

**Effects of anthropogenic noise on songbirds and how mitigation may differ in high and
low-income countries**

by

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Abstract

The negative effects of anthropogenic noise on wildlife, particularly birds, have been widely studied but major gaps in scientific knowledge remain. The inequality of information available and studies conducted between the high-income countries of the Global North, and middle- and low-income countries of the Global South is limiting the applicability and implementation of conservation projects. I investigated the effects of noise in two different contexts: effects of noise from oil extraction in the North American grasslands on chestnut-collared longspurs (*Calcarius ornatus*) and effects of noise from urban activity in the Caribbean island of Grenada on house wrens (*Troglodytes aedon*). I tested whether distance from oil development, distance from infrastructure noise, brood size, and parent size and weight affected nestling sex ratio allocation in chestnut-collared longspurs. Large broods were skewed towards male nestlings, and bigger females and older social males reared more male nestlings, indicating that competitiveness and experience may be valuable traits for successful breeding and greater fitness in adults. Male nestlings were also more likely to be produced further from screw pump and silent playback treatments, suggesting that habitat farthest from anthropogenic development favours production of male nestlings. My results suggest that both biological and environmental characteristics interact to regulate sex ratio allocation in my study population. Conservation managers should focus on improved planning to limit landscape fragmentation and reduce the acoustic footprint of oil development. In contrast, I tested whether Grenadian house wrens living in urban and rural areas sing differently. I found that Grenadian house wrens in urban habitats sang shorter introductions, faster trills, and increased the low frequencies of their introductions and whole songs. My result demonstrated that Grenadian house wrens adjusted their song to counteract acoustic masking from anthropogenic noise using some strategies that are unlike their mainland

cousins and adapted for urban environments in Small Island Developing States. Additional research is needed to understand the challenges faced by wildlife in the Global South, including in Small Island Developing States. Conservation efforts in the Global South should focus on education and public outreach that include local and Indigenous communities to create community-based conservation programs and research.

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Dedication

Je dédie ce mémoire à mes parents qui m'ont toujours supporté dans mes ambitions. Il me serait impossible d'être où je suis aujourd'hui sans votre confiance et votre amour. Merci.

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Contributions of Authors

Chapter 3 of this thesis was published in October 2020 and was the result of a collaborative effort. Song recordings were collected by Andrew Horn, Kimberley Wetten, and me. I conducted all song measurements and statistical analyses. I wrote the first draft of this manuscript, which was then edited with the help of Nicola Koper and Miyako Warrington. We also received analytical and editorial advice and help from Claire Curry and Andrew Horn.

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Chapter 1: Introduction

Human alteration of landscapes has been global in scale (McDonald et al. 2008), and species have been negatively affected by the resulting habitat loss and fragmentation. Species are pushed out of their natural habitat and forced to adapt to and cope with their newly modified environments through behavioural and physiological mechanisms (Isaksson et al. 2018). With the increased impacts of anthropogenic surface area cover, human population growth, and increasing resource use, wildlife populations have been decreasing in numbers and extinction rates increasing across many taxa (McDonald et al. 2008, Ceballos et al. 2020). Birds are of special concern because they are vulnerable to environmental changes across both their breeding and wintering grounds. Birds also provide ecological, economical, social, cultural, and recreational services (BirdLife International 2018, Michel et al. 2020).

Avian conservation has been studied more than any other taxon, but still suffers from biases that result in important knowledge gaps (BirdLife International 2018, Devenish-Nelson et al. 2019, Moussy et al. 2021). In particular, although there have been improvements over the past decades, socio-economic and demographic biases in research remain (Freile et al. 2014, Devenish-Nelson et al. 2019, Moussy et al. 2021). The abundance of research conducted and published in and about high-income countries of the Global North is in strong contrast with the scarce literature available from low-income countries of the Global South (Ducatez and Lefebvre 2014, Marzluff 2016, Moussy et al. 2021). The use of the Global South and Global North terminology is controversial because it can be defined in various ways (Mahler 2017, 2018). For this thesis, I use Montgomery et al.'s (2020) definition of the Global South as “countries in South America, Central America, Africa, and Asia that are low and middle income relative to countries in the Global North”. This definition also accommodates the use of the terms high, middle, and low incomes, which are often

used in research because of their more quantitative attribute. Some researchers may prefer to use the Global North and Global South terminology with caution and remove the geographic component of its definition, opting instead for a definition that “address spaces and peoples negatively impacted by globalisation” (Mahler 2018).

Discrepancy in how much research has been conducted between the Global North and Global South regions raises concerns about the applicability of current scientific knowledge and implementation of conservation projects in low-income countries (Montgomery et al. 2020). The Global South faces unique socio-political issues that can make research and implementation of conservation projects challenging (Montgomery et al. 2020, Moussy et al. 2021). For instance, armed conflicts (Gaynor et al. 2016), ineffective governance (Baynham-Herd et al. 2018), and human-wildlife conflicts (Michalski et al. 2020) in the Global South have been shown to negatively affect wildlife. With global population growth, habitat conversion and natural resources demand due to urban development are increasing with potentially devastating consequences for wildlife, particularly in ecosystems of particular biological importance (McDonald et al. 2008, Isaksson et al. 2018). Notably, urban development and human activities produce noise, which can have pervasive effects on the environment (Shannon et al. 2015). Effects of noise have gained attention over the past decades, but more research is needed to understand the significance of species and context, such as a countries’ socioeconomics (Shannon et al. 2015). In this paper, I focus on the effects of noise pertaining to two different contexts: effects of noise from oil extraction in the North American grasslands and effects of noise from urban activity in the Caribbean island of Grenada.

Research needs: Towards a better understanding of the effects of urbanization and noise

By 2050, world-wide population growth is predicted to more than double city land cover, number of automobiles, and fuel demand with the most drastic changes happening in low-income countries (Angel et al. 2011, World Energy Council 2011, Organisation for Economic Co-operation and Development 2019). Human presence and activities associated with urbanization produce noise that can negatively affect wildlife (Laiolo 2010, Kunc and Schmidt 2019, Jerem and Mathews 2021). Anthropogenic noise has been studied since the 1990s with a sharp increase in research published in all taxa in 2011 (Shannon et al. 2015, Marzluff 2016), with most publications studying the effects of noise focus on birds (Shannon et al. 2015, Jerem and Mathews 2021). Sound plays an important role in many aspects of avian biology, making birds particularly susceptible to noise and likely to use a variety of mechanisms to cope with the potentially negative effects of noise (Warren et al. 2006, Laiolo 2010).

In line with global research trends, birds from high-income countries have received more research effort, and studies here have been more likely to focus on behavioural adjustments to noise (Brito and Oprea 2009, Marzluff 2016). Research on urban birds in low-income countries focused proportionally more on changes in abundance, richness, and density in response to noise (Marzluff 2016). Moreover, bird species from the Neotropics, which consist mainly of low-income countries, are among the least studied while being under increasing pressure from urbanization and associated human activities (Lugo et al. 2012, Williams 2013, Ibáñez-Álamo et al. 2017). Neotropical research has tended to focus on just three countries since the 1970s (Freile et al. 2014): in 2011, over 50% of published research on Neotropical bird species was from Mexico, Argentina, and Brazil (Freile et al. 2014). A part of the Neotropics, the hotspot of the Caribbean islands is of conservation concern as almost 50% of the vegetation is vulnerable to urban disturbance (Williams

2013, Devenish-Nelson et al. 2019). Much of the Caribbean islands are underrepresented in the literature, emphasizing the need for research on urbanization and conservation throughout the region (Williams 2013, Freile et al. 2014, Devenish-Nelson et al. 2019).

Effects of noise

Numerous studies have demonstrated that chronic noise reduces habitat quality for animals, particularly for species relying heavily on acoustic signals (Reijnen and Foppen 1995, Peris and Pescador 2004, Bayne et al 2008). Acoustic signals play major roles in avian communication (Bradbury and Vehrencamp 2011). Songs and calls are essential for birds to attract mates (Catchpole 1983, Horn and Falls 1991); demonstrate their quality (Lampe and Espmark 2002); build and maintain social bonds between pairs (Tomaszycki and Adkins-Regan 2005), parents and offspring (Magrath et al. 2010), and among conspecifics (Kalb and Randler 2019); indicate the presence of threats (Leavesley and Magrath 2005, Suzuki 2011); defend their territories (Catchpole 1983, Horn and Falls 1991, de Kort et al. 2009); protect their paternity (Baldassare et al. 2016); and defend resources (Lampe and Espmark 2002, Diniz et al. 2019). Songs are also an integral part of social learning by offspring; songs are innate in some species but learned in others (Brenowitz and Beecher 2005). Offspring can learn songs from adult birds through memorization and imitation that can result in syllable types and repertoires different from the originals (Marler and Peters 1981, Marler and Peters 1982). Song species can also learn songs through their lives (Mountjoy and Lemon 1995). Song learning can lead to the development of long-lasting local dialects that can become indicators of mate quality and influence mating success (Rothstein and Fleischer 1987).

