

**Effects of oil infrastructure and associated noise on the stress physiology,
growth and development of an altricial grassland songbird nestling**

by

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Abstract

In recent decades, oil and gas development has increased in central North America, fragmenting grassland ecosystems and introducing anthropogenic noise to the soundscape. Chronic exposure to anthropogenic noise on the landscape may increase corticosterone levels in altricial songbird nestlings, potentially influencing growth rate, fledgling success, and adult behaviour. To determine how anthropogenic disturbance and chronic noise impacts the development of Chestnut-collared Longspur (*Calcarius ornatus*) nestlings, I isolated noise from the associated infrastructure by broadcasting generator-powered screw pump recordings on the short- and mixed- grass prairies of southeastern Alberta, and compared these impacts with those of real wells and controls. I measured basal corticosterone and stress response in nestlings and mothers as well as mass and outer primary length in nestlings as a metric for fitness. Surprisingly, I found nestlings closer to anthropogenic noise exhibited down-regulated HPA-axis activity as well as evidence to suggest that maternal stress mediated the relationship between noise and basal corticosterone. Mothers that responded strongly to novel stressors produced nestlings with longer primaries. In addition, across all sites nestlings with lower corticosterone were heavier. These results suggest that nestlings may benefit from living in noisy environments and that mothers may prepare their offspring for living in sub-optimal environments or growing up with sub-optimal care.

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Dedication

This thesis is for Nick Bergen, without your love and support this would not have been possible.

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Introduction

Grassland ecosystems across the planet are facing increasing threats due to agricultural intensification, habitat fragmentation and, more recently, oil and gas expansion (Hoekstra et al. 2005, Askins et al. 2007). Consequently, up until the 1990's grassland songbirds were experiencing the most dramatic declines of any other guild of birds in North America (Downes et al. 2011, North American Bird Conservation Initiative 2019). A number of individual species have continued to experience these declines, including the Chestnut-collared Longspur (*Calcarius ornatus*), a species listed as Threatened under Schedule 1 of the Species at Risk Act (SARA). Results from the Breeding Bird Survey have shown a 6% annual decline in Chestnut-collared Longspurs from 1970 to 2012 (Environment and Climate Change Canada 2017). In southeastern Alberta, the Chestnut-collared Longspur is relatively abundant and their population overlaps with intense energy-extraction activities, making them susceptible to the effects of energy development (Askins et al. 2007, Environment and Climate Change Canada 2017).

Oil extraction activities introduce anthropogenic noise to the grasslands. Research has shown that exposure to anthropogenic noise can have multiple impacts on individuals, including causing avoidance of noisy areas, masking communication, and altering behaviour (McClure et al. 2013, McIntyre et al. 2014, Ng et al. 2019). Chronic anthropogenic noise can also act as a stressful stimulus on the landscape and may directly or indirectly impact the physiology of individuals, though the results are inconsistent (Wright et al. 2007). Over the past few decades, conservation physiologists have used physiological mediators, such as glucocorticoids, as a tool to measure the non-lethal effects of disturbance on populations (Wikelski and Cooke 2006). Glucocorticoids, often referred to as stress hormones, can provide a rapid assessment of how individuals are able to cope in challenging environments (Walker et al. 2005).

Determining the impacts of anthropogenic noise on individuals can be challenging as noise is often confounded by physical disturbance, such as habitat alteration and visual stimuli. Experimental studies, which isolate noise from physical disturbance, have helped researchers to separate the effects of noise from the presence of infrastructure (Campo et al. 2005, Chloupek et al. 2009, McClure et al. 2013, Potvin and MacDougall-Shackleton 2015). However, many experimental studies fail to accurately reproduce anthropogenic noise on the landscape scale. Often noise is broadcasted for short periods of time, and low-quality recordings or low-fidelity speakers are used which do not accurately reproduce sound that emulates the original acoustic environment (Rosa et al. 2015). To combat this, my study used high-quality recordings and high-fidelity speakers to reproduce noise from the original source (Rosa et al. 2015). Large-scale experimental playbacks, like the one employed in this study, provide insight into the biologically relevant responses an individual might express in a natural environment (Kight and Swaddle, 2011). Identifying the underlying mechanisms leading to the decline of grassland songbirds will aid land managers in the difficult task of mediating human impact during vulnerable stages of their life history

Literature Review

The decline of North American grasslands and grassland birds

North American grasslands are undergoing intense habitat conversion and fragmentation due to increased human activities, such as agricultural land conversion and the expansion of energy development (Roch and Jaeger 2014). Over the past 150 years the Great Plains have been reduced by approximately 70% of their original land cover. While tall grass prairies have suffered the most extreme losses and retain only 13% of their original land area, mixed-grass prairies have also been impacted, retaining only 29% of their historic extent (Samson et al.

2004). Land conversion in the Great Plains has not only reduced the total grassland habitat available but has also fragmented the remaining habitat. As more intact habitat is fragmented, patch size decreases and the proportion of edge habitat increases (Fletcher 2005). Some grassland songbirds are area-sensitive, meaning they avoid small prairie fragments, while others avoid habitat edges, both of which ultimately reduce the total available habitat on the prairies (Herkert 1994, Winter and Faaborg 1999, Sliwinski and Koper 2012, Thompson et al. 2015). A study by Davis (2004) demonstrated that an increase in the edge to habitat ratio explained the decreased abundance of three grassland obligates: Sprague's Pipit (*Anthus spragueii*), Baird's Sparrow (*Ammodramus bairdii*), and Chestnut-collared Longspurs. Edges may decrease habitat quality by altering the density of predators and nest parasites and changing the structure and composition of vegetation, which has been shown to affect reproductive success in some species (Winter et al. 2000, Benson et al. 2013, Ludlow et al. 2015). In the remaining grasslands, humans have disrupted natural disturbance regimes, altering the ecological integrity of these ecosystems. Historically, grasslands were maintained through fire and grazing, which prevented the encroachment of woody vegetation and created heterogeneity on the landscape (Brennan and Kulvesky 2005, Askins et al. 2007). The eradication of Bison (*Bison bison*) and the suppression of fire has removed the disturbance that once maintained the shifting mosaic of diverse habitat that supported grassland songbirds (Brennan and Kulvesky 2005).

As a result of these changes, grassland songbird obligates have experienced steep declines (Brennan and Kulvesky 2005). A recent report on the state of Canada's birds found an 87% decline in grassland obligates from 1970 to 2016 (North American Bird Conservation Initiative 2019). Because much of the grasslands were lost prior to the initiation of the monitoring programs such as the Breeding Bird Surveys, population declines are likely much

greater (North American Bird Conservation Initiative 2012, Sauer et al. 2013). Unfortunately, temperate grasslands are poorly protected globally, and it is this disparity between habitat loss and habitat protection that make grassland ecosystems one of the most threatened terrestrial biomes on the planet (Hoekstra et al. 2005).

The effects of oil and gas extraction on passerines

Since 2000, there has been a rapid increase in oil and gas development in central North America, with an average of 50,000 new wells dug every year (Allred et al. 2015). The land area occupied by oil and gas activities in the Great Plains was recently estimated to be approximately 3 million hectares (Allred et al. 2015). This expansion includes not only the physical footprint of the well pad but also the corresponding network of linear features, such as roads, power lines and fences, which can further exacerbate habitat loss (Copeland et al. 2011, Thompson et al. 2015).

The effects of oil and gas extraction on grassland songbird abundance have been well documented but the results have been inconsistent among studies and species. Multiple studies have shown that Sprague's Pipits and Baird's Sparrows are found at lower abundances in the presence of energy infrastructure (Hamilton et al. 2011, Nenninger and Koper 2018) but not all studies support these findings (Bogard and Davis 2014). Similarly, studies examining the abundance of Chestnut-collared Longspurs have also yielded mixed results. Bogard and Davis (2014) found that Chestnut-collared Longspurs avoided gas wells, while Nenninger and Koper (2018) found no significant effect of oil wells on their presence in the area. Oil infrastructure may also reduce the nesting success of grassland songbirds. In my study system in southeastern Alberta, multiple studies have shown that nesting success is species specific. Bernath-Plaisted and Koper (2016) found that in the presence of oil infrastructure both Savannah Sparrows (*Passerculus sandwichensis*) and Vesper Sparrows (*Pooecetes gramineus*) had reduced nesting

success, while Chestnut-collared Longspurs were not affected. A subsequent study conducted by Des Brisay (2018) also found no effect of oil infrastructure on nesting success of Chestnut-collared Longspurs but contradicted the results for Savannah Sparrows. Des Brisay (2018) found that distance to oil infrastructure did not affect Savannah Sparrow nesting success (Des Brisay 2018).

The presence of oil infrastructure on the prairies can have present multiple disturbances to grassland birds including altering vegetation composition, predator-prey interactions and introducing anthropogenic noise to the soundscape (Francis et al. 2009, Nasen et al. 2011, Rosa et al. 2015). Historically, non-native grasses such as crested wheatgrass (*Agropyron cristatum*) were used to re-vegetate disturbed areas around newly constructed wells and pipelines (Dale et al. 2009). The high seed-production factor of this species makes it an aggressive invader of prairies leading to creation of monocultures as it outcompetes native grasses (Dale et al. 2009). Vegetation structure and composition can impact both the occurrence of grassland birds as well as their reproductive success (Davis and Duncan 1999, Ludlow et al. 2015). Lloyd and Martin (2005) found that Chestnut-collared Longspurs that nested in monocultures of crested wheatgrass had lower nesting success than those that nested in native prairie.

The introduction of aboveground infrastructure can increase the availability of perch sites on an otherwise planar landscape, affecting the occupancy and abundance of avian predators and brood parasites (Benítez-López et al. 2010, Bernath-Plaisted et al. 2017). A recent study by Bernath-Plaisted et al. (2017) showed an increase in relative abundance of Brown-headed Cowbirds (*Molothrus ater*), an obligate brood parasite, as well as an increase in brood parasitism in the presence of oil infrastructure and associated linear developments. The survival and productivity of the host species is often reduced as brood parasitism has been shown to increase

the risk of abandonment, decrease hatching success and decrease the probability of nest survival (Smith et al. 2003, Ludlow et al. 2014, Bernath-Plaisted et al. 2017). Energy development and the associated habitat loss and fragmentation can also impact predator assemblages and densities (Chalfoun et al. 2002, Herkert et al. 2003, Benítez-López et al. 2010, Hethcoat and Chalfoun 2015). Hethcoat and Chalfoun (2015) documented an increase in predator activity resulting from habitat loss due to natural gas development, which in turn resulted in an increased probability of nest predation. Changes to the predator community could be one of the mechanisms explaining the reduction in reproductive fitness that is commonly associated with energy development (Herkert et al. 2003, Hethcoat and Chalfoun 2015, Bernath-Plaisted and Koper 2016). Conversely, some predators may be deterred from noisy environments if their ability to detect prey species is compromised, which can have an indirect positive effect on nest success (Francis et al. 2009). In predator-dense environments, grassland songbirds that exhibit behavioural plasticity may be able to adapt to altered predator communities by adjusting their level of parental care to avoid attracting predators to their nest (Eggers et al. 2008). In southeastern Alberta, a recent study by Ng et al. (2019) demonstrated that in the presence of oil infrastructure and noise, Chestnut-collared Longspurs reduced their level of parental care. These studies suggest that the effects of oil and gas can extend far beyond the physical footprint of the disturbed area.

The effects of anthropogenic noise on passerines

Over the past few decades, the study of anthropogenic noise and its effects on passerines has received increasing attention. As human populations continue to grow and expand, anthropogenic noise has become pervasive in natural environments. In grassland ecosystems, where topography is generally flat and vegetation is short, there are fewer barriers affecting

attenuation of sound. Noise will likely travel farther here than in ecosystems with taller vegetation such as forests (Ortega 2012). This suggests that noise-emitting infrastructure on the prairies has a much larger acoustic footprint than those in forested ecosystems. Research has shown that noise has the potential to deter individuals from otherwise suitable habitat (McClure et al. 2013), impair acoustic communication (Barber et al. 2010), alter behaviour (Antze and Koper 2018) and impact stress physiology (Injaian et al. 2018).

