

**Proximity to Conventional Oil and Gas Development is Associated with Reduced Parental
Care in Chestnut-collared Longspurs (*Calcarius ornatus*)**

by
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ABSTRACT

Anthropogenic disturbances such as energy extraction may affect how songbirds perceive and respond to risk during the breeding season. I examined how the incubation and parental behaviours of the chestnut-collared longspur (*Calcarius ornatus*), a threatened grassland songbird, changed with proximity to conventional oil wells and compressor stations and with proximity to roads. I also evaluated any effects of industrial noise by comparing responses of active wells to inactive wells and control sites. Longspurs consistently reduced parental care in the presence of all three factors of energy extraction, though males and females were sensitive to different factors. Females consistently altered behaviours when nesting near roads, while males were sensitive to industrial noise. Fewer offspring successfully fledged at nests near roads and these offspring fledged at a later age, possibly as a result of decreased female provisioning. The effects of noise on behaviour differed from the effects of oil wells and compressor stations, indicating that inactive infrastructure still poses a disturbance on the landscape. These findings suggest that energy development in the grasslands increases perceived risk and influences songbirds' reproductive strategies, likely with consequences for reproductive fitness. Effective mitigation measures must address all three related disturbances of physical infrastructure, roads, and noise to be successful.

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CHAPTER 1: INTRODUCTION

1.1 Background

Grassland songbirds have experienced greater and more consistent population declines than birds of any other North American biome over the past several decades (Knopf 1994; Peterjohn and Sauer 1999; Sauer et al. 2014). This decline is largely due to the destruction and degradation of the prairie habitats where they breed in the spring and summer (Samson and Knopf 1994). Among the species in decline is the chestnut-collared longspur (*Calcarius ornatus*; hereafter “longspurs”), which is listed as threatened in Canada (Peterjohn and Sauer 1999; Sauer et al. 2014; COSEWIC 2015). This ground-nesting passerine breeds in the mixed- and short-grass prairies, and its reliance on native grassland habitat means it is sensitive to ongoing disturbance and fragmentation and destruction of the prairies (Bleho et al. 2015; COSEWIC 2015).

Energy extraction is a major industry in the Great Plains of North America, with over 2.5 million hectares occupied by oil and gas development across rangeland and cropland (Allred et al. 2015). In the prairies of central Canada, oil wells are especially dense in Alberta (Schneider et al. 2003; Askins et al. 2007; Copeland et al. 2011). Oil and natural gas development is associated with abundant infrastructure, noise, human presence, roads, and exotic vegetation (Askins et al. 2007; Copeland et al. 2011; Nasen et al. 2011). Research into the effects of the oil and gas industry on grassland-obligate songbird abundance and reproductive success is increasing, and the results have generally indicated a negative impact of development on abundance and reproductive fitness (e.g. Linnen 2008; Dale et al. 2009; Hethcoat and Chalfoun 2015).

The effects of anthropogenic disturbance on songbird reproductive behaviour are less well understood. Birds balance their current reproductive fitness with their survival and future

fitness, and variables such as predation risk, anthropogenic disturbances, and habitat quality may, thus, influence reproductive behaviour and output (e.g. Conway and Martin 2000; Mazumdar and Kumar 2014; Niederhauser and Bowman 2014). Quantifying changes in behaviour at nests allows us to see how birds adjust their reproductive strategies in response to disturbance by using trade-offs; for instance, a reduction in parental care under perceived high predation risk may be due to reducing current reproductive fitness in favour of future fitness (Niederhauser and Bowman 2014). We can infer changes in longspur reproductive strategy by quantifying changes in behaviour at nests near to oil and gas infrastructure, roads, and industrial noise. Technological advances in recent years, such as the increasingly accessible use of surveillance cameras to monitor nests (Pietz and Granfors 2012), allow us study nonlethal changes in parental behaviour. This information would contribute to our knowledge of the proximate and nonlethal effects of oil and gas development. As nonlethal effects may signal long-term trends for population health (Cresswell 2008), studying the nonlethal effects of energy development will allow us to make more informed long-term management decisions for this threatened prairie obligate.

1.2 Purpose and objectives

The purpose of this study was to determine whether incubation and parental behaviours of chestnut-collared longspurs at nests are affected by oil and gas infrastructure, roads, and industrial noise in southeastern Alberta. Specifically, I examined whether the quality of parental care was impacted by focusing on the duration parents spent at the nest and the frequency of nest visits and provisioning at sites with and without industrial noise. Additionally, I examined whether fledging age was affected by energy development.

To meet these objectives I:

- 1) Video-recorded parental activity at chestnut-collared longspur nests during both incubation and nestling stages and
- 2) Analyzed nest footage to quantify the duration and frequency of key parental behaviours, including incubation, mate provisioning, brooding and shading, and nestling provisioning.

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CHAPTER 2: LITERATURE REVIEW

2.1 Grassland songbird decline

North American grassland songbirds have been in consistent decline since the beginning of the Breeding Bird Survey in 1966, with all 16 grassland obligates experiencing significant declines (Peterjohn and Sauer 1999; Sauer et al. 2013; Sauer et al. 2014). As a group, obligate grassland species have declined 37.8% from 1968 – 2011 (Sauer et al. 2013). This decline corresponds with the widespread loss and degradation of the prairies, which are among the most threatened of North American ecosystems (Samson and Knopf 1994; Noss 1995). Mixed-grass prairies, though spared the extreme losses experienced by tall-grass prairies, only cover approximately 28% of their original area (Samson et al. 2004). Over the last several centuries, remaining grasslands have been subject to the removal of native grazers, a shift from free-range to pasture-based grazing, suppression of fires, encroachment by woody plants, invasions by non-native plants, and drainage (Knopf 1994). Grasslands today continue to be converted to croplands across the Northern Great Plains, removing vital habitat for grasslands birds (Gage et al. 2016).

2.2 Oil and gas extraction in the grasslands

Oil and gas extraction has been a major industry in central Canada for the last several decades (Schneider et al. 2003, see Fig. 2.1, p.11 in Copeland et al. 2011). The Western Canadian Sedimentary Basin encompasses the majority of Alberta, and has been developed since the 1950s (Schneider et al. 2003). Alberta contains one of the largest crude oil reserves in the world, and the oil and gas industry in Alberta continues to expand; between 2003 and 2013, Alberta's oil and gas industry nearly tripled (Government of Alberta 2016). In 2011, 5.8% of the grasslands in western North America were affected by active oil and gas leases (Copeland et al. 2011); including both active and inactive leases, a total of 13% of the grasslands were affected

by oil and gas leases (Copeland et al. 2011). Extraction of oil and gas is associated with a potentially expansive network of infrastructure, including well pads, and linear features such as access roads and pipelines, which remove and degrade habitat (Copeland et al. 2011). Additionally, energy extraction is associated with ambient industrial noise (see Koper et al. 2015), and roads and leases are associated with invasive and non-native vegetation (Sutter et al. 2000; Nasen et al. 2011).

2.3 Effects of oil and gas extraction on birds

There are several demonstrated effects of oil and gas development on bird abundance and reproductive success, though results have sometimes been inconsistent among studies from different areas. In southeastern Alberta, where my study took place, nesting success, defined as the proportion of nests that fledged at least one offspring, was lower in grassland songbirds at infrastructure sites compared to controls, and lower at grid-powered oil wells compared to generator-powered (Bernath-Plaisted and Koper 2016). Two species of grassland obligates, Baird's sparrows (*Ammodramus bairdii*) and Sprague's pipits (*Anthus spragueii*), showed reduced abundance at infrastructure sites and with proximity to infrastructure (Nenninger 2016). Baird's sparrows and Sprague's pipits also had reduced abundance near roads but chestnut-collared longspurs (*Calcarius ornatus*) showed increased abundance with proximity to roads (Nenninger 2016). There was no difference in nest success or abundance between active and inactive infrastructure sites in southeastern Alberta (Bernath-Plaisted and Koper 2016; Nenninger 2016). In other studies, prairie obligate songbird species, including chestnut-collared longspurs, Baird's sparrows, and Sprague's pipits, avoided oil wells by up to several hundred metres (Linnen 2008; Thompson et al. 2015). Greater sage-grouse (*Centrocercus urophasianus*)

avoid nesting in areas with high density of oil wells, and experienced higher offspring mortality when in oil well-dense areas (Aldridge and Boyce 2007).

Oil and gas development presents multifaceted disturbances to grassland songbirds, combining effects of physical infrastructure, anthropogenic noise, fragmentation and edge effects caused by roads, human disturbance, and increased prevalence of exotic vegetation (Ingelfinger and Anderson 2004; Aldridge and Boyce 2007; Askins et al. 2007; Linnen 2008; Dale et al. 2009; Nasen et al. 2011). The presence of large infrastructure and associated power lines breaks up the horizon and provides perches and possibly nesting sites for avian nest predators such as common ravens (*Corvus corax*) and raptors, possibly leading to higher abundances and more nest depredation (Ingelfinger and Anderson 2004; Aldridge and Boyce 2007; Benítez-López et al. 2010). Higher amounts of linear perch such as transmission lines and fences were associated with reduced Baird's sparrow and Sprague's pipit abundance in this region, and Baird's sparrows and chestnut-collared longspurs were less abundant near to perches (Nenninger 2016). One study found that rodents, which are common nest predators of grassland songbirds, increased in abundance with energy infrastructure-caused habitat loss (Hethcoat and Chalfoun 2015).

Anthropogenic noise may interfere with intraspecific communication or serve as a distraction, resulting in lower reproductive success and lower abundances near noisy infrastructure or traffic (Bayne et al. 2008; Schroeder et al. 2012; Ware et al. 2015). High levels of ambient noise may also interfere with the antipredator response of breeding songbirds (Antze 2016). However, recent studies from this region have found that nest success and abundance are more impacted by the presence of infrastructure than industrial noise (Bernath-Plaisted and Koper 2016; Nenninger 2016).

Roads and anthropogenic edges represent another potential form of disturbance to grassland birds. In Saskatchewan, chestnut-collared longspurs, Sprague's pipits, and Baird's sparrows, all grassland obligates, were significantly less abundant near large roads compared to two-track trails (Sutter et al. 2000), and in North Dakota, grassland songbirds, as a whole, avoided secondary gravel roads, such as access roads (Thompson et al. 2015). Sagebrush songbirds showed reduced abundance within 100 m of even very lightly-travelled roads (<12 cars per day) and sagebrush sparrows (*Artemisiospiza nevadensis*) showed reduced density along natural gas pipelines that featured surface disturbance but no traffic (Ingelfinger and Anderson 2004). Sprague's pipits avoided two-track trails (Dale et al. 2009).

Exotic vegetation, such as crested wheatgrass (*Agropyron cristatum*), is commonly associated with oil infrastructure as it was used to reseed pipelines and well footprints until the 1980s and has since aggressively spread from the original plantings (Dale et al. 2009). Chestnut-collared longspurs nests are less successful when in pastures of crested wheatgrass (Lloyd and Martin 2005; see section 2.8). Sprague's pipits avoided crested wheatgrass (Dale et al. 2009). Separately and in combination, these disturbances associated with oil and gas development contribute to a range of negative responses in birds.

2.4 History of grassland nest video surveillance

Monitoring songbird nests in the grasslands is difficult as the open environment prohibits the use of conspicuous, bulky cameras and the dense vegetation around the cryptic nests requires a camera to be positioned very near the nest (Pietz and Granfors 2000; Pietz et al. 2012a). Since 1996, video surveillance systems have been successfully used to monitor grassland nest activity, though many of the initial studies focused on identifying nest fate and nest predators (Pietz and Granfors 2000; Pietz et al. 2012a). More recently, video surveillance has been used to quantify

information on incubation, parental, and even nestling behaviour of grassland songbirds, such as incubation rhythm and provisioning rate (Adler and Ritchison 2011; Davis and Holmes 2012; Kirkham and Davis 2013). Nest footage has already added to the information available on chestnut-collared longspur incubation behaviour, including hatching and fledging times and lengths, the confirmation that males will briefly shield eggs in the absence of the female, and disproving the assumption that males did not provision for incubating females (Wyckoff 1983; Pietz et al. 2012b; Kirkham and Davis 2013; Bleho et al. 2015).

Although researchers are now able to quantify the basic behavioural patterns of reproductive birds more easily and thoroughly than ever, we still know very little about what these patterns mean for reproductive fitness and how they vary across populations. Often information is only available for a specific population and cannot necessarily be extrapolated to the species as whole; for instance, the only video study on incubation or parental chestnut-collared longspur behaviour was based out of a community pasture in Saskatchewan (Kirkham and Davis 2013). Studies linking behavioural patterns to actual risk are inconsistent. For example, one study on Brewer's sparrows (*Spizella breweri*) found that there was no initial difference in behaviour between pairs that had successful first clutches and those that lost theirs to nest predation (Chalfoun and Martin 2010), contrary to other studies that found correlations between parental activity and nest success (e.g. Martin et al. 2000). Very little is known about what effects anthropogenic disturbances have on breeding behaviour, and what the consequences of these changes are. Many of the few existing studies have focused on anthropogenic noise (e.g. Schroeder et al. 2012; McIntyre et al. 2014; Meillère et al. 2015), and to my knowledge, none have focused on grassland songbirds. Considerably more research is needed to identify how

behavioural patterns change with disturbances, and what these changes mean to reproductive fitness.

2.5 Incubation and parental behaviour

Behaviour of reproductive birds is often a balance of trade-offs between current reproductive fitness and self-preservation for future fitness (Conway and Martin 2000; Kirkham and Davis 2013). We can gain insights into the reproductive strategies of parental birds by quantifying and comparing their behaviour. For instance, experimentally inflated predation risk is linked to reduced parental care or reduced male mate provisioning in a variety of songbird species, including two species of nuthatches (*Sitta carolinensis* and *S. canadensis*; Ghalambor and Martin 2000), pied flycatchers (*Ficedula hypoleuca*; Tilgar et al. 2010), common blackbirds (*Turdus merula*; Bonnington et al. 2013), and Florida scrub jays (*Aphelocoma coerulescens*; Niederhauser and Bowman 2014). This reduction in parental care is hypothesized to be the result of trade-offs in reducing the current reproductive effort to increase adult survivorship, especially when the danger is from predators of adults versus those of nests. Also, during the incubation stage, birds nesting in areas of perceived higher risk often reduce the activity around the nest by minimizing the number of trips they take to and from the nest (Conway and Martin 2000; Ghalambor and Martin 2000; Mazumdar and Kumar 2014). During the nestling stage, competing strategies exist: parents can continue reducing care as they had during incubation (Chalfoun and Martin 2010; Niederhauser and Bowman 2014), or parents in risky environments can increase parental care to encourage earlier fledging (Remeš and Martin 2002; Cheng and Martin 2012).

The effects of other characteristics such as habitat quality and disturbance on parental behaviour can also be studied. Energy extraction is associated with fragmentation of the landscape, resulting in smaller and potentially poorer quality habitat patches. In eastern yellow

robins (*Eopsaltria australis*), females nesting in smaller, low quality patches foraged more frequently during the incubation period, while males provisioned incubating females less frequently (Zanette et al. 2000). Purple sunbirds (*Nectarinia asiatica*) nesting in urban landscapes took longer recess bouts and provisioned nestlings less frequently than those nesting in rural landscapes (Mazumdar and Kumar 2014). Again, few if any studies have examined these effects in the grasslands.

The two most common metrics of incubation behaviour in the literature are incubation rhythm, defined as the length of on- (incubation) and off-nest (recess) bouts, and incubation attentiveness, the percentage of daylight hours spent incubating (Hill 1997; Conway and Martin 2000; Kirkham and Davis 2013). Like other grassland songbirds, incubating chestnut-collared longspurs spend the majority (98%) of the night on the nest without taking recesses, and this behaviour is presumed to not differ much among nests (Slay et al. 2012; Kirkham and Davis 2013). Percentage of time on the nest at night is a third and less common metric of incubation behaviour (Slay et al. 2012; Kirkham and Davis 2013). Provisioning rate of the male to the incubating female in female-only incubation species can also be measured (Kirkham and Davis 2013). After hatching, length of brooding bouts (consisting of sitting on the nest to warm and shield nestlings) and provisioning rate can be quantified (Hill 1997; Adler and Ritchison 2011). Brooding and provisioning rates vary with habitat quality, food availability, and predation risk (Zanette et al. 2000; Newhouse et al. 2008; Mazumdar and Kumar 2014; Niederhauser and Bowman 2014).

2.6 Chestnut-collared longspurs

The chestnut-collared longspur, referred to hereafter as “longspurs,” is a migratory songbird species that breeds in the short- and mixed-grass prairies of North America (Bleho et al.

2015). In Canada, longspurs breed in southern Alberta, Saskatchewan, and southwestern Manitoba (Sauer et al. 2014; Bleho et al. 2015; COSEWIC 2015). They prefer to nest in disturbed grasslands, such as pastures grazed by bison or cattle, or grasslands disturbed by fire or mowing (Owens and Myers 1973; Bleho et al. 2015). In the fall, longspurs migrate in large flocks to southern United States and Mexico, where they overwinter in dry grasslands, deserts, and plateaus (Bleho et al. 2015).