Since different noises are generated by various types of anthropogenic activities, avian communities may demonstrate diverse responses. Therefore, a vast body of literature has focused

on the effects of chronic anthropogenic noise on birds and their implications for conservation (Slabbekoorn and Ripmeester. 2008, Barber et al. 2010, Blickley and Patricelli 2012, Ortega 2012). Noise can affect many aspects of reproductive success and fitness (Halfwerk et al. 2011a, Blickley and Patricelli 2012), for instance, by altering conspecific communication (Langemann et al. 1998) and, in doing so, negatively impact pairing success (Habib et al. 2007) and other aspects of reproduction. In monogamous avian species, noise can deteriorate and weaken bonds between social mates, and alter mate preferences for example, both of which may favor extra-pair behaviours (Swaddle and Page 2007, Huet des Aunay et al. 2014).

To avoid the deleterious effects of noise, birds use a variety of different adaptive strategies. Birds can modify their songs and calls in order to produce sounds outside of the noise's range and, thus, be heard. For example, since noise produced by oil infrastructures - like most anthropogenic sounds - is low-frequency, some bird species increase the frequency of their songs partially or in totality to minimize risks of masking (Francis et al. 2011a). In other species, the males may sing louder because, among other reasons, high amplitude sounds carry over longer distances (Brumm 2004). The duration of songs and individual syllables might be altered as well (Gough et al. 2014). Moreover, noise exposure can have long-term consequences on nestlings and on their calls (Sobrian et al. 1997, Leonard and Horn 2008). Consequently, species with greater song plasticity may be more likely to adapt to anthropogenic noises (Slabbekoorn and Peet 2003, Cunningham and Fahrig 2010, Francis et al. 2011b).

In some species, however, females prefer males with lower-frequency songs, which are more energetically demanding (Halfwerk et al. 2011b). Therefore, males may experience reduced pairing success when singing at high frequencies and may have to adapt their behaviour to counter this problem. For instance, if noise is periodic, such as noise caused by road traffic, birds can shift

their morning chorus to avoid the periods of peak intensity (Ortega 2012). In urban environments, a coping strategy can be to sing during nighttime, a behavioural modification recorded in European robins (*Erithacus rubecula*) (Fuller et al. 2007). However, temporal shifts would be ineffective for birds in chronic noise conditions since noise levels remain stable throughout the day.

Anthropogenic noise can have a variety of additional negative impacts on birds. For example, individuals might be at higher risk of predation (Read et al. 2014), have difficulty finding a breeding partner (Riebel 2003, Habib et al. 2007, Blickley and Patricelli 2012), change their parental behaviour (Platzen and Magrath 2004, Leonard and Horn 2005, Haff and Magrath 2011) and favor vigilance over foraging (Krebs et al. 1997, Quinn et al. 2006). All of those factors may impact reproductive success and fitness (Lind and Cresswell 2005, Blickley and Patricelli 2006, Halfwerk et al. 2011a, Blickley and Patricelli 2012). Consequently, birds that cannot alter their songs to avoid masking may have no other choice but to move to other locations with better quality habitats for nesting and breeding, resulting in a reduction in bird abundance around the source of the noise (Reijnen et al. 1995, Bayne et al. 2008, Francis et al. 2011c).

Given that responses to noise tend to be species-specific, community diversity and composition can be affected (Stone 2000, Francis et al. 2009), which may alter heterospecific interactions. For instance, noise can create settlement patterns around its source based on song parameters (frequency, amplitude, duration) and flexibility (Rheindt 2003; Francis et al. 2009, 2011c), as well as individual quality (Habib et al. 2007). If birds relocate as a result of noise, noise may influence nesting density (Reijnen et al. 1995, Bayne et al. 2008), which may alter depredation risk among other things (Picman 1988). However, studies demonstrate that anthropogenic noise can also act as a protection against predators (Francis et al. 2012).

Chronic noise exposure can result in stressful environmental conditions that can greatly impact songbirds. One measure of stress is levels of corticosterone, a stress hormone in birds and other vertebrate groups. Under typical conditions, corticosterone levels are maintained in homeostasis through physiological processes (Romero et al. 2009). Altered levels of this hormone are, therefore, considered the result of some kind of stimulus that can negatively affect well-being (Romero et al. 2009). Little research has been done specifically on the physiological response to noise in birds, but studies have shown that high levels of corticosterone can, for example, cause delayed hatching in eggs (Rubolini et al. 2005) and anxiety in offspring (Campo et al. 2005). Also, during breeding season, male greater sage-grouse (*Centrocercus urophasianus*) were found to have greater concentrations of the stress hormone, which could be correlated to the population decline of this species (Blickley et al. 2012). However, no hormonal increase was found in California spotted owls (*Strix occidentalis occidentalis*) subjected to anthropogenic noise, but noise amplitude was only 50-60 dB and individuals were exposed for only short-term periods (one hour per day for approximately two weeks, repeated twice) (Tempel and Gutierrez 2003).

Mixed-grass prairie ecosystem

Prairies are among the most threatened ecosystems in North America and their rapid disappearance has important consequences to the biodiversity that relies on them (Bragg and Steuter 1996, White et al. 2000). Habitat loss from land conversion for agriculture and fragmentation due to energy development have contributed to grassland birds declining and continue to threaten grassland populations (Brennan and Kuvlesky 2012, Roch and Jaeger 2014, Allred et al. 2015, Sauer et al. 2017). Grassland birds are of significant concern since almost every obligate grassland species suffered from significant declines in population size over the last half

of the century, and many are now classified as threatened or vulnerable (Sauer et al. 2001, Askins et al. 2007).

In Canada, grassland birds have declined by 57% since 1970, with prairie obligates having declined by 87% (North American Bird Conservation Initiative 2019). According to the North American Bird Conservation Initiative (2009, 2014), populations of some species of grassland songbirds appear to have stabilized from the drastic declines mentioned above because of improved grazing practices and pasture management. However, 74% of grassland species continue to decline due to habitat loss and pesticide use, including the Chestnut-collared Longspur (*C. ornatus*), McCown's Longspur (*Rhynchophanes mccownii*), Sprague's Pipit (*Anthus spragueii*), Western Meadowlark (*Sturnella neglecta*), Bobolink (*Dolichonyx oryzivorus*), Baird's Sparrow (*Ammodramus bairdii*), Lark Bunting (*Calamospiza melanocorys*) (Stanton et al. 2018, Rosenberg et al. 2019).

Energy development for oil and gas exploitation requires the use of infrastructures that modify the physical and acoustic landscapes and can negatively impact grassland birds (Bayne et al. 2008). The chronic noise produced by extraction infrastructures could have particularly pervasive effects because it increases the footprint of infrastructures beyond their physical footprint (Rosa and Koper 2018). For instance, a 50 x 50 m area usually makes up the oil well pad of screw pumps, however, the acoustic footprint of generator-powered screw pumps can reach up to 295 m radius from the infrastructure (Rosa and Koper 2018).

Caribbean ecosystems

The Caribbean, also referred to as the West Indies and Antilles, consist of over a hundred islands in three clusters: the Greater Antilles, the Lesser Antilles, and the Bahamas (Levy 2008,

Lugo et al. 2012). While 2% of the world's plant and vertebrate species are found in the Caribbean, the islands make up less than 0.5% of the world's land (Myers et al. 2000). The Caribbean hotspot has the highest ratio of species per square kilometre throughout the Americas (Myers et al. 2000).