Anthropogenic noise may act as a deterrent for some species causing them to avoid noisy environments (Francis et al. 2009, Blickley et al. 2012a, Ware et al. 2015). However, some species may experience indirect positive effects from living in noisy environments (Francis et al. 2011). Noise can also hinder an individuals' ability to accurately assess habitat quality (Bock and Jones 2004). A recent experimental study by Rosa (2019), which isolated noise from its physical disturbance, found that Chestnut-collared Longspurs avoided noise-emitting oil infrastructure despite experiencing increased reproductive productivity close to noise.

For individuals that do settle in noisy environments, there is a reduction in the distance that avian acoustic signals can be perceived, which can interfere with the ability to detect vocalizations from conspecifics (Habib et al. 2007, Slabberkoorn and Ripmeester 2008). This can be particularly challenging for birds as they rely on auditory communication for many important life history strategies including territorial displays, mate attraction, predator alarms calls, and parent-offspring communication (Slabberkoorn and Ripmeester 2008, Barber et al. 2010). Industrial noise broadcasts across a wide range of frequencies (0-21 kHz), though typically dominates the soundscape at lower frequencies (Wood and Yezerinac 2006, Warrington et al. 2018). This generally overlaps with the frequencies where avian hearing is most sensitive (1-4 kHz). When anthropogenic noise and acoustic signals have similar frequency profiles,

acoustic communication is masked (Beason 2004, Rosa et al. 2015). Some species may exhibit song plasticity and will modify their acoustic signal in loud environments to mitigate acoustic masking, allowing them to be heard in noisy environments (Wood and Yezerinac 2006, Curry et al. 2018).

Studies have shown that anthropogenic noise may elicit inappropriate behavioural responses in both adults and nestlings (McIntyre et al. 2014, Antze and Koper 2018). In response to conspecific alarm calls, adult Savannah Sparrows decreased feeding latency in noisy environments compared to quiet ones, which could increase predation risk if parental presence at the nest signals the nest location to predators (Antze and Koper 2018). Additionally, nestlings may be more vulnerable to predators in noisy environments if they are unable to detect or appropriately respond to parental alarm calls as predators can use nestling begging calls to locate nests (Haff and Magrath 2011). Parental alarm calls should serve as a signal to silence begging nestlings when predation risk is high (McIntyre et al. 2014). But as one study demonstrated, in noisy environments nestlings may miss these acoustic cues and continue to beg despite the increased predation risk (McIntyre et al. 2014).

Anthropogenic noise also has the potential to act as a physiological stressor for some species. Laboratory experiments where individuals were exposed to noise have shown that changes to the acoustic environment can increase levels of glucocorticoids (Chloupek et al. 2009). However, in the wild, the results have been inconsistent (Crino et al. 2011, 2013, Blickley et al. 2012b, Potvin and MacDougall-Shackleton 2015, Injaian et al. 2018). For example, Blickley et al. (2012b, a) found that male Greater Sage-Grouse (*Centrocercus urophasianus*) avoided experimental playbacks, while those that remained behind had elevated levels of immunoreactive corticosterone metabolites in fecal samples. Conversely, a study by

Angelier et al. (2016) found no effect on anthropogenic noise on either body condition or corticosterone levels in House Sparrows (*Passer domesticus*). Differences between study species, age, sex and even noise sources will all impact how an individual will respond to noise, which can likely explain the majority of the differences in results amongst studies (Romero et al. 2009).

Stress Physiology

In the face of changing environmental conditions, organisms use physiological mediators to maintain homeostasis (McEwen and Wingfield 2003). In mammals and birds, this is typically accomplished through the activation of the hypothalamic-pituitary-adrenal (HPA) axis, prompting the release of physiological mediators such as glucocorticoids (Wingfield et al. 1997). Corticosterone, the primary avian glucocorticoid, triggers the conversion of fat and protein to useable carbohydrates (Wingfield et al. 1997). Individuals experience predictable daily and seasonal changes that require the release of physiological mediators to meet their energetic demands. When individuals encounter unpredictable or threatening environmental stimuli they may increase the level of mediators needed to re-establish homeostasis, pushing the organism into reactive homeostasis (Wingfield et al. 1998, Romero et al. 2009). This is generally referred to as the stress response (Romero et al. 2009).

Increases in corticosterone, the primary glucocorticoid released during the stress response in birds, mobilize energy and cause individuals to adopt behaviours that promote immediate survival such as increased foraging and vigilance (Wingfield et al. 1997, McEwen and Wingfield 2003, Romero et al. 2009). These coping mechanisms can be adaptive in the short-term, allowing individuals to cope with environmental perturbations and re-establish homeostasis (Romero 2002). However, when individuals are exposed to an extreme stressor, the concentration of the physiological mediator released may exceed that of their normal reactive homeostatic range,

pushing the individual into homeostatic overload (Romero et al. 2009). As a result, individuals enter an ‘emergency life history stage’ where normal life history strategies and behaviours, such as reproduction and development, are suspended until the individual can re-establish homeostasis (Wingfield et al. 1998). During life history stages where energetic requirements are high, as in the case with breeding or parental care, an individual may be more susceptible to entering homeostatic overload (Romero et al. 2009).

Continuous exposure to a stressor can keep an individual in the reactive homeostasis range for long periods of time. The cumulative effects of maintaining corticosterone levels within the reactive homeostasis range leads to increased wear and tear on an individual and a gradual decrease in the ability of that individual to respond to a stressor (Romero et al. 2009). The accumulation of these costs over time makes the individual more vulnerable to entering homeostatic overload at lower intensity disturbances (Romero et al. 2009). Different species and individuals vary in their ability to cope with stressful stimuli. Their ability to cope can depend on their genetic makeup, social status and energy requirements at the time of the stressful event (McEwen and Wingfield 2003). The long-term impacts of sustained corticosterone release include immunosuppression, causing greater susceptibility to disease and infection, muscle deterioration, reduced growth rate, and decreased reproductive output (Wingfield et al. 1997, Sapolsky et al. 2000, Love et al. 2004).

Short-term secretions of glucocorticoids can be adaptive in organisms by redirecting behaviour to promote immediate survival, but long-term activation of the HPA-axis carries significant costs (Wingfield et al. 1998, Wingfield et al. 1997). It is this negative association between elevated corticosterone levels and metrics of fitness that led to the creation of the Corticosterone-Fitness hypothesis (Bonier et al. 2009). Despite the general acceptance of this

hypothesis in some fields, research on the effects of corticosterone on fitness has been inconsistent. The relationship between corticosterone and fitness measures has been found to be positive in some studies (Cyr and Romero 2002, Crino et al 2011), neutral (Tilgar et al 2010, Angelier et al. 2016), but negative in others (Angelier et al. 2010, Kitaysky et al. 2001). Romero (2002) suggests that selection may favour low corticosterone or high corticosterone during different life history stages, which might explain the inconsistency of the results. Due to the difficulty associated with tracking wild organisms throughout their lifetime, the majority of studies use some measure of individual quality to represent fitness. This suggests that studies evaluating corticosterone levels in birds should be accompanied by data collection on individual health or quality, to allow the researcher to interpret the implications of variation in corticosterone levels.

While the majority of studies to date have focused on the effects of corticosterone on adults, an increasing number are exploring these effects on nestlings. In comparison with adults, altricial nestlings may be more vulnerable to the effects of elevated corticosterone during development, a critical time period in their lives.

Nestling Physiology, Growth and Development

Altricial nestlings are blind and unable to thermoregulate immediately after hatching, leaving them completely dependent on parental care for food, warmth, shelter and protection from predators. In response to environmental stressors adults may adopt behaviours that promote immediate survival in order to avoid the deleterious consequences of sustained corticosterone release (Wingfield et al. 1997). Altricial nestlings are more limited in their behavioural flexibility and are unable to move away from stressful stimuli and therefore may be more susceptible to the effects of corticosterone during development (Lima and Dill 1990, Crino et al. 2013). Research

has shown that after birth, mammals experience a hyporesponsive period where the HPA-axis is unresponsive to stressful stimuli (Sapolsky and Meaney 1986). This has also been documented in altricial nestlings; as nestlings develop in the nest, the HPA-axis develops as well, and their capacity to respond to stressful stimuli grows (Sims and Holberton 2000, Blas et al. 2006, Wada et al. 2007). This period of hyporesponsiveness at a younger age is likely an adaptive response to the deleterious effects of corticosterone during a critical period of development and growth (Sims and Holberton 2000). Because of their vulnerability during development, nestlings are sensitive to the environmental conditions in which they are raised. Changes in corticosterone can be associated with sibling competition (Saino et al. 2003), food availability (Pravosudov and Kitaysky 2006), parental care (Rensel et al. 2010), and noise (Injaian et al. 2018). Studies have shown that there can be a cost associated with elevated corticosterone during development, including reduced growth rates (Spencer and Verhulst 2007) and slower plumage development (Saino et al. 2005). Nestlings that receive exogenous corticosterone treatments are often in worse body condition or exhibit suppressed growth rates suggesting that increased levels of corticosterone can negatively impact individual quality (Spencer and Verhulst 2007). The effects of corticosterone can persist into adulthood and influence phenotype later in life. A study by Spencer and Verhulst (2007) found that experimentally elevated corticosterone levels in Zebra Finch (*Taeniopygia guttata*) nestlings led to sex-specific changes in personality. At 50 days post exposure, corticosterone-elevated males exhibited neophobic behaviour and reduced dominance compared to controls, which could have significant impacts on fitness (Spencer and Verhulst 2007).

However, short-term elevation of corticosterone levels during the developmental period can also be adaptive. A greater responsiveness to stressful stimuli, like the sound of a predator

approaching, could promote fitness by triggering predator-evading behaviours (Wright et al. 2007). A study by Chin et al. (2009) experimentally elevated corticosterone levels of European Starling (*Sturnus vulgaris*) eggs and found that in comparison to controls, nestlings exposed to corticosterone had heavier pectoral muscles relative to body mass. Fledglings are extremely vulnerable to predation during the post-fledgling period (Naef-Dantzer et al. 2001) so more rapid development of traits that enhance mobility can promote post-fledgling survival (Jones et al. 2017). Therefore, similar to the functioning of the stress response in adults, a short-term increase in corticosterone may facilitate survival of nestlings. However, when environmental stressors persist or if parents cannot meet the needs of the offspring, homeostatic overload may follow (Kitaysky et al. 2001).

Over the past decade, researchers have demonstrated that the quality of the both the pre-natal and post-natal environment can impact the development of nestling physiology, growth and development. Stressed mothers can transfer glucocorticoids to their eggs (Love et al. 2005, Bowers et al. 2016), which in turn can have consequences for her offspring in the form of elevated corticosterone levels, reduced growth and poor body condition (Hayward and Wingfield 2004, Saino et al. 2005). Conversely, maternal stress can also result in an adaptive response in offspring. A study by Love and Williams (2008) injected corticosterone into the yolks of eggs to mimic the effect of a poor-quality mother on offspring. They found that nestlings exposed to elevated corticosterone during development had a dampened stress response at fledging. In unpredictable environments where resources may be scarce or maternal quality low, a dampened stress response can reduce the negative effects of inappropriately releasing corticosterone (Love and Williams 2008).

Study Species

The Chestnut-collared Longspur is a migratory grassland songbird that breeds in the short- and mixed-grass Northern Great Plains of the United States and Canada (COSEWIC 2009). This species overwinters from western Oklahoma to south-eastern Arizona and down to northern Mexico (COSEWIC 2009). Chestnut-collared Longspurs are socially monogamous and double-brooded with both parents investing heavily in parental care and males actively defending the nest and feeding the offspring (Lynn and Wingfield 2003). Males arrive on the breeding grounds in Canada prior to females and have established territories by early to mid-May (COSEWIC 2009). Females typically lay 3-5 eggs which are incubated for 10-12.5 days by the female followed by 10 days in the nest before fledging (COSEWIC 2009).

