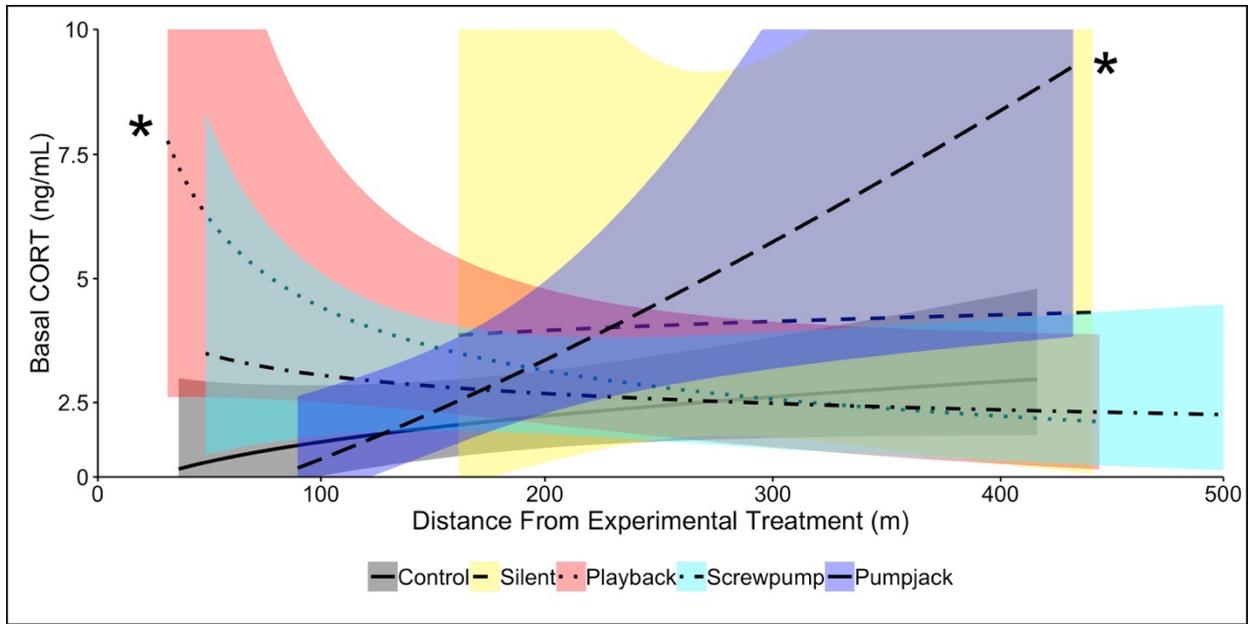


Figure 3. Female Chestnut-collared Longspur basal corticosterone levels relative to proximity of experimental feature (Control, Silent infrastructure, Audio playback without infrastructure, Screwump, or Pumpjack).

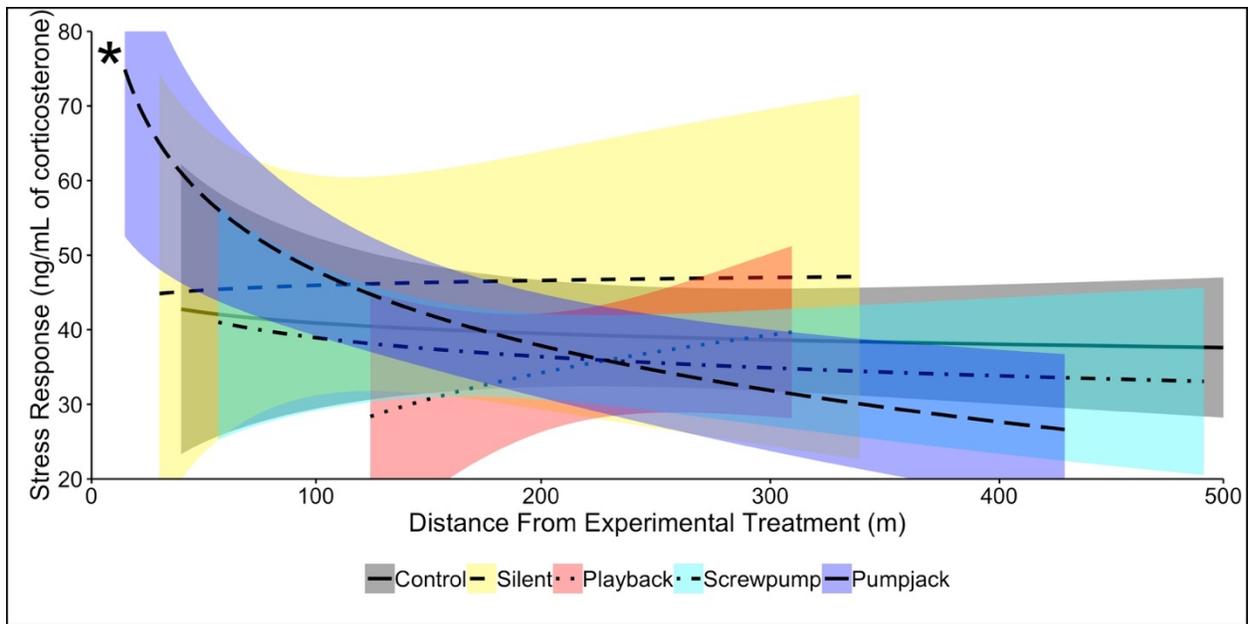


Figure 4. Male Savannah Sparrow stress response corticosterone level in response to each treatment type. Males closer to pumpjacks has significantly higher stress response corticosterone levels.

Table 8. Influence of distance from any type of oil well (Log(m)), distance from road (Log(m)), weight, age (see footer), and day on basal corticosterone levels (Log (ng/ml)) in female and male Chestnut-collared Longspur, male Baird’s Sparrow, and male and female Savannah Sparrow. Samples were obtained during the breeding seasons of 2015 to 2016 in Southern Alberta.

Basal Predictor	Female Chestnut-collared Longspur			Male Chestnut-collared Longspur			Male Baird’s Sparrow			Female Savannah Sparrow			Male Savannah Sparrow		
	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p
(Intercept)	1.40	0.56	0.02	0.76	0.56	0.18	12.4	3.39	0.01	1.00	1.49	0.52	4.72	0.66	<0.01
Distance from Oil Well	0.03	0.10	0.74	0.04	0.09	0.69	-0.15	0.17	0.38	-0.02	0.23	0.94	-0.03	0.07	0.69
Distance from Road	-0.11	0.09	0.22	-0.05	0.07	0.50	-0.16	0.19	0.40	0.19	0.26	0.48	-0.01	0.10	0.91
Age: ASY				0.20	0.24	0.40							0.34	0.13	0.01
Weight							-0.30	0.13	0.02						
Season Day							-0.01	0.01	0.01				-0.01	0.00	<0.01
n	63			88			42			18			89		
R ² / adjusted R ²	0.026 / -0.006			0.013 / -0.022			0.224 / 0.140			0.041 / -0.087			0.210 / 0.173		

ASY: After second year bird – a bird in its third calendar year since hatching, indicating a mature adult bird.

Table 9. Influence of distance from any type of oil well (Log(m)), distance from road (Log(m)), time of day, and basal corticosterone level on stress response corticosterone levels (ng/ml) in female and male Chestnut-collared Longspur, male Baird's Sparrow, and male and female Savannah Sparrow. Samples were obtained during the breeding seasons of 2015 to 2016 in Southern Alberta.

Stress Response	Female Chestnut-collared Longspur			Male Chestnut-collared Longspur			Male Baird's Sparrow			Female Savannah Sparrow			Male Savannah Sparrow		
	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p
Intercept	25.86	7.60	0.01	10.37	4.61	0.03	145	29.9	<0.01	-25.6	23.5	0.29	46.0	11.4	<0.01
Distance from Oil Well	0.55	0.99	0.584	0.14	0.77	0.85	3.25	4.22	0.446	6.88	3.56	0.07	-1.61	2.00	0.42
Distance from Road	-1.38	0.89	0.12	0.43	0.62	0.49	-13.6	4.81	0.01	-3.04	4.12	0.47	0.26	2.8	0.92
Time of Day	-0.02	0.01	0.05				-0.09	0.03	0.01						
Basal CORT										11.2	4.01	0.01			
n	61			86			41			18			87		
R ² / adjusted R ²	0.088 / 0.040			0.008 / -0.016			0.318 / 0.263			0.466 / 0.351			0.013 / -0.011		

Table 10. Influence of distance to oil well types and noise playback treatment sites, age (see footnote), weight (g), and day, on basal corticosterone levels (Log (ng/ml)) in female and male Chestnut-collared Longspur, male Baird's Sparrow, and male and female Savannah Sparrow. Samples were obtained during the breeding seasons of 2015 to 2016 in Southern Alberta. Distances from center of each site or infrastructure/ playback unit and are measured in Log(m).

Predictors	Female Chestnut-collared Longspur			Male Chestnut-collared Longspur			Male Baird's Sparrow			Female Savannah Sparrow			Male Savannah Sparrow		
	Estimates	std. Error	p	Estimates	std. Error	p	Estimates	std. Error	p	Estimates	std. Error	p	Estimates	std. Error	p
(Intercept)	-1.25	1.31	0.343	0.52	1.73	0.763	8.06	2.35	0.002	3.95	2.72	0.170	3.38	1.18	0.005
Control	0.39	0.24	0.114	0.06	0.31	0.854	0.42	0.16	0.014	-0.33	0.48	0.502	0.27	0.17	0.122
Silent	-0.28	0.87	0.750	-0.15	0.58	0.792	-0.18	1.04	0.862				-0.68	0.34	0.047
Playback	-0.88	0.36	0.016	-0.26	0.50	0.602	-13.96	9.32	0.143	1.50	1.60	0.365	-0.37	0.70	0.598
Pumpjack	0.92	0.54	0.095	0.12	0.55	0.833							-0.23	0.25	0.371
Screwump	-0.58	0.37	0.122	-0.00	0.39	0.992	-0.38	0.35	0.275	-0.37	1.16	0.753	0.04	0.31	0.899
Age: ASY				0.32	0.22	0.148							0.29	0.14	0.040
Weight							-0.29	0.10	0.006						
Season Day							-0.02	0.01	0.002				-0.02	0.00	<0.001
Observations	84			115			46			20			104		
R ² / adjusted R ²	0.193 / 0.095			0.041 / -0.051			0.473 / 0.322			0.213 / -0.150			0.251 / 0.162		

ASY: After second year bird – a bird in its third calendar year since hatching, indicating a mature adult bird. 'Pumpjack' refers to propane-powered pumpjack oil wells that draw oil from underground using a vertical see-saw motion. 'Screwump' refers to

propane-powered screw pump oil wells, another type of oil well without the associated large movements of a pumpjack. 'Playback' is a high-fidelity experiential noise treatment, broadcasting the sound of a screw pump oil well 24h a day in field absent of oil infrastructure throughout the breeding season. 'Silent' treatments have the same fencing and build as the playback infrastructure, but do not broadcast noise. Controls are field with no infrastructure nor experimental playback manipulations.

Table 11. Influence of distance oil wells types and noise playback treatment sites, basal corticosterone level (Log), time of day, and day of season, on stress response corticosterone levels (ng/ml) in female and male Chestnut-collared Longspur, male Baird's Sparrow, and male and female Savannah Sparrow. Samples were obtained during the breeding seasons of 2015 to 2016 in Southern Alberta. Distances from center of each site or infrastructure/ playback unit and are measured in Log(m).

Predictors	Female Chestnut-collared Longspur			Male Chestnut-collared Longspur			Male Baird's Sparrow			Female Savannah Sparrow			Male Savannah Sparrow		
	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p
(Intercept)	35.2	14.3	0.02	18.4	14.9	0.22	71.9	40.2	0.08	27.0	52.9	0.62	61.8	30.3	0.05
Control	-2.11	2.41	0.38	-0.70	2.66	0.79	1.63	5.51	0.76	-3.30	8.88	0.71	-3.45	4.24	0.41
Silent	7.20	9.90	0.46	2.98	5.11	0.561	18.6	34.4	0.59				6.10	8.49	0.47
Playback	4.37	3.56	0.22	-2.53	4.30	0.558	-129	313.	0.68	24.9	28.5	0.40	19.6	19.36	0.31
Screwump	1.98	3.79	0.60	1.11	3.36	0.742	5.59	12.6	0.66	28.0	20.4	0.19	0.79	7.67	0.91
Pumpjack	6.62	5.45	0.23	0.45	4.66	0.92							-10.6	6.16	0.09
Basal corticosterone										10.9	4.96	0.05	3.75	2.54	0.14
Time of Day	-0.03	0.01	0.01				-0.09	0.04	0.03						
Season Day													-0.08	0.11	0.46 4
n	81			111			45			19			102		
R ² / adjusted R ²	0.140 / 0.017			0.051 / -0.033			0.248 / 0.054			0.542 / 0.251			0.174 / 0.073		

'Pumpjack' refers to propane-powered pumpjack oil wells that draw oil from underground using a vertical see-saw motion. 'Screwump' refers to propane-powered screwump oil wells, another type of oil well without the associated large movements of a pumpjack. 'Playback' is a high-fidelity experiential noise treatment, broadcasting the sound of a screwump oil well 24h a day in field absent of oil infrastructure throughout the breeding season. 'Silent' treatments have the same fencing and build as the playback infrastructure, but do not broadcast noise. Controls are field with no infrastructure nor experimental playback manipulations.

Individual Quality

Heavier female Chestnut-collared Longspurs and Savannah Sparrows were associated with metrics of increased productivity compared to lighter females (Table 18; Figure 5). Heavier female Chestnut-collared Longspurs produced broods with greater biomass while heavier female Savannah Sparrows had heavier individual nestlings. Male age, weight, and size were not correlated with productivity for Chestnut-collared Longspur or Savannah Sparrow (Table 18), nor were these physical characteristics correlated with the weight of their socially bonded female (Table 19). My sample size of Baird's Sparrows was too small to analyse.