The Caribbean islands' fauna and flora have undergone unique historical changes from human settlement, slave trade, and economic trade (Lugo et al. 2010, 2012). Species, mainly plants, have been introduced and naturalized (Acevedo Rodriguez and Strong 2008, Lugo et al. 2012). Extinctions and extirpations due to habitat loss and conversion for plantations, human-wildlife conflicts, and introduction of non-native species have also been reported (Brash 1987, Woods 1996). Colonization by Spanish explorers and missionaries date back to the early 1500s and the islands were found to be inhabited by various Indigenous groups (Levy 2008). European settlers deliberately introduced various species of birds to the islands, notably turkeys and a variety of waterfowl (Levy 2008). Trade and sell of native and non-native wildlife between islands and mainland countries also became common practice (Levy 2008). In the late 1800s, small Indian mongoose (*Urva auropunctata*) were introduced as a means of pest control in Jamaica (Scott 1903). Mongoose were then introduced to other Caribbean islands where they became invasive as they did in Jamaica (Scott 1903, Levy 2008). To this day, the mongoose remains an invasive species throughout the Caribbean (Louppe et al. 2020, Louppe et al. 2021). Many Caribbean species of reptiles, birds and mammals have been extirpated and gone extinct following the introduction of mongoose (Berentsen et al. 2018). Mongoose are also known carriers of parasites and diseases, including rabies, that can spread to native wildlife (Johnson et al. 2016, Cheng et al. 2018, Jaffe et al. 2018, Shiokawa et al. 2019). The Caribbean's unique wildlife sparked the interest of scientists of that time (Levy 2008, Latta 2012).

Research into the Caribbean's biodiversity and ecosystems prior to the 1970s focused almost exclusively on describing species and their natural history (Levy 2008, Latta 2012). After the 1970s, research focus became more diverse with ecology and genetics garnering particular interest over time (Devenish-Nelson et al. 2019). However, conservation and management studies have recently become more common (Levy 2008, Latta 2012, Freile et al. 2014).

Research objectives

To study the effects of various anthropogenic noise sources on birds living under different ecological contexts and the conservation implications of noise, I will focus my research on a North American grassland obligate, the chestnut-collared longspur (*Calcarius ornatus*) and on the Caribbean island of Grenada's sub-population of house wrens (*Troglodytes aedon*). My objectives are to:

- (i) Determine if industrial chronic noise from infrastructures used for oil extraction and infrastructure presence have an impact on nestling sex ratio allocation of chestnut-collared longspurs.
- (ii) Determine if Grenada's house wrens adjust their songs in urban environments.
- (iii) Determine if variations in Grenadian house wren songs can be explained by the acoustic and physical landscape associated with urban living in Grenada.
- (iv) Assess the differences and challenges of management implications of noise mitigation in high-income and low-income countries.

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Chapter 2. Effects of oil infrastructure and associated noise on nestling sex ratio allocation of Chestnut-collared Longspur (*Calcarius ornatus*)

CONNECTING TEXT

Discrepancies in research effort between the Global North and Global South are common in avian conservation research, especially regarding effects of human activities, urbanization, and anthropogenic noise. Research is needed to comprehend the pressures on birds in contrasting socioeconomic and environmental contexts of the Global North and Global South. In Canada, a high-income country of the Global North, oil development is widespread throughout the prairies and results in chronic noise. The potential for negative effects of anthropogenic noise on the breeding biology and reproductive success of grassland birds is particularly concerning considering many of them are listed as species at risk, including the chestnut-collared longspur (Species at Risk Act 2002).

ABSTRACT

North American prairies have experienced steep declines in land cover due to habitat conversion and fragmentation due in part to oil development. Number of oil wells continues to increase rapidly and pose a threat to wildlife by altering the landscape and soundscape of the prairies. Chronic anthropogenic noise from oil wells could affect aspects of the reproductive biology of birds, such as nestling sex ratio. I investigated the effects of generator-powered screw pumps, a type of oil infrastructure, and associated noise on nestling sex ratio of the chestnut-collared longspur (*Calcarius ornatus*). I isolated noise from infrastructure presence by broadcasting high-fidelity recordings of generator-powered screw pumps in the prairies of Southern Alberta. I used four treatments: generator-powered screw pumps, active playbacks, silent

playbacks, and controls. I assessed whether distance from oil development, distance from infrastructure noise, brood size, and parental factors affected nestling sex ratio. I found that nestlings in large broods were more likely to be males, perhaps to safeguard from variations in reproductive output of male offspring due to intraspecific competition. Also, bigger females and older social males reared more male nestlings, indicating that competitiveness and experience may be valuable traits for successful breeding and greater fitness in adults. Male nestlings were also more likely to be produced further from screw pump and silent playback treatments, suggesting that habitat farthest from anthropogenic development may be better quality or perceived as such by social parents. My results suggest that both biological and environmental characteristics interact to regulate sex ratio allocation in my study population of chestnut-collared longspurs.

INTRODUCTION

Grassland species are of particular conservation concern in North America, having declined 33% - 70% in the past 50 years. Their natural habitat has changed considerably over that period and is continuing to do so (Sauer et al. 2015, North American Bird Conservation Initiative 2016). Historical changes due to European settlement, such as land conversion for agriculture and ranching, have evolved into large-scale intensive monocultures and farming (Samson et al. 2004, Hoekstra et al. 2005, Sylvester et al. 2013). Energy development has since also started taking place throughout North American grasslands (Askins et al. 2007). Infrastructure used for oil extraction - as well as associated features like roads - is becoming more abundant and spread out, resulting in further pressure on grassland ecosystems (Askins et al. 2007).

Oil extraction and associated infrastructure alter landscapes visually and acoustically, resulting in a multitude of negative effects on wildlife (Rosa and Koper 2018). For instance, oil extraction can reduce reproductive success (Halferk et al. 2011), pairing success (Habib et al.

2007), nesting success (Bernath-Plaisted and Koper 2016) and reduced parental care (Ng and Koper 2018). By their physical presence, oil extraction infrastructure can cause avoidance (Thompson et al. 2015) and hypervigilance (Krebs et al. 1997, Quinn et al. 2006). However, the noise produced by infrastructure might add to this disturbance, resulting in particularly large ecological footprints (Rosa and Koper 2018). Noise can mask acoustic signals, forcing species to modify their singing to improve communication (Warrington et al. 2018), although not all species seem capable of song plasticity (Slabbekoorn and Peet 2003, Francis et al. 2011). In birds, noise can impair communication between paired individuals and cause pair bond degradation (Swaddle and Page 2007, Huet des Aunay et al. 2014), and noise can result in deteriorated communication between parents and their offspring (Antze and Koper 2018). Moreover, by altering the acoustic landscape, noise can affect predator communities (Campos et al. 2009, Francis et al. 2009), resulting in increases (Campos et al. 2009, Bernath-Plaisted et al. 2016) or decreases (Francis et al. 2009) in predation rates. Noise can cause predators to avoid areas, limiting predation opportunities, or conceal prey by masking acoustic signals like calls and sounds from movements (Francis et al. 2012). Conversely, noise can also mask sounds made by approaching predators and cause prey to be distracted (Chan et al. 2010).

Environmental variability requires individuals to adapt over both short and long time periods, and North American birds need to have particularly flexible behavioural strategies because they migrate and use different territories seasonally (Doligez et al. 2003, Askins et al. 2007). Since consequences on reproductive success and fitness can be considerable during their short breeding season, it should be expected that birds will make short-term adjustments to their behaviour or reproductive output during that time to improve their own fitness and that of their

young (Hedenström 2007). Among adjustments pairs and individuals could make to their breeding strategies, there is the potential for sex ratio manipulation (Bell et al. 2014, Bowers et al. 2015).

Sex ratios within avian nests are thought to be flexible to optimize offspring quality and viability, which, in turn, benefits parents' reproductive fitness (Trivers and Willard 1973, Whittingham and Dunn 2000). Since male offspring can contribute in greater number to the lifetime reproductive output by proxy of their biological parents, males should be preferable in broods (Trivers and Willard 1973, Whittingham and Dunn 2000). However, male offspring might be more costly to produce (Westneat et al. 2002). Males raised in lower-quality environments and by lower-quality parents have shown decreased fitness compared to their female siblings (Bowers et al. 2015); hence, male-biased broods might not always be advantageous (Trivers and Willards 1973, Bowers et al. 2015). The underlying mechanisms of sex ratio allocation are not well understood (Hasselquist and Kempenaers 2002). Some studies suggest it is random (Westneat et al. 2002), while others point to the influence of environmental conditions (Bell et al. 2014), and others indicate a degree of choice and parental control (Hasselquist and Kempenaers 2002). Females that are older (Blank and Nolan 1983), bigger (Wiebe and Bortolotti 1992), and in better body condition (Nager et al. 1999, Whittingham and Dunn 2000) tend to rear more male offspring. These trends have also been observed with breeding males (Ellegren et al. 1996, Svensson and Nilsson 1996, Kölliker et al. 1999). Pairing of males and females according to their body condition and age can also influence brood sex ratio (Rathburn and Montgomerie 2004, Pryke et al. 2011). Furthermore, pair quality might be a secondary factor in sex allocation when faced with harsh environmental conditions where offspring survival could be jeopardized regardless of parental body condition and experience (Bell et al. 2014, Bowers et al. 2015).