2.6.1 Chestnut-collared longspur reproductive behaviour

Chestnut-collared longspurs often nest semi-colonially, clustering in suitable habitat (Owens and Myers 1973; Bleho et al. 2015). Males secure territories before attracting a mate (Bleho et al. 2015). In Alberta, the average territory size is 1 ha (Bleho et al. 2015). Males defend territories by chasing away other males in addition to performing aerial song displays and singing while perched (Harris 1944). Longspurs form socially monogamous pairs and remain together for the entire breeding season, and occasionally multiple breeding seasons (Harris 1944; Bleho et al. 2015). This species often raises two broods in a breeding season, and may attempt up to four clutches if they experience successive failures (Bleho et al. 2015). Both sexes engage in extra-pair copulations, and second broods are more likely to contain offspring resulting from extra-pair copulations (Hill 1997).

Female chestnut-collared longspurs spend an average of 5.5 days constructing a nest in short and sparse grass after first creating a shallow depression (Bleho et al. 2015). Nest sites typically have little dead standing vegetation and litter, resulting in nests that are relatively exposed (Davis 2005). Females lay 3 – 6 eggs per clutch with eggs laid on successive days, typically in the early morning (Harris 1944; Bleho et al. 2015). During nest building and laying periods, the pair spends most of their time within 10 m of each other (Hill 1997). After the

female lays the last or penultimate egg of the clutch, continuous incubation begins and the pair spends less time in close proximity to one another (Hill 1997). The incubation period typically lasts between 10 – 12.5 days after the last egg is laid (Harris 1944; Jones et al. 2010) True incubation is undertaken exclusively by the female, which develops a brood patch to do so, though males have been documented to occasionally sit on the nest, shielding or shading eggs, for up to 17 min in the female's absence, promptly leaving when the female returns (Wyckoff 1983; Kirkham and Davis 2013). Male chestnut-collared longspurs sometimes provision to their mates during the incubation period (Kirkham and Davis 2013). During the incubation period, females spent an average of 62.2% of daylight hours on the nest (Kirkham and Davis 2013). Incubation bouts lasted an average of 15.2 minutes in Alberta (Hill 1997) and 11.6 min in Saskatchewan (Kirkham and Davis 2013). Mean length of incubation recesses were 13.7 min in Alberta (Hill 1997) and 7.2 min in Saskatchewan (Kirkham and Davis 2013). In Saskatchewan, incubation bouts ranged from 3 s to 2.3 h in duration, and recess bouts ranged from 6 s to 2.13 h in duration (Kirkham and Davis 2013). Time of day has a major effect on incubation patterns, with females most likely to be incubating during and just after sunrise, and during and just before sunset (Kirkham and Davis 2013). Conversely, females incubate least in the late afternoon (Kirkham and Davis 2013). Females remain on the nest overnight, spending over 98% of the night incubating (Kirkham and Davis 2013). It is inconclusive if ambient temperature affects incubation patterns (Kirkham and Davis 2013).

Both parents care for nestlings by brooding and feeding. Parents typically alternate between foraging away from the nest and brooding or guarding the nest (Lynn and Wingfield 2003). While both parents brood on nestlings, females do 95% of the brooding (Hill 1997). Parents brood less as nestlings age, and may cease to brood by day 5 (Harris 1944; Hill 1997).

Male parental care is essential for nest success, possibly because two parents are required to provide adequate defence against nest predators (Lynn and Wingfield 2003). Longspurs respond to avian predators by mobbing, and dive-bomb rodents and snakes (Lynn et al. 2002; Kirkham and Davis 2013; Bleho et al. 2015). Both parents also maintain the nest by removing fecal sacs and waste (Hill 1997). Mean fledging age for chestnut-collared longspurs is 10 or 11 days, though they may fledge as early as 7 days if disturbed, or fledge as late as 15 days (Harris 1944; Lynn et al. 2002; Jongsomjit et al. 2007; Bleho et al. 2015).

2.6.2 Chestnut-collared longspur conservation concerns

Chestnut-collared longspurs, like other North American grassland birds, have experienced a considerable decline over the past few decades and are declining at a rate of 4.3 %/year across North America, and 7.4 %/year in Alberta (Peterjohn and Sauer 1999; Sauer et al. 2013; Sauer et al. 2014; Bleho et al. 2015). They are listed as threatened in Canada (COSEWIC 2015). Longspurs no longer inhabit much of their historical breeding range, largely due to urbanization and conversion of the prairies to agriculture (Bleho et al. 2015). The likelihood of longspurs to select and successfully use a patch of habitat is strongly affected by the vegetation features of the area (Owens and Myers 1973; Bleho et al. 2015). Longspurs do not breed in agricultural crop lands, but can breed in pastures seeded with exotic vegetation (Owens and Myers 1973; Lloyd and Martin 2005; Bleho et al. 2015). However, longspur nestlings in pastures dominated by the introduced species crested wheatgrass may fledge later and at a smaller mass, and each nest may produce fewer fledglings than nests in native mixed-grass prairies (Lloyd and Martin 2005). Longspurs also significantly preferred grazed, and to a lesser extent, mown pastures (Owens and Myers 1973). Longspur population health is therefore dependent on the availability of suitable grazed, native prairie habitat.

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CHAPTER 3: CHESTNUT-COLLARED LONGSPURS REDUCE PARENTAL CARE IN THE PRESENCE OF CONVENTIONAL OIL AND GAS INFRASTRUCTURE, ROADS, AND INDUSTRIAL NOISE

Abstract

Anthropogenic disturbances such as energy extraction may affect how songbirds perceive and respond to risk during the breeding season. I examined how the incubation and parental behaviours of the chestnut-collared longspur (*Calcarius ornatus*), a threatened grassland songbird, changed with proximity to conventional oil wells and compressor stations and with proximity to roads. I also evaluated any effects of industrial noise by comparing responses of active wells to inactive wells and control sites. Longspurs consistently reduced parental care in the presence of all three factors of energy extraction, though males and females were sensitive to different factors. Females consistently altered behaviours when nesting near roads, while males were sensitive to industrial noise. Fewer offspring successfully fledged at nests near roads and these offspring fledged at a later age, possibly as a result of decreased female provisioning. The effects of noise on behaviour differed from the effects of oil wells and compressor stations, indicating that inactive infrastructure still poses a disturbance on the landscape. These findings suggest that energy development in the grasslands increases perceived risk and influences songbirds' reproductive strategies, likely with consequences for reproductive fitness. Effective mitigation measures must address all three related disturbances of physical infrastructure, roads, and noise to be successful.

3.1 Introduction

Grassland songbirds have been the focus of conservation interest recently due to concern about their consistent and steep population declines (Knopf 1994; Peterjohn and Sauer 1999; Sauer et al. 2013). Temperate grasslands remain one of the most endangered biomes in North America, having experienced significant historical losses and ongoing degradation in the form of anthropogenic disturbances such as energy extraction (Samson and Knopf 1994; Noss 1995). An estimated 13% of the grasslands remaining in North America, comprising nearly 10,000 ha, are

affected by oil and gas leases (Copeland et al. 2011). Oil and gas wells are associated with linear features such as access roads, pipelines, and transmission lines. These associated structures and their edge effects extend the effects of oil and gas leases beyond their immediate footprint (Copeland et al. 2011; Koper et al. 2014). These structural networks are a particularly significant problem in grasslands as ecological effects of infrastructure may extend particularly far in non-forested landscapes (Benítez-López et al. 2010).

Energy extraction in grassland and steppe ecosystems has been documented to have several negative effects on breeding birds, including reductions in available habitat through direct habitat loss, avoidance of oil and gas infrastructure (Linnen 2008; Dale et al. 2009; Nenninger 2016), avoidance of roads (Ingelfinger and Anderson 2004), and reduced nest success, which is the proportion of nests that produce at least one fledgling (Hethcoat and Chalfoun 2015a; Bernath-Plaisted and Koper 2016). Infrastructure and roads are also associated with modified predator communities, including changes in nest predators. Avian nest predators such as corvids and raptors may be more abundant in the presence of artificial structures, which can serve as perches or even nesting sites (Ingelfinger and Anderson 2004; Benítez-López et al. 2010), and rodent nest predators may also be more abundant with increasing densities of energy infrastructure (Hethcoat and Chalfoun 2015b). Proximate causes of these impacts are poorly studied, and little is known about what mechanisms explain them. Lethal effects from altered predator communities may be one of the proximate causes of reduced nest success, but there are likely also hidden nonlethal effects, such as behavioural modifications associated with species perceptions of risk.

Differences in reproductive behaviours enable us to understand the life histories of birds, which must balance the well-being of their offspring against their own survival and future

reproductive opportunities. In communities where nest predation risk is unpredictable and relatively high compared to risk at other life stages, such as grassland songbirds (Pietz and Granfors 2000; Chalfoun and Martin 2010), reproductive strategies reflect both the degree and source of perceived risk (e.g. Conway and Martin 2000; Niederhauser and Bowman 2014). Skutch (1949) proposed the hypothesis that the smaller clutch sizes (number of eggs) of tropical birds are an evolutionary adaptation to high nest predation rates; parents can reduce how often they need to return to the nest to provision, and thus reduce the likelihood that they inadvertently lead a predator back to the nest, by reducing brood size (number of nestlings). This hypothesis has often been expanded to include species from temperate climates and reinterpreted to suggest that higher rates of parental activity at the nest would lead to higher rates of nest depredation; therefore, parents must balance the developmental needs of eggs or nestlings against the possibility of attracting predators (summarized in Roper and Goldstein 1997; Martin et al. 2000). Behaviours to reduce the likelihood of predation include avoiding the nest when a predator is present (e.g. Ghalambor and Martin 2000; Eggers et al. 2008), and/or lengthening incubation and recess bouts to minimize number of trips to and from the nest (Conway and Martin 2000).

Parents may selectively exhibit such antipredator behaviours based on the types of perceived risk and context for trade-offs. In some species, parents do respond to predators of adult birds by avoiding the nest, but show no or weaker changes in the presence of nest predators (e.g. Tilger et al. 2011; Bonnington et al. 2013); this difference suggests that these parents may risk offspring safety before their own. Parents may also reduce parental care to promote their own body condition; for example, females in small, low quality patch sizes may take more frequent recess bouts to forage, leaving their eggs unprotected (Zanette et al. 2000). Because migratory birds must reproduce and raise young in a short breeding season while maintaining

sufficient body condition to migrate afterwards, parents must manage time and energy to balance risk to their nest (current reproductive effort) against risk to themselves (future reproductive fitness). While most songbirds use antipredator behaviours, species in environments characterized by diverse and unpredictable risks, such as grasslands, may possess greater behavioural plasticity to make more drastic behavioural changes in response to risks (Chalfoun and Martin 2010).

New studies have increasingly shown that anthropogenic disturbances and changes to the landscape also influence avian behaviour. Economic models of antipredator trade-offs argue that nonlethal anthropogenic disturbances, such as traffic noise or activity at infrastructure, trigger generalized antipredator behaviours (Frid and Dill 2002). In landscapes dense with energy development, this may lead to an artificially inflated perception of risk, causing reproducing birds to make unnecessary trade-offs in response. These behavioural trade-offs may result in parents favouring self-maintenance and adult safety over offspring development or favouring offspring safety over development (e.g. by reducing activity at nests and slowing development). The trade-offs triggered by perceived risk can have fitness consequences as reduced effort in parenting young may result in fewer fledglings or lower quality fledglings with reduced survival rates (e.g. Dunn et al. 2010; Zanette et al. 2011; Hua et al. 2014). Nonlethal effects may have significant long-term repercussions for populations if they lower overall reproductive success or alter population demographics (Frid and Dill 2002; Cresswell 2008; Leshyk et al. 2012). Despite its importance to conservation, to my knowledge, this is the first study to examine the nonlethal behavioural effects of conventional oil and gas extraction, along with associated roads and industrial noise, on passerine parental behaviour during both the incubation and nestling rearing periods.

Anthropogenic noise may explain some effects of industrial activities on songbird behaviour. Acoustic communication plays a key role in both antipredator behaviour (e.g. alarm calls) and reproductive behaviour (e.g. nestling begging calls). High levels of ambient noise may mask these calls, reducing the effectiveness of acoustic communication. Experimentally increased ambient noise reduced the ability of tree swallow (*Tachycineta bicolor*) nestlings to respond appropriately to parental alarm calls (McIntyre et al. 2014). Ambient noise from oil and gas infrastructure reduced the antipredator response of adult Savannah sparrows (*Passerculus sandwichensis*), reducing the delay between hearing conspecific alarm calls and returning to the nest (Antze 2016). Anthropogenic noise may also contribute to the perception of risk across a landscape (Shannon et al. 2014), or distract birds from completing fitness-related behaviours (Ware et al. 2015). Anthropogenic noise can delay responses even when visual cues are present, as Caribbean hermit crabs (*Coenobita clypeatus*) subjected to anthropogenic noise responded more slowly to the sight of a simulated predator's approach (Chan et al. 2010).

However, the physical structures associated with infrastructure, such as buildings, transmission lines, and roads, can also influence avian behaviour. Nest success in Savannah sparrows and vesper sparrows (*Pooecetes gramineus*) was lower at oil well sites relative to control sites regardless of noise intensity (Bernath-Plaisted and Koper 2016). Similarly, Baird's sparrows (*Ammodramus bairdii*) and Sprague's pipits (*Anthus spragueii*) showed reduced abundance near both active and inactive infrastructure (Nenninger 2016). Industrial mitigation efforts are often focused on reducing the amplitude and spatial footprint of noise (e.g. Bayne et al. 2008), but these recent studies suggest that noise mitigation might not always decrease ecological footprints of industrial activities. It is important to distinguish between behavioural effects caused by the physical presence of infrastructure from the effects caused by noise

generated by active infrastructure because these effects are likely driven by separate ecological mechanisms. For example, physical infrastructure, with their associated with predators, may cause heightened perceived risk in the local environment while the noise generated by infrastructure may mask communication and distract animals. Therefore, different management and mitigation strategies may be required to reduce impacts of the built environment versus anthropogenic noise.

I studied the effects of energy extraction on the reproductive behaviour of chestnut-collared longspurs (*Calcarius ornatus*) in southeastern Alberta, a region heavily affected by oil and gas development (Schneider et al. 2003; Askins et al. 2007; Copeland et al. 2011). Chestnut-collared longspurs (hereafter “longspurs”) are threatened short- and mixed-grass prairie obligates (Bleho et al. 2015; COSEWIC 2015). Longspurs appear sensitive to oil and gas infrastructure, and sometimes have lower abundances near oil wells (e.g. Linnen 2008; Thompson et al. 2015; but see Nenninger 2016). Longspurs in this region may also have smaller clutch sizes near roads associated with energy extraction (Bernath-Plaisted, unpublished data). The primary cause of nest failure in longspurs is nest predation (Hill 1997; Bernath-Plaisted 2015), and thus longspurs’ reproductive strategies are expected to be highly attuned to the perception of risk of nest predation. In addition to heightened perceived risk from anthropogenic disturbances, oil and gas infrastructure and roads may increase actual risk by altering predator communities or increasing predator abundance. Changes in the reproductive strategy used by longspurs may serve as an early indicator of long-term population health, as nonlethal effects in the form of trade-offs favouring parent safety have the capacity to reduce reproductive success (Cresswell 2008). Managers should study nonlethal effects to avoid underestimating the impact of disturbances, to

gauge effectiveness of mitigation strategies, and to predict long-term trends (Frid and Dill 2002; Cresswell 2008).

To understand how energy extraction affects chestnut-collared longspur reproductive behaviour, I monitored parental behaviour at longspur nests at conventional oil wells and compressor stations (hereafter “infrastructure”) and control sites using nest surveillance cameras. I hypothesized that the presence of 1) infrastructure, 2) roads, and/or 3) industrial noise would heighten the perception of predation risk in breeding longspurs. I predicted that incubating birds would respond by minimizing trips to and from the nest, resulting in higher incubation frequency (number of incubation bouts) and shorter incubation and recess bout means at nests away from infrastructure, roads, and/or industrial noise. I predicted that parents would promote earlier fledging to minimize the chance of nest depredation, resulting in lower visit and provisioning frequencies, lower nest attentiveness (proportion of time at nest), lower cumulative and mean brood and shade length, and later fledging age at nests farther from infrastructure, roads, and industrial noise.

3.2 Methods

3.2.1 Study area

My research was carried out in Newell County in southeastern Alberta, Canada. My study sites were centred on Brooks, Alberta (50° 33' 51"N 111° 53' 56" W, 760 m above sea level), with all sites within 60 km of the city centre (see Appendix I). This region is composed of native mixed-grass prairie and dominated by native vegetation such as needle-and-thread (*Hesperostipa comata*), blue grama (*Bouteloua gracilis*), western wheatgrass (*Pascopyrum smithii*), June grass (*Koeleria macrantha*) and silver sagebrush (*Artemisia cana*) (Bailey et al.