Table 12. Influence of female weight, age (see footnote), size (tarsus) on total nestling biomass and individual nestling mass. Additionally, influence of brood size and average nestling age on total nestling biomass, and influence of nestling age on individual

Predictor	CCLO Nestling Combined Weight			SAVS Nestling Combined Weight			CCLO Individual Nestling Mass			SAVS Individual Nestling Mass		
	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p
(Intercept)	20.7	54.0	0.70	-121	466	0.80	4.56	8.36	0.58	-6.08	33.9	0.86
Female Weight	3.29	1.46	0.03	5.05	5.78	0.41	0.14	0.22	0.51	0.97	0.42	0.05
Female Age: SY	-2.51	3.73	0.50	-0.49	19.0	0.98	-0.33	0.57	0.56	-2.24	1.34	0.14
Female Tarsus	-4.36	2.67	0.11	2.67	20.2	0.90	0.03	0.42	0.94	-0.58	1.49	0.71
Brood Size	12.1	1.36	<0.01	4.88	7.91	0.56						
Average Nestling Age	0.50	2.27	0.82	1.13	14.2	0.94						
Nestling age							0.78	0.34	0.02	2.13	1.04	0.08
Random Effects												
σ^2							3.14			1.21		
τ_{00}							1.88 _{nest_id}			1.44 _{nest_id}		
ICC							0.37 _{nest_id}			0.54 _{nest_id}		
Observations	40			12			178			36		
R ² / adjusted R ²	0.738 / 0.700			0.159 / -0.541			0.067 / 0.417			0.338 / 0.699		

SY: Second year bird – a bird in its second calendar year, one year after hatching.

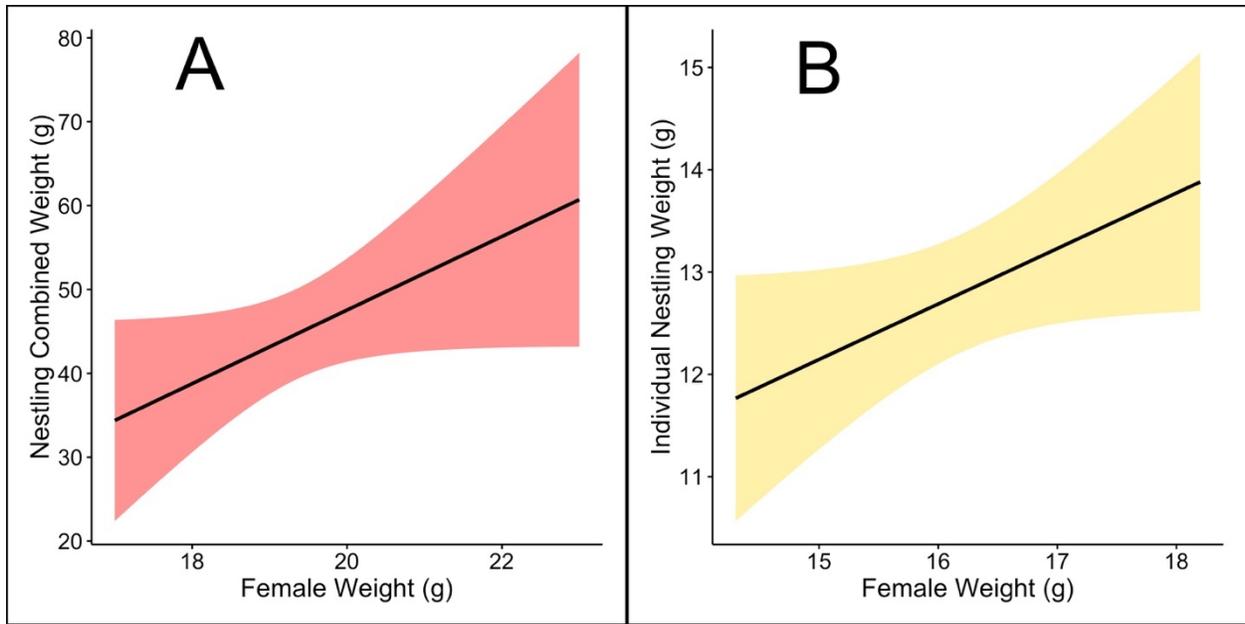


Figure 5. Heavier females are associated with A) A higher combined nestling weight in Chestnut-collared Longspur and B) heavier individual nestling weights in Savannah Sparrows.

Table 13 Associations in individual quality between socially paired male and female Chestnut-collared Longspur and Savannah Sparrows. Male weight, age, or tarsus length were not predictive of being paired with a heavier (higher-quality) female.

<i>Predictors</i>	CCLO Female Weight			SAVS Female Weight		
	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	16.89	4.76	0.001	13.37	24.82	0.628
Male Weight	0.21	0.16	0.183	0.34	0.58	0.595
Male Age: SY	-0.04	0.36	0.912	0.94	1.02	0.427
Male Tarsus	-0.07	0.22	0.747	-0.16	0.85	0.865
Observations	53			7		
R ² / adjusted R ²	0.037 / -0.022			0.327 / -0.347		

Habitat Selection

From 2015 to 2017, I took morphometric measurements from 411 adult birds (Table 11). Female Chestnut-collared Longspurs were older and heavier closer to oil wells but were smaller near roads (Table 12-14; Figure 6). I found no spatial pattern in male Chestnut-collared Longspur age, weight, or size, in response to oil wells, roads (Tables 12-14). Male Savannah Sparrows were lighter and female Savannah Sparrows were smaller near screwpumps (Tables 16-17). Male Baird's Sparrows were heavier near screwpumps (Table 17). I found no effect of noise *per se* on habitat selection for any species or sex (Tables 15-17).

Table 14. Number of adult Chestnut-collared Longspur, Baird's Sparrow, and Savannah Sparrow caught and banded by species and year, excluding recaptures in Southern Alberta from breeding seasons of 2015 – 2017.

Year	Chestnut-collared Longspur		Baird's Sparrow		Savannah Sparrow	
	Females	Males	Females	Males	Females	Males
2015	28	50	2	18	2	60
2016	50	61	1	35	21	47
2017	17	23	0	27	2	15
Total	95	134	3	80	25	122

Table 15. Influence of distance from oil well and roads on age class (Second Year or After Second Year) of female and male Chestnut-collared Longspur, male Baird's Sparrow, and male and female Savannah Sparrow. Birds were captured during the breeding seasons of 2015 to 2017 in Southern Alberta. Distances are from the nearest infrastructure and road measured in Log(m). Model was fitted with a binomial distribution.

Age	Female Chestnut-collared Longspur			Male Chestnut-collared Longspur			Male Baird's Sparrow			Female Savannah Sparrow			Male Savannah Sparrow		
	Log-Odds	std. Error	p	Log-Odds	std. Error	p	Log-Odds	std. Error	p	Log-Odds	std. Error	p	Log-Odds	std. Error	p
(Intercept)	2.81	1.61	0.08	1.94	1.47	0.18	0.67	2.83	0.81	-2.70	3.78	0.47	-2.46	1.37	0.07
Distance from Oil Well	-0.53	0.28	0.06	-0.11	0.25	0.66	-0.07	0.38	0.84	-0.42	0.53	0.42	0.32	0.22	0.14
Distance from Road	0.20	0.25	0.42	0.01	0.20	0.95	-0.01	0.40	0.98	0.90	0.70	0.20	0.07	0.28	0.80
n	73			102			74			23			105		
Cox & Snell's R ² / Nagelkerke's R ²	0.050 / 0.069			0.002 / 0.003			0.001 / 0.001			0.082 / 0.110			0.039 / 0.051		

Table 16. Influence of distance from oil well and roads on size (tarsus length in mm) of female and male Chestnut-collared Longspur, male Baird's Sparrow, and male and female Savannah Sparrow. Birds were captured during the breeding seasons of 2015 to 2017 in Southern Alberta. Distances are from the nearest infrastructure and road measured in Log(m).

Tarsus	Female Chestnut-collared Longspur			Male Chestnut-collared Longspur			Male Baird's Sparrow			Female Savannah Sparrow			Male Savannah Sparrow		
	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p
Intercept	19.2	0.41	<0.01	19.7	0.42	<0.01	20.1	0.97	<0.01	19.3	1.28	<0.01	20.8	0.5	<0.01
Distance from Oil Well	-0.05	0.07	0.48	-0.05	0.07	0.50	0.03	0.13	0.82	0.01	0.18	0.96	-0.05	0.08	0.47
Distance from Road	0.15	0.07	0.03	0.07	0.06	0.24	0.19	0.14	0.16	0.06	0.21	0.77	-0.02	0.10	0.82
n	73			102			74			23			105		
R ² /adjusted R ²	0.068 / 0.042			0.014 / -0.006			0.035 / 0.008			0.006 / -0.093			0.012 / -0.008		

Table 17. Influence of distance from oil well and roads on weight (g) of female and male Chestnut-collared Longspur, male Baird's Sparrow, and male and female Savannah Sparrow. Birds were captured during the breeding seasons of 2015 to 2017 in Southern Alberta. Distances are from the nearest infrastructure and road measured in Log(m).

Predictor	Female Chestnut-collared Longspur			Male Chestnut-collared Longspur			Male Baird's Sparrow			Female Savannah Sparrow			Male Savannah Sparrow		
	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p	Estimate	std. Error	p
(Intercept)	23.8	1.49	<0.01	20.80	1.12	<0.01	23.8	1.64	<0.01	18.3	3.32	<0.01	18.9	1.06	<0.01
Distance from Oil Well	-0.26	0.14	0.06	-0.08	0.10	0.40	-0.13	0.16	0.43	-0.03	0.27	0.91	0.07	0.11	0.54
Distance from Road	-0.02	0.13	0.90	0.03	0.08	0.68	-0.16	0.17	0.35	0.04	0.32	0.89	-0.08	0.14	0.59
Season Day	-0.02	0.01	0.02	-0.01	0.01	0.32	-0.02	0.01	0.01	-0.01	0.01	0.35	-0.01	0.01	0.29
n	72			101			73			23			103		
R ² / adjusted R ²	0.135 / 0.096			0.018 / -0.012			0.131 / 0.093			0.051 / -0.099			0.019 / -0.010		

Table 18. Influence of distance to type of oil infrastructure or experimental noise playback on age class (second year or After Second Year) of female and male Chestnut-collared Longspur, male Baird’s Sparrow, and male and female Savannah Sparrow. Birds were captured during the breeding seasons of 2015 to 2017 in Southern Alberta. Distances from center of each site or infrastructure/ playback unit and are measured in Log(m). Model was fitted with a binomial distribution.

Predictors	Female Chestnut-collared Longspur			Male Chestnut-collared Longspur			Male Baird’s Sparrow			Female Savannah Sparrow			Male Savannah Sparrow		
	Log-Odds	std. Error	P	Log-Odds	std. Error	P	Log-Odds	std. Error	P	Log-Odds	std. Error	P	Log-Odds	std. Error	P
(Intercept)	5.35	3.81	0.160	0.37	3.34	0.912	0.27	2.86	0.926	2.84	6.46	0.661	0.61	2.57	0.814
Distance to Control	-0.91	0.68	0.180	0.15	0.60	0.807	-0.08	0.49	0.872	-0.58	1.14	0.608	-0.09	0.46	0.839
Distance to Silent	0.57	1.32	0.666	-1.71	1.45	0.240	2.20	1.96	0.261				0.26	1.04	0.804
Distance to Playback	1.00	0.94	0.286	0.73	1.00	0.463	-2.14	2.58	0.408	-7.43	13.25	0.575	-1.51	2.94	0.608
Distance to Screwump	0.89	1.04	0.390	0.52	0.83	0.532	0.58	1.18	0.626	-0.29	2.26	0.899	0.26	0.77	0.732
Distance to Pumpjack	-3.98	3.42	0.245	-2.84	1.91	0.137							0.49	0.86	0.566
Observations	95			134			78			25			121		
Cox & Snell's R ² / Nagelkerke's R ²	0.090 / 0.125			0.062 / 0.096			0.069 / 0.092			0.159 / 0.213			0.074 / 0.099		

‘Pumpjack’ refers to propane-powered pumpjack oil wells that draw oil from underground using a vertical see-saw motion.

‘Screwump’ refers to propane-powered screwump oil wells, another type of oil well without the associated large movements of a pumpjack. ‘Playback’ is a high-fidelity experiential noise treatment, broadcasting the sound of a screwump oil well 24h a day in field

absent of oil infrastructure throughout the breeding season. 'Silent' treatments have the same fencing and build as the playback infrastructure, but do not broadcast noise. Controls are field with no infrastructure nor experimental playback manipulations.

Table 19. Influence of distance to type of oil infrastructure or experimental noise playback on size (Tarsus length mm) of female and male Chestnut-collared Longspur, male Baird's Sparrow, and male and female Savannah Sparrow. Birds were captured during the breeding seasons of 2015 to 2017 in Southern Alberta. Distances from center of each site or infrastructure/ playback unit and are measured in Log(m).

Predictors	Female Chestnut-collared Longspur			Male Chestnut-collared Longspur			Male Baird's Sparrow			Female Savannah Sparrow			Male Savannah Sparrow		
	Estimate <i>s</i>	std. Error	<i>p</i>	Estimate <i>s</i>	std. Error	<i>p</i>	Estimate <i>s</i>	std. Error	<i>p</i>	Estimate <i>s</i>	std. Error	<i>p</i>	Estimate <i>s</i>	std. Error	<i>p</i>
(Intercept)	19.66	0.88	<0.001	17.85	1.07	<0.001	20.49	0.98	<0.001	22.62	2.12	<0.001	21.17	0.86	<0.001
Distance to Control	-0.00	0.16	0.995	0.35	0.19	0.074	0.18	0.17	0.288	-0.49	0.37	0.206	-0.16	0.15	0.300
Distance to Silent	0.36	0.31	0.238	-0.50	0.33	0.129	-0.47	0.52	0.366				0.24	0.33	0.477
Distance to Playback	-0.10	0.24	0.669	-0.49	0.31	0.121	-0.38	0.58	0.519	-0.72	1.36	0.601	-0.26	0.70	0.705
Distance to Screw pump	0.04	0.27	0.884	-0.27	0.26	0.304	-0.82	0.40	0.044	1.41	0.74	0.074	0.20	0.25	0.425
Distance to Pumpjack	-0.11	0.40	0.789	-0.45	0.41	0.273							-0.27	0.29	0.350
Observations	95			134			78			25			121		
R ² / adjusted R ²	0.081 / -0.016			0.070 / 0.002			0.090 / -0.001			0.268 / 0.023			0.080 / 0.005		

'Pumpjack' refers to propane-powered pumpjack oil wells that draw oil from underground using a vertical see-saw motion. 'Screwump' refers to propane-powered screwump oil wells, another type of oil well without the associated large movements of a pumpjack. 'Playback' is a high-fidelity experiential noise treatment, broadcasting the sound of a screwump oil well 24h a day in field absent of oil infrastructure throughout the breeding season. 'Silent' treatments have the same fencing and build as the playback infrastructure, but do not broadcast noise. Controls are field with no infrastructure nor experimental playback manipulations.