Chestnut-collared Longspur population sizes have decreased by approximately 90% since the late 1960s, likely due to habitat loss of short- and mixed- grass prairies (COSEWIC 2009). The species is listed as Threatened federally and as Sensitive by the province of Alberta (COSEWIC 2009, Cerney and Calon 2015). With the rapid expansion of oil wells in central North America, as well as the increasing conversion to agricultural cropland, suitable grassland habitat is disappearing (Askins et al. 2007, Allred et al. 2015). Chestnut-collared Longspurs have shown mixed responses to the presence of oil infrastructure in the prairies (Hamilton et al. 2011, Bogard and Davis 2014). Possible explanations for their sustained decline could include the impacts of edge effects, invasive vegetation or noise pollution (Davis 2004, Lloyd and Martin 2005, Koper and Schmiegelow 2006, Rosa and Koper 2016).

Research Objectives

The expansion of oil and gas development in the grasslands has had mixed effects on Chestnut-collared Longspurs abundance (Nenninger and Koper 2018, Rosa 2019). Studies in

southeastern Alberta found that nesting success of longspurs was not affected by oil and gas well presence (Bernath-Plaisted and Koper 2016), but parental care was consistently reduced in the presence of oil and gas infrastructure, noise and associated roads (Ng et al. 2019). Additionally, adult females had elevated levels of basal corticosterone near experimental playbacks of oil well noise, indicating that anthropogenic noise does impact physiology of Chestnut-collared Longspurs (Des Brisay 2018).

Given that nesting success of Chestnut-collared Longspurs is unaffected by oil wells and noise but parental care is reduced, I sought to determine whether nestlings raised in close proximity to oil wells and noise are bearing the cost of being raised in disturbed environments. Based on previous studies that have demonstrated a direct or indirect effect of maternal stress and quality on nestling stress physiology, and that previous studies in this area have shown that female Chestnut-collared Longspur stress physiology is influenced by noise (Des Brisay 2018), I also investigated whether maternal stress mediated the impact of oil wells and noise on offspring (Love and Williams 2008). To assess the effects of oil infrastructure and its associated noise on nestlings I used solar-powered playback units broadcasting oil extraction recordings to isolate effects of noise from the physical source of disturbance and compared these impacts with those of real wells. I measured corticosterone levels and indices of growth and development (mass and outer primary feather length, hereafter referred to as p9 length) to determine if nestlings were affected by infrastructure or noise. Female Chestnut-collared Longspur corticosterone was assessed in a concurrent study (Des Brisay 2018) and these data were used to test the mediating effect maternal stress had on nestling stress. Based on previous research (Love and Williams 2008, Injaian et al. 2018), I expected to see higher elevated corticosterone levels and a reduction in body condition as distance from oil infrastructure and experimental playback decreased. If

effects of oil infrastructure were due to the built environment itself, rather than the noise it produces, I would expect this to be true only at infrastructure sites. Additionally, I examined the direct relationship between corticosterone levels and nestling body condition to determine if there were consequences of elevated corticosterone levels on nestling growth and development.

Methods

This study was accomplished under the 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

My study took place within 60 km of Brooks (50°33'51"N, 111°53'56"W, 760 MASL) in the mixed-grass prairies of southeastern Alberta, Canada from May to August 2016. The vegetation on our sites was predominantly composed of native grasses such as blue gramma (*Bouteloua gracilis*), needle-and-thread (*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), as well as native forbs and shrubs such as pasture sagewort (*Artemisia frigida*) and silver sagebrush (*Artemisia cana*). Exotic vegetation such as smooth brome (*Bromus inermis*) and crested wheatgrass (*Agropyron cristatum*) were present on our sites at low abundances. Study sites were located on topographically flat, annually grazed pastures owned by the Eastern Irrigation District (EID).

Treatments

Four treatments, each with 3 replicates, were used to examine the effects of oil infrastructure and associated noise on Chestnut-collared Longspur nestlings. The first treatment consisted of a 2500 m² fenced-in gravel pad that housed a generator-powered screw pump connected to a network of gravel roads. Screw pumps are a common type of oil well in southeastern Alberta that are approximately 2.7 m tall and consist of a horizontal spinning mechanism that extracts oil out of the ground. Generator-powered oil wells are powered by propane-fuel generators and are noisier than grid-powered screw pumps, which lack a generator but are connected via power lines to the electrical grid (Warrington et al. 2018). To distinguish between the effects of the physical infrastructure and noise, an experimental playback system was used as the second treatment type. High-fidelity recordings of generator-powered screw pumps were broadcasted on to the prairies to emulate the sound of real infrastructure in the absence of the physical presence of the wells (Rosa et al. 2015). The fidelity of the broadcast system was confirmed by comparing the spectral composition and spatial attenuation of sound at playback sites to real infrastructure using sound pressure level measurements at four cardinal direction 100 m transects (see Rosa et al. 2015). The recordings were broadcasted continuously throughout the entire breeding season (approximately May 1st to July 31) and were installed prior to the establishment of territories to mimic the effects of noise on settlement patterns. Each playback system (hereafter referred to as ‘experimental playback’) was powered by a solar panel array connected to a charge-controller, batteries, inverter, 2 high-fidelity speakers and an iPod (Apple) that was housed in a 1.2 m plywood box. The plywood box had 2 screened holes on either side from which the speakers projected the high-fidelity generator-powered screw pump recording (Rosa et al. 2015). The unit was surrounded by a 1 m high, 7.3 m long and 4.9 m wide

technical fence that protected it from grazing cattle. I included an additional treatment referred to as ‘silent playback’ to control for the presence of the playback unit itself and the effect it might have on habitat selection or corticosterone. The silent playback housed the same structure as the experimental playback but did not broadcast noise on the landscape. The final treatment included in this study were control sites. Control sites were located on native mixed-grass prairies and were free of both noise-emitting and silent infrastructure. Centre points were located at least 800 m from any infrastructure, playback unit or road.

Field Methods

We searched for Chestnut-collared Longspur nests using adult behavioural cues such as territorial displays, singing, and carrying nesting material or food. A GPS coordinate was taken each time a nest was found. The nest was then marked with a brightly coloured bamboo stick 10 m to the south, and a nail with a coloured survey marker 10 m to the west. Nests were assigned an alphanumeric “Nest ID” based on the site name and the order in which nests were found (i.e. C3-CN1). Nests were monitored every 1-2 days until the eggs hatched. Nestlings were aged using visual cues such as individual feather tracts, eye and ear development and emergence of pins (Jongsomjit et al. 2007). After nestlings hatched, monitoring took place every 2-4 days until the nest failed or fledged. A nest was considered successful if at least one nestling successfully fledged.

As part of a concurrent study examining the effects of oil infrastructure on adult stress physiology and demographics (Des Brisay 2018), colleagues and I captured female Chestnut-collared Longspurs on the nest using a walk-in drop trap that consisted of a wire frame covered in mist net material propped open with a stick. A 50 m piece of twine was tied to the stick and held by an observer hidden in a blind. When the female returned to the nest to attend to the

nestlings the observer would pull the twine to dislodge the stick, trapping the female inside. Observers would attempt to trap the female for a maximum of 30 minutes per day. Drop trapping was not performed on nestlings between days 1 and 3, to mitigate nest abandonment, or on the day of blood sampling so as not to affect corticosterone levels.

On day 7 post hatch, we returned to the nest to band and sample blood of nestlings between the hours of 10 AM and 2 PM to control for hormonal changes in circadian rhythm. Day 7 was chosen as the sampling date as it was anticipated that individuals would be old enough to mount a stress response, without being so old that our activities would be likely to force-fledge the nestlings. While no studies have examined the hyporesponsive period in Chestnut-collared Longspurs, a study by Wada et al. (2007) on Nuttall's White-crowned Sparrow nestlings (*Zonotrichia leucophrys nuttalli*) showed that nestlings as young as 4 days old could mount a stress response. Though not closely related to Chestnut-collared Longspurs, Nuttall's White-crowned Sparrows also nest on the ground, produce altricial nestlings, and have a similar nestling period (approximately 10 days) to Chestnut-collared Longspur so it was expected that Chestnut-collared Longspur nestlings would also be capable of responding to a novel stressor at day 7. I found evidence to suggest that at day 9 Chestnut-collared Longspur nestlings were capable of mounting a stress response that was qualitatively similar to an adult stress response. My results suggest that at day 7 nestlings were still in the hyporesponsive period but were able to mount a stress response. Nestlings were occasionally sampled a day earlier due to field logistics (poor weather) or sampled later if nests were found when nestlings were older, which allowed us to evaluate effects of nestling age on the stress response. Both adults and nestlings were banded with a CWS aluminum band with a unique number as well as a unique combination of plastic colour bands for subsequent identification in the field. In adult females, we assessed age and

weight while in nestlings we assessed weight, tarsus length and the length of the outer primary feather (hereafter referred to as p9).

Circulating levels of basal corticosterone were assessed by taking an initial blood sample within 3 minutes of capture or removal from the nest (Romero and Reed 2005). The initial 3-minute basal blood sample reflects the circulating levels of basal corticosterone in an individual which is representative of the energetic demands an individual faces daily (McEwen and Wingfield 2003). Blood was extracted from the brachial vein using a 27-gauge needle drawn into a heparinized microcapillary tube. Approximately 70 μ L of blood was drawn from adults while approximately 50 μ L was drawn from nestlings. A second acute blood sample was taken 12 minutes later following a standardized capture-restraint protocol to assess the change in corticosterone following a novel stressor (Wingfield et al. 1992). The acute blood sample reflects the peak corticosterone released after a stressful stimulus which, in the case of this study, was handling and restraint. I chose a 12-minute handling protocol to sample acute corticosterone levels based on a study by Lynn et al. (Lynn et al. 2003) that demonstrated after 10 minutes of handling and restraint Chestnut-collared Longspur corticosterone levels had reached peak levels. Approximately 30-70 μ L was drawn from the adult birds while only 30-40 μ L was drawn from nestlings. The total amount of blood drawn from nestlings was less than 1% of their body weight and nestlings under 8 g were not subject to the capture-restraint blood sampling (Sheldon et al. 2008). Blood samples were stored on ice for no more than 6 hours until the plasma and hematocrit were separated using a centrifuge and subsequently frozen at -20°C until analysis in the lab.

Radioimmunoassay Procedure

Plasma corticosterone was determined following a radioimmunoassay (Sheriff et al. 2011). Corticosterone was extracted from plasma using a 12:1 ratio of absolute ethanol to plasma then centrifuged at 13000 rpm for 3 minutes at 4°C. The supernatant was extracted, and the process repeated once more. The pooled supernatants were then dried down in a centrifugal evaporator (Savant® ISS110 SpeedVac® Concentrator), sealed with parafilm and stored at -20°C until the day of the assay. Extraction efficiency of corticosterone from plasma was 113.2%.

On the day of the assay the samples were reconstituted in 100 µL RIA buffer (phosphate buffer, sodium chloride and bovine serum albumen) for 1 hour. I then combined 100 µL of 1:6000 diluted corticosterone antibody (Antibodies-online, cat no. ABIN343319) with 100 µL of 3H-labeled corticosterone (Perkin Elmer) and 100 µL of reconstituted sample or known concentrations of corticosterone (standards). The mixture was incubated for one hour at 24°C and then stored at 4°C overnight. The following day I added dextran-coated charcoal, a separation buffer, to remove unbound corticosterone. The tubes were vortexed then left on ice for 15 minutes before being centrifuged at 2500G for 30min at 4°C. The supernatant was then poured into scintillation vials and combined with 4 mL of Ultima Gold scintillation fluid (Perkin Elmer). Radioactivity was measured in a scintillation counter (TriCarb 3100 LSC, Perkin Elmer, Waltham, MA, USA), where each vial was counted for 5 minutes each. Using the known concentrations of corticosterone from the standard curve, I interpolated corticosterone of each sample using Prism 6 (Graphpad). All samples were run in duplicate and standards run in triplicate to improve the accuracy of our results. The inter-assay coefficient of variation was 14.5% and the intra-assay coefficient of variability was 13.4 %. A pooled sample of Chestnut-

collared Longspur plasma was serially-diluted and compared to serially-diluted standard concentrations to confirm that parallelism was achieved.