2014). Newell County is also notable for its high density of conventional oil and natural gas wells and associated infrastructure.

Newell County follows Mountain Daylight Time (UTC -6:00) during the breeding season. In 2014, sunrise during the breeding season ranged from 0515 on June 21 to 0552 on July 30, the last day of recorded footage (USNO 2016). Sunset ranged from 2143 on June 21 to 2115 on July 30 (USNO 2016).

3.2.2 Field methods

I collected continuous digital video footage between May and July of 2013 and 2014 from chestnut-collared longspur nests found as part of a concurrent study on the impacts of oil and gas infrastructure on grassland songbird nest success and nest predation (Bernath-Plaisted and Koper 2016). Nest searches were conducted at 47 rotationally-grazed native mixed-grass prairie sites throughout Newell County, and included both control and infrastructure sites. Sites were 800 m by 200 m, and the centre points of control sites were ≥ 800 m from infrastructure sites. Each rectangular site was oriented in a cardinal direction. Infrastructure sites had compressor stations or oil wells as their centre points.

I focused on the effects of conventional oil wells and compressor stations on chestnut-collared longspur behaviour because these were the largest and/or noisiest energy development structures in the region. Shallow gas wells are also abundant, but are motionless, less than 1.5 m tall, do not produce mechanical industrial noise, and are visited only once annually for maintenance; thus, shallow gas wells less likely to influence avian behaviour. Compressor stations typically consisted of a fenced-in gravel pad containing one or more buildings, sheds, generators, and other large structures, and had permanent gravel roads entering them.

Compressor stations pump raw natural gas from wellheads throughout the regional pipeline system (CAPP 2015). Oil well pads typically consisted of a fenced-in gravel substrate, generators or transmission lines, and either a pumpjack or screw pump overground structure to pump oil to the surface, which use either a vertical pumping motion or horizontal spinning mechanism, respectively. Other common features of oil well pads include permanent gravel access roads, sheds, and storage tank batteries. At focal sites in Newell County, the average fenced-in area around pumpjacks was 3,787 m² ($n = 4$) while the average area for screw pumps was larger at 10,636 m² ($n = 3$) (Bernath-Plaisted 2015). Well pad sizes in this study were typical of those throughout the Western Canadian Sedimentary Basin: 1 ha, with an additional estimated 1 ha is disturbed to provide access to leases (Van Wilgenburg et al. 2013). My study included 14 sites: three with compressor stations (including one disassembled compressor), seven with oil wells, and four control sites (see Appendix II). To distinguish effects of the presence of infrastructure from effects of the noise and human activity associated with active infrastructure, five of the infrastructure sites (two compressor stations and three oil wells) were active (moving, noisy, visited regularly for maintenance) while the other five infrastructure sites were inactive (turned off, quiet, not visited for maintenance). Technicians confirmed whether the infrastructure was active and noisy or inactive and quiet during each visit for nest searching (3 visits per season). Ambient noise at control sites was 52 ± 5.0 dB(C) ($n = 11$; see Koper et al. 2015). Active compressor stations were loudest on average at 82 ± 3.1 dB(C) at 10 m ($n = 4$). Active pumpjacks produced noise at an average amplitude of 68 ± 7.0 dB(C) at 10 m ($n = 8$), and active screw pumps generated an amplitude of 69 ± 10.7 dB(C) at 10 m ($n = 10$). The average amplitude of noise generated by the combined infrastructure types is 71 ± 9.9 dB(C) at 10 m ($n = 22$). Because of our small sample size, we combined compressor stations, screw pumps, and

pumpjacks as “infrastructure” when calculating distance to the nearest infrastructure. Roads in this study included gravel range and township roads and gravel or dirt access roads.

We searched for nests systematically by dragging a 30-m long weighted rope over each site, designed to flush birds from their nests (Winter et al. 2003). Rope dragging was carried out three times over each breeding season for each 800 m by 200 m site. Fenced-in areas around infrastructure were not searched. To maximize our chances of locating nests, searching efforts were carried out early in the morning when the likelihood of adults being on the nest was at its maximum (Kirkham and Davis 2013). To minimize the chance of eggs or nestlings chilling or overheating, rope dragging only occurred between 10 °C and 30 °C, and when vegetation had dried following rain or dew. We located the nest based on where the bird emerged from the grass, and marked it with a bamboo stake wrapped in pink flagging 10 m south and a pink trail chaser (a small, highly visible plastic trail marker) staked 10 m west of the nest. Nests were assigned an alphanumeric “nest ID” (e.g. “CN1”) at discovery. We also photographed the nest and its contents and took GPS coordinates. A nest card was filled out at discovery and updated at subsequent nest checks with the status of the nest, including number of eggs, number of nestlings, age of nestlings, evidence of brown-headed cowbird (*Molothrus ater*) parasitism, and presence and activity of parents. Nestlings were aged visually based on developmental cues, such as by presence and development of pin sheaths (Jongsomjit et al. 2007). All nests, including chestnut-collared longspur nests, were checked every 2 – 5 days. In 2014, nests were checked for fledging daily or almost daily once nestlings were 8 or more days old.

We set up video surveillance cameras at longspur nests to record parental behaviour at the nest. We used weather-proof Specto Technologies® cameras (model CVC-628M), which have a wide-angle focal length of 3.6 mm, 21 infrared light-emitting LEDs enabling low light

recording, and a resolution of 420 television lines. The nest camera set-up also consisted of a 704 x 480 resolution miniature digital-video recorder (DVR), a 12V-35ah rechargeable lead-acid battery, and a 30 m combined power-video BNC, with the battery and DVR contained in a waterproof plastic ammunition case. The nest cameras were placed approximately 20 cm from the nest and camouflaged with burlap and native vegetation (see Appendix III). The field of view across nests was not quantified, but examples of camera stills can be seen in Chapter 4 (Figures 4.1 and 4.3). We secured the BNC cable into the ground, under existing vegetation, with around half a dozen U-nails to reduce the likelihood of it being seen or damaged by potential nest predators, and whenever possible, the ammunition case was concealed, usually in silver sagebrush (*Artemisia cana*) shrubs or depressions. Cameras recorded continuously from when they were deployed to when the nest was terminated, except for brief pauses at battery changes. Technicians exchanged the battery and 32GB SD card for a fresh battery and SD card every 3 – 4 days during a nest check. To reduce risk of abandonment, cameras were set up once laying was complete (Kirkham and Davis 2013). At nests discovered during the nestling stage, cameras were most often set up the day following nest discovery or at the next nest check.

3.2.3 Footage review methods

I and six technicians reviewed the video recordings of each nest. Observational data from footage was divided into “incubation stage” and, post-hatch, “nestling stage.” During the incubation stage, the footage was watched in its entirety. Footage from the hour of set-up and battery changes was excluded due to the artificial disturbance from researchers. Footage from nestling stage was subsampled so that six staggered hours between 0500 and 2200, inclusive, of every day were watched when possible, with the initial hour of 0500, 0600, or 0700 randomized for each day of footage. The hours of 0500 and 2200 were chosen as the earliest and latest hours

watched to capture activity during sunrise and any activity leading up to nocturnal brooding. As sunrise and sunset consistently fell within a clock hour (0500 and 2100 respectively) across the field season, I chose to follow the protocol described in Kirkham and Davis (2013) and analyzed footage by standard clock time. A regularly staggered six hours could not be watched on the first day of recording and on nest termination days (i.e. depredation, or last nestling fledging). In situations where a scheduled hour was unavailable to watch, disrupted, or incomplete, a randomly selected, non-overlapping hour between 0500 and 2200 was used to replace the incomplete or missing hour, such that a total of six hours were still watched for each day provided that at least six full hours were recorded. Footage between 2300 and 0500 was considered nocturnal footage, and only watched during incubation stage. For this study I was primarily interested in daytime behaviour, but included nocturnal incubation footage to compare to previous incubation studies. I watched footage using VideoLAN VLC Media Player version 2.2.4, with footage speed of no more than 10x between events, and slowed down to between 0.1x to 1x during events.

At incubation stage, I recorded the time when female birds entered and exited the nest. Using these times, I calculated the length of each incubation session (“incubation bout”), the length of each break from incubation (“recess bout”), and the proportion of each hour spent incubating (“incubation attentiveness”). I also counted how many incubation bouts were initiated each hour (“incubation frequency”). I considered nocturnal incubation (“nocturnal attentiveness”), the total time spent incubating overnight, to encompass all incubation between 2300 and 0500 as well as incubation bouts that overlapped 2300 or 0500. The full duration of any incubation bout that extended into 2300 or lasted past 0500 were included for nocturnal attentiveness. I also recorded male activity at the nest, including all visits and mate provisioning,

to calculate incubation visit frequency and mate provisioning frequency. Longspur males have been documented briefly “brooding” on eggs (Wyckoff 1983; Kirkham and Davis 2013); however, this behaviour is not considered true incubation, and only females develop a brood patch (Bhelo et al. 2015). Henceforth, I refer to this male behaviour as “egg shielding.”

A mean hatch period for chestnut-collared longspurs is known from a previous study which used nest cameras raised on dowels, allowing researchers to see into the nest from above (Pietz et al. 2012). In my study, cameras were level with nests because nest vegetation at our sites was often sparse and short. Combined with the minimum distance of 20 cm from nests, they were too far from nests to directly observe eggs hatching. Hatching was inferred to have begun when a parent was seen removing a piece of eggshell or the female brought food to the nest. At this point, the nest was considered at nestling stage. Hatch times for the rest of the clutch were estimated based on the known mean hatching period for chestnut-collared longspurs (Pietz et al. 2012) or based on the confirmed number of nestlings if a nest check occurred during the hatching period. I estimated hatch times to approximate nestling number, as brood size may affect provisioning frequency of parents (e.g. Conrad and Robertson 1993; Adler and Ritchison 2011). The mean hatching period, or the elapsed time between the first and last eggs hatching in a nest, was 34 hours for a clutch of four ($n = 5$, Pietz et al. 2012). Using this mean, I approximated the hatch time of the first nestling as when I first saw evidence of hatching activity (e.g. parents removing eggshell fragments). For clutches of four or five, I approximated the hatching period to be complete and the last egg hatched after 34 hours. I estimated the middle two or three hatch times to be staggered evenly by 11.3 hours for four-egg clutches or 8.5 hours for five-egg clutches. As data were not available for hatching periods for clutches of three, I used the same

staggered 11.3 hour hatch times as for four-egg clutches, for an overall hatch period of 22.6 hours for three-egg clutches. Hatch day nestlings were considered to be 0 days old.

At the nestling stage, I recorded all visits by both parents and whether provisioning was evident, to calculate visit frequency and provisioning frequency. In some cases, typically as vegetation grew up to reduce visibility, it was not possible to tell whether parents brought food or had deposited food into the nestlings' mouths, so the provisioning frequency for some nests may have been underestimated. I also recorded the start and end time of visits to calculate the proportion of when hour one or both parents were present, the "nest attentiveness." As it was sometimes difficult to distinguish between brooding (sitting on the nest to shield and warm nestlings) and shading (protecting nestlings from the heat of direct sunlight) activity, I did not differentiate between the two behaviours, and recorded all time spent in and directly above the nest as "brood and shade" when calculating cumulative time spent in and above the nest ("cumulative brood and shade") and mean brood or shade bout length ("brood and shade mean") for each hour. As nestlings often left the nest for a few seconds to a few hours prior to actual fledging, I used the time that an individual left the nest without returning as the actual fledge time (Pietz et al. 2012).

Distances to infrastructure and roads were calculated using the measurement tool in ArcGIS 10 (see Bernath-Plaisted and Koper 2016).

3.2.4 Analyses

I used R version 3.3.2 for all statistical analyses (R Core Team 2014). I evaluated significance with an alpha value of 0.1 to compensate for small sample sizes and to avoid invoking a Type II error, or falsely concluding no effect, which presents significant problems in ecology (Taylor and Gerrodette 1993). I developed linear mixed-effects models and generalized

linear mixed-effects models with the package “lme4” (Bates et al. 2014), and extracted p -values for linear mixed-effects models using the package “lmerTest” (Kuznetsova et al. 2016). I produced all figures with the package “ggplot2” (Wickham 2009). Error bars for the barplot were produced using “Hmisc” (Harrell 2016).

I used AIC_c to determine whether including the covariates quadratic hour, Julian date, and year improved model fit (Akaike 1974; Anderson 2008; Arnold 2010). I also tested for the inclusion of one of two additional fixed-effects variables, male visit frequency and male mate provisioning frequency, on all daytime incubation models (excluding male behavioural models) as female incubation behaviours may be significantly influenced by male activity (e.g. Matysioková et al. 2011). I did not observe any nocturnal male visits. I selected the model with the fewest terms within $\Delta AIC_c < 2$ of the lowest AIC_c value (Arnold 2010). I used AIC_c values generated by package “AICcmodavg” (Mazerolle 2016). Once I determined whether nuisance variables should be included in my models, I followed a frequentist approach (Mundry 2011).

I analyzed incubation stage and nestling stage footage separately. All dependent variables regarding time, including frequencies, cumulative sums, and means, were calculated by the hour. The exception was nocturnal attentiveness, which was calculated per night. Distance to infrastructure and distance to road were log-transformed to linearize the relationship between distances and dependent variables. The presence of noise was included as a two-factor categorical variable: absent (“quiet”) or present (“active”). I used graphical diagnostic tools such as q-q plots and histogram plots of residuals to determine model distributions and assess whether assumptions of models were met.

Daytime incubation-stage models tested for the effects of distance to infrastructure, distance to road, and presence of noise from active compressor stations or oil wells on the

following response variables: incubation frequency, incubation attentiveness, incubation bout mean, recess bout mean, male visit frequency, male mate provisioning frequency, and male egg-shielding likelihood (see Appendix IV). Incubation bout mean and recess bout mean were square-root transformed to fit a normal distribution. Male egg-shielding likelihood was analyzed using a binomial generalized linear mixed model. A binomial response variable was used instead of duration because egg-shielding behaviour was present in less than 0.05% of the analyzed hours ($n = 564$), resulting in a positively skewed data set. Clutch size and hour were included as additional fixed-effects variables in all daytime incubation models. All models included nest ID as a random effect.

To test the impact of anthropogenic disturbance on nocturnal incubation, I evaluated the effects of distance to infrastructure, distance to roads, and presence of noise on the response variable nocturnal attentiveness. I controlled for potential effects of clutch size by including this variable in the models as a fixed effect, and included nest ID as a random effect.

I evaluated the effects of distance to infrastructure, distance to roads, and presence of noise on the following nestling stage response variables: visit frequency, provisioning frequency, nest attentiveness, cumulative brooding and shading, and brood and shade mean (see Appendix V for nestling stage models). Because footage during nestling stage was subsampled, I excluded any brooding or shading bout that did not occur entirely within the hour (i.e. partial bouts) for brood and shade mean to avoid underestimations. I included partial bouts when calculating nest attentiveness and cumulative brood and shade because these variables measured total time spent at the nest within each hour. Visit frequency, provisioning frequency, cumulative brood and shade, and brood and shade mean were all analyzed both separately by sex and with both sexes combined. Nest attentiveness, cumulative brood and shade, and brood and shade mean were log-

transformed to better approximate a normal distribution. In addition to distance to infrastructure, distance to road, and presence of noise, fixed-effects included nestling age, number of nestlings, and hour. All nestling stage models included nest ID as a random effect.

For each nest, I evaluated the effects of distance to infrastructure, distance to road, and presence of noise on the mean fledging age. In addition, I evaluated the effects of distance to infrastructure, distance to road, and presence of noise on number of nestlings fledged at each nest. For number of nestlings fledged (“number fledged”), I only included nests where outcomes (fledge, depredation, or other causes of mortality) were captured on footage.

3.3 Results

3.3.1 General results

Cameras were deployed on a total of 39 chestnut-collared longspur nests in 2013 and 2014. In all, 28 nests were used in this study because eight nests were abandoned, one nest camera failed to record entirely, and two nests were rejected due to poor footage quality. The footage of six nests included in the study was partially compromised due to some form of camera failure, often from animals (cattle or wildlife) disturbing or damaging the cameras or cables. Of the nests used in this study, 12 were from 2013 and 16 were from 2014 (see Appendix II). I initiated video recording 12 nests at incubation stage, totalling 564 hours of daytime footage and 30 nights of nocturnal footage. Nine of these 12 nests were recorded also recorded during nestling stages. We recorded 25 nests at nestling stage, and reviewed 962 hours of nestling stage footage. We captured the outcomes of 20 nests; of these, ten fledged. Nests were 24 – 1398 m from the nearest infrastructure, with a mean of 339.25 m (SD = 325.19), and 11 – 606 m from the nearest road, with a mean of 162.36 m (SD = 159.16) (see Appendix II). Ten nests were at

active infrastructure sites. Nests at quiet sites were an average of 388.94 m (SD = 395.28) from the nearest infrastructure, and nests at active sites were an average of 214.20 m (SD = 123.60) from the nearest infrastructure.