Table 20. Influence of distance to type of oil infrastructure or experimental noise playback on weight (g) of female and male Chestnut-collared Longspur, male Baird's Sparrow, and male and female Savannah Sparrow. Birds were captured during the breeding seasons of 2015 to 2017 in Southern Alberta. Distances from center of each site or infrastructure/ playback unit and are measured in Log(m).

Predictors	Female Chestnut-collared Longspur			Male Chestnut-collared Longspur			Male Baird's Sparrow			Female Savannah Sparrow			Male Savannah Sparrow		
	Estimate <i>s</i>	std. Error	<i>p</i>	Estimate <i>s</i>	std. Error	<i>p</i>	Estimate <i>s</i>	std. Error	<i>p</i>	Estimate <i>s</i>	std. Error	<i>p</i>	Estimate <i>s</i>	std. Error	<i>p</i>
(Intercept)	22.44	1.93	<0.001	20.33	1.84	<0.001	20.36	1.72	<0.001	21.21	3.41	<0.001	21.42	1.51	<0.001
Distance to Control	-0.17	0.30	0.572	0.19	0.30	0.522	0.12	0.23	0.601	-0.70	0.61	0.269	-0.42	0.23	0.063
Distance to Silent	-0.01	0.01	0.032	-0.01	0.01	0.068	-0.01	0.01	0.045	-0.00	0.01	0.820	-0.01	0.01	0.189
Distance to Playback	-0.48	0.58	0.417	-0.75	0.51	0.142	-0.54	0.70	0.449				0.89	0.49	0.073
Distance to Screwump	0.10	0.45	0.833	-0.52	0.49	0.287	-0.73	0.81	0.373	-1.87	2.15	0.397	-0.40	1.03	0.700
Distance to Pumpjack	-0.72	0.50	0.154	0.17	0.40	0.681	-0.82	0.55	0.137	0.88	1.15	0.453	0.83	0.37	0.028
Season Day	-0.74	0.74	0.320	-0.45	0.64	0.482							-0.03	0.42	0.938
Observations	94			133			77			25			119		
R ² / adjusted R ²	0.163 / 0.062			0.110 / 0.037			0.138 / 0.036			0.356 / 0.091			0.113 / 0.031		

'Pumpjack' refers to propane-powered pumpjack oil wells that draw oil from underground using a vertical see-saw motion. 'Screwump' refers to propane-powered screwump oil wells, another type of oil well without the associated large movements of a pumpjack. 'Playback' is a high-fidelity experiential noise treatment, broadcasting the sound of a screwump oil well 24h a day in field absent of oil infrastructure throughout the breeding season. 'Silent' treatments have the same fencing and build as the playback infrastructure, but do not broadcast noise. Controls are field with no infrastructure nor experimental playback manipulations.

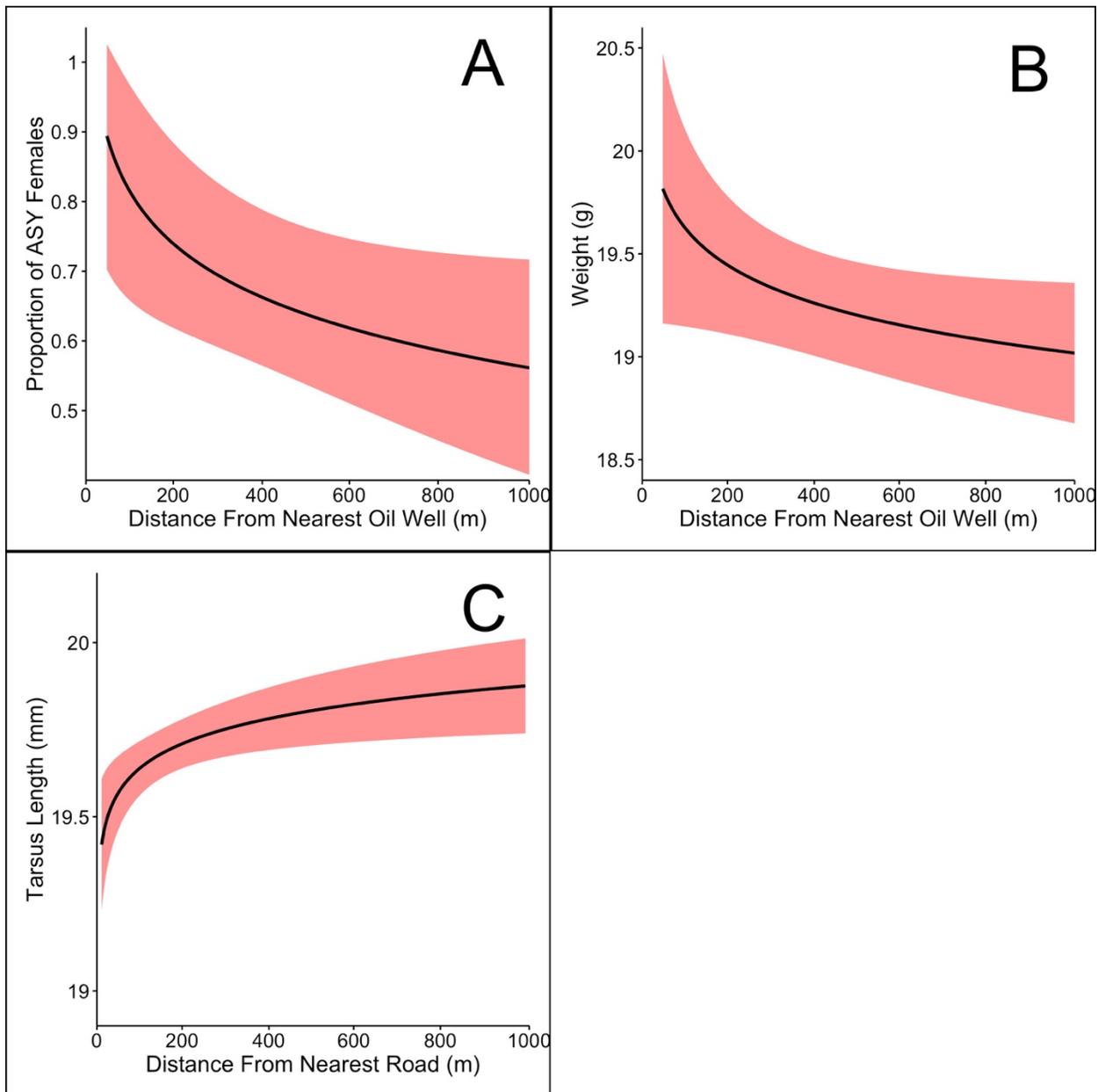


Figure 6. Female Chestnut-collared Longspur habitat selection. A) Females closer to oil wells are significantly older B) Females closer to oil wells are significantly heavier, and C) Females closer to roads are significantly smaller.

Discussion

Corticosterone levels suggest that habitat quality was reduced in some cases by the presence of oil wells, simulated oil well noise, or roads. Higher levels of corticosterone in individuals near these disturbances suggest that those birds require more effort to meet their daily metabolic demands and thus are experiencing physiological stress (Romero et al. 2009). This conclusion is consistent with other research conducted in this region, which demonstrated that productivity near wells is low (Bernath-Plaisted and Koper 2016), brood parasitism rates are high (Bernath-Plaisted et al. 2017), and that parental care of nests near wells is low (Ng et al. 2018), all of which suggest that habitat quality near oil wells is low, but also highlights previously undocumented effects on individual health. I also found evidence that these anthropogenic disturbances impact the perceived habitat quality for some breeding grassland songbirds. However, perceived habitat quality and realized habitat quality were not always affected synchronously. Both Chestnut-collared Longspurs and Savannah Sparrows exhibited signs of stress near some types of infrastructure, but higher-quality (heavier) Chestnut-collared Longspur females preferentially selected nest sites near oil infrastructure while higher-quality Savannah Sparrows avoided it. These two opposite responses suggest that there may be a fundamental difference in how Chestnut-collared Longspurs and Savannah Sparrows assess habitat quality and integrate novel information about landscape into that perception. Relative ability to match habitat selection to habitat quality in anthropogenically modified landscapes may help explain why Savannah Sparrows successfully adapt to anthropogenically modified habitats (Wheelright and Rising 2008) while Chestnut-collared Longspur populations are declining precipitously (Sauer et al. 2017).

Nest Success

I did not find an effect of oil wells, simulated oil well noise, or roads on nesting success of Chestnut-collared Longspurs, Baird's Sparrow or Savannah Sparrow. However, it seems likely that risk of nest predation is higher near wells since several species experience lower nesting success near these wells in this region, including 15% lower nest success for Savannah Sparrow at sites with oil wells, with screw pumps having a particularly strong negative impact (Bernath-Plaisted et al. 2016). Increased predator densities have also been found in other regions impacted by energy development (Hethcoat and Chalfoun 2015). It is possible that many species, including Chestnut-collared Longspurs and Savannah Sparrows, are able to compensate for increased real or perceived predation risk behaviourally (e.g. Ng et al. 2018, Antze and Koper 2018). However, Ng et al. (2018) demonstrated that altered parental care decreases numbers of fledglings produced per nest near roads, suggesting that productivity, and thus fitness, of individuals near oil development may still be reduced. This suggests that there is some cost to nesting close to disturbance, despite behavioural responses to risk. Higher basal corticosterone found in female Chestnut-collared Longspurs near simulated oil well noise supports the hypothesis that more effort is required to breed in impacted habitat. However, without tracking lifetime reproduction or survival the extent to which this affects fitness is unknown.

Corticosterone

While corticosterone responses varied by species, there were several cases where oil infrastructure, roads, or noise altered corticosterone levels. As the intensity of the disturbance increases, so too should levels of corticosterone in the blood rise until that individual can no longer maintain increased expression, at which point corticosterone should decrease as that individual is

no longer able to cope with that disturbance (Busch and Hayward 2009). Female but not male Chestnut-collared Longspurs showed increased basal corticosterone in the presence of simulated oil well noise, suggesting noise induces stress. Female longspurs also had lower basal corticosterone near pumpjacks than at control sites, which might indicate that pumpjacks are actually the more stressful disturbance than noise alone if this is indicative of an inability to cope with disturbance. Savannah Sparrow with territories near pumpjacks also showed a heightened stress response. These results also suggest that these individuals are experiencing stressful conditions, which may result in short- or long-term health effects (Busch and Hayward 2009). Baird's Sparrows with territories near roads showed an elevated stress response. This suggests an increased sensitivity of the HPA axis (Wingfield et al. 1998, Busch and Hayward 2009), which could be caused by more frequent exposure to disturbances in the habitat adjacent to roads. These effects are not restricted to songbirds, as chronic noise from energy development also increased fecal corticosterone levels in Greater Sage-Grouse on leks (Blickley et al. 2012).

A recent similar study also found changes in corticosterone in response to disturbances from energy infrastructure across multiple songbird species (Kleist et al. 2018). Interestingly, Kleist et al. (2018), found that basal corticosterone was consistently lower near chronic anthropogenic noise from natural gas compressor stations and attributed the associated declines in productivity to that increased noise. Natural gas compressor stations are much louder than oil wells (Rosa et al. 2015, Kleist et al. 2018), so perhaps this disturbance has pushed the surrounding individuals past the tipping point of maximum corticosterone output. Differences in corticosterone responses to disturbance can be expected in cases where the intensity of disturbance and the capacity of an organism to respond differ (Busch and Hayward 2009). The cavity nesting birds sampled in Kleist et al. (2018) are taxonomically (Tyrannidae, Turdidae) distinct from the families

represented in my study (Passerellidae, Calcariidae), so it is possible that their capacity to respond to disturbances may be bounded by different thresholds. Since the response in corticosterone and the associated capacity for an organism to respond to disturbance are not linear, organisms experiencing challenging environmental conditions may show positive or negative changes in circulating corticosterone depending on the severity of the disturbance (Busch and Hayward 2009). Repeated measures of an individual during exposure may help determine species-specific values of corticosterone to indicate the coping ability of an individual.

Phylogenetic differences between passerellids and calcariids may at least partially explain differences I observed in their corticosterone responses. In birds, sex (gonadocorticoid) and stress (glucocorticoid) hormones share a single binding globulin (corticosteroid-binding globulin; CBG) that modulates the activity of steroids in the blood (Breuner and Orchinik 2002). However, testosterone seems to be a more important regulator of CBG quantities in the blood than corticosterone (Deviche et al. 2001). Beyond the inherent differences in circulated corticosterone demonstrated in this study and others (Lynn et al. 2003, Crino et al. 2011), male calcariids also have different circulating levels of testosterone than many other songbirds (Lynn and Wingfield 2008). Once a male longspur's socially bonded female is incubating, his levels of circulating testosterone are reduced, possibly to facilitate greater parental care (Lynn et al. 2002, Lynn and Wingfield 2008), which is essential for longspur nestling survival (Lynn and Wingfield 2003). Physiological mechanisms that control male longspur insensitivity to testosterone during brood rearing (Lynn et al. 2002) may also reduce sensitivity to corticosterone. For example, if the mechanism for testosterone insensitivity is increased CBG quantities in the blood, the activity of corticosterone could also be reduced (Breuner and Orchinik 2002, Van Duyse et al. 2004, Krause et al. 2014). Since I was measuring the total concentration of corticosterone in blood, not the

proportion that was bound or unbound to CBG (Breuner and Orchinik 2002), this may explain why I may not have had the resolution in my data to detect a response from male Chestnut-collared Longspur around oil infrastructure.

Measures of corticosterone can be particularly useful to contextualize impacts within an affected population by identifying individuals or groups with increased susceptibility to habitat disturbance. However, care must be taken to interpret corticosterone levels within an ecological context (Dantzer et al. 2014). Basal corticosterone levels are known to vary by species, season, age, sex, and breeding status (Wingfield et al. 1995, Dantzer et al. 2014). Similarly, the magnitude of a bird's stress response can vary with developmental stage, body condition, or parental investment (Romero et al. 2009). Therefore, aspects of a bird's biology and life stage can impact measures of baseline and stress-induced corticosterone, which may mimic chronic stress. However, I controlled for seasonal and age effects on corticosterone, so this does not impact the interpretation of my results. My results also highlight the importance of experiments, as departures from normal circulating levels of corticosterone may indicate stress regardless of direction due to the nonlinear nature of corticosterone expression in response to environmental disturbance.