In the Canadian prairies, oil extraction and associated infrastructures have caused habitat loss and fragmentation by their physical and acoustic footprints, possibly creating sub-optimal breeding habitats (Bernath-Plaisted and Koper 2016). The Chestnut-collared longspur is a prairie obligate species breeding in the mixed-grass prairies of Southern Alberta. Populations of chestnut-collared longspurs have declined 95% in the past 50 years (COSEWIC 2019). The species was recognized as ‘Threatened’ and listed under Schedule 1 of the Species at Risk Act (2002). Chestnut-collared longspurs have shown diminished parental care (Ng et al. 2019), but no decline in nest success (Bernath-Plaisted and Koper 2016, Des Brisay 2018, Rosa 2019) in proximity to roads and oil wells. Studies have found contradictory results regarding avoidance of oil infrastructure. Nenninger and Koper (2018) have shown no change in abundance of chestnut-collared longspurs near oil wells, whereas Rosa (2019) found they avoided areas with noise from two types of oil infrastructures: drilling rigs and power-grid pumpjacks. Sex ratio allocation might be adjusted by breeding individuals to compensate for the negative effects of oil development and optimize their fitness potential.

Few studies have investigated the impacts of human development on offspring sex ratio of birds, but diverse types of anthropogenic disturbances have been found to impact offspring sex ratio of birds. For instance, in Algonquin Provincial Park, ovenbirds (*Seiurus aurocapilla*) in undisturbed forests typically reared female-biased broods but when nesting in forests altered by logging adults produced male-biased broods; the shift in sex ratio grew with the intensity level of logging practices (Leshyk et al. 2012). Great tits (*Parus major*) breeding in orchards in southeastern France had fledgling sex-ratios skewed towards females in habitats where more chemical pesticides were used for pest management, which are presumably the most disturbed habitats (Bouvier et al. 2016). However, no effect of pesticide use on offspring sex ratio of white-

crowned sparrows (*Zonotrichia leucophrys*) was found in forests of Western Oregon (Rivers et al. 2017). In the grassland of the Tibet Plateau, nestling sex ratio of Isabelline wheatears (*Oenanthe isabellina*) was more male-biased in areas subjected to low-intensity grazing, which more closely resembles normal grazing by native species, compared to areas ungrazed and with high-intensity grazing (Lin et al. 2018). Prior et al. (2011) found similar effects of grazing intensity on offspring sex ratio of the meadow pipit (*Anthus pratensis*) in Scotland. Moreover, increase in forest fragmentation resulted in a shift from male-biased to female-biased broods of Eurasian treecreepers (*Certhia familiaris*) in Finland (Suorsa et al. 2003). My study is the first to my knowledge to examine the effects of oil development on offspring sex ratio and has the added benefit of a noise experiment component that distinguishes it from most studies on the effects of anthropogenic noise on wildlife.

Changes in sex ratio allocation could inform conservation measures as an indicator of compensatory behaviours in response to environmental disturbances. Avian sex is determined by sex chromosomes Z and W, with females being the heterogametic sex (ZW) and males being homogametic (ZZ) (Ioannidis et al. 2021). Z chromosomes normally carry the DMRT1 gene, which in concert with estrogen, plays a key part in sex determination by causing the development of testes (Ioannidis et al. 2021). Disturbances could cause shifts in nestling sex ratio towards one sex and, as a result, alter the sex ratio of adults in a population and affect reproductive competition (Wilson and Pianka 1963, Clutton-Brock 2017, Kus et al. 2017). For instance, a population with more females may impact mating behaviour, alter population dynamics, and increase male-male competition (Kus et al. 2017, Heinsohn et al. 2018). However, these effects might only occur in areas with small populations of chestnut-collared longspurs, such as the edges of their habitat range, where gene flow might be more limited. Sex ratio adjustment probably acts as a minor

coping mechanism, especially given that the global population of chestnut-collared longspur is estimated over 3 million individuals, with 680 000 individuals in the Canadian population (COSEWIC 2019, Rosenberg et al. 2019).

I used a manipulative, large-scale field of four treatment types to differentiate whether the presence of real oil wells, noise from operating oil wells, and parental factors affect sex ratio allocation in chestnut-collared longspurs. I hypothesized that if oil extraction infrastructure lowers the quality of the environment and makes it more difficult for males and females to provide for their offspring, then sex ratio in disturbed environments should be close to 1:1 or be biased towards female offspring. If noise produced by infrastructure lowers the quality of the environment and makes it more difficult for males and females to provide for their offspring, then sex ratio in noisy environments should be close to 1:1 or be biased towards female offspring. If the quality of the environment is not a limiting factor for offspring condition and male offspring provide greater fitness gain to females, then high-quality females and high-quality males should rear male-biased broods regardless of the environment of their breeding ground.

METHODS

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

Study area and design

My study took place in the mixed-grass prairies of Southern Alberta, in the County of Newell. My study sites were situated on lands belonging to Cenovus Energy and the Eastern

Irrigation District (EID). During the breeding period (May to August) of 2016, I captured adult chestnut-collared longspurs and monitored nests.

To identify the effects of oil extraction infrastructure on sex ratio allocation of chestnut-collared longspurs, I used a playback system to isolate the impacts of oil extraction infrastructures and chronic noise produced. In total, I used four treatment types and 12 64-ha sites (three sites per treatments). Three sites of native prairie, with minimal presence of invasive species, hydrological features, oil wells, and roads, were used as control sites. The second treatment type included real infrastructure at the centre of each site, hereafter ‘active infrastructure.’ I used generator-powered screw pumps because screw pump noise overlaps the frequencies of chestnut-collared longspur vocalizations, resulting in the risk of acoustic masking (Rosa and Koper 2018). Screw pumps are situated on 50 x 50 metre fenced oil well pads and can measure up to 2.7m high. Screw pumps that are generator-powered are louder than those powered by the grid, producing chronic noise of 79 dB(C) at 10 m (Rosa and Koper 2018). For chestnut-collared longspurs, generator-powered screw pumps have an acoustic footprint of energetic masking of 205 m radius and an acoustic footprint of informational masking of 295 m radius (Rosa and Koper 2018). The third treatment (‘active playback’) used a broadcasting system consisting of two speakers positioned north and south powered by four 12 volt batteries connected to five solar panels (Rosa 2015). The solar panels charged the batteries throughout the day so the system could broadcast uninterrupted, even at night. Speakers broadcast high-fidelity WAV file recordings of generator-powered screw pumps stored on media players (Rosa 2015). The speakers, batteries, and media players were placed in wooden boxes to protect them from the elements. The whole broadcasting system was surrounded by technical fences to protect them from disturbance from cattle and native ungulates. The fourth (‘noiseless playback’) treatment complements the active playbacks, allowing us to isolate effects

of noise from the confounding factor of the broadcasting system. The noiseless playback treatment appeared the same as the active playback's system with the distinction that it did not include the broadcasting equipment that would normally be in the wooden box; therefore, it did not broadcast noise. The screw pumps or playback systems, active and noiseless, were used as center-points for those sites, while the centre of the control sites had no infrastructure. Data were collected within a 400-m radius of site center-points. Sites were located at least 800 m from each other or from any other oil well. All oil wells and linear features within a 1000-m radius of sites were mapped.

Data collection

Nest search and monitoring

To locate nests, assistants and I followed individual adult birds that exhibited behaviours indicating the presence of a nest, such as territory defense, mate guarding, flight displays, alarm calling, distraction displays, or food and nesting material foraging. Once nests were found, they were monitored and visited every two days until completion. I considered nests successful when, at a nest visit, an empty nest was found to have no signs of predator disturbance (scats, remains, or other); signs of nestling leaving the nest (such as flattened edges, adults calling in surrounding, adults carrying food); nestling age - at estimated fledgling time - was at least 7 days old (Des Brisay 2018); or presence of fledglings around nests (Martin et al. 1997). During nest monitoring, nest stage (eggs or nestlings), clutch size, and brood size were reported and the age of nestlings was estimated (Jongsomjit et al. 2007). I also approximated nest initiation date considering the incubation period of chestnut-collared longspurs last up to 15 days (Jones et al. 2010).

When possible, adults and nestlings associated with nests were marked and sampled. Nestlings were banded when they were at least 7 days old. Prior to that, nestling would be too

small to ensure the band does not slide off and does not cause injury during growth. Adult males and females were captured at or around nests using active mist netting and drop traps (Sutherland et al. 2004). All individuals were banded with one numbered aluminium band and three colored bands of unique color combination (Environment and Climate Change Canada 2013, US Geological Survey Bird Banding Laboratory 2016).