3.3.2 Effects of anthropogenic disturbance on incubation behaviour

Only one (8.3%, $n = 12$) incubating female appeared to interrupt incubation because of the camera's presence. Twenty-seven hours from that nest over the course of three days were excluded from incubation frequency, mean incubation bout, and mean recess bout calculations because the female's behaviour was clearly disrupted by the camera as she interrupted incubation frequently to examine the nest camera. The female stopped visibly reacting to the camera by nestling stage.

Females took shorter breaks from incubation when farther from both infrastructure and roads, expressed as a lower recess bout mean with increasing distance from infrastructure ($\beta = -7.750$, $SE = 3.301$, $p = 0.039$) and roads ($\beta = -3.925$, $SE = 1.814$, $p = 0.062$) (see Table 3.1). On average, females within 100 m of infrastructure spent an additional minute away from the nest each recess compared with females 250 m away, and spent an additional two minutes away compared to females 600 m from infrastructure (see Figure 3.1a). When two outliers were removed, nocturnal attentiveness was lower at active sites ($\beta = -0.389$, $SE = 0.202$, $p = 0.065$), with females incubating for almost half an hour less overnight in the presence of industrial noise (see Figure 3.2). Nocturnal attentiveness was unaffected by distance to infrastructure or distance to roads, and incubation frequency, incubation attentiveness, and incubation bout mean were unaffected by distance to infrastructure, distance to roads, or noise (Table 3.1).

Male behaviours were affected by both distance to infrastructure and presence of active infrastructure, but not by distance to roads. Male visit frequency ($\beta = 0.390$, $SE = 0.155$, $p =$

0.036) and mate provisioning frequency ($\beta = 0.272$, $SE = 0.085$, $p = 0.001$) were both higher farther from infrastructure (see Figure 3.1b). Males mate-provisioned more frequently at active sites ($\beta = 0.094$, $SE = 0.055$, $p = 0.091$; Figure 3.1c). Male egg-shielding likelihood did not change due to any anthropogenic disturbance.

Table 3.1. Anthropogenic effects on chestnut-collared longspur reproductive behaviours and fledging in southeastern Alberta in 2013 and 2014. Significant results are bolded.

	Oil and Gas Infrastructure			Road			Noise		
	β	SE	<i>p</i>	β	SE	<i>p</i>	β	SE	<i>p</i>
Incubation Stage									
Incubation Frequency	0.625	0.564	0.283	0.427	0.313	0.197	-0.153	0.344	0.664
Incubation Attentiveness	5.410	6.451	0.414	-0.345	3.859	0.930	1.221	3.833	0.755
Incubation Bout Mean	-2.304	6.797	0.740	-6.389	3.754	0.115	4.586	4.127	0.287
Recess Bout Mean	-7.750	3.301	0.039	-3.925	1.814	0.062	0.025	1.839	0.990
Nocturnal Attentiveness (outlier)	-1.214	1.149	0.299	0.087	0.727	0.905	-0.609	0.810	0.458
Nocturnal Attentiveness (no outlier)	-0.268	0.297	0.374	-0.039	0.186	0.836	-0.389	0.202	0.065
Male Visit Frequency	0.390	0.155	0.036	0.116	0.092	0.241	0.152	0.101	0.168
Male Mate Provisioning Frequency	0.272	0.085	0.001	0.070	0.051	0.172	0.094	0.055	0.091
Male Egg Shielding Likelihood	1.905	3.174	0.548	2.323	1.954	0.235	0.330	2.055	0.872
Nestling Stage									
Visit Frequency									
Total	0.391	1.118	0.730	-0.458	1.123	0.687	-0.327	1.051	0.758
Male	-0.087	0.825	0.917	-1.098	0.826	0.197	-0.980	0.776	0.220
Female	0.224	0.560	0.693	1.467	0.606	0.023	0.515	0.526	0.339
Provisioning Frequency									
Total	-0.018	1.091	0.987	-0.354	1.095	0.749	-0.790	1.026	0.449
Male	-0.115	0.701	0.871	-1.020	0.704	0.162	-1.308	0.660	0.060
Female	-0.104	0.600	0.864	1.409	0.648	0.040	0.408	0.564	0.477
Nest Attentiveness									
Total	0.178	0.099	0.087	-0.110	0.099	0.280	-0.017	0.093	0.861
Cumulative Brood and Shade									
Total	0.336	0.178	0.073	-0.120	0.178	0.507	-0.045	0.167	0.790
Male	-0.334	0.240	0.180	-0.088	0.240	0.718	-0.321	0.226	0.171
Female	0.430	0.173	0.022	-0.107	0.174	0.544	-0.060	0.163	0.716
Brood and Shade Mean									
Total	0.241	0.151	0.125	-0.112	0.151	0.467	-0.029	0.142	0.838
Male	-0.294	0.202	0.162	-0.066	0.202	0.748	-0.278	0.190	0.161
Female	0.292	0.149	0.064	-0.078	0.149	0.607	-0.075	0.140	0.595
Fledging									
Fledging Age	0.078	0.770	0.923	-3.221	1.584	0.088	-2.104	1.291	0.154
Number Fledged	-0.047	0.719	0.949	2.509	0.830	0.009	0.244	0.855	0.780

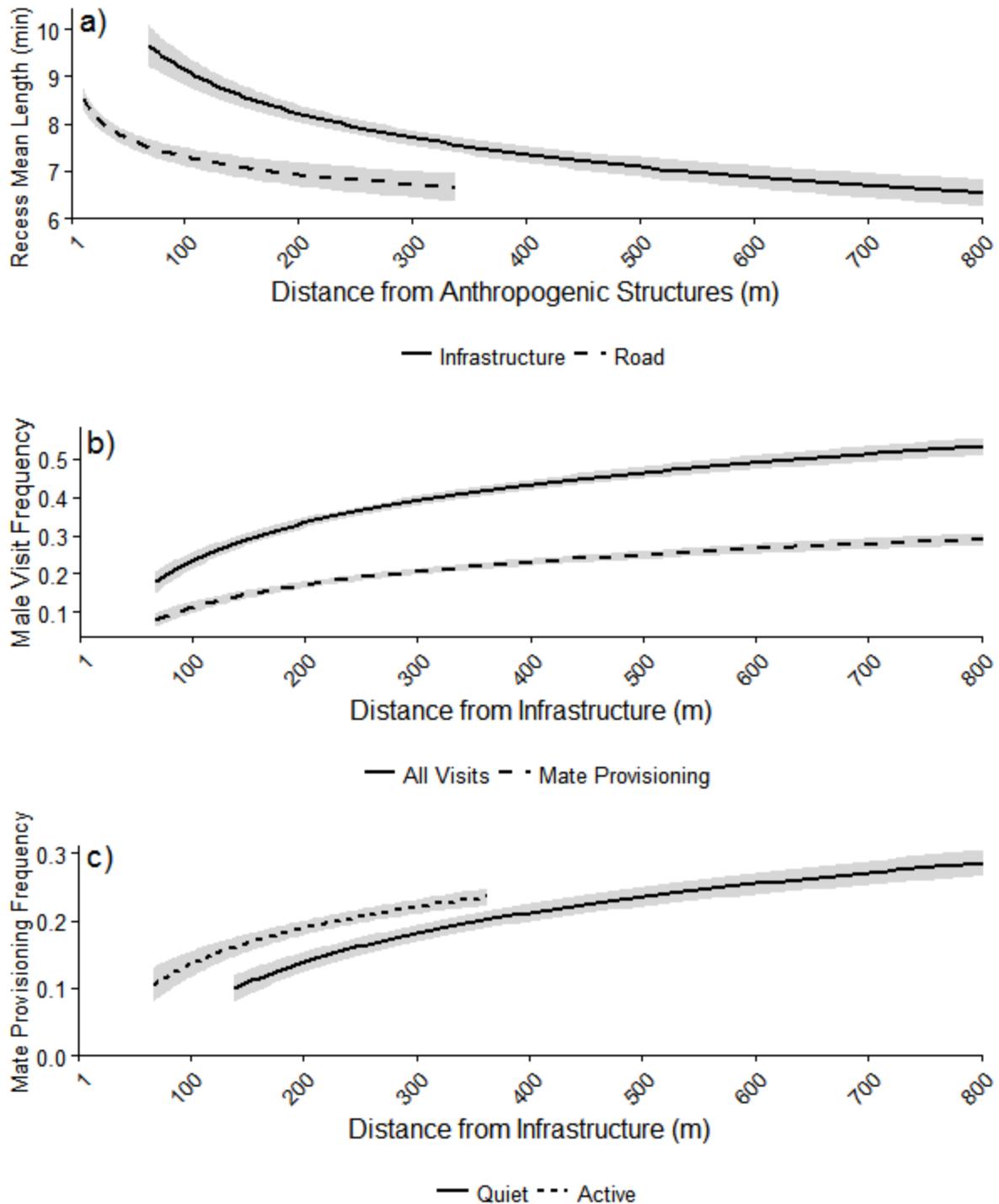


Figure 3.1. Significant effects of anthropogenic disturbances on daytime incubation-stage behaviours of chestnut-collared longspur (*Calcarius ornatus*) in southeastern Alberta in 2013 and 2014 included: a) distance from conventional oil and gas infrastructure and roads on incubation recess bout length of females, b) distance from conventional oil and gas infrastructure on male nest visitation and mate provisioning, and c) distance from conventional oil and gas infrastructure and industrial noise on male mate provisioning. Grey fill indicates 95% confidence intervals.

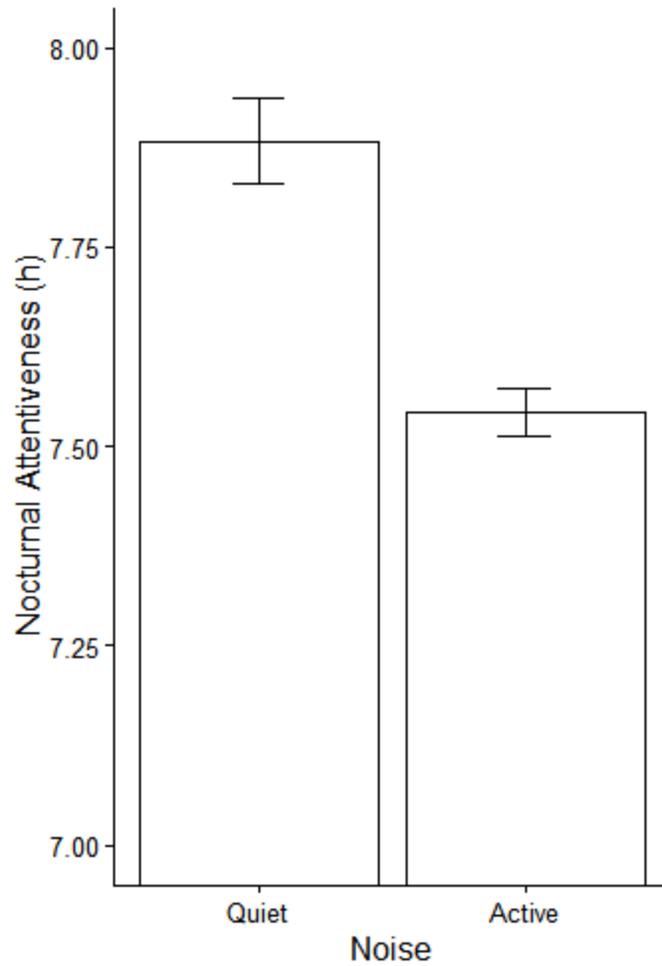


Figure 3.2. Effect of industrial noise from conventional oil wells and compressor stations on female chestnut-collared longspur (*Calcarius ornatus*) nocturnal incubation attentiveness in southeastern Alberta in 2013 and 2014 (with outliers removed). Error bars represent 95% confidence intervals.

3.3.3 Effects of anthropogenic disturbance on nestling-stage parental behaviour

Nest attentiveness was higher farther from infrastructure ($\beta = 0.178$, $SE = 0.099$, $p = 0.087$), increasing from an average of 10 min per hour at a distance of 50 m to 15 min at 500 m (Figure 3.3a). This is likely driven by the higher total ($\beta = 0.336$, $SE = 0.178$, $p = 0.073$) and female ($\beta = 0.430$, $SE = 0.173$, $p = 0.022$) cumulative brood and shade bouts farther from infrastructure (Figure 3.3b). Female brood and shade bout mean was also higher farther from infrastructure ($\beta = 0.292$, $SE = 0.149$, $p = 0.064$) (Figure 3.3b).

Females visited ($\beta = 1.467$, $SE = 0.606$, $p = 0.024$) and provisioned ($\beta = 1.409$, $SE = 0.648$, $p = 0.040$) nestlings more frequently with increasing distance from roads (Figure 3.3d). Males provisioned nestlings less frequently at active sites ($\beta = -1.308$, $SE = 0.660$, $p = 0.060$), resulting in an average of one less provisioning visit per hour regardless of nestling age (Figure 3.4). Total and male visit frequency, total provisioning frequency, male cumulative brood and shade, and total and male brood and shade mean were all unaffected by the presence of infrastructure, roads, or noise (Table 3.1).

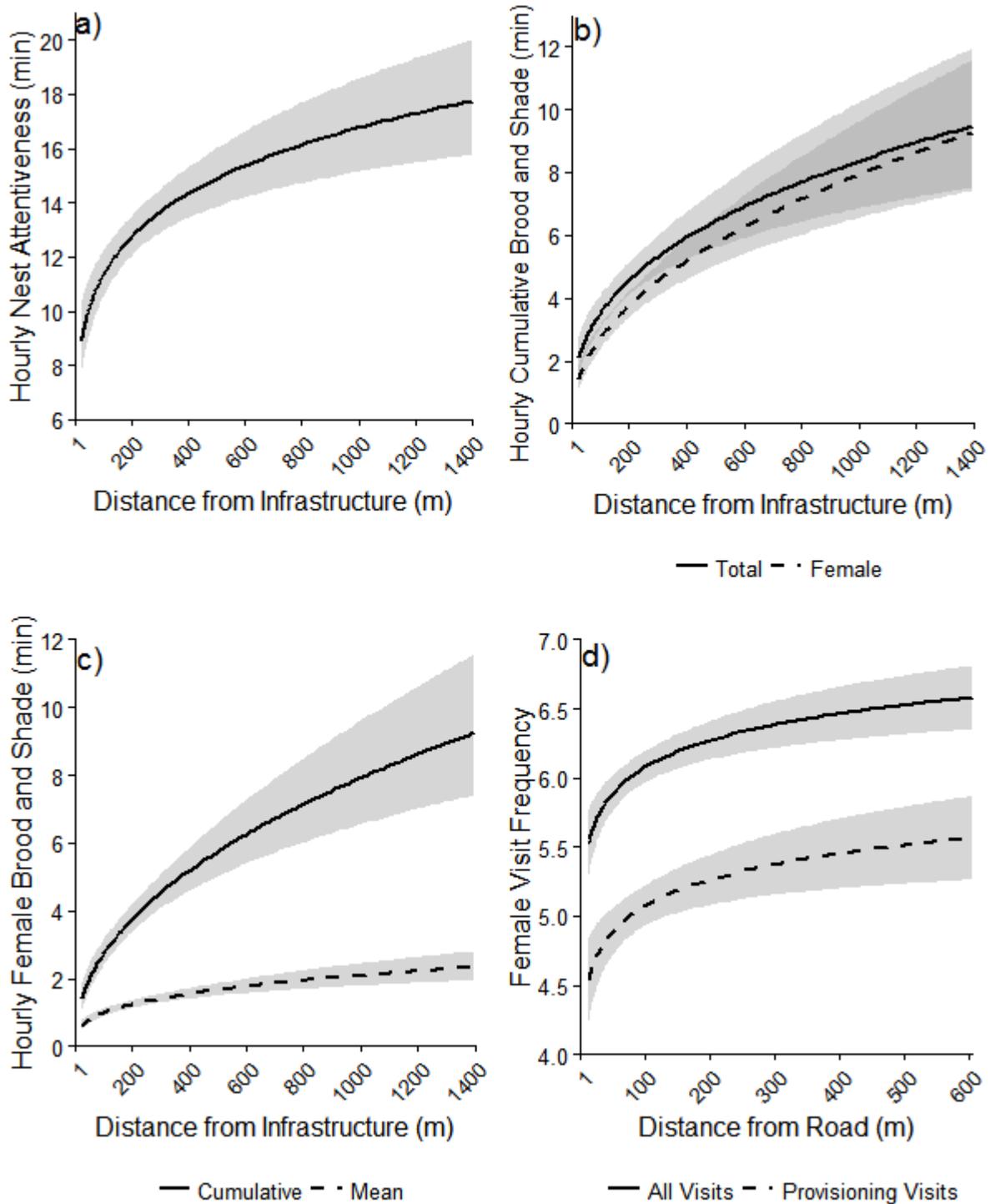


Figure 3.3. Significant effects of anthropogenic disturbances on nestling stage behaviours of chestnut-collared longspur (*Calcarius ornatus*) in southeastern Alberta in 2013 and 2014 included effects of distance from conventional oil and gas infrastructure on a) nest attentiveness, b) cumulative brood and shade, and c) cumulative and average length of female brood and shade bouts, and effect of distance from road on d) female visitation and provisioning frequency. Grey fill indicates 95% confidence intervals.