Habitat Selection

I found that higher-quality female Chestnut-collared Longspur were more likely to nest far from roads and that male Baird's Sparrow had higher stress responses near roads. Both results could be due to frequent exposure to the unpredictable disturbance of passing cars (Francis and Barber 2013a), increased predator activity near roads (Chalfoun et al. 2002), changes to vegetation characteristics (Koper et al. 2014) or invertebrate abundances near roadsides. The negative impact of roads on wildlife is well established and many other studies have also found negative effects of

roads on birds (Laurance et al. 2004, Sliwinski and Koper 2012), and even effects of isolated road noise (McClure et al. 2017). Roads around my study sites are used daily by service vehicles and trucks visiting the oil wells. However, these roads are unpaved and traffic volume is very low, often less than 5 vehicles per hour (per. obs.). My results add to this literature by suggesting that even small, infrequently used roads may have ecological impacts.

Male Chestnut-collared Longspurs did not show signs of selecting territories based on the presence of oil disturbances, nor did they suffer any negative consequences of interacting with these disturbances. This is surprising given the number of significant effects I detected for female longspurs. However, since females alone incubate (Lloyd and Martin 2005), perhaps they are more susceptible to certain type of disturbance, such as chronic noise, from which they cannot move away. Nevertheless, my results suggest that males settle the landscape according to the ideal free distribution, but that neither male age nor size appear to be factors that females use to select a mate. Males establish territories in early May, which they actively defend against rivals while advertising to females (Harris 1944). However, once in a socially monogamous pair, the female appears to select the actual nest location as she alone builds the nest (Lloyd and Martin 2005). Female Chestnut-collared Longspurs seem to show a preference for nesting near oil wells. Females nesting close to oil wells were more likely to be experienced breeders (older) and were heavier, which suggests that they may be more competitive and higher quality than younger, lighter females.

Interestingly, female longspurs had elevated basal corticosterone at sites with playback of noise from screw pumps, suggesting that these females were experiencing greater physiological stress than those farther from noise, although higher quality females preferentially selected these sites. One explanation for this discrepancy could be related to vegetation characteristics. Building

oil wells in an otherwise featureless landscape shifts grazing patterns since cattle are neophilic (Koper et al. 2014). These more heavily grazed areas near oil wells may produce a concentration of desirable nesting locations for Chestnut-collared Longspurs (Davis 2005, Lloyd and Martin 2005), explaining the stronger attraction for females than males. Either the deterrence of the stressful environment near oil wells is outweighed by the preference for these vegetation characteristics for nesting, or the source of the stress, noise, is not considered by females during mate selection. This suggests that experienced breeders are choosing males with territories close to oil wells based on vegetation characteristics for nest sites. This mismatch in perceived and realized habitat quality suggests an ecological trap (Robertson and Hutto 2016), whereby individuals are attracted to habitats that are of lower quality. There is evidence that Chestnut-collared longspurs may also fall into an equal-preference ecological trap by not avoiding nesting in patches of Crested Wheatgrass but suffering reduced nest success as a result (Lloyd and Martin 2005), and that Savannah Sparrows may not always preferentially settle in the habitat that affords the highest reproductive success (Vickery et al. 1992a). As suggested by Battin (2004), the prevalence and consequences of ecological traps should continue to be an active area of research for conservation biologists.

Noise

It is clear that noise *per se* does not drive most of the patterns in habitat perception I observed; simulated oil well noise, when independent of real infrastructure, failed to produce an effect on demographic structure of my study species. This indicates that either 1) birds are not using sound of any type as a mechanism for habitat selection, therefore anthropogenic noise could not influence habitat selection, 2) anthropogenic noise specifically is a novel habitat feature that is

not yet integrated into the perception of habitat quality by grassland songbirds, 3) oil well noise in this system is insufficiently loud to influence grassland songbird behaviour or habitat selection, or 4) birds are able to adapt to oil well noise as it is predictable and continuous (Francis and Barber 2013a). Scenario 3) or 4) are perhaps the most likely given Savannah and Baird's Sparrows have the ability to adapt to noise (Curry et al. 2017) and Savannah Sparrows can effectively compensate for the interference behaviourally (Curry et al. 2018). This adaptive flexibility likely evolved as a response to natural noises in this ecosystem, such as wind, which has the capacity to severely distort acoustic signals (Green 1992, Curry et al. 2017). Low cost behavioural changes such as a head tilt or singing louder may be all that is necessary to compensate. Similarly, the lack of effect of noise *per se* on nesting success suggests that the effectiveness of nest predators is not influenced by noise. Perhaps key nest predators in this system rely more heavily on visual cues (e.g. birds of prey) or olfactory cues (e.g. snakes).

The only evidence of a negative impact of noise on habitat quality was that basal corticosterone of female Chestnut-collared Longspurs was higher in proximity to simulated oil well noise. This result is a contradiction to that of Kleist et al. (2018), who attributed changes in corticosterone levels to the noise produced by natural gas compressor station. Despite their physiological response, female Chestnut-collared Longspurs do not appear to take noise cues into account during territory establishment. The reason that Savannah Sparrows avoid oil wells is not noise *per se* either, as they did not avoid the sites with simulated oil well noise, and interestingly, the individuals near silent playback infrastructure had lower basal corticosterone suggesting the physical infrastructure, not noise, is driving deviations in corticosterone. Perhaps this is because they can effectively compensate for the effects of noise on communication with vocal plasticity (Curry et al. 2017) and behavioral shifts (Curry et al. 2018). If noise is not the driving mechanism

for most of the impacts observed in this system, then there is little value in its mitigation. Similarly, Bernath-Plaisted and Koper (2016) and Nenninger and Koper (2018) both suggest that inactive oil wells have similar effects to active oil wells, suggesting noise does not explain impacts of wells on abundance or nest success of grassland songbirds.

The general lack of significant impacts from noise *per se* in this study system is a curious and interesting result, as many studies have concluded that noise influences productivity, stress, or settlement patterns in birds (Habib et al. 2007, Bayne et al. 2008, Francis et al. 2012a, Kleist et al. 2016, 2018). This could be because other studies have incorrectly attributed impacts of above-ground infrastructure to impacts of noise. For example, shallow gas wells, a small (often only 1 m high), silent piece of infrastructure associated with natural gas extraction has negative effects on grassland bird abundance completely in the absence of noise (Rodgers and Koper 2017). This fact illustrates the importance of experiments to disentangle effects of noise from infrastructure. Additionally, predictable noises, such as the chronic drone of an oil pump generator, might not have negative impacts if birds can adapt more easily to them than to unpredictable noise (Francis and Barber 2013a). My results suggest that mitigation of cyclic or predictable noise may not be as effective as making management decisions to address the spatial distribution the physical oil wells. Future research on noise in this system should focus on determining the impact of noise predictability as much as amplitude.

Conclusions

Mismatches in perceived and realized habitat quality that result in either an ecological (Robertson and Hutto 2016) or perceptual trap (Gilroy and Sutherland 2007) are of particular concern for species at risk. My results suggest that Chestnut-collared Longspurs, a Threatened

species in Canada, may experience an ecological trap as a result of oil wells: females preferentially nest near oil wells, where their corticosterone levels are higher, parental care of nests is lower (Ng 2017), nest predators are more abundant (Chalfoun et al. 2002), and nest predation risk is higher (Bernath-Plaisted and Koper 2016). In addition to the effects of the oil infrastructure itself, the presence of roads increases stress in Baird's Sparrows and are perceived as poor-quality habitat by Chestnut-collared Longspurs. This highlights the importance of all aspects of human influence on the landscape, even an innocuous-looking dirt road. In order to get a full estimate on the impact of oil development on species at risk, it will be necessary to determine the effect on population vital rates, such as post fledgling survival and lifetime reproductive success of individuals interacting with disturbance. Of the species I examined, the species at risk seem to be more likely to fall victim to mismatches between perceived and realized habitat quality, which could be a contributing factor to their declines.

Oil development in the mixed grass prairies of Canada poses a significant threat to birds that rely on the few remaining intact patches of grassland habitat. Noise appears to be a relatively unimportant mechanism by which oil wells affect grassland songbird communities; the main problem is the physical infrastructure itself. However, female Chestnut-collared Longspurs did respond to noise *per se*, so to protect habitat for the most sensitive species at risk we must minimize both the above-ground infrastructure and noise. Nevertheless, it is clear that our first priority should be reducing human presence on the landscape by concentrating above ground infrastructure using techniques such as directional drilling, decommissioning old well heads, reclaiming under used roads, and generally reducing vehicle traffic. Future energy development should be undertaken while minimizing the construction of new roads and lease sites.

Chapter 3: General Discussion and Management Implications

My results suggest that individual grassland songbird species can respond more strongly, or be most sensitive to, different aspects of oil development in the prairies. Consequently, conservation management for a single species compared to taking a multi species approach may be less effective, which has important conservation and management implications (Brennan and Kuvlesky 2005, Gerber 2016). Unfortunately, current resource allocation for conservation often plays a bigger role dictating a management approach than science-based long-term planning (Gerber et al. 2018). This often results in on-the-ground actions to mitigate the effects of human activities, including natural resources development, being reactive and focusing solely on whatever species is of greatest conservation concern (Martin et al. 2018b, Burgar et al. 2018). These mitigative actions rely on legal precedence to enforce environmental protective measures (Gerber 2016), of which our strongest legislation is the Species at Risk Act (SARA). However, in the context of oil development in the prairies, this means that despite the guild-wide declines seen in grassland songbirds (Sauer et al. 2017), legal protection for non-listed species is crippled in habitat where species at risk are absent, or on private land where SARA cannot be implemented. Additionally, mitigation strategies aimed at Chestnut-collared Longspur, the species of greatest conservation concern I examined, may not have many positive impacts for Baird's Sparrow as, unlike Chestnut-collared Longspur, they seem to simply avoid all disturbances.

Since there is realistically little chance that oil development in the Great Plains will cease any time soon, I feel that the principle for prioritizing conservation efforts proposed by Wilson et al. (2006), to “maximize short-term gain, minimize short-term loss”, may be an appropriate way to move forward. Therefore, in this chapter I will discuss some of the implications of species-specific responses to oil development, the utility of using corticosterone as a tool for conservation,

a summary of the impact of oil development in this study system. I conclude with implications of how my study suggests we should address these impacts, avenues for future research that support conservation of these at-risk species, and the grassland songbird community

Species-Specific Responses

Species-specific differences in nesting behaviour may affect susceptibility to reduced nesting success near oil development. I did not find reduced nest success for Chestnut-collared Longspur or Savannah Sparrow, however, Savannah Sparrow have been found to suffer reduced daily probability of nest survival in proximity to oil wells in the same study area (Bernath-Plaisted and Koper 2016). While the specific nest predators of Chestnut-collared Longspur and Savannah Sparrow are not well documented, the general guild of songbird nest predators in the grasslands is well known (Pietz and Granfors 2000, Klug et al. 2009, Ng 2017). Variation in foraging behaviour among predator types, combined with differences in Chestnut-collared Longspur and Savannah Sparrow nesting microhabitat preferences (Davis 2005, Wheelright and Rising 2008) may make each species more susceptible to certain types of nest predators. For example, open nests such as those of Chestnut-collared Longspurs, are more susceptible to diurnal predators than nocturnal predators (Pietz and Granfors 2000). However, human activity around oil wells can prompt shifts the peak activity of two nest predators, coyotes and rodents, from day to night in order to avoid human interactions (Lendrum et al. 2017). Additionally, rodents may be less likely to leave cover while foraging nocturnally due to perceived predation risk (Ceradini et al. 2017). Since Savannah Sparrows select nest sites with denser grass cover and are more likely to nest in patches of introduced grasses (Wheelright and Rising 2008), they may be more susceptible to changes in small mammal nest predation near oil wells than Chestnut-collared Longspurs. To know how to

best mitigate reductions in nesting success for some species, the effects of development on specific predator guilds will need to be examined.

I found associations of higher corticosterone with anthropogenic disturbance for all three species I examined, but there were clear phylogenetic differences in the type or response of disturbance that elicited it. There was no impact of the disturbances I examined on male Chestnut-collared Longspurs, while males of both sparrows showed increased stress responses when living beside disturbances. Savannah Sparrows were impacted most strongly by tall infrastructure associated with constant mechanical movement of the pump head sweeping vertically over several meters. In contrast, corticosterone levels of Baird's Sparrows indicate sensitivity to roads, a linear disturbance that can result in a wide variety of ecological impacts, including: shifts in predator communities (Chalfoun et al. 2002), barriers to movement (Laurance et al. 2004), unpredictable noise (Ware et al. 2015), and direct mortality due to road use (Northrup and Wittemyer 2013).

I also detected differences between sexes. High-quality female longspurs selected males with territories near oil wells and nested in sites that caused increased basal corticosterone. However, I found no trend in corticosterone of male longspurs in the same area, even when in a breeding pair with an aforementioned female. Sex differences were not as pronounced in the passerelids as they were longspurs. For example, both sexes of Savannah Sparrow seem to perceive the area around screw pumps as poor-quality habitat. The ability of both sexes of Savannah Sparrow to accurately perceive habitat quality could be a factor contributing to their relatively stable population trend range-wide (Environment and Climate Change Canada 2017), when compared to other grassland birds. As generalist species can be more adaptable (Damas-Moreira et al. 2018), it is possible that Savannah Sparrows, being a generalist (Wheelright and Rising 2008), are more flexible at integrating novel habitat information into their territory selection.

Conversely, the say the difference between perceived and actual habitat quality could be a contributing factor to ongoing declines in Chestnut-collared Longspurs. My results suggest that a combination of differences in sensitivity to disturbance and ability to identify high-quality habitat might explain why species that share ecological niche space may suffer disproportionate rates of decline. However, it will be necessary to examine a broader suite of species to confirm this hypothesis.