Sampling and measurements

I collected blood samples and recorded morphometric measurements for all captured adults and 7-day old nestlings. Blood samples of 30 – 40 μL from nestlings and 30 - 70 μL from adults were collected from the brachial vein using capillary tubes and stored in lysis buffer at room temperature (20°-24°C) (Seutin et al. 1991, Longmire et al. 1997). For safety, blood samples never exceeded 1% of body weight (Sheldon et al. 2008). I recorded indicators of body condition and development of nestlings (Table 1). Handling time was restricted to 20 minutes to limit the risk of abandonment by parents.

Table 1. Morphometric measurements and information collected from sampled adults and nestlings that were used during analyses.

Morphometrics and indicators recorded		
Adults and nestlings	Adults only	Nestlings only
Age*	Tail length	Outer primary feather length (P9 length)
Mass	Reproductive status***	Unsheathed outer primary feather length (Unsheathed P9 length)
Tarsus length		
Wing chord length		
Sex **		

* Age was determined based on Pyle et al. (2008).

** Adults were sexed based on plumage because Chestnut-collared longspurs are sexually dimorphic. Genetic testing was used to sex nestlings.

*** The reproductive status of adults was determined using the appearance of the cloacal protuberance or the presence of a brood patch.

Data analysis

Assessing Sex of Nestlings

I extracted DNA from blood samples following Ivanova et al. (2006). I sexed all nestlings using PCR amplification of chromo-helicase-DNA (CHD1) binding genes from avian W and Z sex chromosomes (Griffiths et al., 1998). I used the following PCR mixture: 2.0 μ l 5x reaction buffer (Promega, Madison, WI, USA), 2.0 mM MgCl₂ (Promega, Madison, WI, USA), 0.5 μ M forward primer, 0.5 μ M reverse primer, 0.2 mM deoxyribonucleotide triphosphate (dNTP; each), 1 μ l of 4X BSA (ThermoFisher), 1 U GoTaq Flexi DNA Taq polymerase (Promega, Madison, WI, USA), 1 μ L DNA template, and 4.0 μ L DNA grade ddH₂O (Fisher Scientific, Hampton, New Hampshire) to a final volume of 10.0 μ l per sample. I used the following PCR conditions for amplification: initial denaturation at 94 °C for 2 minutes, followed by 40 cycles at 94 °C for 45 seconds, 48 °C for 45 seconds, 72 °C for 45 seconds, and a final elongation at 72 °C for 5 minutes.

After amplification, a mixture of PCR products and bromophenol blue loading dye was loaded into gel wells before being separated by gel electrophoresis on 1% agarose gels stained with GelRed® (Biotium). Gels ran at 95 volts and 220 amps current for 90 minutes. Gels were viewed under UV lights with a BioRad GelDoc XR+ Imager. Samples showing two bands were designated as females and those with one band were marked as males.

Statistical analyses

Statistical analyses were performed in R Studio (R Core Team 2019). In R Studio, I used the package ‘lmerTest’ (Kuznetsova et al. 2017) to develop linear mixed models (LMM) and generalized linear mixed models (GLMM) and ‘ggplot2’ (Wickam 2016) to test and plot models. Outputs of models were rendered into tables using the R package sjPlot (Lüdtke 2020). When

interpreting results, I used an alpha level of 0.1 to decide significance because, in conservation biology, Type II errors can have serious consequences and, therefore, their risk should be limited (Taylor and Gerrodette 1993). I included ‘nest ID’ as a random variable in all relevant models to control for the presence of multiple nestlings per nest. For all GLMM models predicting nestling sex ratios, I used a binomial distribution with a logit link function with nestling sex as the response variable being either male or female. Female was used as the reference category so that female was coded as 0 and male as 1.

I evaluated effects of four components on sex ratios: effects of nestling morphometrics, Julian date and brood size; effects of parental condition; effects of treatment on nestlings; and effects of treatments on adults. Each analysis used a different dataset to predict the effects of each factor. I did not have information on body condition of both social parents at every nest sampled because of difficulty capturing adult birds. Nests that failed prior to day 7 were not included in analyses because no blood samples could be collected from nestlings for sexing.

When studying the influence of maternal and paternal morphometrics on offspring, I analysed the effects of known mothers and social males separately, because too few nests had both the female and social male captured and sampled. I could not analyse the additive or interactive effect of parental characteristics on nestling due to small sample size. The identity of the biological father was often not known so analyses did not assess the effect of extra-pair mates and, instead, focused on social parents. When investigating hypotheses relating only to nestlings, such as nestling body condition and sex ratio distribution relative to treatment types, all sampled nests and individual nestling with available information were included in the analyses.

The inclusion of nest ID as a random variable increased complexity of models so I compared the results with and without random variable and found no quantitative difference in results, which enable me to remove the random variable from some models.

Results of GLMMs using binomial distributions are presented in log odds ratio. The log odds ratio is the coefficient of the odds ratio and can be transformed into the odds ratio using the natural exponential function. Odds ratio values are always positive whereas log odds ratio can have negative values. Significant negative log odds ratio and odds ratio below 1 both signify that the predictor reduces the likelihood of the outcome.

Effects of nestling morphometrics, Julian date and brood size on nestling sex ratio allocation

I first investigated nestling morphometrics, brood size, and nest initiation date as predictive variables for nestling sex ratio allocation. I used nestling sex as the binomial response variable and tested all available morphometrics as explanatory variables. I tested the effects of Julian date, squared Julian date and brood size on nestling sex in separate models. If there was a significant correlation between nestling sex and nesting morphometrics, Julian date, and brood size, subsequent models included that explanatory variable.

Effects of parental body condition, morphometrics, and age on nestling sex ratio allocation

I assessed what morphometrics of males and females should be included in models of effects of parent condition on nestling sex ratio allocation based on their correlation coefficient. A correlation coefficient of 0.7 demonstrates high collinearity and can distort the results, which can be avoided by removing one of the collinear variables (Dormann et al. 2013). Male and females were analyzed separately and to avoid converge issue due to sample size. Female morphometrics

were included in two models to determine their significance. Significant explanatory variables were then included in their own individual models with brood size to determine if there an interaction with female tarsus length and female tail length.

Effect of treatments on nestling sex ratio allocation

Four separate models were used to assess the effects of treatments on nestling sex ratio allocation. The first model determined the effect of treatment on the sex allocation of all sampled nestlings, not just at nests with known parents, and included brood size as an explanatory variable. The second and third models included female morphometrics, brood size, treatment types, and distance from treatments on nestling sex allocation. The fourth model assesses the effect of male body condition, brood size, treatment type, and distance from treatment type on nestling sex ratio allocation. Data sets differed for each model because female and male parent morphometrics were not available for all nestlings.

Effects of treatments on demographic spatial patterns

I modelled the effects of treatments on morphometrics that were correlated significantly with nestling sex ratio, to determine whether treatment affected the settlement of individuals. Sexes were modelled separately. Female morphometrics were modelled using an LMM, whereas male age was modelled using a GLMM with a binomial response variable and logit link function. After second year males were coded as 1 and second-year males as 0. Hence, the reference category was being second year.

RESULTS

I recorded and monitored 138 chestnut-collared longspur nests during the breeding season of 2016. Of those, 68 nests contained nestlings aged 7 days or older. In total, I sampled 236

nestlings of which 111 were females and 122 were males. Three nestlings were not sexed because gels showed unclear bands. I collected blood samples and morphometrics of female parents and social males of 25 nests. At 18 nests, I was only able to sample the females. At 11 nests, only the social males were sampled. 14 nests, I was unable to sample any associated adults.

For four analyses, the amount of variation explained by the random variable was extremely small (variance $< 2.00 \times 10^{-19}$), resulting in a singularity in the model. This suggests that the random variable accounted for little variability in the model, and thus was not necessary. In these cases, we removed the random variable from these models to eliminate the problem with singularity.

Effects of nestling morphometrics, Julian date and brood size on nestling sex ratio allocation

I found no difference in morphometrics of male and female nestlings, indicating that nestling growth and development does not appear to be sexually dimorphic (Table 2). There was no seasonal change in nestling sex ratio allocation (Table 3). However, larger broods had higher ratios of male nestlings (Table 3, Figure 1). As a result, brood size was included in subsequent models. Most nests contained broods of four as expected for chestnut-collared longspurs (Yoo 2014).

Table 2. Predicted effect of sex on five morphometrics obtained from chestnut-collared longspur nestlings in Southern Alberta, 2016. Female was used as the reference category.