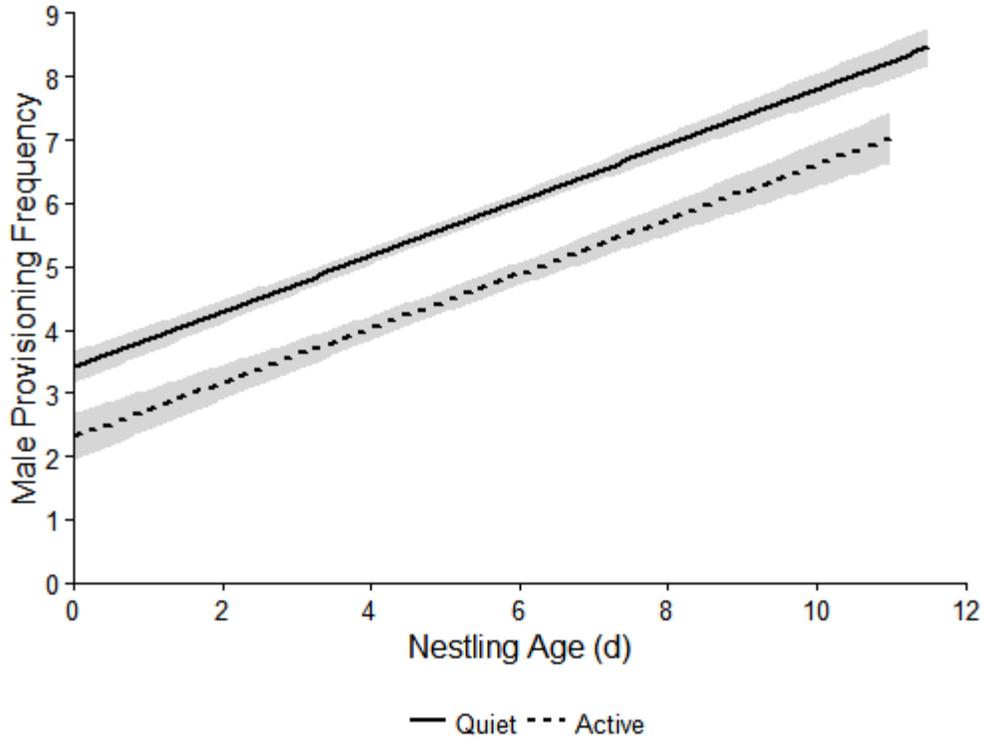


Figure 3.4. Effect of industrial noise from active conventional oil and gas infrastructure on male chestnut-collared longspur (*Calcarius ornatus*) hourly nestling stage provisioning frequency by nestling age in southeastern Alberta in 2013 and 2014. Grey fill indicates 95% confidence intervals.

3.3.4 Effects of anthropogenic disturbance on fledging

The average age of fledging per nest was lower farther from roads ($\beta = -3.221$, SE = 1.584, $p = 0.088$) (Figure 3.5a). Nests 600 m away from roads fledged almost a day earlier than nests within 100 m of roads. More nestlings fledged on average from nests farther from roads ($\beta = 2.509$, SE = 0.830, $p = 0.009$) (Figure 3.5b). On average, nests within 50 m of roads failed or produced only one fledgling. At 150 m, nests produced an average of two fledglings, and nests at 500 m away and farther produced three fledglings. Fledging was unaffected by infrastructure or noise (see Table 3.1).

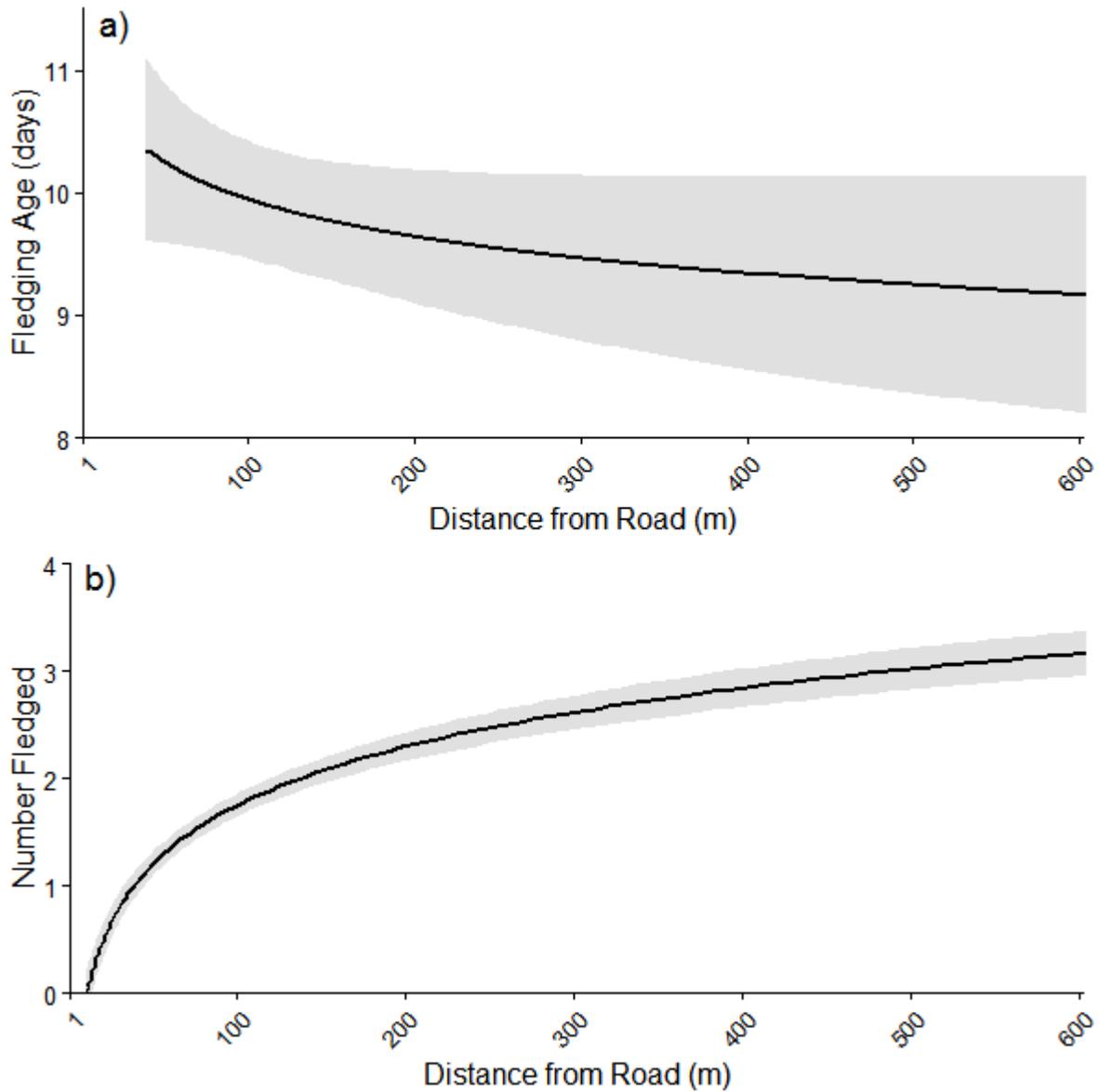


Figure 3.5. Effects of roads on chestnut-collared longspur (*Calcarius ornatus*) fledging in southeastern Alberta in 2013 and 2014: a) mean fledging age, and b) number fledged per nest. Grey fill indicates 95% confidence intervals.

3.4 Discussion

Industrial activity can trigger unnecessary or detrimental behavioural trade-offs in songbirds by altering their perception of risk, which may have long-term fitness consequences (e.g. Schroeder et al. 2012). Chestnut-collared longspurs consistently reduced parental care in the presence of conventional oil and gas infrastructure, roads, and industrial noise, in partial accordance with my incubation stage predictions, although opposite to my nestling stage predictions. Two mechanisms may explain these behavioural modifications. One mechanism may be heightened perceived rather than actual predation risk, as longspur nest success is apparently unaffected by these three disturbances (Bernath-Plaisted and Koper 2016). Heightened perceived risk from anthropogenic disturbances such as chronic noise can trigger antipredator behaviours and increase reactivity to potential threats (e.g. Owens et al. 2012; Meillère et al. 2015; Antze 2016). Alternatively, it is possible that predation risk is indeed higher in the presence of roads and oil wells, but longspurs' behavioural plasticity was successful in compensating for this change. Physical infrastructure seems to increase predation risk in other species of this region, as the nests of co-occurring species were depredated more frequently at oil well and compressor station sites in southeastern Alberta (Bernath-Plaisted and Koper 2016). Longspurs may have been able to avoid similar increased nest predations because they reduced both activity near nests (consistent with Skutch's hypothesis) and presence at nests. Longspurs' behavioural changes in response to the different anthropogenic disturbances are likely caused by a combination of both perceived risk and increased predation risk. As grassland songbird nests in this region were not less successful in the presence of roads or noise (Bernath-Plaisted and Koper 2016), perceived risk may be the underlying mechanism at these disturbances.

3.4.1 Effects of oil wells and compressor stations on behaviour

Anthropogenic structures and energy extraction may attract relatively high abundances of predators, including Accipitriformes, Falconiformes, and rodents (Benítez-López et al. 2010; Hethcoat and Chalfoun 2015b), which may be the drivers behind the changes in both male and female longspur behaviour in the presence of oil wells and compressor stations. Species of all three orders have been documented to depredate longspur nests (Bernath-Plaisted 2015), and several of these species also prey on adults (Bleho et al. 2015). Reduced nest attentiveness and brooding in the presence of a predator is one strategy parents can use to minimize risk to themselves. Especially when the threat is a predator of adult birds, parents often prioritize their own safety above the temporary well-being of their nestlings (e.g. Tilgar et al. 2011; Neiderhauser and Bowman 2014). However, this trade-off can be prevented if conditions are otherwise favourable; for example, Florida scrub jays (*Aphelocoma coerulescens*) did not reduce their brooding in the presence of a predator decoy when also supplemented with food (Niederhauser and Bowman 2014). Though both male and female longspurs brood and shade, females carried out the majority of this responsibility (Figure 3.3b), so the decrease in nest attentiveness near infrastructure can be partially attributed to the decreased amount of brooding and shading provided by females.

The longer incubation stage recess bouts by females may partially be explained by male behaviour. Male mate provisioning during incubation is hypothesized to improve the duration and quality of incubation by reducing the females' need to forage, resulting in higher incubation attentiveness and shorter recess bouts (e.g. Matysioková et al. 2011), consistent with my results (see Chapter 4). Male longspurs reduced their support of incubating females as proximity to infrastructure increased, which may have caused the females' longer recess bout mean; therefore, the extended absences shown by incubating females may be both a direct and an indirect effect

of infrastructure. Mate provisioning behaviour can change with predation risk (Ghalambor and Martin 2002; Fontaine and Martin 2006; Matysioková et al. 2011) and habitat quality (Zanette et al. 2000), both of which may be impacted by the presence of infrastructure. Because nests were left unattended longer during both incubation and nestling stages, nests close to infrastructure may be more vulnerable to depredation, especially by small predators longspurs may be able to actively defend nests against, such as rodents (Lynn et al. 2002; Pietz and Granfors 2005) and potentially even carnivores and snakes (Pietz and Granfors 2005; Ellison and Ribic 2012).

3.4.2 Effects of roads on behaviour

Female longspurs reacted somewhat differently to the presence of roads than they did to infrastructure, primarily reducing their activity levels with increasing proximity to roads instead of reducing their presence at nests. Like infrastructure, roads and edges promote generalist predators (Chalfoun et al. 2002; Benítez-López et al. 2010). It is likely that roads represent a different risk to birds than physical infrastructure because while oil wells and compressor stations disrupt the horizon and provide elevated perches for avian predators and brood parasites, roads disrupt the landscape linearly, creating edges and mammalian travel corridors, increasing adult mortality rates, and fragmenting the landscape (Frey and Conover 2006). Occasional traffic may also pose a more frequent and unpredictable disruption than maintenance at active infrastructure. Therefore, it is not surprising that songbirds may require different behavioural strategies to compensate for oil wells and compressor stations compared with roads.

Female longspurs reduced their nestling stage visit and provisioning rates when their nests were near roads, a strategy that suggests prioritizing their own safety or offspring safety over nestling development, consistent with Skutch's hypothesis of minimizing activity to avoid depredation. For example, reduced provisioning is a common response to inflated perceived

predation risk (e.g. Dunn et al. 2010; Zanette et al. 2011; Bonnington et al. 2013). However, reduced provisioning is not a viable strategy over an extended period, as this reduction prolongs the nesting period, during which offspring are vulnerable and dependent in a nest (e.g. Bjørnstad and Lifjeld 1996). In addition, severely reduced provisioning may cause offspring mortality (Zanette et al. 2011; Greggor et al. 2017) or delayed growth among surviving offspring resulting in smaller and weaker fledglings (Metcalf and Monaghan 2001; Dunn et al. 2010; Zanette et al. 2011). Roads also fragment the landscape, indirectly causing songbirds to reduce provisioning frequency. Both eastern yellow robins (*Eopsaltria australis*; Zanette et al. 2000) and female spectacled tyrants (*Hymenops perspicillatus*; Pretelli et al. 2016) reduced provisioning frequency in more fragmented landscapes.

Females lengthened their recess bouts when close to both infrastructure and roads, but near roads there was no concurrent increase in male mate provisioning to explain this change. Recess lengths are partially dictated by effort needed to self-forage before the female resumes incubating (Conway and Martin 2000), and food-supplemented females typically improve their attentiveness or bout length (Pearse et al. 2004; Boucaud et al. 2016). As grassland songbirds are generally not food-limited (Kennedy et al. 2008), the longer absences of females nesting near roads are probably not driven by a greater need to forage. Therefore, the longer recess bouts of females near to roads are likely a direct response to perceived risk, and again, leave eggs more vulnerable to depredation.

3.4.3 Effects of industrial noise on behaviour

Surprisingly, none of the effects of physical infrastructure can be attributed to industrial noise as there was no overlap in observed behavioural modifications between the two disturbances. For example, while males decreased their frequency of mate provisioning near

infrastructure, they mate-provisioned more frequently in the presence of noise (Figure 3.1c), so the effect of infrastructure was not caused by its noise. These results support the idea that physical infrastructure and noise must be managed separately when mitigating the effects of development.

Beyond the effects of mate provisioning on incubation parameters and hatching success, mate provisioning is generally poorly studied, especially in response to disturbance and risk. Males adjusted their nestling provisioning in the presence of noise only, with no change near infrastructure. Male longspurs provisioned nestlings less in the presence of noise, a response that to my knowledge has not been documented in any other songbird species. A study on the effects of generator noise on house sparrows (*Passer domesticus*) found that only females reduced their provisioning in the presence of noise (Schroeder et al. 2012), while a study on Savannah sparrows found parents increased provisioning rate when exposed to active compressor stations (Antze 2016). Unlike house sparrows, where male provisioning behaviour is relatively constant (Nakagawa et al. 2007), both male and female longspurs exhibited flexible provisioning frequencies in my study. While it is possible that noise masked nestlings' begging calls, resulting in reduced provisioning, it seems probable that this explanation would have affected both male and female provisioning. The impact of noise may have fitness consequences as male-specific provisioning may impact nestling body mass (Ardia 2007). While males showed a mix of positive and negative changes in the presence of noise, the detrimental impact of reduced male provisioning at nestling stage probably outweighs the benefits of increased mate provisioning during incubation, especially as the latter did not result in females demonstrating concurrent changes in incubation behaviour in the presence of noise.

Nocturnal attentiveness may be affected by the presence of noise. When I excluded two nights of nocturnal footage where females failed to incubate through the majority of the night, females spent less time incubating overnight at active sites. This result may be because females breeding under chronic noise are more vigilant and are disturbed more easily (Meillère et al. 2015), causing them to settle down later at night and leave earlier in the morning. Reduced nocturnal attentiveness may increase nest vulnerability to nocturnal and crepuscular predators such as rodents.