The upper and lower detection limits of my radioimmunoassay were 3.0 ng/mL and 0.2 ng/mL respectively. Some of my samples failed to produce corticosterone concentrations that fell within the interpretable range of our assay due to low concentrations of corticosterone in the sample. Following a technique defined in Des Brisay (2018) I calculated the minimum detectable corticosterone based on the lower detection limit of my radioimmunoassays (i.e. 0.2 ng./mL) and the sample specific duplicate plasma volume for samples that had adequate plasma volume (minimum 10 uL per duplicate),. Although I cannot be sure of the actual concentration of corticosterone in these samples, this method of assigning corticosterone concentrations is conservative as biologically the concentration must fall between 0 and 1-2.0 ng/mL. This method of assigning corticosterone levels avoids the consequences of assigning all low samples with an arbitrary value (i.e. 1 ng/mL), which can artificially lower standard error. By using this approach, I retained a large number of samples that would otherwise have been lost. Obtaining blood samples from a federally threatened species is extremely difficult and so retaining as many samples as possible is extremely important.

Nestling Sexing

Nestlings were sexed using a Polymerase Chain Reaction based on techniques used by Griffith et al. (1998). Primers P2 and P8 were used in the PCR amplification with 1 uL of DNA. The final reaction conditions were: 0.5 ul of each primer, 4.0 ul of H₂O, 2.0 ul of (5x) Buffer, 0.6 ul of MgCl₂, 0.2 ul of dNTP, 1 ul of BSA and 0.2 ul of Taq polymerase (Promega). Thermal cycling was carried out in a BioRad C1000 Thermal Cycler at 94°C/2min followed by 40 cycles

of 94 C/45s, 48 C/45s, 72 C/45s and 72 C/5min. PCR products were separated by gel electrophoresis on a 1% agarose gel stained with ethidium bromide for 90 minutes at 95 Volts.

Statistical Analysis

All analyses were done in R Studio (R Core Team 2018) using an alpha level of 0.1 to reduce the risk of a Type II error, which can have critical consequences in conservation biology (Taylor and Gerrodette 1993). I developed linear mixed models using the package ‘lmerTest’ (Kuznetsova et al. 2019), created figures using the package ‘ggplot2’ (Wickham, 2016) and used ‘sjplot’ to create tables of model outputs (Lüdtke 2019). Nest ID was included in all models as a random variable to account for the relatedness of nestlings within a nest. In this study, nestling and maternal stress refers to both basal corticosterone levels and the stress response of individuals, where stress response is defined as the difference between acute and basal corticosterone levels and reflects how strongly an individual responds to a stressor.

Based on previous studies (Love and Williams 2008, Injaian et al. 2018, Kleist et al. 2018) and work done in this system (Ng et al. 2019), I expected oil wells and their associated noise could affect nestling stress physiology, growth and development and that maternal stress could mediate that relationship. Due to the difficulty associated with quantifying both basal and acute corticosterone in nestlings as well as successfully capturing and quantifying basal and acute corticosterone of their mothers in a wild system, I was not able to acquire a sufficient sample size at each treatment to effectively analyze the two effects together. By including maternal stress in analyses the sample size was reduced considerably, so in order to retain enough power to detect an effect of treatment type on response variables I analyzed a large data set without maternal corticosterone in the model, and then in a subsequent model with both treatment and maternal corticosterone.

Nestling Hyporesponsive Period

I initially tested whether the capacity to respond to a novel stressor increased during the nestling period by comparing the stress response of nestlings as they aged (day 6-10). To test this, I ran a linear model with nestling stress response as the response variable and an interaction with age and mass as predictor variables.

Preliminary Models

I ran two preliminary models to determine which biologically important variables impact basal corticosterone and stress response and thus should be included in subsequent models to control for their effects. All basal corticosterone concentrations were log transformed to reduce skewness. The biological variables included in the preliminary model for nestling physiology were age, mass, sex, brood size (number of nestlings in the nest at the time of sample), Julian date, and time of day of the sample. In the stress response model, I also included an age and mass interaction and basal corticosterone as a predictor variable. Significant predictor variables were carried forward in subsequent models.

I ran a second set of preliminary models to determine which biological variables should be included in growth and development models (mass and p9 length as response variables, respectively). I included age, sex, brood size, Julian date, and time of day of the sample as predictor variables for mass. For the length of p9, I included all the variables mentioned above as well as mass. Significant predictor variables were carried forward in subsequent models.

Effects of infrastructure on nestling physiology, growth and development

To test for the effect of oil well infrastructure and associated noise on nestling physiology, growth and development I ran four linear mixed models with (1) basal

corticosterone, (2) stress response, (3) mass and (4) p9 length as the response variables. I included treatment type (screwump, experimental playback, silent playback and control), distance to the experimental treatment or control and an interaction between the two as the predictor variables as well as any biological variables found to be significant from the preliminary models described above.

Mediating role of maternal stress on nestling physiology, growth and development

To models 1 to 4, I added maternal basal corticosterone (log transformed) and maternal stress response as predictor variables to test whether maternal stress mediated the impact of treatment type on nestling physiology, growth and development. This hierarchical modelling approach was chosen as the sample size was considerably reduced with the addition of maternal stress to models 1 to 4.

Effects of corticosterone on nestling growth and development

To test whether corticosterone levels impact nestling growth and development I ran two linear mixed models with mass and p9 length as the response variables and basal corticosterone and stress response as the predictor variables, also including biologically influential variables as determined above.

Results

Throughout the breeding season I monitored 138 Chestnut-collared Longspur nests and banded 236 nestlings from 68 different nests. I took 222 basal and 217 acute blood samples from these nestlings. Of those, I was able to recover and analyze corticosterone from 187 basal and 206 acute samples. Seven nestlings had a lower acute corticosterone level than basal corticosterone and so were omitted from the analyses as I was unable to confirm whether these

differences were naturally occurring or due to human error in the field or lab. In all other cases, the 12-minute acute sample had a higher corticosterone level than the 3-minute basal sample (Figure 1). We captured and banded 42 females associated with the above nests. Of those, I was able to recover, pair and analyze 28 basal corticosterone and stress response samples with nestling basal corticosterone and stress response levels.

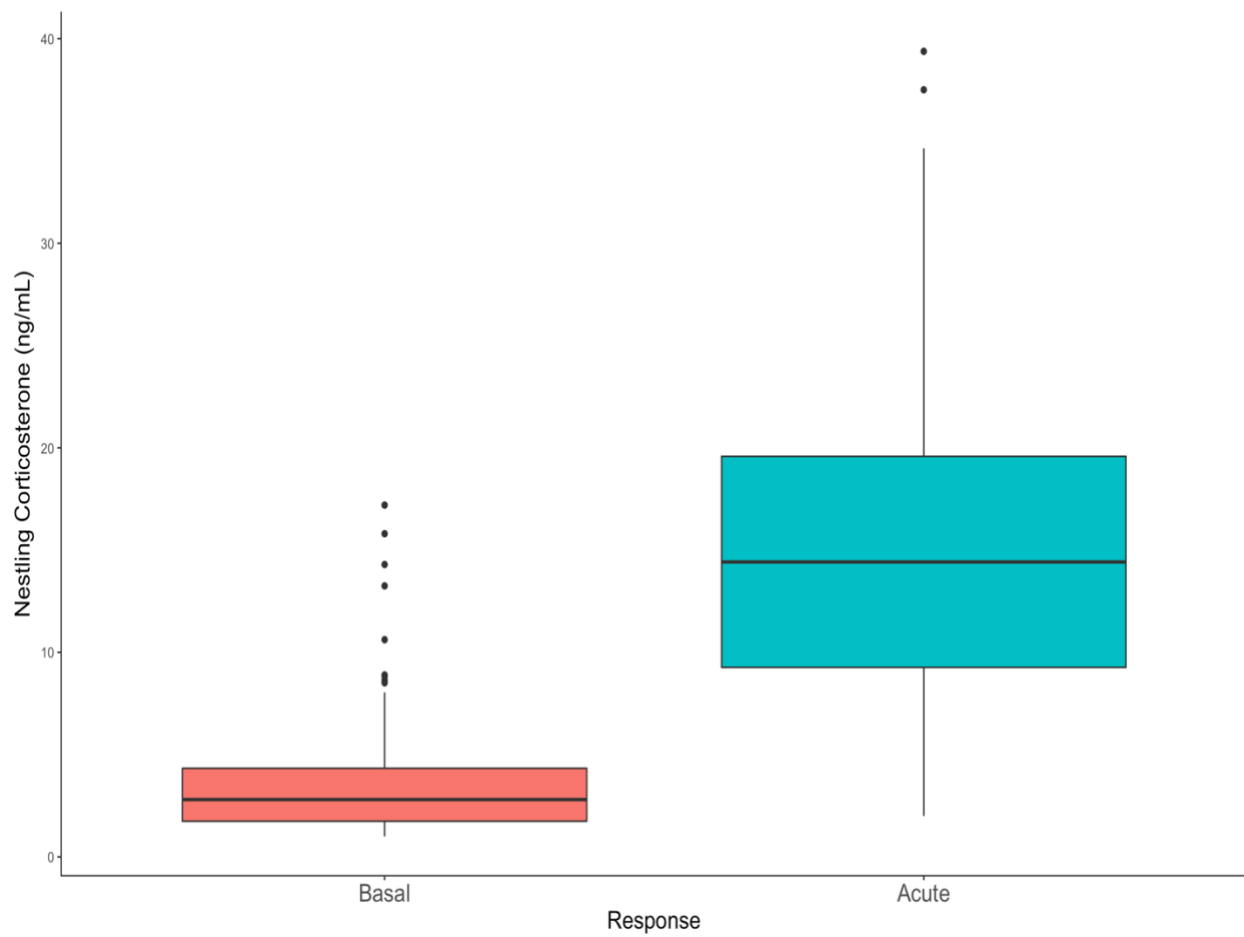


Figure 1. Corticosterone values from basal (under 3 minutes) and acute (approximately 12 minutes) blood samples of Chestnut-collared Longspur nestlings in southeastern Alberta, 2016.

Nestling Hyporesponsive Period

As nestlings aged, they responded more strongly to novel stressors, indicating that Chestnut-collared Longspur nestlings do experience an initial period of hyporesponsiveness (Figure 2). I also found that the effect of mass on stress response increased with age: older, lighter nestlings responded more strongly to a novel stressor (Figure 3).