Corticosterone as a Management Tool

In a phylogenetically controlled meta-analysis Martin et al. (2018a) determined that corticosterone levels were not intrinsically linked to conservation status in birds. My data also support this finding, albeit with a much narrower spectrum of species, and despite substantial variation in the basal and stress induced corticosterone between the two families I sampled. These taxonomic differences in the expression of corticosterone could be a result of differential production of corticosterone (i.e. the amount of corticosterone produced by stimulating the HPA axis) or differences in other aspects of an individual's endocrinology (Busch and Hayward 2009). Other hormones circulating in the blood can interact with corticosterone to change its activity (Krause et al. 2014). The number of receptors in a tissue can be different between bodily regions and can change over time, or in response to chronic exposure to a stressor (Romero et al. 2009). Baird's Sparrows and Savannah Sparrows did not differ significantly in their basal or stress induced corticosterone, but both had significantly higher basal and stress induced corticosterone than Chestnut-collared Longspurs. This demonstrates that care must be taken to construct stress hypotheses within an ecological context, and between-species conclusions must be conservative (Dantzer et al. 2014). For example, if I had only measured corticosterone at infrastructure sites it

would have seemed as though Savannah and Baird's Sparrows were reacting much more strongly to disturbance than Chestnut-collared Longspurs, as their circulating levels of corticosterone are much higher.

Within-species variation in basal corticosterone levels is expected by season, age, sex, and breeding status (Wingfield et al. 1995, Dantzer et al. 2014). Similarly, the magnitude of a bird's stress response can vary with developmental stage, body condition, or parental investment (Romero et al. 2009). Therefore, if I had not been able to confirm breeding condition for the individuals in my study I also could have come to misleading conclusions. For example, if I had only captured unpaired male Chestnut-collared Longspurs near infrastructure and paired males far from infrastructure, I might have concluded that oil wells increased corticosterone simply because corticosterone is higher in unpaired males (Lynn and Wingfield 2008). Notably, caring for a larger brood is linked to higher baseline corticosterone (Love et al. 2004), possibly to facilitate increased provisioning rates (Wingfield et al. 1998, Pereyra and Wingfield 2003, Crossin et al. 2012). Therefore, the influence of increased parental investment on measures of baseline and stress-induced corticosterone may be similar to the increased metabolic demands associated with environmental stress.

The way in which the corticosterone is measured also affects the inferences that can be drawn from those data. Corticosterone, from blood plasma, feces, hair, or feathers, all represent a different timeframe of deposition and therefore the interpretation of the results (Busch and Hayward 2009). Blood plasma represents a near instantaneous measure of corticosterone, which allowed me to measure both basal and stress induced corticosterone (Wingfield 2013). This is important because I would not have been able to detect effects in the passerelids with only a measure of basal corticosterone; HPA activity reflected in a heightened stress response changed in

response to disturbance for Baird's and Savannah Sparrows. A downside to measuring corticosterone from plasma is that it is potentially sensitive to stochastic events that happened to an individual immediately before I captured it. Similarly, corticosterone quantification methods - whether the total amount corticosterone in the plasma is measured, as I did, or only unbound (active) portion is independently quantified - can affect results as only molecules of corticosterone not bound to binding globulins in the blood are free to interact with target tissues (Breuner et al. 2013).

Measures of corticosterone can be a powerful accompanying metric for conservation research and action, but without context, they can be almost meaningless. Importantly, unless a clear connection between changes in an individual's corticosterone levels and reduced lifetime fitness, it can be difficult to confirm that changes in corticosterone are a sign of negative environmental conditions (Madliger and Love 2016). Despite a myriad of issues and considerations surrounding the application of corticosterone as a conservation tool, I was still able to detect an effect of anthropogenic disturbances on grassland songbirds. Taken together, I think my results highlight some of the easily overlooked effects of oil development while corroborating some that were previously found.

The Impacts of Oil Development

In recent years research on the effects of oil development on birds has increased the mechanistic understanding of why we see greater than expected effects of disturbing a relatively small amount of grassland habitat to construct oil wells and service roads (Koper and Nudds 2011, Ortega and Francis 2012, Francis and Barber 2013a, Northrup and Wittemyer 2013). Two main consequences of oil development in the prairies are structural changes to habitat (Koper et al.

2014), and anthropogenic noise (Francis et al. 2011, Rosa et al. 2015). Both of these disturbances result in proximate functional changes in the distribution or behaviour of some species of grassland birds, but the effects are far from ubiquitous (Bernath-Plaisted and Koper 2016; Curry et al. 2017, 2018; Nenninger and Koper 2018). Ultimately, the biggest impact of oil development in the Canadian prairies may be the contribution to global climate change of combusting the extracted hydrocarbons. Climate change is expected increase the unpredictability of precipitation and storm intensity, which will have major ramifications for the songbirds breeding in the Great Plains (Langham et al. 2015). However, in an effort to “maximize short-term gain, minimize short-term loss” (Wilson et al. 2006), my results corroborate some best management practices.

Southeastern Alberta is a globally important area for threatened grassland songbirds as it holds some of the largest remaining tracts of intact mixed-grass prairie in Canada (Samson et al. 2004). However, population trends for my study species in this region have still been drastically negative in recent decades (-2.29 to -7.71; Environment and Climate Change Canada 2017). Without knowing the source-sink dynamics and range-wide connectivity of these populations, the contribution of the southeastern Alberta populations to their species survival is difficult to determine (Perkins et al. 2003). However, a strong case can be made that the best course of action to protect species experiencing precipitous declines is to sufficiently protect their core range. To do this, it is clear that we must reduce the overall footprint of built structures and roads on the landscape. Some of this is relatively simple; decommissioning of inactive oil wells and reclamation of underused roads are easy actions that will address many of the effects seen in my study and others (Bernath-Plaisted and Koper 2016, Nenninger and Koper 2018). Burying infrastructure whenever possible, and careful reseeding with native grasses, may also benefit the birds communities even when the disturbance from infrastructure may seem small (Rodgers and Koper

2017). While noise appears to be a limited stressor in this system, I still see effects on some of the most sensitive species, and others have identified its importance in similar contexts (Kleist et al. 2018), suggesting that sound should at least be considered. As others have also suggested (Allred et al. 2015, Thompson et al. 2015), the best way to address all of these impacts in concert moving forward is by concentrating above-ground infrastructure such that number of well heads per well pad are maximized. This could be achieved using existing directional drilling technology, thus minimizing the construction of new roads and lease sites, and reducing vehicle traffic, fragmentation, and noise.

Future Research

Habitat loss from a variety of anthropogenic disturbances (agriculture, oil development, urbanization) continues to contribute to declines of grassland birds (North American Bird Conservation Initiative 2016, World Wildlife Fund 2017). However, these disturbances are not occurring at the same intensity across the Great Plains. Oil development is a particularly patchily distributed disturbance (Alberta Energy 2012). A combination of resource distribution maps and breeding bird survey data could be used to identify regions where oil development is most likely to be limiting population growth and stability. While this might be achievable for the breeding ground for many grassland birds, it is important to consider that this is just one threat in one part of the life cycle of a migratory bird and that activities not on the breeding grounds can have severe impacts on vital rates (Baker et al. 2004). For example, we currently do not have estimates on first year survival for most of these species that are in decline. Full annual cycle modeling on these species is necessary to identify the bottleneck and determine the cause of declines (Marra et al. 2015). A synthesis of threats on the migratory pathways and overwintering ranges, in addition to

the breeding grounds, is needed to direct conservation efforts, particularly to most effectively purchase and restore land (Pool et al. 2014, Ellison et al. 2017).

It is also concerning that male and female Chestnut-collard Longspurs do not seem to be impacted by infrastructure in the same way. It will be necessary to understand what is driving this difference in susceptibility to disturbance in order to fully mitigate the effects of oil development on this Species At Risk. It is possible that there is some other more suitable metric for quantifying male quality than I used, such as song (Phillips and Derryberry 2017) or plumage (Hill 1991). Additionally, brood size or total brood weight, and rates of extra pair paternity in this population could provide further information regarding male quality. Chestnut-collared Longspurs can exhibit extra pair paternity rates as high as 42.9% (Hill 1997), however, male characteristics associated the highest rates of extra pair offspring while minimizing opportunities for their mates to engage in extra pair copulations are currently unknown. Future work should assess quality of males relative to landscape characteristics using a broader range of variables. However, if it is true that oil wells are acting as an ecological trap for female but not male longspurs due to vegetation characteristics around oil wells (Koper et al. 2014), managers could focus of increasing the diversity of grazing intensities away from oil wells to increase to attractiveness of this habitat for female longspurs.

For species that avoid oil development, calculating the effects of infrastructure on their vital rates is a relatively straight forward matter quantifying habitat loss. However, to get a holistic picture of the effects of oil development on grassland birds we must measure changes in population vital rates (Daniel 2015), which requires input informed by basic aspects of a species biology that remains unknown for many grassland songbirds. First-year survival, migratory connectivity, and lifetime reproductive success all influence population trends (Marra et al. 2015). However,

gathering data on many of these metrics has been difficult for grassland birds since they have low site fidelity, relatively few people are studying them, and that they are small, so tracking technology is challenging to do safely, and affordably (Bridge et al. 2011). Hopefully in the next 5-10 years the means to answer to some of these questions will become achievable.

Conclusions

Our most important piece of legislation for supporting conservation in Canada is the SARA. In order to list species as At Risk under SARA, we need sound science and rigorous species assessments to persuade legislators to list and protect species. Only once a species is listed can we enforce stricter guidelines to limit industrial activity in remaining intact critical habitat. However, one of the weaknesses of SARA is its single-species centric approach, which can make balancing the needs of different at-risk species difficult. My results suggest that managing for the most sensitive species could be an effective tool for protecting grassland birds in Canada, as I and others have found that even abundant species such as Savannah Sparrow are impacted by some facet of anthropogenic disturbance on the landscape. I believe we should continue to explore innovative techniques that can help contribute to conservation, such as assays for stress, and new tracking devices and biologgers to assess population connectivity and facilitate full annual cycle research. Finally, in order to gain an understanding of the true impact of oil development, we need to contextualize the observed effects on songbird species within future climate models, and within the full annual cycle, to assess what the future may hold for grassland songbirds.

Literature Cited

- Ahlering, M. A., D. H. Johnson, and J. Faaborg (2009). Factors Associated with Arrival Densities of Grasshopper Sparrow (*Ammodramus savannarum*) and Baird's Sparrow (*A. bairdii*) in the Upper Great Plains. *The Auk* 126:799–808.
- Alberta Energy (2012). Alberta's Energy Industry. An Overview. 1–6.
- Allred, B. W., W. K. Smith, D. Twidwell, J. H. Haggerty, S. W. Running, D. E. Naugle, and S. D. Fuhlendorf (2015). Ecosystem services lost to oil and gas in North America. *Science* 348:401–402.
- Andersson, M., J. Wallander, and D. Isaksson (2009). Predator perches: a visual search perspective. *Functional Ecology* 23:373–379.
- Angelier, F., J. C. Wingfield, H. Weimerskirch, and O. Chastel (2010). Hormonal correlates of individual quality in a long-lived bird: a test of the “corticosterone-fitness hypothesis”. *Biology letters* 6:846–849.
- Antze, B., and N. Koper (2018). Noisy anthropogenic infrastructure interferes with alarm responses in savannah sparrows (*Passerculus sandwichensis*). *Royal Society Open Science* 5:172168.
- Arlt, D., and T. Pärt (2007). Nonideal breeding habitat selection: a mismatch between preference and fitness. *Ecology* 88:792–801.
- Askins, R. A., F. Chávez-Ramírez, B. C. Dale, C. A. Haas, J. R. Herkert, F. L. Knopf, and P. D. Vickery (2007). Conservation of Grassland Birds in North America: Understanding Ecological Processes in Different Regions. *Ornithological Monographs* 64:1–46.
- Astheimer, L., W. Buttemer, and J. C. Wingfield (1995). Seasonal and acute changes in adrenocortical responsiveness in an arctic-breeding bird. *Hormones and Behavior* 45:442–

457.

- Baker, A. J., P. M. González, T. Piersma, L. J. Niles, I. de L. S. do Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts (2004). Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings. Biological sciences* 271:875–82.
- Battin, J. (2004). When good animals love bad habitats: Ecological traps and the conservation of animal populations. *Conservation Biology*.
- Bayne, E., L. Habib, and S. Boutin (2008). Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. *Conservation Biology* 22:1186–1193.
- Bernath-Plaisted, J., and N. Koper (2016). Physical footprint of oil and gas infrastructure, not anthropogenic noise, reduces nesting success of some grassland songbirds. *BIOC*. <https://doi.org/10.1016/j.biocon.2016.11.002>
- Bernath-Plaisted, J., H. Nenninger, and N. Koper (2017). Conventional oil and natural gas infrastructure increases brown-headed cowbird (*Molothrus ater*) relative abundance and parasitism in mixed-grass prairie. *Royal Society Open Science* 4:170036.
- BirdLife International (2018). State of the world's birds: taking the pulse of the planet.
- Bland, L. M., B. Collen, C. D. L. Orme, and J. Bielby (2015). Predicting the conservation status of data-deficient species. *Conservation Biology* 29:250–259.
- Bleho, B. I., N. Koper, and C. S. Machtans (2014). Direct effects of cattle on grassland birds in Canada. *Conservation Biology* 28:724–734.
- Blickley, J. L., K. R. Word, A. H. Krakauer, J. L. Phillips, S. N. Sells, C. C. Taff, J. C. Wingfield, and G. L. Patricelli (2012). Experimental Chronic Noise Is Related to Elevated Fecal

- Corticosteroid Metabolites in Lekking Male Greater Sage-Grouse (*Centrocercus urophasianus*). *PLoS ONE* 7:e50462.
- Bókony, V., Z. Lendvai, A. Liker, F. Angelier, J. C. Wingfield, and O. Chastel (2009). Stress Response and the Value of Reproduction: Are Birds Prudent Parents? 173.
- Boonstra, R., D. Hik, G. Singleton, and A. Tinnikov (1998). The Impact of Predator-Induced Stress on the Snowshoe Hare Cycle. *Ecology Monographs* 79:371–394.
- Boulinier, T., and E. Danchin (1997). The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology* 11:505–517.
- Brennan, L. A., and W. P. Kuvlesky (2005). North American Grassland Birds: An Unfolding Conservation Crisis? *Journal of Wildlife Management* 69:1–13.
- Breuner, C. W., B. Delehanty, and R. Boonstra (2013). Evaluating stress in natural populations of vertebrates: Total CORT is not good enough. *Functional Ecology* 27:24–36.
- Breuner, C. W., and M. Orchinik (2002). Plasma binding proteins as mediators of corticosteroid action in vertebrates. *Journal of Endocrinology* 175:99–112.
- Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, P. Hartl, R. Kays, J. F. Kelly, W. D. Robinson, and M. Wikelski (2011). Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds. *BioScience* 61:689–698.
- Burgar, J. M., A. C. Burton, and J. T. Fisher (2018). The importance of considering multiple interacting species for conservation of species at risk. *Conservation Biology*. <https://doi.org/10.1111/cobi.13233>
- Busch, D. S., and L. S. Hayward (2009). Stress in a conservation context: A discussion of glucocorticoid actions and how levels change with conservation-relevant variables. *Biological Conservation* 142:2844–2853.