3.4.4 Sex-based differences in behavioural responses

Male and female longspurs appear to be sensitive to different features associated with energy extraction. For example, at nests near roads females consistently reduced parental care while males failed to adjust any behaviour. Males of some species are possibly less sensitive to perceived risk than females (see also Florida scrub jays: Niederhauser and Bowman 2014). This explanation may also explain the lack of any male-specific behavioural change during nestling-stage in response to infrastructure. Conversely, males appear to be more sensitive to industrial noise. Males may have altered their behaviour in noisy environments because they rely heavily on acoustic communication after the courtship stage. Male longspurs are responsible for maintaining territory boundaries, typically through direct confrontation, perched singing, or aerial song displays (Harris 1944). High levels of ambient noise may have impacted the ability of territorial males to respond appropriately to acoustic cues. For example, high levels of broadband and low frequency noise impaired the ability of Savannah sparrows to distinguish between biologically relevant and irrelevant sounds, causing parents to delay provisioning in response to both alarm calls and the nonthreatening song of a co-occurring species (Antze 2016). In addition, noisy environments created by compressor stations can also delay the response of territorial

males to conspecifics' songs, possibly because males are unable to quickly identify the song as belonging to a conspecific, or because they are unable to easily locate the source location (Kleist et al. 2016). Consequently, males may spend more time on territory defence, reducing the amount of time they can spend parenting. As female behaviour was only minimally affected by noise, changes in male behaviours are likely due to acoustic masking rather than distraction. Because males and females carry out different roles during the breeding season, it is unsurprising that different aspects of energy extraction affect their behaviour.

3.4.5 Effects of energy extraction on fledging

In contrast to my predictions, fledging age was higher closer to roads and was unaffected by infrastructure or noise. Together with the lower number of nestlings fledged near roads, these results suggest that the underlying mechanism behind fledging effects is the female response to roads. Female provisioning was lower in the presence of roads, and a prolonged nesting period is consistent with the idea that female provisioning affects nestling growth rate (Ardia 2007). Reduced female provisioning may have directly affected number fledged by increasing nestling mortality (Greggor et al. 2017). Additionally, initial clutch size may have been reduced near roads as a result of females' perception of risk (Bernath-Plaisted, unpublished data). Clutch size, egg mass, hatching success, nestling condition, and nestling mortality may all be adversely affected by females' perception of risk, and in combination, these can lead to significant a reduction in number fledged (Zanette et al. 2011; Hua et al. 2014). Alternatively, fledging effects could have been caused by higher rates of parasitism or disease near roads, though preliminary studies suggest low rates of blood parasites in this system (Des Brisay, unpublished data), and few nests in this study experienced death by natural causes other than predation ($n_{\text{nests}} = 3$).

3.4.6 Management implications

Conventional oil and gas development in the grasslands alters the perception of risk across the landscape, significantly impacting the reproductive behaviour of chestnut-collared longspurs. This study demonstrates that longspurs can exhibit behavioural plasticity to reduce some of the perceived and actual risk, though likely with long-term fitness consequences. Managers must consider the effects of physical oil and gas infrastructure, roads, and industrial noise if they are to better mitigate the negative impacts of energy extraction on grassland birds as all three disturbances caused significant behavioural modifications. To reduce the effects of infrastructure, managers should remove the overground structures of dry and abandoned wells as soon as possible, though work should not be conducted during breeding seasons to avoid disturbing parents at nests. Elevated perches should also be minimized, and the installation of overhead transmission lines should be avoided. As the effects were most pronounced within 400 m of infrastructure, managers should aim to cluster infrastructure where possible to leave larger tracts of land undisturbed and reduce the mileage of access roads needed (see Thompson et al. 2015). To minimize the impacts of roads on reproductive success, construction of gravel access roads should be limited, and access roads leading to abandoned oil wells should be reclaimed and reseeded with native vegetation. Alternative technologies can be used to reduce amplitude of industrial noise, and sound barrier walls can also limit the extent of compressor station noise (Francis et al. 2011).

3.5 Conclusion

As we learn more about how anthropogenic disturbances and reproductive behaviour intersect to impact reproductive fitness, it becomes obvious that nonlethal trade-offs have the potential to cause cascading effects on long term population health. Managers should consider monitoring reproductive behaviour of focal species when assessing effectiveness of disturbance

mitigation regimes, as changes in reproductive strategies may predict future population trends. I found that energy extraction contributed directly and indirectly to behavioural changes in a threatened songbird species, resulting in a consistent reduction of parental care that lowered reproductive success. I was also able to confirm that the effects of physical infrastructure and noise are non-overlapping; these represent separate disturbances that must both be managed. If managers remove unnecessary infrastructure from the landscape and limit access roads in addition to mitigating noise, parental behaviour and fledging success of chestnut-collared longspurs may be less disrupted.

3.6 Literature cited

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CHAPTER 4: SUPPORTIVE PARENTS AND DUTIFUL PARTNERS: MALE CHESTNUT-COLLARED LONGSPURS PROVIDE CONSISTENT CARE THROUGHOUT THE PARENTAL PERIOD

Abstract

Biparental care is a well-known aspect of chestnut-collared longspur (*Calcarius ornatus*) reproductive behaviour, but little research has focused on the relative contributions of males across the parental period, from incubation to fledging. I examined the reproductive behaviour of chestnut-collared longspurs in southeastern Alberta in 2013 and 2014 by using nest cameras to continuously record activity at 28 nests during both incubation ($n_{\text{nests}} = 12$, $n_{\text{daylight hours}} = 564$, $n_{\text{nights}} = 30$) and nestling ($n_{\text{nests}} = 25$, $n_{\text{hours}} = 962$) stages. I found that males consistently provisioned their mates with food during the incubation stage, and did so up to three times an hour. Increased mate provisioning was associated with higher incubation attentiveness and shorter recesses among females. Four males also shielded eggs a total of 20 times. During the nestling stage, males fed nestlings more frequently than females, especially when offspring were younger, though females visited nests more and carried out the majority of the brooding and shading. While both sexes provisioned more frequently to larger broods, males responded to brood size more strongly than females; conversely, as nestlings aged, females increased their provisioning frequency more than males. Males and females provisioned up to 21 and 20 times per hour, respectively. At one nest, the male disappeared six days post-hatch; at this nest, only one out of five nestlings survived to fledge. These results emphasize the consistency and necessity of male parental care in this species.

4.1 Introduction

A long-standing hypothesis to explain the biparental care typical of many socially monogamous bird species is that this reproductive strategy evolved in environments where the support of both parents is necessary for reproductive success (e.g. Wittenberger and Tilson 1980). For example, two parents may be required to meet the brooding (thermoregulatory), nutritional, and protection requirements of young altricial nestlings (Wittenberger and Tilson 1980). Though females of some species are able to compensate in part for male removal (e.g.

snow buntings (*Plectrophenax nivalis*; Lyon and Montgomerie 1985)), the necessity of male care for reproductive success in certain species is hypothesized to explain the apparent testosterone insensitivity found in these species of monogamous songbirds, such as species of the genus *Calcarius* (Hunt et al. 1999; Lynn et al. 2002). In most seasonally breeding and socially monogamous songbirds, high testosterone levels are associated with sexual behaviour and a reduction of parental care. However, Lapland longspurs (*Calcarius lapponicus*) and chestnut-collared longspurs (*Calcarius ornatus*) have some degree of behavioral insensitivity to testosterone during the nestling stage, which allowed males with supplemental testosterone to raise nestlings of similar mass to control males (Hunt et al. 1999; Lynn et al. 2002).

Biparental care is essential for reproductive success in chestnut-collared longspurs (Lynn and Wingfield 2003), a threatened, socially monogamous, and sexually dimorphic songbird (Hill 1997; COSEWIC 2015). During the nestling stage, males brood and provision nestlings, and defend the nest against predators (Hill 1997; Bleho et al. 2015). During incubation, males may provision females (Kirkham and Davis 2013), and have been documented shielding or shading eggs (Wyckoff 1983; Kirkham and Davis 2013). However, the patterns of male behaviour are not well understood, especially during nestling stage, which had never been studied in this species for the entire hatching to fledging period.

Technological improvements have allowed for the use of small, weatherproof, and continuously recording cameras to record activity at longspurs nests with minimal disturbance to the birds. My primary objectives for this study were to quantify male and female parental care at nests during the nestling stage, including brooding and provisioning behaviours, and determine the effects of brood size (number of nestlings) and nestling age on parental care. My secondary objectives were to quantify and determine patterns of male support during the incubation stage,

and to quantify incubation behaviour and determine incubation patterns of female longspurs for comparisons with other populations of this songbird.

4.2 Methods

See section 3.2 for methods.

4.3 Results

4.3.1 Descriptive incubation results

Males at 11 nests ($n = 12$) visited during daytime incubation as many as 4 times in one hour, and males successfully provisioned the female up to 3 times per hour (see Figure 4.1a); the one nest without any male visitation only had two hours of incubation footage recorded prior to hatch, suggesting I had insufficient data to assess male provisioning behaviour at that nest. Males visited their nests a mean of 0.38 times per hour ($SD = 0.68$), and successfully provisioned a mean of 0.20 times per hour ($SD = 0.45$). Males shielded eggs at four nests a total of 20 times, with these bouts lasting up to 10 min 13 s.

Females initiated an average of 2.20 ($SD = 1.65$) incubation bouts were initiated per hour during the day. The mean length of incubation bouts initiated each hour ranged from 4 s to 2 h. The mean length of recess bouts initiated each hour ranged from 12 s to 4 hr 49 min. Females typically incubated throughout the night ($n = 30$ nights), though twice an incubating bird took a recess during the night, and once the female was absent for most of the night and only returned shortly before dawn. Excluding that last event, the latest start of nocturnal incubation was 34 min after sunset, and earliest start of nocturnal incubation was 22 min before sunset. The earliest a female left in the morning was 11 min before sunrise, and the latest a female left was 40 min after sunrise. On average, females began nocturnal incubation 14.13 min past sunset ($SD =$

14.30), and ceased nocturnal incubation 15.48 min past sunrise (SD = 16.46). Nocturnal incubation attentiveness was unaffected by clutch size (see Table 4.1).

Hatching typically occurred in the morning. First detection of hatching (e.g. eggshell removal, see Figure 4.1b) happened as early as 54 min after sunrise ($n = 2$), and as late as 10 hr after sunrise ($n = 1$). On average, hatching began approximately 6.07 hr after sunrise (SD = 3.39, $n = 8$).

a)



b)



Figure 4.1. Images of chestnut-collared longspur (*Calcarius ornatus*) incubation behaviour captured by nest video cameras in southeastern Alberta in 2013 and 2014: a) male mate provisioning incubating female, and b) female removing eggshell fragment from hatching eggs.

4.3.2 Incubation trends

Females generally incubated more with male support. When mate provisioned by males, females exhibited higher incubation attentiveness ($\beta = 3.631$, $SE = 1.662$, $p = 0.029$) and lower mean recess bout length ($\beta = -2.575$, $SE = 0.875$, $p = 0.003$; see Table 4.1). However, higher male visit frequency was correlated with higher incubation frequency ($\beta = 0.375$, $SE = 0.088$, $p = <0.001$).

Time of day affected the majority of behaviours at the nest (Table 4.1). During incubation, hour was positively correlated with incubation frequency ($\beta = 0.366$, $SE = 0.067$, $p = <0.001$) but negatively correlated with incubation attentiveness ($\beta = -5.398$, $SE = 0.830$, $p = <0.001$), male visit frequency ($\beta = -0.025$, $SE = 0.005$, $p = <0.001$), and male provisioning frequency ($\beta = -0.018$, $SE = 0.004$, $p = <0.001$), with no effect on mean incubation or recess bout length. Male egg shielding likelihood may be influenced by hour, but the trend was not significant ($\beta = -0.077$, $SE = 0.048$, $p = 0.104$). Hour*hour was included as a model term and significant for incubation frequency ($\beta = -0.013$, $SE = 0.002$, $p < 0.001$) and incubation attentiveness ($\beta = 0.2119$, $SE = 0.030$, $p < 0.001$). These variables show mirrored relationships with hour, with incubation frequency at a high and incubation attentiveness at a low around 1300 (see Figure 4.2). Julian date had a small effect on incubation frequency ($\beta = -0.035$, $SE = 0.012$, $p = 0.006$). Incubation attentiveness and recess bout mean varied by year (Table 4.1).

Larger clutch sizes were associated with higher incubation attentiveness ($\beta = 6.707$, $SE = 3.205$, $p = 0.050$) and lower recess bout mean ($\beta = -3.593$, $SE = 1.977$, $p = 0.080$). Clutch size had no effect on incubation frequency, male behaviour, incubation mean bout length, or nocturnal attentiveness (Table 4.1).

Table 4.1. Incubation behaviour trends of chestnut-collared longspurs in southeastern Alberta in 2013 and 2014. Models also included anthropogenic disturbance variables (not shown). The “Male Activity” column represents either Male Visit Frequency (“Visit”) or Male Provisioning Frequency (“Prov”). Significant results are bolded, and inapplicable variables are marked with dashes.

	Hour			Clutch Size			Hour*Hour			Date			Year			Male Activity			
	β	SE	p	β	SE	p	β	SE	p	β	SE	p	β	SE	p	β	SE	p	
Incubation Frequency	0.366	0.067	<0.001	-0.258	0.323	0.430	-0.013	0.002	<0.001	-0.035	0.012	0.008	-	-	-	Visit:	0.375	0.088	<0.001
Incubation Attentiveness	-5.398	0.830	<0.001	6.707	3.205	0.050	0.212	0.030	<0.001	-	-	-	-21.132	5.545	0.001	Prov:	3.631	1.662	0.029
Incubation Mean	-0.159	0.106	0.137	-0.530	3.477	0.880	-	-	-	-	-	-	-	-	-	-	-	-	
Recess Mean	-0.051	0.081	0.531	-3.593	1.977	0.080	-	-	-	-	-	-	8.409	2.726	0.008	Prov:	-2.575	0.875	0.003
Nocturnal Attentiveness (outlier)	-	-	-	0.092	0.658	0.889	-	-	-	-	-	-	-	-	-	-	-	-	
Nocturnal Attentiveness (no outlier)	-	-	-	0.015	0.164	0.930	-	-	-	-	-	-	-	-	-	-	-	-	
Male Visit Frequency	-0.025	0.005	<0.001	-0.003	0.085	0.975	-	-	-	-	-	-	-	-	-	-	-	-	
Male Provisioning Frequency	-0.018	0.004	<0.001	-0.034	0.049	0.488	-	-	-	-	-	-	-	-	-	-	-	-	
Male Egg Shielding Likelihood	-0.077	0.048	0.104	-0.953	1.588	0.549	-	-	-	-	-	-	-	-	-	-	-	-	

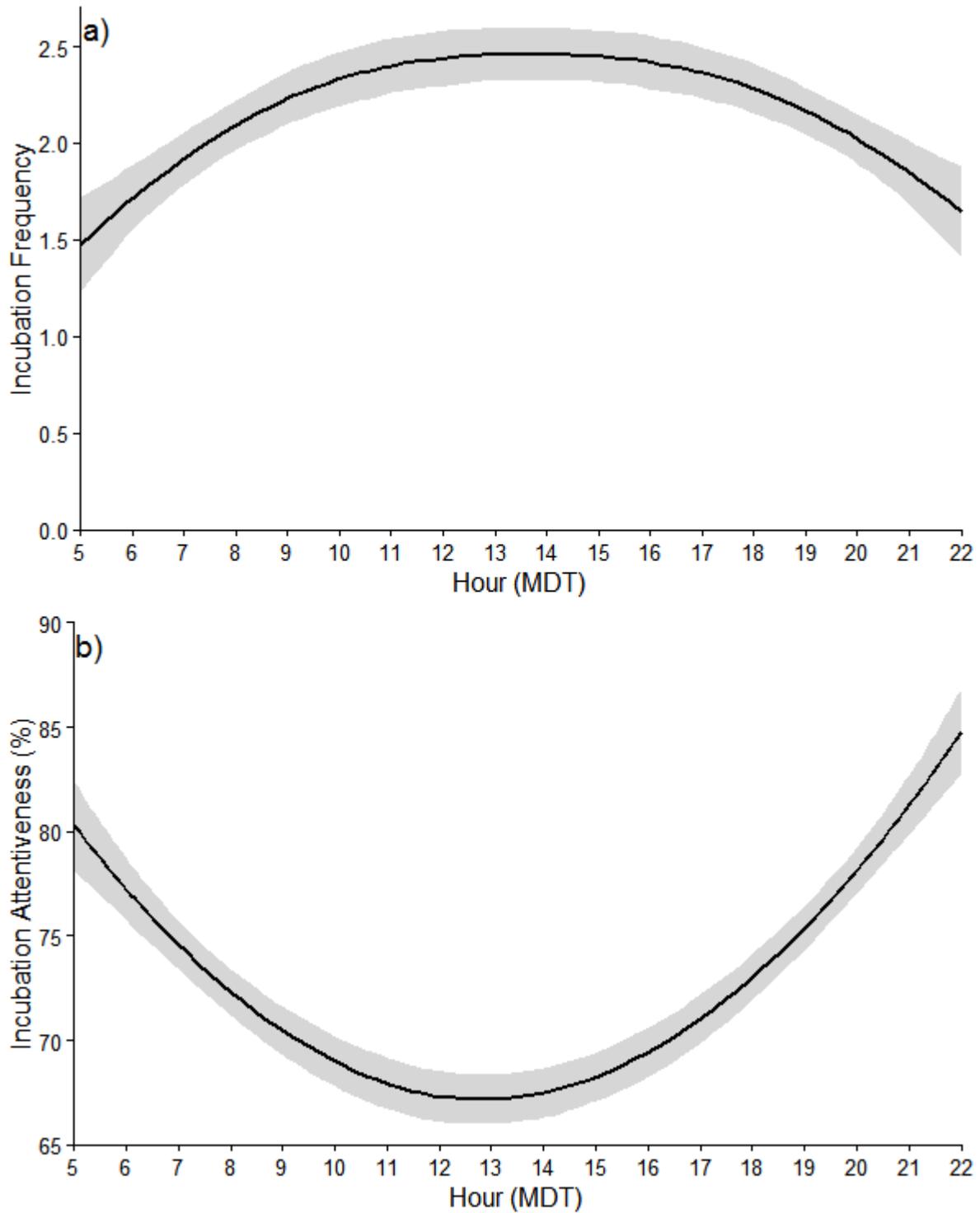


Figure 4.2. Hourly changes in chestnut-collared longspur (*Calcarius ornatus*) incubation behaviour during the day southeastern Alberta in 2013 and 2014: a) incubation frequency, and b) incubation attentiveness. Grey fill indicates 95% confidence intervals.