<i>Predictors</i>	Difference between male and female nestlings		
	<i>Log-Odds</i>	<i>CI</i>	<i>p</i>
(Intercept)	1.67	-2.78 – 6.12	0.537
Nestling tarsus length (mm)	-0.35	-0.74 – 0.04	0.137
Nestling wing chord length (mm)	0.14	-0.05 – 0.33	0.237
Nestling mass (g)	0.11	-0.10 – 0.33	0.386
Nestling P9 unsheathed length (mm)	-0.04	-0.27 – 0.19	0.774
Nestling P9 length (mm)	-0.08	-0.37 – 0.21	0.633
Random Effects			
σ^2	3.29		
$\tau_{00 \text{ nest_id}}$	0.21		
ICC ¹	0.06		
N _{nest_id}	57		
Observations	199		
Marginal R ² / Conditional R ²	0.029 / 0.088		

¹ ICC refers to intraclass correlation coefficient.

Table 3. Predicted effect of brood size and nest initiation date (Julian date or square-root Julian date) on sex ratio allocation of chestnut-collared longspur nestlings from Southern Alberta, 2016. Female was used as the reference category.

Log-odds of nestling being male	Linear seasonal changes			Non-linear seasonal changes		
	<i>Log-Odds</i>	<i>CI</i>	<i>p</i>	<i>Log-Odds</i>	<i>CI</i>	<i>p</i>
<i>Predictors</i>						
(Intercept)	-0.16	-2.68 – 2.36	0.916	1.22	-3.57 – 6.02	0.675
Julian date	-0.01	-0.02 – 0.01	0.317			
Brood size	0.43	0.11 – 0.76	0.029	0.43	0.11 – 0.76	0.029
Square rooted Julian date				-0.22	-0.58 – 0.15	0.336
Random Effects						
σ^2	3.29			3.29		
τ_{00}	0.05 _{nest_id}			0.05 _{nest_id}		
ICC	0.02			0.02		
N	68 _{nest_id}			68 _{nest_id}		
Observations	233			233		
Marginal R ² / Conditional R ²	0.030 / 0.044			0.029 / 0.044		

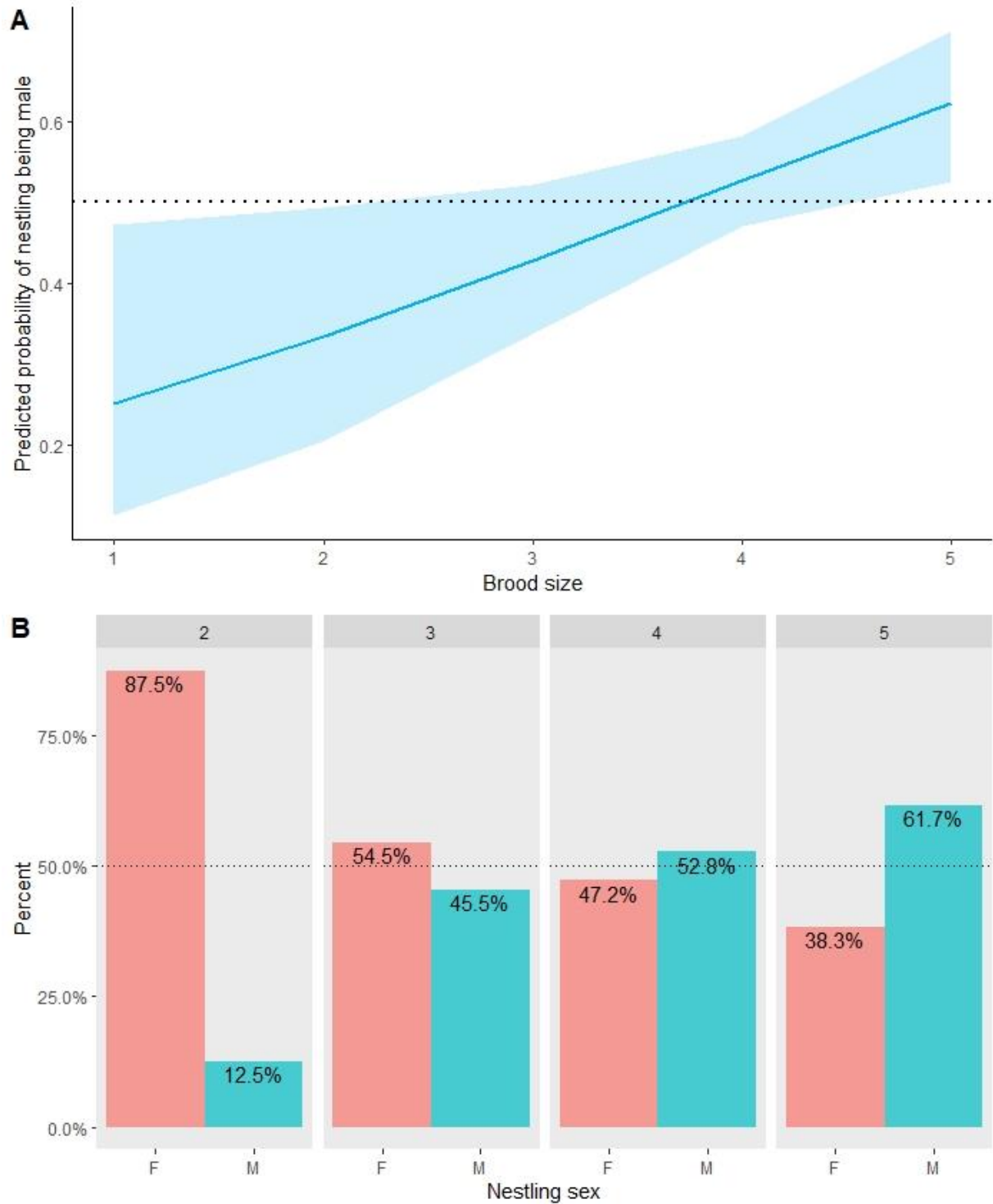


Figure 1. Correlation between nestling sex and brood size as A) the probability of chestnut-collared longspur nestlings being male and B) the percentage estimated from the data of male and female nestlings in nests monitored in Southern Alberta, 2016. The dotted line indicates parity.

Effects of parental body condition, morphometrics, and age on nestling sex ratio allocation

Female morphometrics (mass, tarsus length, wing chord length, and tail length) and age were not strongly collinear (Figure 2). Hence, they were all included in the following analysis of the effect of female morphometrics and age on sex ratio allocation. Male morphometrics and age were not strongly collinear (Figure 3). Wing chord length and age had the highest correlation coefficient at 0.6, which is still within the acceptable range (Dormann et al. 2013).

Odds of nestlings being male was correlated with female parent morphometrics, but not age or body condition of the female parent. When controlling for brood size, mothers with longer tarsi and tails were more likely to produce male offspring (Table 4, Table 5, Figure 4, Figure 5). I had relatively little data for small broods and, therefore, have less confidence regarding those patterns.

Nestling sex ratio allocation was affected by the age of the social male but not their body condition or morphometrics (Table 6). Older males had higher probabilities of having male offspring regardless of brood size (Table 6, Figure 6). Wing chord was dropped from the analyses due to insufficient sample sizes.