- Campos, D. P., L. A. Bander, A. Raksi, and D. T. Blumstein (2009). Perch exposure and predation risk: a comparative study in passerines. *Acta ethologica* 12:93–98.
- Ceradini, J. P., A. D. Chalfoun, C. P. Joseph Ceradini, and W. Cooperative (2017). When perception reflects reality: Non-native grass invasion alters small mammal risk landscapes and survival. *Ecology and Evolution* 7.
- Chalfoun, A. D., F. R. Thompson, and M. J. Ratnaswamy (2002). Nest predators and fragmentation: A review and meta-analysis. *Conservation Biology*.
- Cleasby, I. R., and S. Nakagawa (2012). The influence of male age on within-pair and extra-pair paternity in passerines. *Ibis* 154:318–324.
- Comer, P. J., J. C. Hak, K. Kindscher, E. Muldavin, and J. Singhurst (2018). Continent-Scale Landscape Conservation Design for Temperate Grasslands of the Great Plains and Chihuahuan Desert. *Natural Areas Journal* 38:196–211.
- Cooke, S. J., L. Sack, C. E. Franklin, a. P. Farrell, J. Beardall, M. Wikelski, and S. L. Chown (2013). What is conservation physiology? Perspectives on an increasingly integrated and essential science. *Conservation Physiology* 1:1–23.
- Crino, O. L., B. K. Van Oorschot, E. E. Johnson, J. L. Malisch, and C. W. Breuner (2011). Proximity to a high traffic road: Glucocorticoid and life history consequences for nestling white-crowned sparrows. *General and Comparative Endocrinology* 173:323–332.
- Crossin, G., P. N. Trathan, R. a. Phillips, K. B. Gorman, A. Dawson, K. Q. Sakamoto, and T. D. Williams (2012). Corticosterone predicts foraging behavior and parental care in Macaroni Penguins. *The American naturalist* 180:E31–E41.
- Curry, C. M., P. G. Des Brisay, P. Rosa, and N. Koper (2018). Noise source and individual physiology mediate effectiveness of bird songs adjusted to anthropogenic noise. *Scientific*

Reports 8:3942.

Curry, C. M. C. M., B. Antze, M. H. M. H. Warrington, P. G. Des Brisay, P. Rosa, and N. Koper (2017). Ability to alter song in two grassland songbirds exposed to simulated anthropogenic noise is not related to pre-existing variability. *Bioacoustics* 4622:1–26.

Cutting, K. A., M. L. Anderson, E. A. Beaver, S. R. Schroff, E. Klaphake, N. Korb, and S. McWilliams (2016). Niche shifts and energetic condition of songbirds in response to phenology of food-resource availability in a high-elevation sagebrush ecosystem. *The Auk* 133:685–697.

Damas-Moreira, I., D. Oliveira, J. L. Santos, J. L. Riley, D. J. Harris, and M. J. Whiting (2018). Learning from others: an invasive lizard uses social information from both conspecifics and heterospecifics. *Biology letters* 14:20180532.

Daniel, J. (2015). Landscape-scale effects of oil and gas development on grassland passerines in southern Alberta. Thesis:124.

Davis, S. (2005). Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *The Condor*:605–616.

Davis, S. K. (2004). Area Sensitivity in Grassland Passerines : Effects of Patch Size , Patch Shape , and Vegetation Structure on Bird Abundance and Occurrence in Southern Saskatchewan. *The Auk* 121:1130–1145.

Deviche, P., C. Breuner, and M. Orchinik (2001). Testosterone, corticosterone, and photoperiod interact to regulate plasma levels of binding globulin and free steroid hormone in dark-eyed juncos, *Junco hyemalis*. *General and comparative endocrinology* 122:67–77.

Doligez, B., C. Cadet, E. Danchin, and T. Boulinier (2003). When to use public information for breeding habitat selection? The role of environmental predictability and density dependence.

- Animal Behaviour 66:973–988.
- Done, T., E. Gow, and B. Stutchbury (2011). Corticosterone stress response and plasma metabolite levels during breeding and molt in a free-living migratory songbird, the wood thrush (*Hylocichla mustelina*). *General and comparative endocrinology* 171:176–182.
- Van Duyse, E. L. S., R. Pinxten, V. M. Darras, L. Arckens, and M. Eens (2004). Opposite changes in plasma testosterone and corticosterone levels following a simulated territorial challenge in male Great Tits. *Behaviour* 141:451–467.
- Ellis, R. D., T. J. McWhorter, and M. Maron (2012). Integrating landscape ecology and conservation physiology. *Landscape Ecology* 27:1–12.
- Ellison, K., E. McKinnon, S. Zack, S. Olimb, R. Sparks, and E. Strasser (2017). Migration and winter distribution of the Chestnutcollared Longspur. *Animal Migration* 4:37–50.
- Environment and Climate Change Canada (2017). North American Breeding Bird Survey - Canadian Trends Website, Data-version 2015. *Environment and Climate Change Canada, Gatineau, Quebec, KIA 0H3*. [Online.] Available at <https://wildlife-species.canada.ca/breeding-bird-survey-results/P004/A001/?lang=e&m=s&r=SAVS&p=L>.
- Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, M. Katie, S. A. G. Jr, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, et al. (2016). Conserving migratory land birds in the New World : Do we know enough? *Ecological Applications* 20:398–418.
- Fairhurst, G. D., T. A. Marchant, C. Soos, K. L. Machin, and R. G. Clark (2013). Experimental relationships between levels of corticosterone in plasma and feathers in a free-living bird. *Journal of Experimental Biology* 216:4071–4081.
- Finer, M., C. N. Jenkins, and B. Powers (2013). Potential of Best Practice to Reduce Impacts from Oil and Gas Projects in the Amazon. *PLoS ONE* 8:e63022.

- Francis, C., and J. Barber (2013a). A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Frontiers in Ecology and the Environment*. <https://doi.org/10.1890/120183>
- Francis, C., and J. Barber (2013b). A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Frontiers in Ecology and the Environment* 11:305–313.
- Francis, C., N. Kleist, C. Ortega, and A. Cruz (2012a). Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal. *Proceedings of the Royal Society B* 279:2727–2735.
- Francis, C., C. Ortega, and A. Cruz (2010). Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. *Proceedings of the Royal Society B* 278:2025–2031.
- Francis, C., C. Ortega, R. Kennedy, and P. Nylander (2012b). Are nest predators absent from noisy areas or unable to locate nests. *Ornithological Monographs*:101–110.
- Francis, C., J. Paritsis, C. Ortega, and A. Cruz (2011). Landscape patterns of avian habitat use and nest success are affected by chronic gas well compressor noise. *Landscape ecology* 26:1269–1280.
- Fretwell, S. D. (1972). *Populations in a seasonal environment*. Princeton University Press, Princeton, N.J.
- Fretwell, S. D., and H. L. Lucas (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16–36.
- Gage, A. M., S. K. Olimb, and J. Nelson (2016). Plowprint: Tracking Cumulative Cropland Expansion to Target Grassland Conservation. *Great Plains Research* 26:107–116.
- Gerber, L. R. (2016). Conservation triage or injurious neglect in endangered species recovery.

- Proceedings of the National Academy of Sciences of the United States of America 113:3563–6.
- Gerber, L. R., M. C. Runge, R. F. Maloney, G. D. Iacona, C. A. Drew, S. Avery-Gomm, J. Brazill-Boast, D. Crouse, R. S. Epanchin-Niell, S. B. Hall, L. A. Maguire, et al. (2018). Endangered species recovery: A resource allocation problem. *Science* 362:284 LP-286.
- Gilroy, J. J., and W. J. Sutherland (2007). Beyond ecological traps: perceptual errors and undervalued resources. *Trends in Ecology and Evolution* 22:351–356.
- Government of Canada (2018). Species at Risk Public Registry. [Online.] Available at <http://www.registrelep-sararegistry.gc.ca/>.
- Green, M. T. (1992). Adaptations of Baird’s Sparrows (*Ammodramus bairdsii*) to grasslands: acoustic communication and nomadism [Ph.D. dissertation].
- Griffin, A. S., S. H. Alonzo, and C. K. Cornwallis (2013). Why Do Cuckolded Males Provide Paternal Care? *PLoS Biology* 11:e1001520.
- Guisan, A., and W. Thuiller (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*.
- Habib, L., E. Bayne, and S. Boutin (2007). Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. *Journal of Applied Ecology* 44:176–184.
- Hamilton, L., B. Dale, and C. Paszkowski (2011). Effects of Disturbance Associated with Natural Gas Extraction on the Occurrence of Three Grassland Songbirds. *Avian Conservation and Ecology* 6.
- Harms, N. J., P. Legagneux, H. G. Gilchrist, J. Bêty, O. P. Love, M. R. Forbes, G. R. Bortolotti, and C. Soos (2015). Feather corticosterone reveals effect of moulting conditions in the autumn on subsequent reproductive output and survival in an Arctic migratory bird.

- Proceedings of the Royal Society B 282:20142085.
- Herkert, J. R. (1995). The University of Notre Dame An Analysis of Midwestern Breeding Bird Population Trends : 1966-1993 An Analysis of Midwestern Breeding Bird Population Trends : 1966-1993. *American Midland Naturalist* 134:41–50.
- Hethcoat, M. G., and A. D. Chalfoun (2015). Towards a mechanistic understanding of human-induced rapid environmental change: A case study linking energy development, nest predation and predators. *Journal of Applied Ecology* 52:1492–1499.
- Hill, C. E., Ç. Akçay, S. E. Campbell, and M. D. Beecher (2011). Extrapair paternity, song, and genetic quality in song sparrows. *Behavioral Ecology* 22:73–81.
- Hill, D. P. (1997). The influence of actual paternity and assessment of paternity on the parental care of male Chestnut-collared Longspurs (*Calcarius ornatus*) [Ph.D. dissertation].
- Hill, G. E. (1991). Plumage coloration is a sexually selected indicator of male quality. *Nature* 350:337–339.
- Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts (2005). Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecology Letters* 8:23–29.
- Holmes, R., P. Marra, and T. Sherry (1996). Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. *Journal of Animal Ecology* 65:183–195.
- Horváthová, T., S. Nakagawa, and T. Uller (2011). Strategic female reproductive investment in response to male attractiveness in birds. *Proceedings of the Royal Society B: Biological Sciences* 279:163–170.
- Jones, S. L., J. S. Dieni, M. T. Green, and P. J. Gouse (2007). Annual return ratios of breeding grassland songbirds. *The Wilson Journal of Ornithology* 119:89–94.

- Jongsomjit, D., S. L. Jones, T. Gardali, G. R. Geupel, and P. J. Gouse (2007). A Guide to Nestling Development and Aging in Altricial Passerines - Biological Technical Publication BTP-R6008-2007.
- Kleist, N. J., R. P. Guralnick, A. Cruz, and C. D. Francis (2016). Sound settlement: Noise surpasses land cover in explaining breeding habitat selection of secondary cavity nesting birds. *Ecological Applications* 27:260–273.
- Kleist, N. J., R. P. Guralnick, A. Cruz, C. A. Lowry, and C. D. Francis (2018). Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. *Proceedings of the National Academy of Sciences* 115:201709200.
- Klug, P., L. L. Wolfenbarger, and J. P. McCarty (2009). The nest predator community of grassland birds responds to agroecosystem habitat at multiple scales. *Ecography* 32:973–982.
- Koper, N., K. Molloy, L. Leston, and J. Yoo (2014). Effects of Livestock Grazing and Well Construction on Prairie Vegetation Structure Surrounding Shallow Natural Gas Wells. *Environmental Management* 54:1131–1138.
- Koper, N., and T. Nudds (2011). Progress in Research on Grassland Bird Conservation and Ecology. *Avian Conservation and Ecology* 6:6.
- Kort, S. de, and E. Eldermire (2009). The deterrent effect of bird song in territory defense. *Behavioral Ecology*. <https://doi.org/10.1093/beheco/arn135>
- Krause, J. S., D. Dorsa, and J. C. Wingfield (2014). Changes in plasma concentrations of progesterone, dehydroepiandrosterone and corticosterone in response to acute stress of capture, handling and restraint in two subspecies of white-crowned sparrows. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 177:35–40.
- Langham, G. M., J. G. Schuetz, T. Distler, C. U. Soykan, and C. Wilsey (2015). Conservation

- Status of North American Birds in the Face of Future Climate Change. *PLOS ONE* 10:e0135350.
- Laurance, S. G. W., P. C. Stouffer, and W. F. Laurance (2004). Effects of Road Clearings on Movement Patterns of Understory Rainforest Birds in Central Amazonia. *Conservation Biology* 18:1099–1109.
- Lendrum, P. E., K. R. Crooks, and G. Wittemyer (2017). Changes in circadian activity patterns of a wildlife community post high-intensity energy development. *Journal of Mammalogy* 98:1265–1271.
- Linhart, P., and R. Fuchs (2015). Song pitch indicates body size and correlates with males' response to playback in a songbird. *Animal Behaviour* 103:91–98.
- Lloyd, J. D., and T. E. Martin (2005). Reproductive success of Chestnut-collared Longspurs in native and exotic grassland. *The Condor* 107:363.
- Loman, J. (2003). Small habitat islands are inferior breeding habitats but are used by some great tits - Competition or ignorance? *Biodiversity and Conservation* 12:1467–1479.
- Love, O. P., C. W. Breuner, F. Vézina, and T. D. Williams (2004). Mediation of a corticosterone-induced reproductive conflict. *Hormones and Behavior* 46:59–65.
- Lüdtke, B., I. Moser, D. Santiago-Alarcon, M. Fischer, E. K. Kalko, H. M. Schaefer, M. Suarez-Rubio, M. Tschapka, and S. C. Renner (2013). Associations of Forest Type, Parasitism and Body Condition of Two European Passerines, *Fringilla coelebs* and *Sylvia atricapilla*. *PLoS ONE* 8:e81395.
- Lynn, S. E., L. S. Hayward, Z. M. Benowitz-Fredericks, and J. C. Wingfield (2002). Behavioural insensitivity to supplementary testosterone during the parental phase in the chestnut-collared longspur, *Calcarius ornatus*. *Animal Behaviour* 63:795–803.