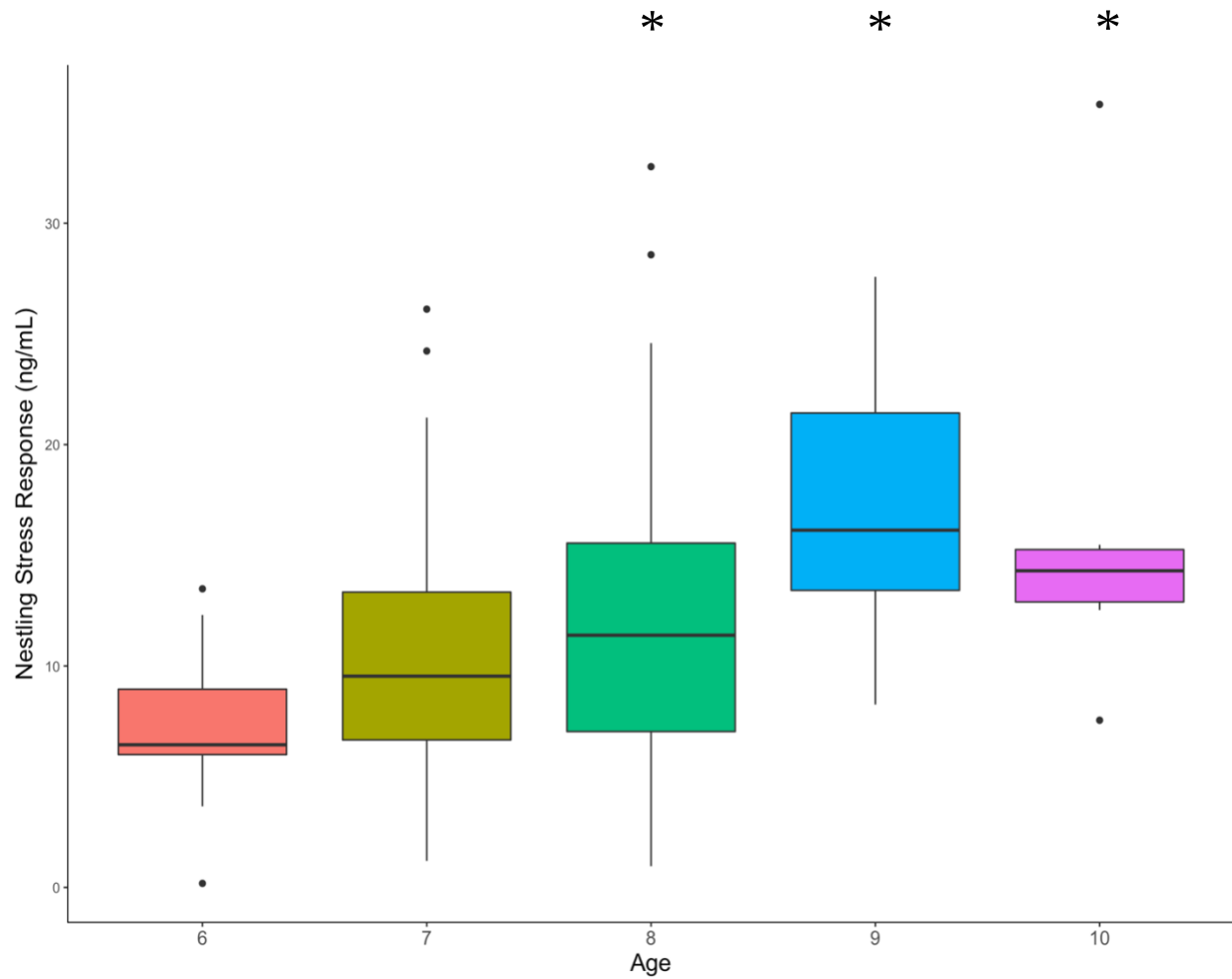


Figure 2. Change in Chestnut-collared Longspur nestling stress response throughout the nestling period in southeastern Alberta, 2016. Asterisk (*) denotes significant differences in nestling stress response from day 6 nestlings.

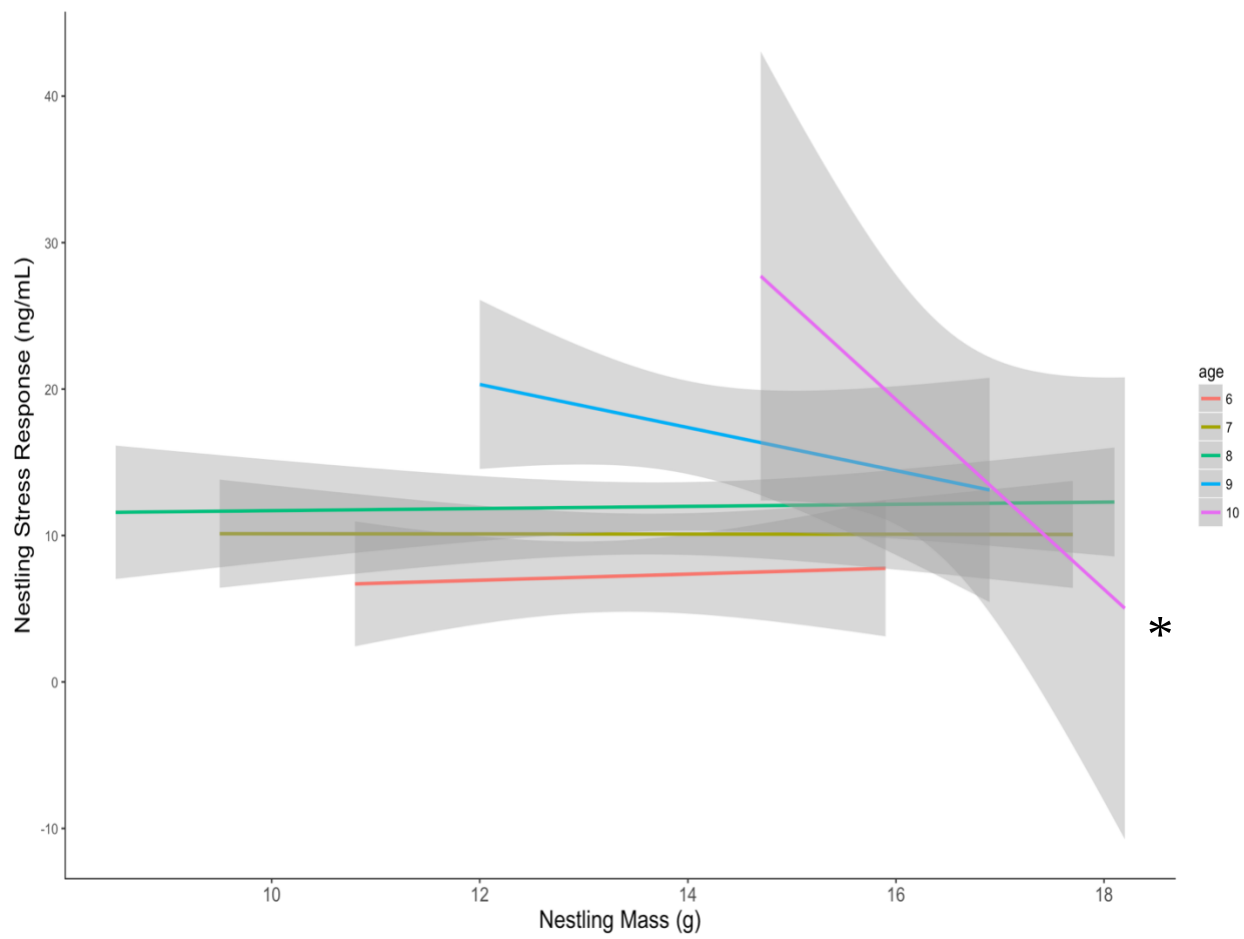


Figure 3 Chestnut-collared Longspur stress response relative to mass throughout the nestling period in southeastern Alberta, 2016. Asterisk () denotes a significant difference.*

Effects of infrastructure on nestling physiology, growth and development

Of the biological variables included in the preliminary model for basal corticosterone, none were strong predictors and were therefore not included in subsequent models (Table 1). Nestlings closer to the experimental playback had a lower baseline corticosterone than those farther away (Table 2, Figure 4). Nestlings closer to screwpumps showed a similar trend to nestlings found close to experimental playbacks; however, the relationship was not significant. We found fewer nests closer to screwpumps, which may have resulted in lower power to detect an effect. Nestling age was a significant predictors of nestling stress response and was included in subsequent models (Table 1). Nestlings closer to screwpumps and experimental playbacks had a lower stress response than those developing farther away (Table 2, Figure 5).

Table 1. Influence of diel, seasonal and biological predictor variables on logged basal corticosterone and stress response of Chestnut-collared Longspur nestlings in southeastern Alberta, 2016.

<i>Predictors</i>	Log of basal corticosterone			Stress response		
	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	0.0546	0.7541	0.942	-6.6170	8.3842	0.430
Age	0.1124	0.0713	0.115	2.4326	0.7987	0.002
Mass	-0.0424	0.0258	0.102	-0.1023	0.2969	0.730
Sex	-0.1304	0.0900	0.147	-1.3709	0.9915	0.167
Brood size	0.0721	0.0692	0.297	-0.2603	0.7641	0.733
Julian date	0.0028	0.0036	0.435	0.0071	0.0395	0.856
Time of sample	0.0011	0.0008	0.155	0.0064	0.0085	0.448
Log of basal corticosterone				-0.1365	0.8754	0.876
Observations	175			165		
Marginal R ₂ / Conditional R ₂	0.067 / 0.281			0.117 / 0.340		

Table 2. Influence of distance to treatment on logged basal corticosterone levels and stress response of Chestnut-collared Longspur nestlings in southeastern Alberta, 2016 compared to controls.

<i>Predictors</i>	Log of basal corticosterone			Stress Response		
	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	1.2348	0.2065	<0.001	-4.8436	5.4595	0.375
Experimental Playback	-0.4720	0.2966	0.112	-6.3590	2.9187	0.029
Screwump	-0.3776	0.3303	0.253	-6.8498	3.4185	0.045
Silent Playback	-0.0664	0.3447	0.847	0.2105	3.3490	0.950
Distance	-0.0004	0.0007	0.544	-0.0101	0.0070	0.148
Distance to Experimental Playback	0.0018	0.0011	0.090	0.0253	0.0108	0.019
Distance to Screwump	0.0013	0.0012	0.267	0.0247	0.0124	0.047
Distance to Silent Playback	-0.0003	0.0012	0.808	-0.0078	0.0119	0.512
Age				2.5758	0.6891	<0.001
Observations	180			170		
Marginal R ² / Conditional R ²	0.045 / 0.270			0.186 / 0.324		

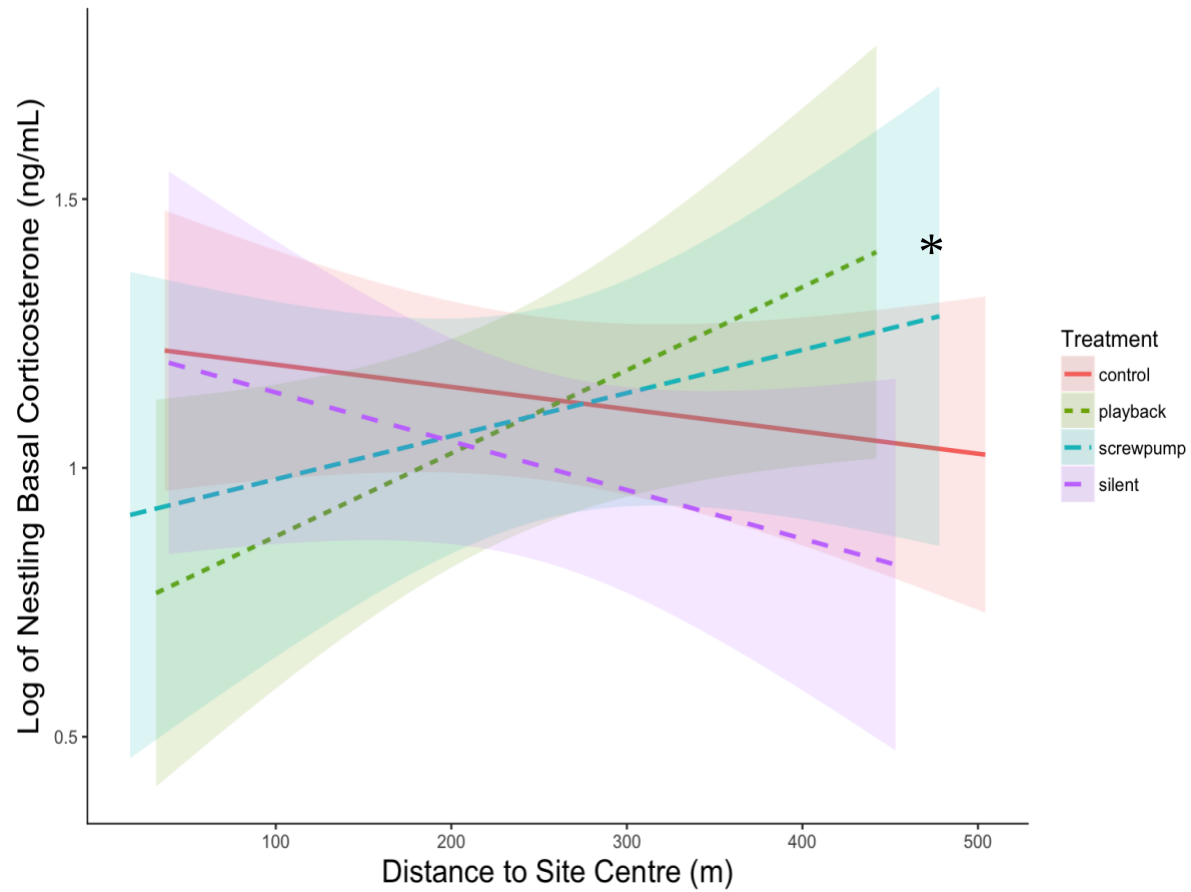


Figure 4. Logged basal corticosterone levels of Chestnut-collared Longspur nestlings relative to the experimental treatment (control, experimental playback, screwpump and silent playback). Statistical significance is denoted by an asterisk (*). Shaded area represents 95% confidence intervals.