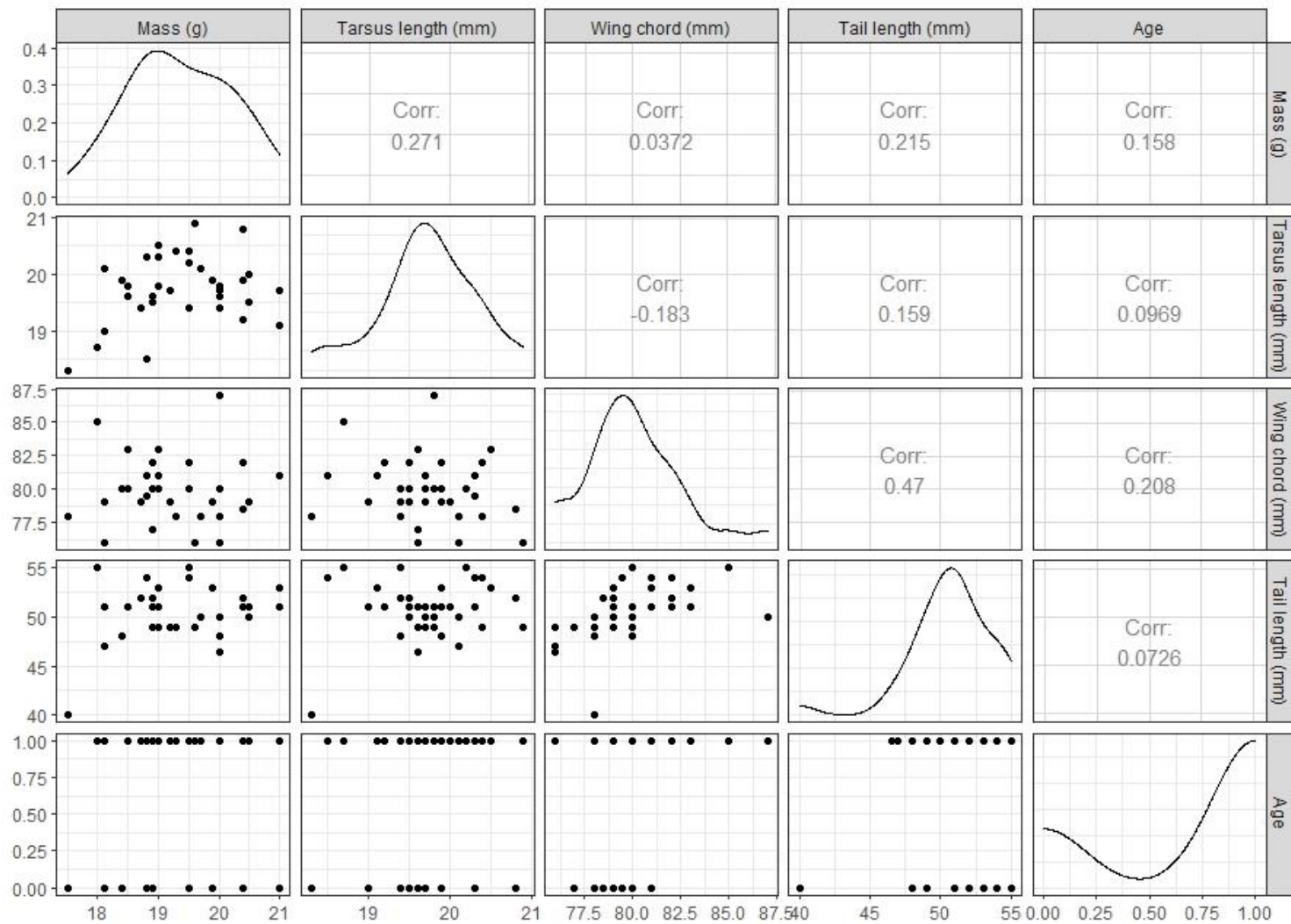


Figure 2. Scatterplot, density plot, and correlation matrix of morphometrics collected from female chestnut-collared longspurs in Southern Alberta, 2016.

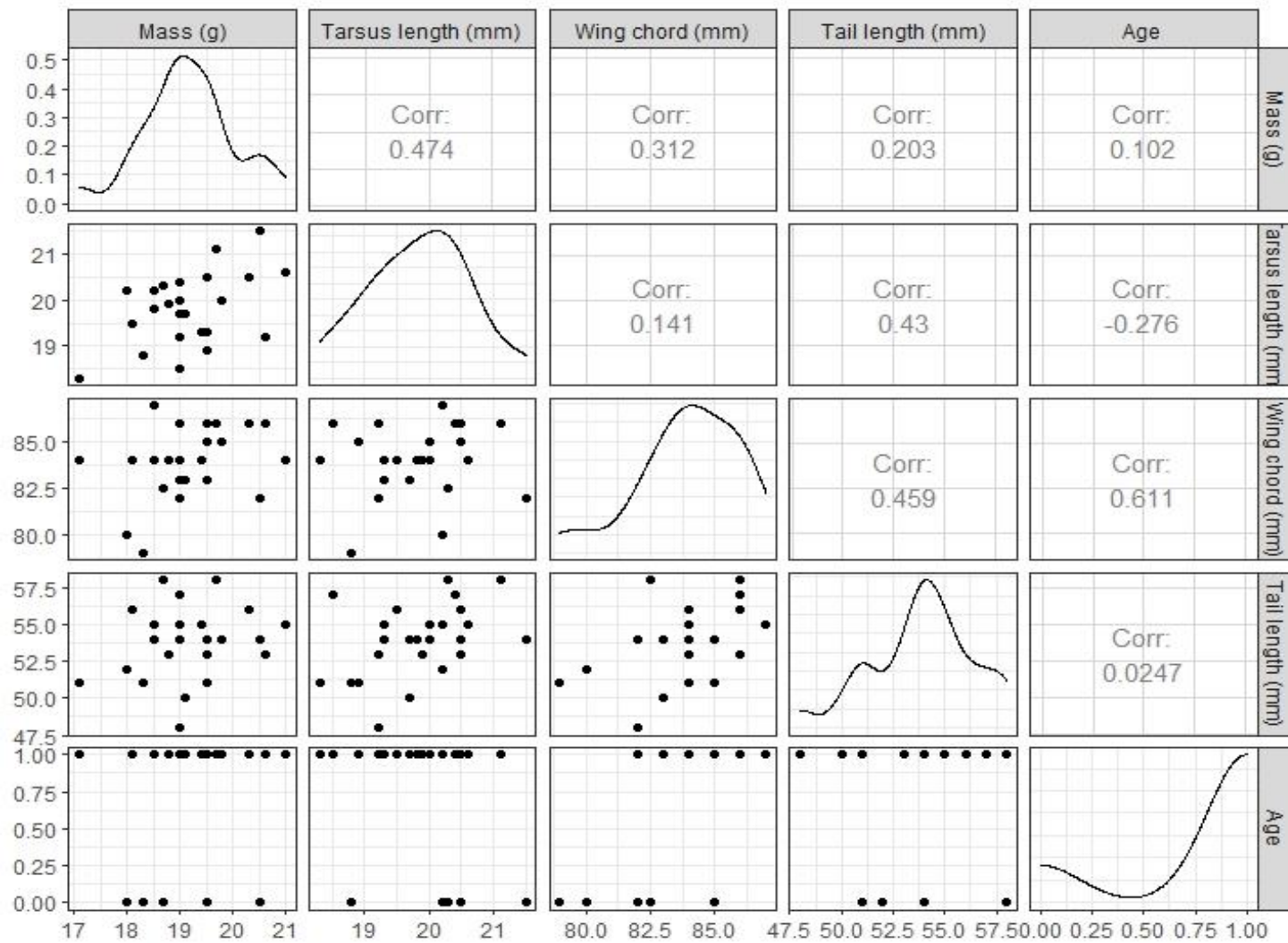


Figure 3. Scatterplot, density plot, and correlation matrix of morphometrics collected from male chestnut-collared longspurs in Southern Alberta, 2016.

Table 4. Predicted effects of four morphometrics and age collected from female chestnut-collared longspurs on offspring sex ratio allocation in Southern Alberta, 2016. Female was used as the reference category. All female morphometric variables were tested under two models to reduce overparameterization.

Log-odds of nestlings being male	Model 1: 3 explanatory variables Tarsus length, wing chord length and mass			Model 2: 2 explanatory variables Tail length and age		
Predictors	Log-Odds	CI	p	Log-Odds	CI	p
(Intercept)	-20.14	-37.04 – -3.24	0.050	-6.71	-12.60 – -0.83	0.061
Female tarsus length (mm)	0.66	0.10 – 1.22	0.052			
Female wing chord length (mm)	0.08	-0.05 – 0.22	0.312			
Female mass (g)	0.03	-0.32 – 0.37	0.903			
Female tail length (mm)				0.13	0.01 – 0.24	0.064
Female age [SY] ¹				0.62	-0.13 – 1.37	0.177
Random Effects						
σ ²	3.29			3.29		
τ ₀₀	0.08 _{nest_id}			0.14 _{nest_id}		
ICC	0.02			0.04		
N	36 _{nest_id}			36 _{nest_id}		
Observations	124			124		
Marginal R ² / Conditional R ²	0.054 / 0.076			0.054 / 0.092		

¹ SY refers to second year birds.

Table 5. Predicted effect of female parent tarsus length (mm), tail length (mm), and brood size of their nest on sex ratios chestnut-collared longspur nestlings monitored in Southern Alberta, 2016. Female was used as the reference category.