- Lynn, S. E., and J. C. Wingfield (2008). Dissociation of testosterone and aggressive behavior during the breeding season in male chestnut-collared longspurs, *Calcarius ornatus*. *General and Comparative Endocrinology* 156:181–189.
- Lynn, S. E., and J. C. Wingfield (2003). Male Chestnut-Collared Longspurs Are Essential for Nestling Survival : A Removal Study. *The Condor* 105:154–158.
- Lynn, S., K. Hunt, and J. C. Wingfield (2003). Ecological factors affecting the adrenocortical response to stress in chestnut-collared and McCown's longspurs (*Calcarius ornatus*, *Calcarius mccownii*). *Physiological and Biochemical Zoology* 76:566–576.
- Madliger, C. L., and O. P. Love (2016). Conservation implications of a lack of relationship between baseline glucocorticoids and fitness in a wild passerine. *Ecological Applications* 26:2730–2743.
- Madliger, C. L., C. A. D. Semeniuk, C. M. Harris, and O. P. Love (2015). Assessing baseline stress physiology as an integrator of environmental quality in a wild avian population: Implications for use as a conservation biomarker. *Biological Conservation* 192:409–417.
- Maron, M., W. Goulding, R. D. Ellis, and F.-S. Mohd-Taib (2012). Distribution and individual condition reveal a hierarchy of habitat suitability for an area-sensitive passerine. *Biodiversity and Conservation* 21:2509–2523.
- Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra (2015). A call for full annual cycle research in animal ecology. *Biology letters* 11:20150552.
- Martin, L. B., M. Vitousek, J. W. Donald, T. Flock, M. J. Fuxjager, W. Goymann, M. Hau, J. Husak, M. A. Johnson, B. Kircher, R. Knapp, et al. (2018a). IUCN Conservation Status Does Not Predict Glucocorticoid Concentrations in Reptiles and Birds. *Integrative and Comparative Biology* 58:800–813.

- Martin, T. G., L. Kehoe, C. Mantyka-Pringle, I. Chades, S. Wilson, R. G. Bloom, S. K. Davis, R. Fisher, J. Keith, K. Mehl, B. P. Diaz, et al. (2018b). Prioritizing recovery funding to maximize conservation of endangered species. *Conservation Letters*.
<https://doi.org/10.1111/conl.12604>
- McClure, C. J. W., H. E. Ware, J. D. Carlisle, and J. R. Barber (2017). Noise from a phantom road experiment alters the age structure of a community of migrating birds. *Animal Conservation* 20:164–172.
- McEwen, B. S., and J. C. Wingfield (2003). The concept of allostasis in biology and biomedicine. *Hormones and Behavior* 43:2–15.
- McEwen, L. C., C. E. Knittle, and M. L. Richmond (1972). Wildlife Effects from Grasshopper Insecticides Sprayed on Short-Grass Range. *Journal of Range Management Archives* 25.
- Nature, I. U. for C. of (2018). The IUCN Red List of Threatened Species. [Online.] Available at <https://www.iucnredlist.org/>.
- Nenninger, H. R., and N. Koper (2018). Effects of conventional oil wells on grassland songbird abundance are caused by presence of infrastructure, not noise. *Biological Conservation* 218:124–133.
- Newcomb Homan, R., J. V. Regosin, D. M. Rodrigues, J. M. Reed, B. S. Windmiller, and L. M. Romero (2003). Impacts of varying habitat quality on the physiological stress of spotted salamanders (*Ambystoma maculatum*). *Animal Conservation* 6:11–18.
- Ng, C. S. (2017). Proximity to Conventional Oil and Gas Development is Associated with Reduced Parental Care in Chestnut-collared Longspurs (*Calcarius ornatus*) of Natural Resources Management Natural Resources Institute.
- Ng, C. S., P. G. Des Brisay, and N. Koper (2018). Chestnut-collared longspurs reduce parental

- care in the presence of conventional oil and gas development and roads. *Animal Behaviour*
In Press.
- Norris, R., and P. P. Marra (2007). Seasonal interactions, habitat quality, and population dynamics
in migratory birds. *The Condor* 109:535.
- North American Bird Conservation Initiative (2016). *The State of the Birds*, 2016.
- North American Bird Conservation Initiative Canada (2012). *The State of Canada's Birds*, 2012.
- Northrup, J., and G. Wittemyer (2013). Characterising the impacts of emerging energy
development on wildlife, with an eye towards mitigation. *Ecology letters* 16:112–125.
- O'Grady, D. R., D. P. Hill, and R. M. R. Barclay (1996). Nest Visitation by Humans Does Not
Increase Predation on Chestnut-Collared Longspur Eggs and Young. *Journal of Field
Ornithology* 67:275–280.
- Ortega, C., and C. Francis (2012). Effects of gaswell-compressor noise on the ability to detect
birds during surveys in northwest New Mexico. *Ornithol. Monogr*:74–78.
- Pereyra, M., and J. C. Wingfield (2003). Changes in plasma corticosterone and adrenocortical
response to stress during the breeding cycle in high altitude flycatchers. *General and
comparative endocrinology* 130:222–231.
- Perkins, D. W., P. D. Vickery, and W. G. Shriver (2003). Spatial Dynamics of Source-Sink
Habitats: Effects on Rare Grassland Birds. *The Journal of Wildlife Management* 67:588.
- Phillips, J. N., and E. P. Derryberry (2017). Equivalent effects of bandwidth and trill rate: support
for a performance constraint as a competitive signal. *Animal Behaviour* 132:209–215.
- Pietz, P. J., and D. a Granfors (2000). Identifying predators and fates of grassland passerine nests
using miniature video cameras. *Journal of Wildlife Management* 64:71–87.
- Pool, D. B., A. O. Panjabi, A. Macias-Duarte, and D. M. Solhjem (2014). Rapid expansion of

- croplands in Chihuahua, Mexico threatens declining North American grassland bird species. *Biological Conservation* 170:274–281.
- Potvin, D. A., and S. A. MacDougall-Shackleton (2015). Traffic noise affects embryo mortality and nestling growth rates in captive zebra finches. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* 323:722–730.
- Powell, L. A., M. J. Conroy, D. G. Krentz, and J. D. Lang (1999). A Model to Predict Breeding-Season Productivity for Multibrooded Songbirds. *The Auk* 116:1001–1008.
- Rich, E. L., and L. M. Romero (2005). Exposure to chronic stress downregulates corticosterone responses to acute stressors. *American journal of physiology. Regulatory, integrative and comparative physiology* 288:R1628-36.
- Robertson, B. A., and R. L. Hutto (2016). A Framework for Understanding Ecological Traps and an Evaluation of Existing Evidence. *Ecology* 53:735–737.
- Roch, L., and J. Jaeger (2014). Monitoring an ecosystem at risk: What is the degree of grassland fragmentation in the Canadian Prairies? *Environmental monitoring and assessment*. <https://doi.org/10.1007/s10661-013-3557-9>
- Rodgers, J. A., and N. Koper (2017). Shallow gas development and grassland songbirds: The importance of perches. *The Journal of Wildlife Management* 81:406–416.
- Romero, L. M., M. J. Dickens, and N. E. Cyr (2009). The reactive scope model - A new model integrating homeostasis, allostasis, and stress. *Hormones and Behavior* 55:375–389.
- Romero, L. M., and M. Wikelski (2002). Severe effects of low-Level oil contamination on wildlife predicted by the corticosterone-stress response: Preliminary data and a research agenda. *Spill Science and Technology Bulletin* 7:309–313.
- Rosa, P., C. R. Swider, L. Leston, and N. Koper (2015). Disentangling effects of noise from

- presence of anthropogenic infrastructure: Design and testing of system for large-scale playback experiments. *Wildlife Society Bulletin* 39:364–372.
- Samson, F. B., F. L. Knopf, and W. R. Ostlie (2004). Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin* 32:6–15.
- Samson, F., and F. Knopf (1994). Prairie conservation in north america. *BioScience* 44:418–421.
- Sauer, J. R., K. L. Pardieck, D. J. Ziolkowski, A. C. Smith, M.-A. R. Hudson, V. Rodriguez, H. Berlanga, D. K. Niven, and W. A. Link (2017). The first 50 years of the North American Breeding Bird Survey. *The Condor* 119:576–593.
- Sherry, T. W., and R. T. Holmes (1996). Winter habitat quality, population limitation, and conservation of neotropical-nearctic migrant birds. *Ecology* 77:36–48.
- Sinclair, S. J., M. D. White, and G. R. Newell (2010). How useful are species distribution models for managing biodiversity under future climates? *Ecology and Society* 15:8.
- Slabbekoorn, H., and E. Ripmeester (2008). Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular Ecology* 17:72–83.
- Sliwinski, M. S., and N. Koper (2012). Grassland Bird Responses to Three Edge Types in a Fragmented Mixed- Grass Prairie. *Avian Conservation and Ecology* 7:6.
- Sorenson, G. H., C. J. Dey, C. L. Madliger, and O. P. Love (2017). Effectiveness of baseline corticosterone as a monitoring tool for fitness: a meta-analysis in seabirds. *Oecologia* 183:353–365.
- Soulé, M. (1985). What is conservation biology? *BioScience* 35:727–734.
- Strasser, E. H., and J. A. Heath (2013). Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. *Journal of Applied Ecology* 50:912–919.

- Taylor, B. L., and T. Gerrodette (1993). The Uses of Statistical Power in Conservation Biology: The Vaquita and Northern Spotted Owl. *Conservation Biology* 7:489–500.
- Thompson, S. J., D. H. Johnson, N. D. Niemuth, and C. A. Ribic (2015). Avoidance of unconventional oil wells and roads exacerbates habitat loss for grassland birds in the North American great plains. *Biological Conservation* 192:82–90.
- Vance, M. D., L. Fahrig, and C. H. Flather (2003). Effect of reproductive rate on minimum habitat requirements of forest-breeding birds. *Ecology* 84:2643–2653.
- Vickery, P. D., and J. R. Herkert (2001). Recent advances in grassland bird research: where do we go from here? *The Auk* 118:11–15.
- Vickery, P. D., M. L. Hunter, and J. V. Wells (1992a). Is Density an Indicator of Breeding Success? *The Auk* 109:706–710.
- Vickery, P. D., M. L. Hunter, J. V. Wells, and J. V. Wells (1992b). Evidence of Incidental Nest Predation and Its Effects on Nests of Threatened Grassland Birds. *Oikos* 63:281.
- Vitousek, M. N., B. R. Jenkins, and R. J. Safran (2014). Stress and success: Individual differences in the glucocorticoid stress response predict behavior and reproductive success under high predation risk. *Hormones and Behavior* 66:812–819.
- Walker, B. L., D. E. Naugle, and K. E. Doherty (2007). Greater Sage-Grouse Population Response to Energy Development and Habitat Loss. *Journal of Wildlife Management* 71:2644–2654.
- Ware, H. E., C. J. W. McClure, J. D. Carlisle, and J. R. Barber (2015). A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. *Proceedings of the National Academy of Sciences* 112:12105–12109.
- Wheelright, N. T., and J. D. Rising (2008). Savannah Sparrow (*Passerculus sandwichensis*). *The Birds of North America*:2173.

- Wiens, J. A., and J. T. Rotenberry (1979). Diet niche relationships among North American grassland and shrubsteppe birds. *Oecologia* 42:253–292.
- Wikelski, M., and S. J. Cooke (2006). Conservation physiology. *Trends in Ecology and Evolution* 21:38–46.
- Wilson, K. A., M. F. McBride, M. Bode, and H. P. Possingham (2006). Prioritizing global conservation efforts. *Nature* 440:337–340.
- Wingfield, J. C. (2013). Ecological processes and the ecology of stress: The impacts of abiotic environmental factors. *Functional Ecology* 27:37–44.
- Wingfield, J. C., D. L. Maney, C. W. Breuner, J. D. Jacobs, S. Lynn, M. Ramenofsky, and R. D. Richardson (1998). Ecological bases of hormone-behavior interactions: the “emergency life history stage.” *American Zoologist* 38:191–206.
- Wingfield, J. C., C. M. Vleck, and M. C. Moore (1992). Seasonal changes of the adrenocortical response to stress in birds of the Sonoran desert. *Journal of Experimental Zoology* 264:419–428.
- World Wildlife Fund (2017). *Living Planet Report Canada*.
- Yoo, J., and N. Koper (2017). Effects of shallow natural gas well structures and associated roads on grassland songbird reproductive success in Alberta, Canada. *PLOS ONE* 12:e0174243.

Appendix 1

A conspicuous absence of haemosporidian parasites in grassland songbirds of the Northern Great Plains

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Abstract

We screened 103 Chestnut-collared Longspurs (*Calcarius ornatus*) and 69 Savannah Sparrows (*Passerculus sandwichensis*) in Alberta, Canada for two genera of haemosporidian parasites (*Haemoproteus* and *Plasmodium*) and detected zero infections. To confirm our laboratory methods could detect infections that were present, we used our methods to sample 22 Swamp Sparrows (*Melospiza georgiana*) in Manitoba and detected 5 infections. No previous studies have documented a lack of blood parasites in grassland songbirds, but it is possible that this is a result of publication bias against null results. As climate change shifts vector ranges, naive populations of grassland songbirds may suffer disproportionately if vector presence or parasite transmission is altered.

Introduction

Grassland songbird populations are declining more rapidly than birds of any other habitat type across North America, and the primary cause of these declines is changes to grassland habitats (Askins et al. 2007). However, the mechanisms that explain why anthropogenic habitat alterations have resulted in these declines are not well understood. One rarely evaluated effect of anthropogenic development of grasslands could be altered disease risk. Conversion of grasslands to other habitat types might affect vector-transmitted disease rates; for example, declines in Greater Sage-Grouse (*Centrocercus urophasianus*) might be indirectly caused by the construction of ponds, which increase exposure and mortality from West Nile virus (Walker et al. 2007). Most haemosporidian disease vectors such as mosquitos (Culicidae), blackflies (Simuliidae), and biting midges (Culicoides) depend on water in some form for larval habitat (Rozendaal 1997), and humans have significantly altered this habitat across grasslands world-wide by creating and manipulating water sources for cattle watering and agriculture (Patz et al. 2008). This may in turn affect transmission of haemosporidian parasites carried by these vectors (Lapointe et al. 2012). If this resulted in naive populations of grassland songbirds being exposed to new insect-borne blood parasites, it could contribute to negative population trends. Habitat degradation may also reduce the ability of birds to allocate resources for immune function, thereby increasing susceptibility to parasitism (Lochmiller et al. 1993, Lüdtkke et al. 2013), exacerbating this effect.