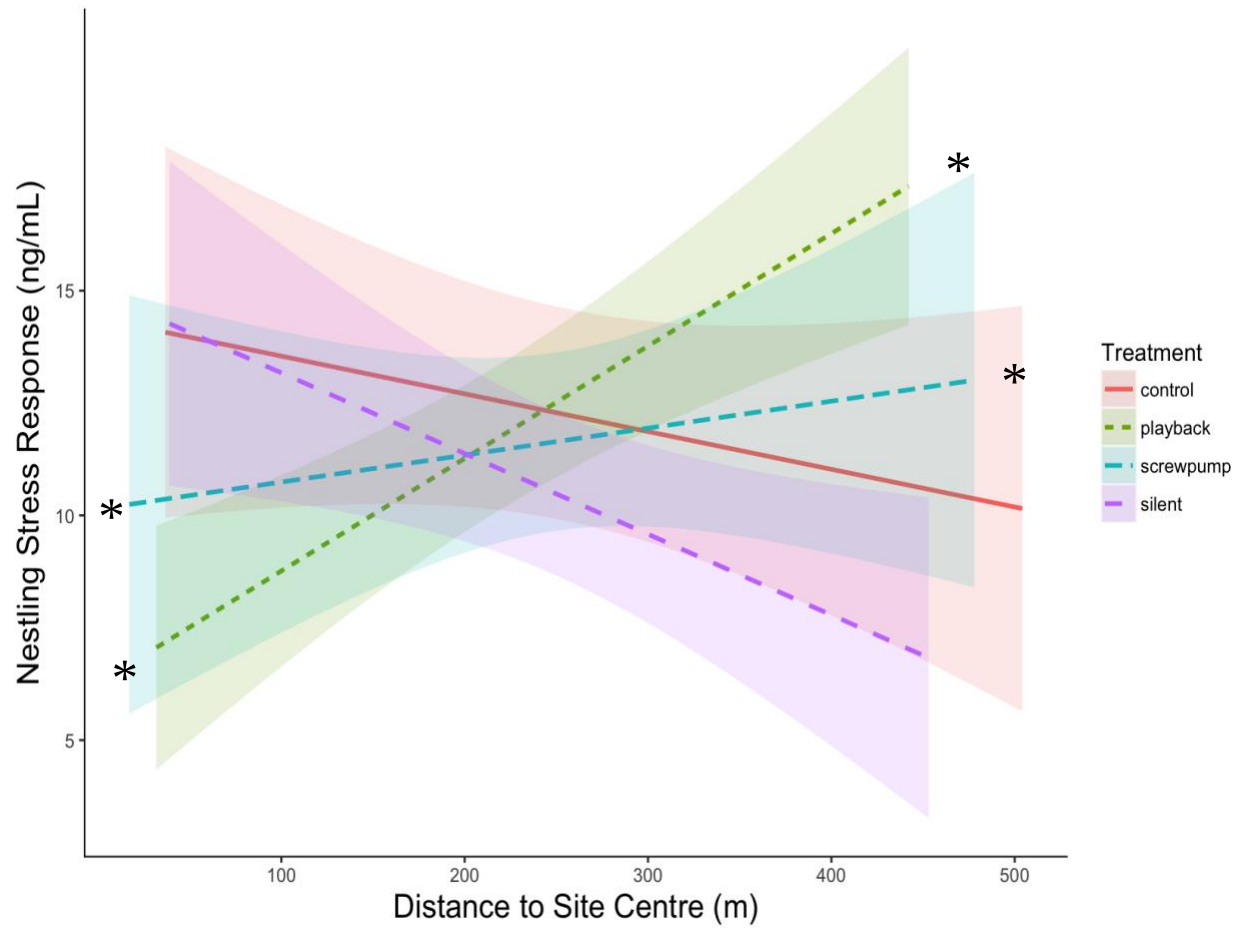


Figure 5. Stress response of Chestnut-collared Longspur nestlings relative to the experimental treatment (control, experimental playback, screwpump and silent playback). Statistical significance is denoted by an asterisk (*). Shaded area represents 95% confidence intervals.

Nestling age significantly predicted mass, while both age and mass predicted p9 length (Table 3). The significant variables were included in all subsequent models where mass or p9 length were the response variables. Neither oil wells or noise had a significant effect on nestling mass or p9 length (Table 4).

Table 3. Influence of diel, seasonal and biological predictor variables on mass and p9 length of Chestnut-collared Longspur nestlings in southeastern Alberta, 2016.

<i>Predictors</i>	Mass			p9		
	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	7.6455	2.2826	0.001	-15.8406	2.6488	<0.001
Age	0.8119	0.2236	<0.001	2.0228	0.2790	<0.001
Sex	0.2728	0.2429	0.261	-0.2495	0.1946	0.200
Brood size	-0.1842	0.2166	0.395	-0.0075	0.2659	0.977
Julian date	0.0002	0.0124	0.986	-0.0019	0.0150	0.899
Time of sample	0.0009	0.0026	0.737			
Mass				1.0109	0.0577	<0.001
Observations	221			221		
Marginal R ₂ / Conditional R ₂	0.142 / 0.468			0.687 / 0.904		

Table 4. Influence of distance to treatment on mass and p9 length on Chestnut-collared Longspur nestlings in southeastern Alberta, 2016, compared to controls.

<i>Predictors</i>	Mass			p9		
	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	7.1668	1.6723	< 0.001	-15.6745	2.2819	< 0.001
Age	0.8318	0.2071	< 0.001	2.0000	0.2814	< 0.001
Experimental playback	1.3679	0.9621	0.155	-2.0236	1.3115	0.123
Screwump	0.0858	1.0765	0.936	-0.5177	1.4614	0.723
Silent playback	0.7453	1.0741	0.488	-0.3815	1.4637	0.794
Distance	-0.0029	0.0024	0.226	-0.0001	0.0032	0.975
Distance to Experimental Playback	-0.0004	0.0036	0.917	0.0043	0.0049	0.380
Distance to screwump	0.0031	0.0040	0.434	0.0014	0.0054	0.795
Distance to silent playback	0.0038	0.0039	0.327	-0.0006	0.0053	0.910
Mass				1.0278	0.0575	< 0.001
Observations	229			229		
Marginal R ₂ / Conditional R ₂	0.209 / 0.475			0.686 / 0.901		

Mediating role of maternal stress on nestling physiology, growth and development

When maternal stress was included in the final model, noise no longer had a significant effect on basal corticosterone (Table 5). This could be due to a mediating effect of maternal corticosterone or the reduction in the sample size with the addition of paired nestling-maternal corticosterone data. However, the considerable change in both the magnitude and the direction of the estimate for experimental noise between the initial treatment model and the maternal mediation model indicates that maternal stress likely mediated the effect of noise on basal corticosterone. To confirm this, I re-ran the initial treatment model (without maternal corticosterone) with the reduced paired nestling-maternal corticosterone data set. I found that the estimate for experimental noise reverted back to the original trend found in the initial treatment model with the full data set. This suggests that there is an impact of noise on nestling basal corticosterone, but it is mediated through maternal corticosterone.

The significant relationship between experimental playback and stress response also disappeared when maternal corticosterone was added to the model. However, unlike the results for basal corticosterone, this is most likely due to a reduction in power as a result of the smaller sample size when maternal corticosterone is included in the model. The direction and magnitude of the estimates for experimental playback and screw pump were the same for both the treatment model and then maternal mediation model (Table 5).

There was no effect of maternal corticosterone on nestling mass, but maternal corticosterone did impact nestling p9 length (Table 6). My results showed a significant, positive correlation between maternal stress response and nestling p9 length (Figure 6).

Table 5. Influence of distance to treatment and maternal stress on logged basal corticosterone and stress response of Chestnut-collard Longspur nestlings in southeastern Alberta, 2016, compared to controls.

<i>Predictors</i>	Log of basal corticosterone			Stress response		
	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	0.9541	0.6377	0.135	8.1092	4.7825	0.090
Maternal basal corticosterone	-0.3039	0.3109	0.328	3.0590	2.4084	0.204
Maternal stress response	0.0137	0.0127	0.279	0.0604	0.0904	0.504
Experimental playback	0.4670	1.0069	0.643	-7.6769	7.6515	0.316
Screwump	0.1911	0.8434	0.821	-7.1056	6.3002	0.259
Silent playback	1.6631	1.3053	0.203	3.6011	9.6743	0.710
Distance	0.0014	0.0028	0.606	-0.0005	0.0210	0.980
Distance to experimental playback	-0.0022	0.0034	0.519	0.0247	0.0260	0.343
Distance to screwump	-0.0009	0.0032	0.776	0.0340	0.0241	0.158
Distance to silent	-0.0061	0.0042	0.153	-0.0217	0.0313	0.487
Observations	80			76		
Marginal R ² / Conditional R ²	0.132 / 0.413			0.240 / 0.270		

Table 6. Influence of distance to treatment and maternal stress on Chestnut-collared Longspur nestling mass and p9 length in southeastern Alberta, 2016, compared to controls.

<i>Predictors</i>	<i>Estimates</i>	Mass		<i>Estimates</i>	p9 length	
		<i>std. Error</i>	<i>p</i>		<i>std. Error</i>	<i>p</i>
(Intercept)	6.5032	4.4093	0.140	-17.2514	4.4202	<0.001
Age	0.4554	0.5248	0.386	2.0648	0.5241	<0.001
Maternal basal corticosterone	-0.2354	0.9164	0.797	-0.4466	0.9046	0.621
Maternal stress response	0.0214	0.0402	0.595	0.1021	0.0405	0.012
Experimental playback	4.4187	3.1089	0.155	-1.1548	3.1121	0.711
Screwump	3.6912	2.6163	0.158	-1.9668	2.6215	0.453
Silent	3.7787	4.0928	0.356	1.8505	4.0774	0.650
Distance	0.0073	0.0084	0.388	-0.0020	0.0084	0.812
Distance to experimental playback	-0.0069	0.0108	0.520	-0.0049	0.0108	0.650
Distance to screwump	-0.0070	0.0098	0.477	0.0069	0.0098	0.482
Distance to silent	-0.0031	0.0131	0.815	-0.0057	0.0131	0.664
Mass				1.1005	0.0841	<0.001
Observations	99			99		
Marginal R ² / Conditional R ²	0.229 / 0.508			0.742 / 0.884		

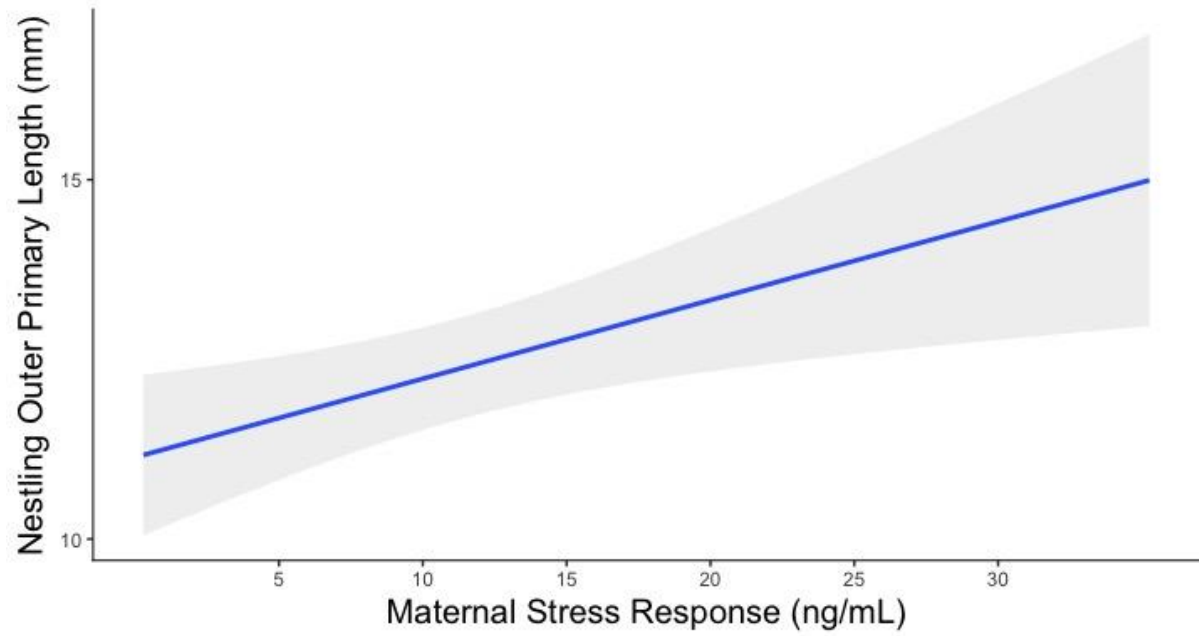


Figure 6. Chestnut-collared Longspur nestling p9 length relative to maternal stress response in southeastern Alberta, 2016.