4.3.3 Descriptive nestling stage results

During the nestling stage, the mean total visit frequency, with both sexes combined, was 12.10 times per hour (SD = 6.38) and the mean total provisioning frequency was 10.55 times per hour (SD = 6.63) (see Figure 4.3a). For males, the mean visit frequency was 5.82 times per hour (SD = 4.07) and the mean provisioning frequency was 5.36 times per hour (SD = 4.04). For females, the mean frequencies for visit and provisioning were 6.12 (SD = 3.63) and 5.11 (SD = 3.82) times per hour respectively. One male abruptly stopped appearing at the nest, possibly due to abandonment or death, so estimates of male effort may be slightly underestimated. The highest number of total visits and total provisioning visits a nest received in an hour were both 35. The maximum male visit frequency and male provisioning frequency were both 21 times in an hour. The maximum female visit frequency was 23 times in an hour, and the maximum female provisioning frequency was 20 times. Females were responsible for 91.4% of all brooding and shading, while males were responsible for 8.1%. The sex of the parent could not be identified for the remaining bouts.

At the nest where the male disappeared the morning of the nestlings' sixth day, the female continued to care for the brood of five, but the overall provisioning rate at the nest was much lower without the male's contributions. For comparison, the mean total provisioning frequency on day five was 20.00 provisioning visits per hour (SD = 2.68), and on day seven it was 11.83 (SD = 2.23). By the tenth day, only one nestling had survived to fledge.

Fledging time and duration were highly variable (Figure 4.3b). Individuals fledged as early as 1 hr 18 min past sunrise and as late as 1 hr 34 min before sunset ($n_{\text{fledglings}} = 33$). The majority of nestlings fledged in the afternoon, with only nine individuals fledging before noon. Cumulatively, the mean fledging time was 9.04 hr after sunrise (SD = 3.75), or 7.17 hr before

sunset (SD = 3.78). Fledging duration, or the difference in fledging time between the first and last individuals in a nest, ranged from 17 s for a brood of three to 45 hr for a brood of four ($n_{\text{nests}} = 10$). Broods of two fledged over an average of 15.77 min ($n = 3$, SD = 25.64), broods of three over an average of 6.64 hr ($n = 3$, SD = 10.97), and broods of four over an average of 19.50 hr ($n = 3$, SD = 22.95). The sole clutch of six fledged over 7 hr 55 min. Cumulatively, the mean fledging duration across all brood sizes was 13.37 hr (SD = 17.96).

a)



b)



Figure 4.3. Images of chestnut-collared longspur (*Calcarius ornatus*) behaviour captured by nest video cameras in southeastern Alberta in 2013 and 2014: a) female with food about to provision nestlings, and b) one day-10 nestling exploring outside nest prior to fledging later that day, with two nestlings still in nest.

4.3.4 Nestling Stage Trends

There were significant differences in parental care between sexes during nestling stage. Visit and provisioning frequencies showed opposite trends, where females visited more ($t = -2.194$, $df = 961$, $p = 0.028$) but males fed more ($t = 1.865$, $df = 961$, $p = 0.063$). Female visit frequency, female provisioning frequency, and number fledged all varied by year (Table 4.2).

Hour was negatively correlated with nest attentiveness ($\beta = -0.103$, $SE = 0.016$, $p = <0.001$) and visit frequency (total: $\beta = -0.278$, $SE = 0.036$, $p = <0.001$; male: $\beta = -0.166$, $SE = 0.022$, $p = <0.001$; female: $\beta = -0.126$, $SE = 0.020$, $p = <0.001$) (Table 4.2). Provisioning frequency, cumulative brood and shade, and brood and shade mean also correlated with hour, though trends were not consistent between total and sex-specific models. Female provisioning frequency increased with hour ($\beta = 0.242$, $SE = 0.119$, $p = 0.042$) while male provisioning frequency decreased ($\beta = -0.169$, $SE = 0.022$, $p = <0.001$). Total brooding and shading behaviours (cumulative: $\beta = -0.182$, $SE = 0.034$, $p = <0.001$; mean: $\beta = -0.019$, $SE = 0.005$, $p = <0.001$) decreased with hour, as did female brooding and shading behaviours (cumulative: $\beta = -0.186$, $SE = 0.036$, $p = <0.001$; mean: $\beta = -0.020$, $SE = 0.006$, $p = <0.001$). Both male cumulative brood and shade ($\beta = 0.073$, $SE = 0.031$, $p = 0.018$) and brood and shade mean ($\beta = 0.061$, $SE = 0.027$, $p = 0.027$) increased with hour, in reverse to how females behaved.

Hour*hour was included in models for several variables, indicating that relationships between these variables and time of day were non-linear. Total and female provisioning frequencies (total: $\beta = -0.018$, $SE = 0.008$, $p = 0.018$; female: $\beta = -0.014$, $SE = 0.569$, $p = 0.005$) declined non-linearly with hour. Total provisioning frequency declined more steeply starting around 1300, and female provisioning frequency did not begin declining until around 1000 (see Figure 4.4a). Nest attentiveness ($\beta = 0.004$, $SE = 0.001$, $p < 0.001$) and cumulative brood and

shade (total: $\beta = 0.007$, $SE = 0.001$, $p < 0.001$; male: $\beta = -0.004$, $SE = 0.001$, $p = 0.002$; female: $\beta = 0.007$, $SE = 0.001$, $p < 0.001$) was lowest at 1100 and 1000 respectively (see Figure 4.4b). Male brood and shade mean ($\beta = -0.003$, $SE = 0.001$, $p = 0.003$) also showed a significant but very weak relationship with the hour*hour term.

Larger broods correlated with higher visit frequencies (total: $\beta = 0.938$, $SE = 0.246$, $p = <0.001$; male: $\beta = 0.740$, $SE = 0.156$, $p = <0.001$; female: $\beta = 0.234$, $SE = 0.137$, $p = 0.088$) and provisioning frequencies (total: $\beta = 1.514$, $SE = 0.241$, $p = <0.001$; male: $\beta = 0.918$, $SE = 0.150$, $p = <0.001$; female: $\beta = 0.547$, $SE = 0.138$, $p = <0.001$), though effects were larger for males. Larger broods were associated with decreased male brood and shade behaviour (cumulative: $\beta = -0.115$, $SE = 0.038$, $p = 0.003$; mean: $\beta = -0.105$, $SE = 0.033$, $p = 0.002$).

Nestling age affected every nestling stage parental behaviour. As nestlings aged, parents made more trips to the nest, resulting in universally higher visit frequencies (total: $\beta = 0.570$, $SE = 0.074$, $p = <0.001$; male: $\beta = 0.227$, $SE = 0.46$, $p = <0.001$; female: $\beta = 0.305$, $SE = 0.041$, $p = <0.001$) and provisioning frequencies (total: $\beta = 0.807$, $SE = 0.072$, $p = <0.001$; male: $\beta = 0.291$, $SE = 0.045$, $p = <0.001$; female: $\beta = 0.515$, $SE = 0.041$, $p = <0.001$) (see Figure 4.4c). Parents spent less time at the nest as nestlings aged (Figure 4.4d), resulting in lower nest attentiveness ($\beta = -0.120$, $SE = 0.012$, $p = <0.001$). All brood and shade behaviour decreased with nestling age, including cumulative brood and shade (total: $\beta = -0.260$, $SE = 0.012$, $p = <0.001$; male: $\beta = -0.145$, $SE = 0.011$, $p = <0.001$; female: $\beta = -0.227$, $SE = 0.012$, $p = <0.001$) and brood and shade mean (total: $\beta = -0.188$, $SE = 0.010$, $p = <0.001$; male: $\beta = -0.127$, $SE = 0.010$, $p = <0.001$; female: $\beta = -0.191$, $SE = 0.011$, $p = <0.001$).

Table 4.2. Nestling stage reproductive behaviours of chestnut-collared longspurs in southeastern Alberta in 2013 and 2014. Models also included anthropogenic disturbance variables (not shown). Significant results are bolded, and inapplicable variables are marked with dashes.

	Age			Number			Hour			Hour*Hour			Year		
	β	SE	<i>p</i>	β	SE	<i>p</i>									
Visit Frequency															
Total	0.570	0.074	<0.001	0.938	0.246	<0.001	-0.278	0.036	<0.001	-	-	-	-	-	-
Male	0.227	0.046	<0.001	0.740	0.156	<0.001	-0.166	0.022	0.000	-	-	-	-	-	-
Female	0.305	0.041	<0.001	0.234	0.137	0.088	-0.126	0.020	<0.001	-	-	-	-1.674	0.531	0.005
Provisioning Frequency															
Total	0.807	0.072	<0.001	1.514	0.241	<0.001	0.192	0.207	0.356	-0.018	0.008	0.018	-	-	-
Male	0.291	0.045	<0.001	0.918	0.150	<0.001	-0.169	0.022	<0.001	-	-	-	-	-	-
Female	0.515	0.041	<0.001	0.547	0.138	<0.001	0.242	0.119	0.042	-0.014	0.004	0.002	-1.792	0.569	0.004
Nest Attentiveness															
Total	-0.120	0.006	<0.001	0.017	0.019	0.361	-0.103	0.016	<0.001	0.004	0.001	0.000	-	-	-
Brood and Shade Sum															
Total	-0.240	0.012	<0.001	0.030	0.039	0.437	-0.182	0.034	<0.001	0.007	0.001	<0.001	-	-	-
Male	-0.145	0.011	<0.001	-0.115	0.038	0.003	0.073	0.031	0.018	-0.003	0.001	0.002	-	-	-
Female	-0.227	0.012	<0.001	0.026	0.041	0.523	-0.186	0.036	<0.001	0.007	0.001	<0.001	-	-	-
Brood and Shade Mean															
Total	-0.188	0.010	<0.001	0.027	0.033	0.419	-0.019	0.005	<0.001	-	-	-	-	-	-
Male	-0.127	0.010	<0.001	-0.105	0.033	0.002	0.061	0.027	0.027	-0.003	0.001	0.002	-	-	-
Female	-0.191	0.011	<0.001	0.005	0.035	0.887	-0.020	0.006	<0.001	-	-	-	-	-	-
Number Fledged															
Fledged	-	-	-	-	-	-	-	-	-	-	-	-	-1.895	0.693	0.016

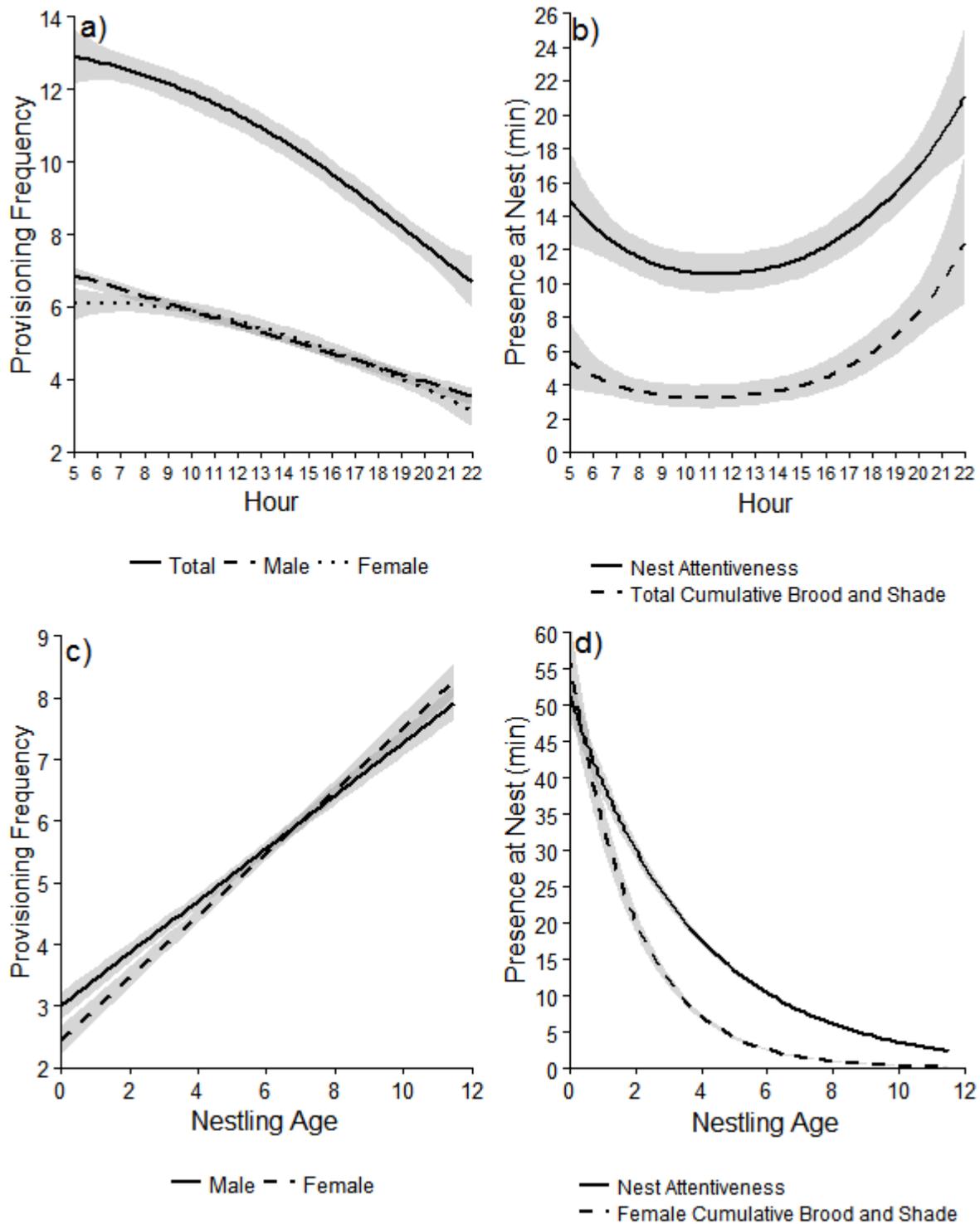


Figure 4.4. Significant effects of hour and age on chestnut-collared longspur (*Calcarius ornatus*) nestling-stage parental behaviour in southeastern Alberta in 2013 and 2014, including effects of hour on a) male and female provisioning frequency, and b) nest attentiveness and total cumulative brood and shade, and effects of nestling age on c) male and female provisioning frequency, and d) nest attentiveness and female cumulative brood and shade. Grey fill indicates 95% confidence intervals.

4.4 Discussion

At my sites with dense oil and gas infrastructure in Alberta, I observed many of the same incubation stage behavioural trends in the chestnut-collared longspurs of a more intact site in southwestern Saskatchewan (Kirkham and Davis 2013). Unlike Kirkham and Davis (2013), not every female in this study incubated throughout every night. Two females took a recess during one night each, and one of these also failed to incubate for one night ($n_{\text{nests}} = 30$). In addition, the incubation attentiveness of Alberta longspurs was higher and followed a slightly different pattern. After adjusting to their incubation parameters, which considered daytime to be between 0500 and 2100, our mean hourly incubation attentiveness was 43.8 min (SD = 11.5) whereas in Saskatchewan incubation attentiveness was 37.3 ± 1.9 min. Additionally, in Saskatchewan, time of day was best explained by a fourth-order polynomial model. The Saskatchewan population experienced two low points of incubation attentiveness at 0900 and 1700, contrasting to our second-order polynomial model with a single low at 1300. We also found an inverse relationship between incubation attentiveness and incubation frequency, though again our population had a single peak incubation frequency at 1400 instead of their dual peaks at 0800 and 1900.

Theory posits that male provisioning would allow females to dedicate more time to incubating instead of self-foraging (Lyon and Montgomerie 1985). My finding that male mate provisioning during incubation increased incubation attentiveness and decreased mean recess bout length is consistent with other studies (e.g. Matysioková et al. 2011). I also found that incubation frequency increased with male visit frequency, but this result may be an artifact as male visit frequency included failed provisioning attempts, when males brought food while the female was absent.