While evaluating the possibility that blood parasites infect grassland songbird populations, we discovered that no previously published studies have described blood parasite communities in grassland songbirds in the Northern Great Plains of North America. To fill this knowledge gap,

we used PCR to document haemosporidian parasitism occurrence in two grassland songbird species, the Savannah Sparrow (*Passerculus sandwichensis*) and federally Threatened Chestnut-collared Longspur (*Calcarius ornatus*) in this region.

Methods

We used mist-nets and drop-traps to capture 103 adult Chestnut-collared Longspurs (*Calcarius ornatus*) and 69 adult Savannah Sparrows (*Passerculus sandwichensis*) within 60 km of Brooks, Alberta, Canada (50°33'51"N 111°53'56"W, 760 MASL), within the mixed-grass prairie ecoregion of the Northern Great Plains, from May-July 2016. Our study sites cover an area of approximately 1300 square kilometers on land owned by the Eastern Irrigation District, which consist of cattle-grazed mixed-grass prairie, consisting mainly of native grasses and forbs: Needle and Thread (*Hesperostipa comata*), Porcupine Grass (*Hesperostipa spartea*), Blue Grama (*Bouteloua gracilis*), Western Wheatgrass (*Pascopyrum smithii*), Pasture Sagewort (*Artemisia frigida*), and Silver Sagebrush (*Artemisia cana*). There are also small intrusions of invasive grasses and forbs (< 3% cover in our sites) including Goatsbeard (*Tragopogon dubius*), Dandelion (*Taraxacum officinale*), Crested Wheatgrass (*Agropyron cristatum*), and Smooth Brome (*Bromus inermis*). This area is typically dry, receiving an average of 252.6 mm of rainfall annually (Environment and Climate Change Canada 2018), and the majority of open standing water sources are man-made dugouts to provide water sources to cattle.

Blood samples (< 70 uL) were collected by brachial venipuncture in heparinized microcapillary tubes and kept iced for < 6 h until centrifuged. The red blood cell fraction (20-40

uL) was added to 600uL Queen's lysis buffer (Seutin et al. 1991) and stored at room temperature until DNA extraction, and the plasma fraction was frozen to be used for hormonal analysis in a different study. To ensure that these blood sampling and storage methods did not affect our ability to detect infections, we collected additional blood samples from 22 Swamp Sparrows (*Melospiza georgiana*) in September 2017 at Delta Marsh Bird Observatory, Manitoba to validate the screening method. We split the blood sample from each Swamp Sparrow at the time of collection, putting ~15 uL directly into Queen's lysis buffer, and centrifuging the remaining 20-50 uL before adding 600uL Queen's lysis buffer to each of the plasma and red blood cell fractions. The red blood cell fraction was equivalent to our Chestnut-collared Longspur and Savannah Sparrow blood samples, while the plasma and whole-blood Swamp Sparrow samples could be used to ensure that infections that were detectable from either of these samples could also be detected in the red-blood-cell-only fraction of the same birds. We extracted DNA from whole blood, red blood cell, and plasma samples using DNEasy kits following the protocol for nucleated blood cells.

We used the nested PCR protocol outlined in Hellgren et al. (2004; Figure 1) to amplify parasite DNA from the DNA extract. The first two primers (HaemNF1 and HaemNR3) amplify a generic region of cytochrome *b* for several parasite families in the order Haemosporidia. Using the product from the first PCR in place of raw DNA, we then performed a second PCR using primers HaemF and HaemR2 to isolate a 480-bp region of cytochrome B specific to *Haemoproteus* and *Plasmodium* parasites. We then used electrophoresis to visualize bands of PCR product and code them as positive infections. As the final PCR process amplified both *Haemoproteus* and *Plasmodium* parasite DNA, we did not determine whether the individual was infected with *Haemoproteus* or *Plasmodium* parasites.

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Results

We found no infections present in the 172 grassland birds screened for *Haemoproteus* or *Plasmodium* infections (Table 1). We screened whole blood samples of 22 Swamp Sparrows, of which five tested positive for *Haemoproteus* or *Plasmodium* infections (Table 1). We then screened the red blood cell and plasma fractions of the blood samples for those five infected individuals and detected the infections again in all five of the red blood cell fractions but only one of the plasma fractions (Table 1).

Discussion

Our results suggest a conspicuous absence of haemosporidian parasites in two widely distributed grassland songbird species. To our knowledge this is the first study to publish haemosporidian parasite prevalence in grassland passerines the North American Great Plains. Only a handful of other studies have assessed haemosporidian infection prevalence for facultative grassland and aridland species outside of the Great Plains (e.g. Kvasager 2015, Walther et al. 2016, Ham-Dueñas et al. 2017). It is possible that the lack of literature on this topic is a result of

publication bias against null results (Fanelli 2010), but we believe that our observation of zero infection rates in this ecosystem is important for understanding the ecology and conservation of grassland songbirds. It is unlikely that our methods were inadequate for detecting infections that were present, because we validated these methods using infected Swamp Sparrows.

There are several possible explanations for the observed pattern. The absence of infections could be due to presence of highly virulent parasites; if infections cause high mortality or low mobility in birds, those individuals would be less likely to be captured in mist-nets (Asghar et al. 2011). However, if there were a highly virulent parasite in the system, capable of causing mortality before a single detection but still abundant enough avoid extirpation, we would expect to have come across sick or injured birds in the field, which we did not observe. Alternatively, the absence of infections could result from an absence of vectors or conditions suitable for transmission in the region (Reisen 2010). However, *Aedes vexans* can transmit *Plasmodium* (Inci et al. 2012) and is present in Southern Alberta (Lysyk 2010). As researchers who have worked in this region for many years, we can attest to the regular abundance of mosquitos. It is also possible that the spatial and temporal scarcity of standing water, or the consistently low overnight temperatures in our study area, are not conducive to parasite transmission (Reisen 2010).

Other studies that have assessed blood parasites in grassland and aridland birds have concluded that their infection rates are similar to those of other bird guilds. In the tall-grass prairie/aspen parkland boundary in Minnesota, 50% of Savannah Sparrows ($n=73$) tested positive for *Haemoproteus* or *Plasmodium* infections (Kvasager 2015). However, this transitional habitat is both geographically distant (approximately 1500 km) and ecologically distinct (over double the

annual rainfall of our study area; National Weather Service 2018) from our study area. In tropical grasslands, infection rates were lower in intact areas of cerrado (tropical savanna in Brazil; 29.3%) than in the cerrado-rainforest transition (40.1%) or urbanised cerrado (41%) (Belo et al. 2011), suggesting that transition habitats may act as parasite reservoirs for less suitable or drier habitats. It is also likely that some taxa are more susceptible to infections. In a riparian zone in California, infection rates ranged from zero for bushtits ($n=31$) and flycatchers ($n=41$) to 13.6-68.6 % in emberizines, including one Savannah Sparrow with a *Leucocytozoon* infection (Walther et al. 2016). Nonetheless, it is clear that at least one of our focal species (Savannah Sparrows) is susceptible to Haemosporidian infection (Kvasager 2015). As no previous studies have measured Haemosporidian infections in Chestnut-collared Longspurs, we cannot evaluate whether this species is also susceptible. However, a congener, *C. pictus*, showed low rates of *Leucocytozoon* infection in the Hudson's Bay Lowlands near Churchill, Manitoba (Bennett et al. 1992), so it is likely *C. ornatus* is susceptible as well. It is clear that we need to increase the spatial and taxonomic breadth of our sampling before we can get a clearer picture of blood parasitism patterns in the grasslands.

As climate change shifts vector ranges (Hongoh et al. 2012), and agricultural intensification and resource development increases across grasslands, naive populations of grassland songbirds may suffer disproportionately if contact with vectors increases. Since naive populations may experience greater susceptibility (Sarquis-Adamson and MacDougall-Shackleton 2016) or more significant physical consequences (Lapointe et al. 2012) from novel exposures, this may pose risks to our focal species in our study area; for example, climate change is expected to render habitat in southern Alberta suitable for *Plasmodium* vector *Culex pipiens* by 2040 (Hongoh

et al. 2012). Conversely, perhaps grassland birds in this region will always be protected from blood-borne disease due to the arid conditions of this ecosystem. These relative risks can only be assessed by collecting more data on parasite and vector prevalence across the Northern Great Plains, and by publishing null results that can be used to develop spatially and temporally explicit infection rate models that accurately reflect the range of infection rates among populations.

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References

- Askins, R. A., F. Chávez-Ramírez, B. C. Dale, C. A. Haas, J. R. Herkert, F. L. Knopf, and P. D. Vickery (2007). Conservation of Grassland Birds in North America: Understanding Ecological Processes in Different Regions. *Ornithological Monographs* 64:1–46.
- Belo, N. O., R. T. Pinheiro, E. S. Reis, R. E. Ricklefs, and É. M. Braga (2011). Prevalence and Lineage Diversity of Avian Haemosporidians from Three Distinct Cerrado Habitats in Brazil. *PLoS ONE* 6:e17654.
- Bennett, G. F., R. Montgomerie, and G. Seutin (1992). Scarcity of Haematozoa in Birds Breeding on the Arctic Tundra of North America. *The Condor* 94:289–292.
- Environment and Climate Change Canada (2018). Canadian Climate Normals 1981-2010 Station Data, Brooks North, Alberta Canada. [Online.] Available at http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?stnID=2197&lang=e&province=AB&provSubmit=go&dCode=0.
- Fanelli, D. (2010). Do Pressures to Publish Increase Scientists' Bias? An Empirical Support from US States Data. *PLoS ONE* 5:e10271.
- Ham-Dueñas, J. G., L. Chapa-Vargas, C. M. Stracey, and E. Huber-Sannwald (2017). Haemosporidian prevalence and parasitaemia in the Black-throated sparrow (*Amphispiza bilineata*) in central-Mexican dryland habitats. *Parasitology Research* 116:2527–2537.
- Hellgren, O., J. Waldenström, and S. Bensch (2004). A new PCR assay for simultaneous studies of *Leucocytozoon*, *Plasmodium*, and *Haemoproteus* from avian blood. *Journal of Parasitology* 90:797–802.
- Hongoh, V., L. Berrang-Ford, M. E. Scott, and L. R. Lindsay (2012). Expanding geographical distribution of the mosquito, *Culex pipiens*, in Canada under climate change. *Applied*

Geography 33:53–62.

- Inci, A., A. Yildirim, K. Y. Njabo, O. Duzlu, Z. Biskin, and A. Ciloglu (2012). Detection and molecular characterization of avian Plasmodium from mosquitoes in central Turkey. *Veterinary Parasitology* 188:179–184.
- Kvasager, D. K. (2015). Prevalence, Statistical Trends and Phylogenetics of Blood Parasites (Haemosporidia: Haemoproteus, Plasmodium and Leucocytozoon) in Songbird Passerines from Grasslands of northwest Minnesota.
- Lapointe, D. a, C. T. Atkinson, and M. D. Samuel (2012). Ecology and conservation biology of avian malaria. *Annals of the New York Academy of Sciences* 1249:211–26.
- Lochmiller, R. L., M. R. Vestey, and J. C. Boren (1993). Relationship between Protein Nutritional Status and Immunocompetence in Northern Bobwhite Chicks. *The Auk* 110:503–510.
- Lüdtke, B., I. Moser, D. Santiago-Alarcon, M. Fischer, E. K. Kalko, H. M. Schaefer, M. Suarez-Rubio, M. Tschapka, and S. C. Renner (2013). Associations of Forest Type, Parasitism and Body Condition of Two European Passerines, *Fringilla coelebs* and *Sylvia atricapilla*. *PLoS ONE* 8:e81395.
- Lysyk, T. J. (2010). Species abundance and seasonal activity of mosquitoes on cattle facilities in southern Alberta, Canada. *Journal of medical entomology* 47:32–42.
- National Weather Service (2018). Climate Graphs, NWS Forecast Office Grand Forks, ND. [Online.] Available at <https://www.weather.gov/fgf/climategraphs>.
- Patz, J. A., S. H. Olson, C. K. Uejio, and H. K. Gibbs (2008). Disease Emergence from Global Climate and Land Use Change. *Medical Clinics of North America* 92:1473–1491.
- Reisen, W. K. (2010). Landscape Epidemiology of Vector-Borne Diseases. *Annual Review of Entomology* 55:461–483.

- Rozendaal, J. A. (1997). Mosquitos and other biting Diptera. In Vector Control. Geneva, Switzerland, pp. 5–177.
- Sarquis-Adamson, Y., and E. A. MacDougall-Shackleton (2016). Song sparrows *Melospiza melodia* have a home-field advantage in defending against sympatric malarial parasites. Royal Society Open Science 3:160216.
- Seutin, G., B. N. White, and P. T. Boag (1991). Preservation of avian blood and tissue samples for DNA analyses. Canadian Journal of Zoology 69:82–90.
- Valkiunas, G. (2004). Avian Malaria Parasites and other Haemosporidia. CRC Press.
- Walker, B. L., D. E. Naugle, and K. E. Doherty (2007). Greater Sage-Grouse Population Response to Energy Development and Habitat Loss. Journal of Wildlife Management 71:2644–2654.
- Walther, E. L., J. S. Carlson, A. Cornel, B. K. Morris, and R. N. M. Sehgal (2016). First molecular study of prevalence and diversity of avian haemosporidia in a Central California songbird community. Journal of Ornithology 157:549–564.

Tables

Table 1. *Haemoproteus* or *Plasmodium* infections detected by positive amplification of CytB from passerine whole blood, red blood cell, and plasma samples in Alberta and Manitoba, Canada, in 2016 and 2017.

Avian species	Location	Fraction	<i>n</i>	Infections detected
<i>Calcarius ornatus</i>	Alberta	Red blood cells	103	0
<i>Passerculus sandwichensis</i>	Alberta	Red blood cells	69	0
<i>Melospiza georgiana</i>	Manitoba	Whole blood	22	5
<i>Melospiza georgiana</i>	Manitoba	Red blood cells	22	5
<i>Melospiza georgiana</i>	Manitoba	Plasma	22	1