Effects of corticosterone on nestling growth and development

I also examined whether changes in nestling stress physiology had an effect on nestling growth and development (Table 7). I found that as basal corticosterone increased, mass decreased (Figure 6). Similarly, older nestlings that responded more strongly to novel stressors were lighter (Figure 3). I found no effect of corticosterone on p9 length.

Table 7. Influence of Chestnut-collared Longspur nestling corticosterone levels on nestling mass and p9 length in southeastern Alberta, 2016.

<i>Predictors</i>	<i>Estimates</i>	Mass		<i>Estimates</i>	p9 length	
		<i>std. Error</i>	<i>p</i>		<i>std. Error</i>	<i>p</i>
(Intercept)	8.1498	1.6124	< 0.001	-16.9148	2.0594	< 0.001
Age	0.8361	0.2154	< 0.001	2.1073	0.2687	< 0.001
Log of basal corticosterone	-0.5572	0.2251	0.013	-0.0244	0.2065	0.906
Stress response	-0.0066	0.0207	0.749	0.0223	0.0183	0.224
Mass				1.0034	0.0724	< 0.001
Observations	165			170		
Marginal R ² / Conditional R ²	0.140 / 0.499			0.680 / 0.900		

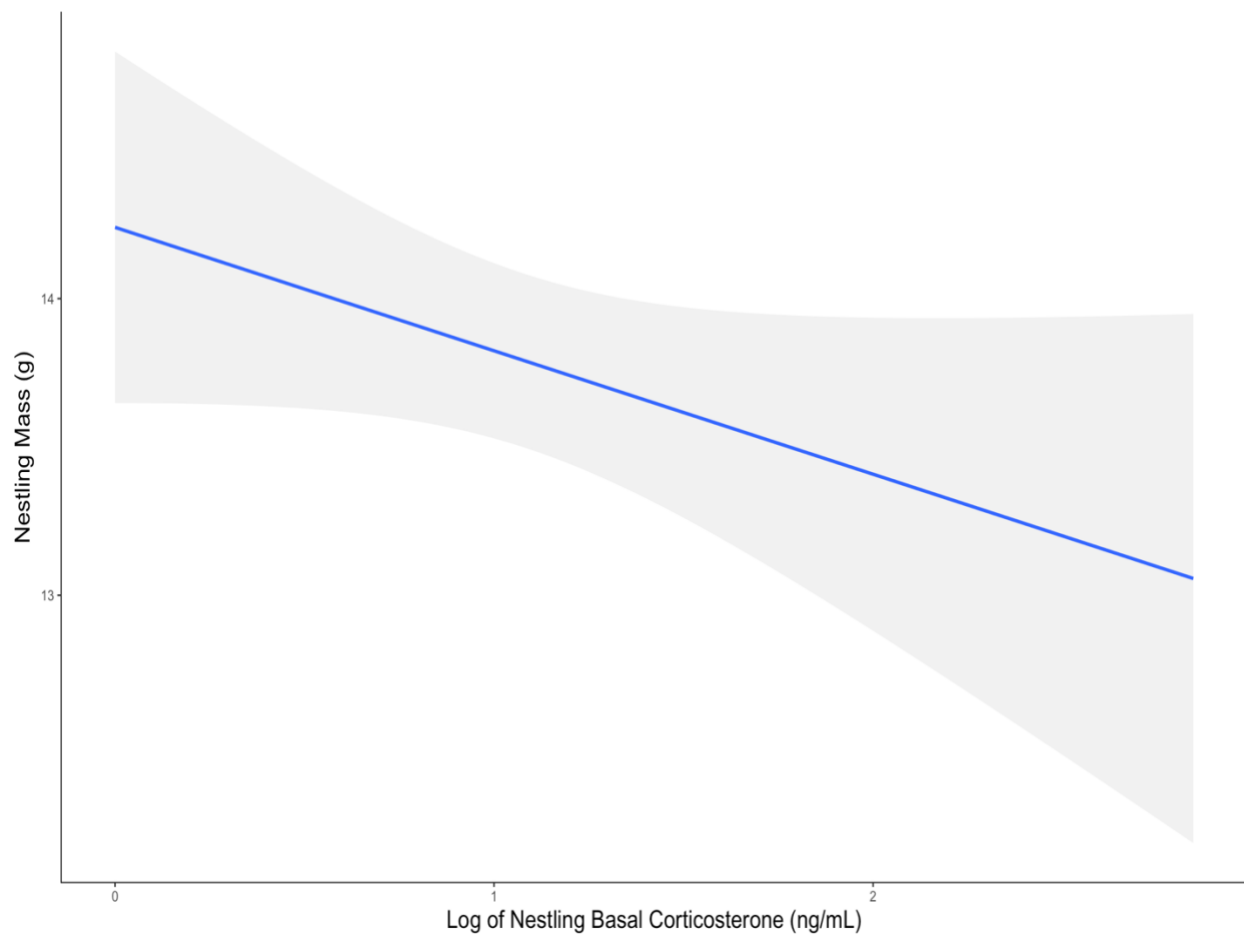


Figure 7. Chestnut-collared Longspur nestling mass relative to log of nestling basal corticosterone in southeastern Alberta, 2016.

Discussion

Nestling Chestnut-collared Longspur corticosterone levels were lower near screw pumps and near playback screw pump noise. This indicates that exposure to noise during development can impact stress physiology, highlighting the importance of separating noise from the confounding effects of infrastructure. Contrary to my predictions, nestling basal corticosterone and stress response were both decreased in the presence of noise. Across all sites nestlings with lower corticosterone were heavier, suggesting that nestlings living in close proximity to oil wells might benefit from living in noisy environments. My results also indicated that maternal stress does mediate the effect of noise on nestling basal corticosterone. Nestling growth and development were unaffected by noise.

There are four possible hypotheses that could explain the down-regulated HPA-axis activity that I observed in this study: 1) hypocorticism, 2) delayed development of the HPA-axis, 3) acoustic masking of stressful stimuli near noise, and 4) maternal mediation. Understanding which of these is most likely to explain the observed patterns is critical for interpreting my results, as research has indicated that there is no consensus regarding the endocrine profile in response to stress, and dysregulation of corticosterone levels are context-dependent (Dickens and Romero 2013).

Decreased basal corticosterone and an attenuated stress response in anthropogenically altered habitats have often been attributed to hypocorticism (e.g. Kleist et al. 2018), a term referring to when individuals are no longer able to secrete glucocorticoids in response to a chronic stressor (Raison and Miller 2003, Fries et al. 2005). Individuals living in sub-optimal habitats may experience increased ‘wear and tear’ as they work harder to meet their energetic demands and maintain homeostasis (Romero et al. 2009). When an individual experiences

prolonged exposure to a stressor, the sustained release of corticosterone may eventually reach a tipping point where that individual is no longer able to cope and the physiological mediator itself begins to have detrimental effects (Busch and Hayward 2009, Romero et al. 2009). After an individual surpasses the tipping point, the physiological mediator can no longer be sustained, and the HPA-axis is down-regulated (Busch and Hayward 2009). However, hypocorticism is a fairly serious indicator of physiological stress, and cannot be assumed based only on decreases in circulating corticosterone levels. Individuals that are experiencing hypocorticism typically show some form of reduced body condition or fitness measure (Rich and Romero 2005, Cyr and Romero 2007). For example, adult European Starlings (*Sturnus vulgaris*) exposed to randomized stressful stimuli (predator decoys and calls, loud radios) for 8 days exhibited both lower basal corticosterone levels compared to controls and reduced reproductive success (Cyr and Romero 2007). Cyr and Romero (2007) propose that females were able to avoid the negative physical consequences typically associated with chronic stress by diverting energy from parental care to self-maintenance. Re-allocating energy under chronic stress may be more challenging for altricial nestlings, which have limited mobility, are reliant on parental care, and, compared to adults, are limited in their range of behavioral responses (Lima 2009). In a similar study to mine, Kleist et al. (2018) found that nestling basal corticosterone was reduced near anthropogenic noise from natural gas compressor stations. Unlike my observations, the authors also found that nestling feather growth and mass were negatively affected by noise, indicating that nestlings were experiencing hypocorticism (Kleist et al. 2018). In contrast, it is unlikely that hypocorticism explains the down-regulated HPA-axis activity observed in my study. I did not find any evidence to indicate that nestlings were suffering from chronic stress, as both nestling mass and p9 length were not affected by noise or infrastructure. In fact, I found that nestlings

with lower basal corticosterone levels were heavier, suggesting that low corticosterone levels and stress responses were associated with higher quality nestlings (Naef-Dantzer et al. 2001) rather than lower quality, as required to support a hypothesis of hypocorticism. Kleist's study focused on noise from compressor stations, which is typically louder than noise from generator-powered screw pumps (Koper et al. 2015). Their study also used tree cavity nesters as model species, which have a longer nestling period than Chestnut-collared Longspurs (Martin and Li 1992). The longer period of exposure to a potentially more extreme stressor may explain the chronic stress documented in their study compared to mine. Regardless, my results are not consistent with the hypocorticism hypothesis as nestlings with low basal corticosterone were of better quality.

Alternatively, the second hypothesis that could explain the attenuated basal corticosterone levels and stress response is that this pattern results from a delay in the development of the HPA-axis. Crino et al. (2013) found that mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) nestlings exposed to experimentally elevated traffic noise had a lower stress response but were in better body condition than controls. The authors propose that noise could indirectly affect nestlings by delaying the development of the HPA-axis, though the mechanisms by which this may occur are poorly understood (Crino et al. 2013). However, this is unlikely to explain the dampened HPA-axis activity I observed, as our results documented an increase in the capacity of Chestnut-collared Longspur nestlings to respond to a novel stressor throughout the nestling period. To validate this, I ran a linear mixed model with stress response as the response variable and an interaction with age and treatment as the predictor variables. I found that stress response did not differ with treatment as nestlings aged suggesting that oil infrastructure and noise did not delay the development of the HPA axis.

While neither of the first two hypotheses can explain the patterns I observed, the remaining two are both possible and could occur concurrently. The third hypothesis that could explain my results is that noise impairs the ability of nestlings to detect stressful stimuli, such as acoustic warnings, and therefore in comparison to controls, nestlings living in noisy environments may not be able to accurately perceive the true risk of predation (Leonard and Horn 2012, McIntyre et al. 2014, Templeton et al. 2016). In adults, anthropogenic noise has been associated with higher perceived predation risk, demonstrated by a shift in behaviour from foraging to increased vigilance in the presence of noise (Quinn et al. 2006). However, it is possible that nestlings living in noisy environments are unable to perceive acoustic signals that provide a warning of potential predators and as a result are less fearful than nestlings living farther from noise. McIntyre et al. (2014) demonstrated that in the presence of noise, nestlings failed to respond appropriately to parental alarm calls and instead continued to beg, suggesting that noise may mask parental alarm calls. Additionally, in a study by Tilgar et al. (2010), Pied Flycatcher (*Ficedula hypoleuca*) nestlings repeatedly exposed to an acoustic warning (nestling distress calls) had higher levels of basal corticosterone than controls, indicating that elevated perceived risk of predation can increase corticosterone levels. Very few studies have directly explored the impacts of perceived predation risk on stress physiology and no studies that I could find have done so in the presence of noise. However, the implications of this hypothesis are important as it suggests that rather than increasing corticosterone levels and the associated negative fitness consequences of their sustained release, noise might have an unexpected positive impact on long-term health.