Two decades prior to my data collection, before the widespread use of video technology to record behaviour, another study on chestnut-collared longspurs in southeastern Alberta also found that males provisioned nestlings more than females (Hill 1997). That study also found that females carried out 95% of the brooding (Hill 1997), similar to my observation that females undertook 91.4% of brooding and shading. Since then, other video camera studies on longspur parental care post-hatch appear to be experimental studies that only recorded on certain days, and did not quantify parental care of the control group (e.g. Lynn et al. 2002).

During the nestling stage, one nest experienced either the abandonment or death of the male. Contrary to a previous study that found artificial removal of males always led to nest failure, likely due to predation (Lynn and Wingfield 2003), in our study one nestling of the original five fledged successfully. However, in the experimental study males were removed at day 1 post-hatch (Lynn and Wingfield 2003), whereas at my nest the male stopped appearing on day 6. Perhaps even severely reduced paternal care improved the likelihood for nest success compared to sole maternal care.

A previous study on grassland songbird hatching and fledging durations found that most chestnut-collared longspurs fledged in the morning (Pietz et al. 2012, $n_{\text{fledglings}} = 13$), but my study found that longspurs fledged throughout the day, and on average fledged in the afternoon. Additionally, I found a much wider range in fledge durations than in their study. Overall, the mean fledge duration they reported of 15 hr 32 min \pm 5 hr 44 min ($n_{\text{nests}} = 3$) is comparable to the 13.37 hr (SD = 17.96) I observed.

4.5 Conclusion

My results emphasize the importance of biparental care in chestnut-collared longspurs during both incubation and nestling stages. Until recently (Kirkham and Davis 2013), it was uncertain if longspur males mate provisioned during incubation (reviewed in Bleho et al. 2015). Excluding one nest with insufficient footage, every male in this study successfully provisioned during incubation. As mate provisioning was correlated with both incubation attentiveness and shorter recess bouts, mate provisioning should be considered an important reproductive behaviour for this species. Additionally, as with previous studies (Wycoff 1983; Kirkham and Davis 2013), I observed males shielding eggs, with a third of all males in my studies briefly shielding their clutches. Male parental care is clearly also important to fledging success. That male disappearance when nestlings were 6 days old resulted in starvation of 4/5 nestlings emphasizes that biparental care is essential for reproductive success in chestnut-collared longspurs.

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CHAPTER 5: MANAGEMENT IMPLICATIONS

Industrial disturbances such as energy extraction can alter real and perceived predation risks for wildlife. Energy extraction fragments the landscape, introduces artificial perches by way of physical infrastructure and transmission lines, and is associated with invasive vegetation, all of which may cause increased predator abundance (Benítez-López et al. 2010; Nasen et al. 2011; Hethcoat and Chalfoun 2015). Beyond altered predator communities, artificial disturbances may present a form of generalized risk to wildlife, and nonlethal effects of this perceived risk can reduce lifelong reproductive fitness and population health (Frid and Dill 2002). In songbirds, high levels of perceived risk can indirectly contribute to the decline of a population by causing a significant reduction in fledging rate, defined as the number of offspring that successfully leave the nest (Zanette et al. 2011; Hua et al. 2014). Changes in reproductive behaviour and strategy are an example of nonlethal effects of disturbance that were difficult to study before the use of continuously recording nest cameras became more practical and accessible.

The presence of conventional oil and gas infrastructure, roads, and industrial noise all impacted chestnut-collared longspur incubation and parental behaviour, indicating that these disturbances likely altered how longspurs perceived risk. In addition, nests near roads took longer to fledge and fledged fewer offspring. The reduction in parental care associated with energy development may affect the quality of fledglings and their chances at successfully surviving to reproductive age.

A reproductive strategy that favours parental fitness over the current reproductive effort in risky environments may result in an ecological trap if the source of risk, for example industrial activity, lasts longer than the lifespan of the longspurs. Longspurs, which were initially attracted to the desirable nesting habitat of rotationally-grazed pastures of native vegetation (Owens and

Myres 1973), may fail to produce high-quality offspring, or worse, fail to reproduce at replacement rate in the presence of industrial development. This reduced reproductive output will be especially damaging if well density continues to increase in the otherwise relatively intact mixed-grass prairies of southeastern Alberta. We should aim to reduce these behavioural changes by mitigating the effects of physical infrastructure, roads, and industrial noise, and preventing both artificially inflated perceived risk and the opportunity for novel or generalist predators to move in. Developing new wells on multi-bore well pads may be preferable to several new single-bore well pads as multi-bore pads have a smaller footprint per well, and multi-bore pads require fewer access roads (see Fig. 4, p. 88 in Thompson et al. 2015). Overall, industry should aim to minimize the placement of new wells and especially new transmission lines and access roads in otherwise minimally disturbed large patches of native prairie.

My results suggest that even inactive wells negatively impact these songbirds. Therefore, where possible, non-operational infrastructure should be disassembled and removed before the next breeding season and well pads and access roads should be reclaimed with native grasses. Inactive pumpjacks are a common sight in Newell County and the surrounding area, and are an unnecessary disturbance. As Alberta legislation requires that surface infrastructure and well pads must be removed within 12 months of operation abandonment (Alberta Energy Regulator 2016), tighter enforcement of industry regulations by provincial and federal government agencies may be required to better protect the threatened longspurs. Finally, noise mitigation strategies should continue to be developed and used. For example, sound barrier walls around compressor stations can limit the spread of noise and reduce the impact of compressor stations on breeding songbirds (Francis et al. 2011); perhaps a similar strategy can be used for the smaller screw pumps, which

may impact grassland specialists more than larger pumpjacks (Bernath-Plaisted and Koper 2016; Nenninger 2016).

Chestnut-collared longspurs are one of several grassland specialists in this region listed as threatened or of special concern by COSEWIC. Co-occurring listed species include burrowing owls (*Athene cunicularia*; endangered), long-billed curlews (*Numenius americanus*; special concern), Baird's sparrows (*Ammodramus bairdii*; special concern) and Sprague's pipits (*Anthus spragueii*; threatened) (COSEWIC 2015). Of the three songbird species, longspurs appear to be the least sensitive to industrial disturbance, sometimes showing no or reduced effects on abundance or nest success even in sites where heterospecifics show a decline (e.g. Linnen 2008; Daniel 2015; Nenninger 2016). Despite longspurs' apparent relative resilience, they exhibited significant behavioural shifts in the presence of infrastructure, roads, and noise. Other grassland specialists may show more extreme changes in parental behaviour, possibly resulting in even more severe impacts on fledging rate, contributing to their continuing population declines (Sauer et al. 2014).

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APPENDIX I

Distribution of sites where chestnut-collared longspur nest footage was collected across County of Newell, in southeastern Alberta, between 2013 and 2014, as part of a study on the effects of oil and gas infrastructure and roads on reproductive behaviour. Brooks, Alberta is marked with a star. Map data © 2016 Google, Landsat, Copernicus.



APPENDIX II

Summary of footage collected from chestnut-collared nests from a study on the effects oil and gas infrastructure, roads, and noise on reproductive behaviour in southeastern Alberta in 2013 and 2014.

Type	Site	Noise	Nest ID	Year	Infrastructure Distance (m)	Road Distance (m)	Incubation Days	Incubation Hours	Incubation Nights	Nestling Days	Nestling Hours
Control	C1	Quiet, control	JSD14	2014	802	338	5	66	4	8	48
Control	C34	Quiet, control	JSD50	2014	252	527	0	0	0	4	22
Control	C34	NA [†]	NS23	2013	760	14	2	27	1	8	44
Control	C34	NA [†]	RC27	2013	374	413	0	0	0	9	51
Control	C35	Quiet, control	HN25	2014	1158	400	0	0	0	7	40
Control	C38	Quiet, control	JSB77	2014	1398	84	0	0	0	7	39
Compressor	59	Quiet, disassembled	KH33	2013	494	604	0	0	0	7	41
Screw pump	129	Quiet, inactive	CN80	2014	206	214	0	0	0	4	24
Screw pump	129	Quiet, inactive	JSB72	2014	48	176	0	0	0	3	18
Screw pump	129	Quiet, inactive	JSD22	2014	24	127	0	0	0	6	30
Screw pump	247	Quiet, inactive	GV2	2014	298	39	0	0	0	1	5
Screw pump	247	Quiet, inactive	JRK3	2014	358	57	2	17	1	2	12
Pumpjack	79	Quiet, inactive	JSB35	2013	166	15	3	33	2	10	57
Pumpjack	79	Quiet, inactive	JSB44	2013	325	31	0	0	0	1	6
Pumpjack	363	Quiet, inactive	JSB38	2013	170	182	2	32	1	10	60
Pumpjack	363	Quiet, inactive	KP11	2014	138	156	1	2	0	9	54
Pumpjack	402	Quiet, disassembled	JW55	2014	190	199	0	0	0	7	42
Pumpjack	402	Quiet, disassembled	LL3	2013	196	207	5	67	4	0	0
Compressor	34	Active	GV4	2014	374	141	0	0	0	9	52
Compressor	34	Active	RC44	2013	363	45	1	2	0	11	66
Compressor	53	Active	TS25	2014	237	23	0	0	0	7	42
Screw pump	80	Active, generator	CN82	2014	200	151	0	0	0	4	24
Screw pump	80	Active, generator	GV20	2014	54	155	0	0	0	3	16
Screw pump	247	Active, generator	LV24	2013	312	11	6	98	5	0	0

Type	Site	Noise	Nest ID	Year	Infrastructure Distance (m)	Road Distance (m)	Incubation Days	Incubation Hours	Incubation Nights	Nestling Days	Nestling Hours
Screw pump	247	Active, generator	LV27	2013	108	58	3	33	2	10	66
Screw pump	247	Active, generator	RC48	2013	316	14	9	152	8	0	0
Screw pump	401	Active, electric	JW16	2014	110	115	0	0	0	8	43
Total per quiet sites [†]							18	217	12	86	498
Total per active sites							22	320	17	63	369

[†] Two control site nests were excluded from noise analyses due to their relative proximity to non-focal infrastructure.

APPENDIX III

Two examples of camouflaged nest cameras facing nests. Circles indicate position of nests.



APPENDIX IV

Chestnut-collared longspur incubation behaviour model comparisons by ΔAIC_c for a study on the impacts of oil and gas infrastructure, roads, and noise from southeastern Alberta in 2013 – 2014. The models with the best fit are bolded.

	K	AIC_c	ΔAIC_c
Incubation Frequency ~ Hour + Clutch + Infrastructure + Road + Noise + (1 Nest.ID)			
Basic	8	1925.74	43.11
Male Visit	9	1912.30	29.67
Male Provisioning	9	1923.02	40.39
Hour*Hour + Mate Provisioning	10	1886.24	3.61
Date + Mate Provisioning	10	1908.32	25.68
Year + Mate Provisioning	10	1914.38	31.74
Hour*Hour + Date + Mate Provisioning	11	1882.64	0.00
Incubation Attentiveness ~ Hour + Clutch + Infrastructure + Road + Noise + (1 Nest.ID)			
Basic	8	4890.28	57.42
Male Visit	9	4892.27	59.41
Male Provisioning	9	4887.35	54.49
Hour*Hour + Mate Provisioning	10	4841.66	8.80
Date + Mate Provisioning	10	4885.77	52.91
Year + Mate Provisioning	10	4878.16	45.30
Hour*Hour + Year + Male Provisioning	11	4832.86	0.00
Incubation Mean ~ Hour + Clutch + Infrastructure + Road + Noise + (1 Nest.ID)			
Basic	8	3644.48	0.80
Male Visit	9	3644.60	0.93
Male Provisioning	9	3646.54	2.87
Hour*Hour	9	3643.68	0.00
Date	9	3645.70	2.02
Year	9	3644.92	1.24

APPENDIX IV (continued)

	K	AIC _c	ΔAIC _c
Recess Mean ~ Hour + Clutch + Infrastructure + Road + Noise + (1 Nest.ID)			
Basic	8	3551.98	9.72
Male Visit	9	3548.72	6.46
Male Provisioning	9	3546.31	4.05
Hour*Hour + Male Provisioning	10	3548.39	6.13
Date + Male Provisioning	10	3548.10	5.84
Year + Male Provisioning	10	3542.26	0.00
Nocturnal Sum (outlier) ~ Clutch + Infrastructure + Road + Noise + (1 Nest.ID)			
Basic	7	39.18	0.00
Date	8	41.80	2.63
Year	8	42.84	3.67
Nocturnal Sum (no outlier) ~ Clutch + Infrastructure + Road + Noise + (1 Nest.ID)			
Basic	7	124.09	0.00
Date	8	127.86	3.76
Year	8	127.85	3.76
Male Visits ~ Hour + Clutch + Infrastructure + Road + Noise + (1 Nest.ID)			
Basic	8	1151.09	0.00
Hour*Hour	9	1153.16	2.07
Date	9	1152.91	1.82
Year	9	1153.08	1.99
Male Provisioning ~ Hour + Clutch + Infrastructure + Road + Noise + (1 Nest.ID)			
Basic	8	678.18	0.00
Hour*Hour	9	679.26	1.09
Date	9	679.55	1.38
Year	9	680.12	1.95
Male Incubation Likelihood ~ Hour + Clutch + Infrastructure + Road + Noise + (1 Nest.ID)			
Basic	8	167.13	0.00
Hour*Hour	9	168.92	1.79
Date	9	167.93	0.79
Year	9	167.48	0.35

APPENDIX V

Chestnut-collared longspur nestling stage behaviour and fledging model comparisons by ΔAIC_c for a study on the impacts of oil and gas infrastructure, roads, and noise from southeastern Alberta in 2013 – 2014. The models with the best fit are bolded.

	K	Total AIC_c	ΔAIC_c	Male AIC_c	ΔAIC_c	Female AIC_c	ΔAIC_c
Visit Frequency ~ Age + Number + Hour + Infrastructure + Roads + Noise + (1 Nest.ID)							
Basic	9	5517.11	0.94	4666.82	0.00	4520.96	6.44
Hour*Hour	10	5518.22	2.05	4668.47	1.65	4520.99	6.47
Date	10	5519.15	2.98	4668.56	1.73	4522.70	8.19
Year	10	5516.17	0.00	4668.79	1.97	4514.61	0.10
Hour*Hour + Year	11	5517.24	1.06	4670.44	3.62	4514.51	0.00
Provisioning Frequency ~ Age + Number + Hour + Infrastructure + Roads + Noise + (1 Nest.ID)							
Basic	9	5484.75	5.41	4638.29	0.00	4515.16	13.74
Hour*Hour	10	5481.18	1.84	4638.76	0.47	4507.63	6.22
Date	10	5486.51	7.17	4640.29	2.01	4516.29	14.87
Year	10	5483.06	3.71	4640.08	1.79	4509.23	7.81
Hour*Hour + Year	11	5479.34	0.00	4640.53	2.25	4501.42	0.00
Nest Attentiveness ~ Age + Number + Hour + Infrastructure + Roads + Noise + (1 Nest.ID)							
Basic	9	1019.23	38.79	-	-	-	-
Hour*Hour	10	980.44	0.00	-	-	-	-
Date	10	1019.56	39.12	-	-	-	-
Year	10	1021.21	40.77	-	-	-	-
Hour*Hour + Date	11	980.84	0.40	-	-	-	-
Hour*Hour + Year	11	982.46	2.02	-	-	-	-

APPENDIX V (continued)

	K	Total AIC _c	ΔAIC _c	Male AIC _c	ΔAIC _c	Female AIC _c	ΔAIC _c
Brood and Shade Sum ~ Age + Number + Hour + Infrastructure + Roads + Noise + (1 Nest.ID)							
Basic	9	2311.32	27.65	2156.13	7.59	2411.30	25.75
Hour*Hour	10	2283.67	0.00	2148.54	0.00	2385.55	0.00
Date	10	2311.72	28.04	2157.88	9.35	2411.54	25.99
Year	10	2313.06	29.39	2157.92	9.38	2413.31	27.76
Hour*Hour + Date	11	2284.14	0.46	2150.27	1.74	2385.86	0.32
Brood and Shade Mean ~ Age + Number + Hour + Infrastructure + Roads + Noise + (1 Nest.ID)							
Basic	9	1842.75	0.00	1930.23	7.11	1942.38	0.00
Hour*Hour	10	1842.86	0.11	1923.12	0.00	1943.56	1.18
Date	10	1844.04	1.29	1932.12	9.00	1943.35	0.98
Year	10	1843.74	0.99	1932.14	9.02	1944.19	1.82
Fledging Age ~ Infrastructure + Roads + Noise							
Basic	5	49.89	0.00	-	-	-	-
Date	6	64.33	14.43	-	-	-	-
Year	6	63.36	13.47	-	-	-	-
Number Fledged ~ Infrastructure + Roads + Noise							
Basic	5	84.48	3.76	-	-	-	-
Year	6	80.73	0.00	-	-	-	-