The fourth hypothesis that could explain the down-regulated HPA-axis activity observed in this study is maternal mediation. Nestlings closer to noise exhibited lower basal

corticosterone. However, my results suggest that this could be an indirect result of noise impacting maternal stress, which in turn impacted nestling basal corticosterone. During laying, offspring can be exposed to the environmental stressors that their mothers face, through the deposition of maternal glucocorticoids in yolk (Hayward and Wingfield 2004, Love et al. 2005). A few studies have suggested that pre-natal maternal stress can be adaptive and may act as a signal, preparing offspring for development in sub-optimal habitat and matching offspring physiology to maternal ability (Gluckman and Hanson 2004, Love and Williams 2008, Tilgar et al. 2016). For example, Tilgar et al. (2016) found that higher embryonic corticosterone resulted in lower basal corticosterone during the nestling period and nestlings raised in resource poor habitats grew more rapidly than controls. Exposure to elevated yolk corticosterone may provide a predictive signal to offspring to down-regulate the HPA-axis activity, which can protect nestlings from the negative effects associated with sustained release of corticosterone during development (Kitaysky et al. 2001, Love and Williams 2008). Additionally, post-natal changes in parental care (i.e. provisioning or nest attendance) can influence nestling corticosterone levels (Rensel et al. 2010, Davis and Guinan 2014). Previous studies from southeastern Alberta have shown that adult Chestnut-collared Longspurs reduce parental care in the presence of infrastructure, however reductions in care are typically associated with elevated corticosterone levels in offspring (Rensel et al. 2010, Davis and Guinan 2014, Lynn and Kern 2014, Ng et al. 2019). In my study system female Chestnut-collared Longspurs had elevated levels of basal corticosterone closer to experimental playback (Des Brisay 2018) therefore, it is possible that stressed mothers send a prenatal hormonal signal to embryos to adjust physiology during the nestling period to match the sub-optimal habitat or reduced ability to provide parental care in disturbed environments.

My results also demonstrated that mothers that responded more strongly to a novel stressor were correlated with nestlings that had a longer p9, providing additional support for the maternal mediation hypothesis. Research shows that stressed mothers can provide a warning to nestlings that speeds up development in uncertain environments (Chin et al. 2009, Coslovsky and Richner 2011). A study by Jones et al. (2017) demonstrated that Dickcissel fledglings (*Spiza americana*) with more advanced wing development were less likely to be preyed upon. The movement of fledglings, tracked using radio-telemetry, showed that those individuals with more advanced wing development were more mobile and, therefore, potentially able to avoid predators more easily (Jones et al. 2017). This result, in combination with the results on nestling physiology, suggests that Chestnut-collared Longspur maternal stress plays a role in shaping offspring phenotype and development.

Costs and benefits of down-regulated HPA-axis activity

Many studies have outlined the deleterious consequences of elevated corticosterone during development (see Schoech et al. 2011 for review). In my study, Chestnut-collared Longspur nestlings with elevated basal corticosterone levels were correlated with lighter mass, while older, lighter nestlings were correlated with a stronger stress response. Together, these results suggest that elevated levels of corticosterone may have consequences on the development of nestlings. While I could not test for lifetime fitness of Chestnut-collared Longspurs, it generally supports the underlying theoretical framework of the corticosterone-fitness hypothesis: individuals with elevated corticosterone levels are in poor condition (Bonier et al. 2009a). However, it should be noted that some studies have demonstrated that after the removal of a chronic stressor during development, nestlings were able to partially or fully compensate for the

delay in growth (Schmidt et al. 2012, Crino et al. 2014), though this too may carry a cost later in life (Metcalf and Monaghan 2003).

Chestnut-collared Longspur nestlings living closer to noise exhibited lower basal corticosterone levels. As basal corticosterone reflects daily energetic demands (McEwen and Wingfield 2003), low basal corticosterone levels (correlated with higher mass) suggest that nestlings closer to noise may enjoy some kind of advantage over nestlings living farther from noise, at least during the nestling period. In another study conducted in southeastern Alberta, Chestnut-collared Longspurs had significantly increased body condition in the presence of noise, providing additional support for this hypothesis (Rosa 2019). The nestling stress response was also lower in close proximity to noise. A dampened stress response could prove to be adaptive if noise is perceived as a stressor, as chronic stimulation of the HPA-axis can have negative impacts on growth and development (Sapolsky et al. 2000, Kitaysky et al. 2003, McEwen and Wingfield 2003). Thus, in low quality environments down-regulated HPA-axis activity could benefit nestlings since consistently elevated corticosterone results in the mobilization of energy and depletion of stored glucose (McEwen and Wingfield 2003). Blas et al. (2007) demonstrated that individuals with lower stress responses earlier in life had greater reproductive success and survival, indicating that a dampened stress response may improve life-long fitness.

However, a dampened stress response could be maladaptive if nestlings are poorly prepared for the environment they are born into. For example, some studies have associated a higher stress response with neophobic behaviours (Fraisse and Cockrem 2006, Baugh et al. 2017). A heightened stress response may promote behaviour that facilitates predator detection and evasion, and therefore in a predator-dense environment where increased fear and vigilance may prepare individuals for a quick escape, a dampened stress response could reduce fitness

(Fraisie and Cockrem 2006, Cockrem 2013, Sheriff and Love 2013, Baugh et al. 2017). This would be consistent with other research in my study area that suggests that in the presence of anthropogenic disturbance and noise, Chestnut-collared Longspurs struggle to accurately perceive habitat quality and may select and settle in unsuitable habitat (Des Brisay 2018, Rosa 2019). Des Brisay (2018) found that older, heavier females preferentially selected habitat close to oil wells, but at a cost. Females found close to experimental playback exhibited elevated basal corticosterone levels. Conversely, Rosa (2019) found that Chestnut-collared Longspurs avoided experimental noise despite increases in productivity (larger clutch sizes, increased nestling body condition) with proximity to noise. Together, these results suggest that female Chestnut-collared Longspurs experience a personal cost (elevated basal corticosterone) but their overall fitness (measured as reproductive success, nestling clutch size and body condition) is not negatively impacted in the presence of anthropogenic noise. Researchers from southeastern Alberta have demonstrated that nest depredation of co-occurring grassland songbirds was higher at oil wells and compressor stations, however, female Chestnut-collared Longspurs seem able to compensate for the increased risk of predation by reducing parental care (Bernath-Plaisted and Koper 2016, Ng et al. 2019). This would suggest that there may be fewer costs associated with a dampened stress response in nestling Chestnut-collared Longspurs during the nestling period though those costs may still be experienced during future life history stages, such as the fledgling period. The interpretation of glucocorticoids is extremely complex and context-dependent. In the face of disturbance, disruptions to the normal functioning of the HPA-axis could be adaptive or maladaptive. In order to determine population level effects, measurements of long-term fitness are necessary (Love et al. 2013). Future research should examine the survival of Chestnut-collared Longspurs fledglings to provide additional context for the results of this study.

Management Implications

Mitigating the Effects of Energy Development

Oil and gas development on the prairies can negatively impact grassland songbirds through a variety of different mechanisms including edge effects, changes to predator-prey interactions, and anthropogenic noise (Barber et al. 2010, Sliwinski and Koper 2012, Hethcoat and Chalfoun 2015). As energy development in Canada continues to expand the associated network of roads, pipelines and powerlines further fragments the landscape and reduces the remaining suitable habitat available (Copeland et al. 2011). In an effort to reduce the overall footprint of oil and gas wells, inactive wells and their associated roads should be decommissioned and re-seeded with a native seed mix. As many other studies have suggested, concentrating above-ground infrastructure and using horizontal drilling to create new wells would reduce both the physical and the acoustic footprint of oil and gas on the landscape (Allred et al. 2015, Thompson et al. 2015, Rosa 2019).

The effects of anthropogenic noise on species are difficult to determine as noise is often associated with other factors such as habitat loss and visual disturbance (Shannon et al. 2016). My results highlight the importance of landscape-scale experimental studies that isolate noise from their source in order to identify the mechanisms that can influence behaviour and physiology. However, many studies have shown that the impacts of oil and gas development are species-specific (Bernath-Plaisted et al. 2017, Rosa 2019). To maximize the effects of mitigation strategies within grassland ecosystems mitigations should target multiple species rather than individual ones. Though my study did not identify noise as a significant stressor to Chestnut-collared Longspurs, other studies in this region have (Des Brisay 2018, Rosa 2019). Therefore, mitigations should address noise as well. Sound barriers may be one tool employed to reduce the

attenuation of noise on the prairies (Francis et al. 2011), though the impacts of this mitigation technique should be investigated prior to widespread use.

Corticosterone as a Management Tool

Over the past few decades glucocorticoids have become a popular tool amongst ecologists as a way to measure the cumulative effects of non-lethal disturbance on individuals. Glucocorticoids can provide a rapid assessment of the impacts of anthropogenic disturbance on individual quality and ultimately fitness, which would otherwise be done through long-term population monitoring (Busch and Hayward 2009, Fefferman and Romero 2013). This provides conservation biologists with a means to identify populations that may be more susceptible to disturbance before the population begins to experience significant declines (Wingfield et al. 1997). However, interpretation of corticosterone is complicated and should be done with caution as the results are species specific and context dependent (Dantzer et al. 2014). Within-species variation in sex, age, breeding status and developmental stage will also affect corticosterone (Dantzer et al. 2014). Research has demonstrated that corticosterone will change depending on life-history stage to provide an adaptive response to meet energetic demands (Bonier et al. 2009b, Madliger and Love 2016). Thus, it is extremely important that the relationship between corticosterone and lifetime fitness be investigated prior to use as a conservation monitoring tool (Madliger and Love 2016).

Glucocorticoids can be measured from a number of sources including plasma, saliva, feces, hair and feathers (Sheriff et al. 2011). Instantaneous measures of corticosterone (i.e. plasms and saliva) provide a snapshot of the physiological state of an organism at any given moment (Sheriff et al. 2011). The downfall of this is that corticosterone levels in the blood are susceptible to that individual's immediate prior experience (i.e. weather events, predator

exposure), which researchers might be unaware of at the time of sampling. Alternatively, integrated measure of corticosterone (i.e. feathers, hair and feces) reflect the average circulating blood corticosterone that individuals have secreted, metabolized or excreted over a specific period of time (Sheriff et al. 2011, Dantzer et al. 2014). While this mode of sampling may be less invasive, there are still some methodological concerns with this measure of stress (Dantzer et al. 2014).

Glucocorticoids are a promising tool that could be used to rapidly assess at-risk populations prior to their decline. However, without context glucocorticoids can be effectively meaningless. Studies have shown that there is no consensus endocrine profile meaning that the results from one study cannot be easily extrapolated to other species or even other stressors (Bonier et al. 2009a, Dickens and Romero 2013). Land managers and biologists considering using glucocorticoids as a tool to assess the health of wild populations must first make the connection between changes in glucocorticoid regulation and lifetime fitness.

Conclusions

This study demonstrates that nestling Chestnut-collared Longspur stress physiology is altered in the presence of noise, highlighting the importance of large-scale experimental playback studies to determine mechanisms that might be affecting sensitive populations. Nestling basal corticosterone and stress response were lower with proximity to noise-emitting infrastructure. While noise did not directly impact nestling physiology growth and development, maternal stress response was correlated with nestling p9 length and lower basal corticosterone levels with greater mass. These results suggest that nestlings living closer to noise may be in better condition, perhaps due to mediating effects of mothers. However, if Chestnut-collared Longspurs are not able to appropriately perceive habitat quality in disturbed or noisy

environments as demonstrated in other studies (Des Brisay 2018, Rosa 2019), there may be future trade-offs that compromise survival and/or fitness. Future studies should investigate the long-term effects of noise on the fitness of Chestnut-collared Longspurs in order to further contextualize these results and validate the use of corticosterone as a tool to measure non-lethal effects of disturbance.

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