Log-odds of nestling being male	Female tarsus length (mm)			Female tail length (mm)		
	<i>Log-Odds</i>	<i>CI</i>	<i>p</i>	<i>Log-Odds</i>	<i>CI</i>	<i>p</i>
Predictors						
(Intercept)	-16.28	-26.95 – -6.07	0.010	-9.53	-15.60 – -3.87	0.007
Female tarsus length (mm)	0.66	0.16 – 1.19	0.032			
Brood size	0.80	0.36 – 1.29	0.004	0.82	0.37 – 1.32	0.004
Female tail length (mm)				0.12	0.02 – 0.23	0.049
Observations	124			124		
R ² Tjur	0.105			0.098		

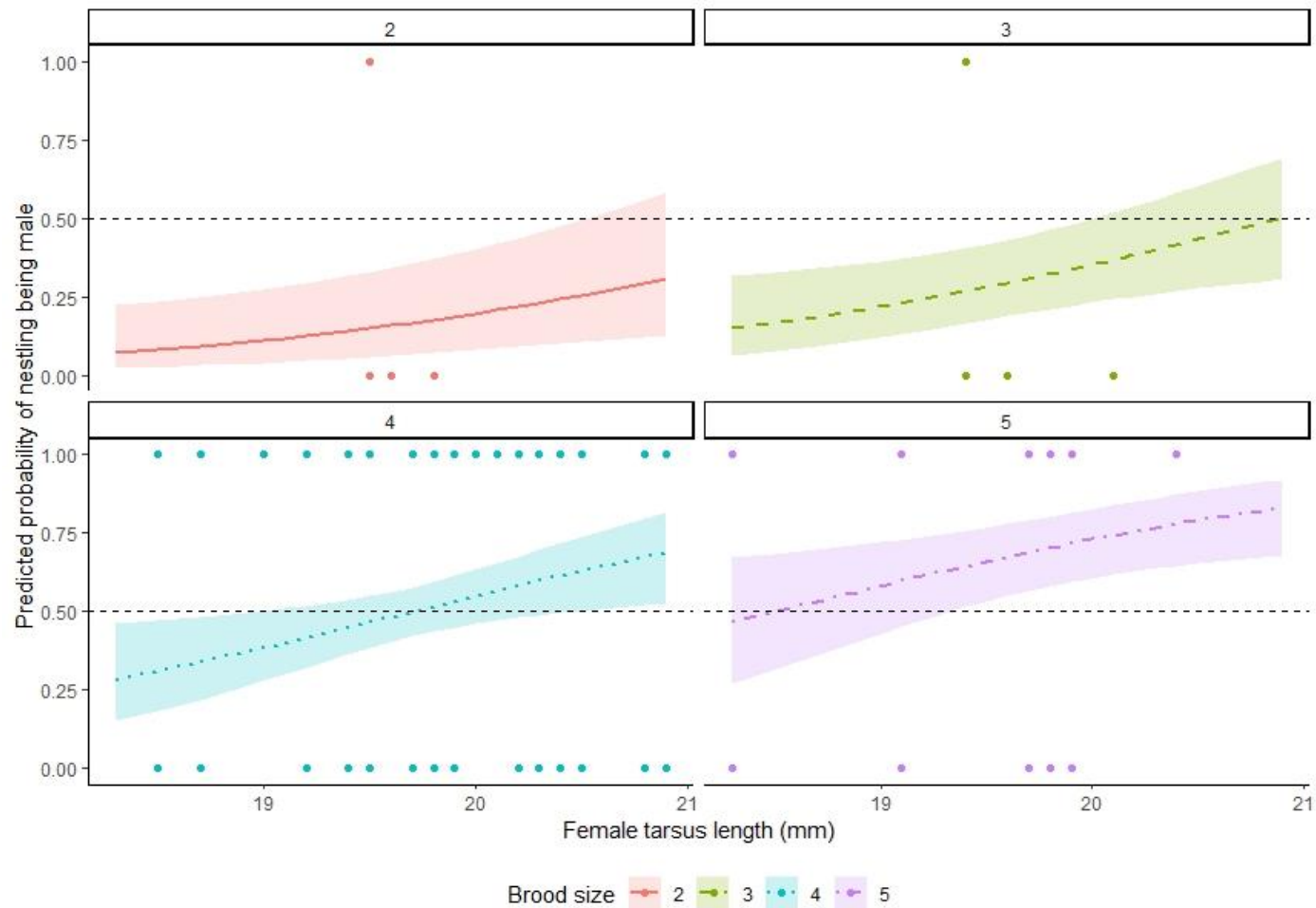


Figure 4. Probability of chestnut-collared longspur nestlings being male relative to female tarsus length (mm) and brood size of nests monitored in Southern Alberta, 2016. The black dashed line indicates parity. The colored dots indicate the raw data points for each associated color of broods: 1 is a male nestling and 0 is a female nestling.

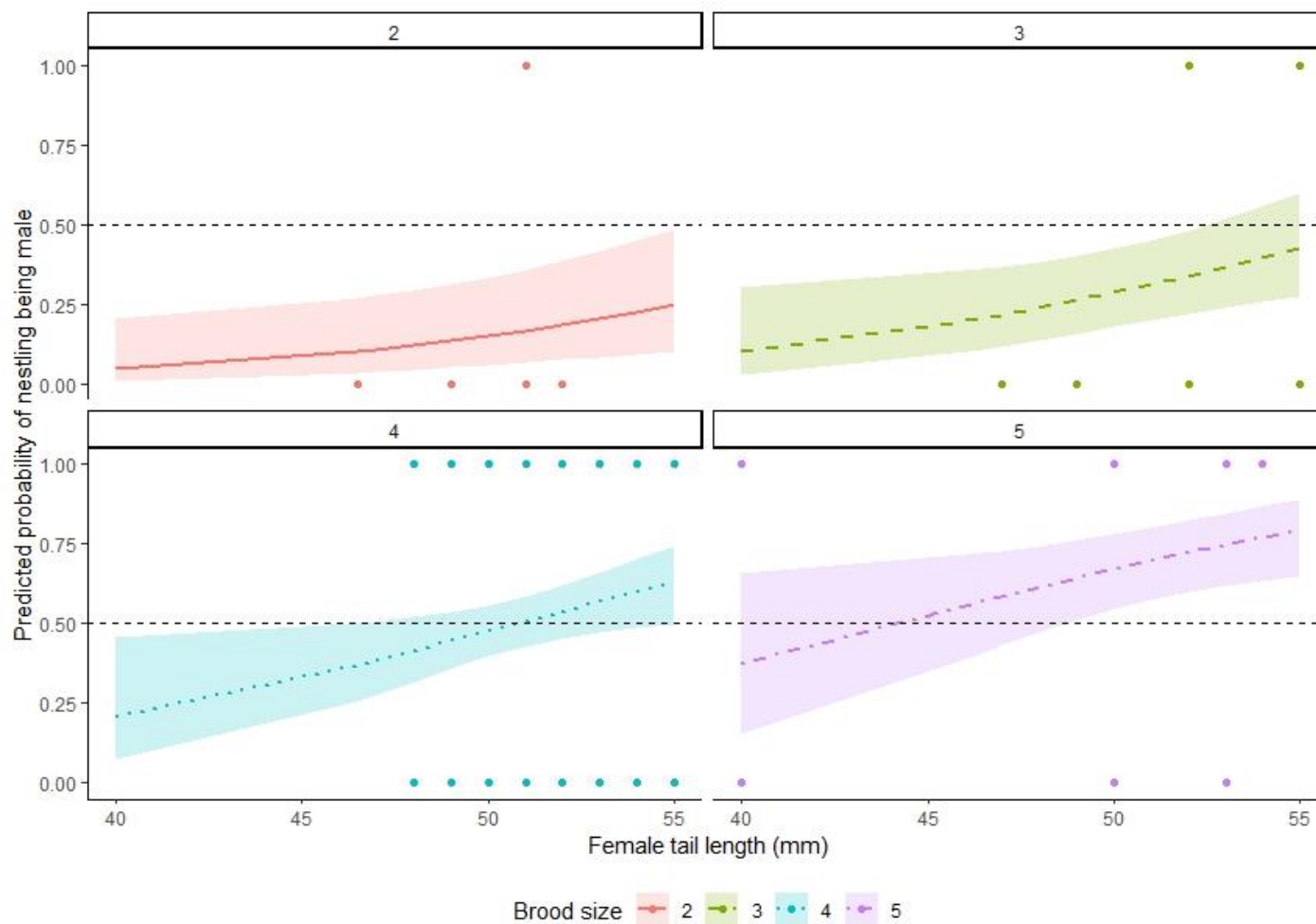


Figure 5. Probability of chestnut-collared longspur nestlings being male relative to female tail length (mm) and brood size of nests monitored in Southern Alberta, 2016. The black dashed line indicates parity. The colored dots indicate the raw data points for each associated color of broods: 1 is a male nestling and 0 is a female nestling.

Table 6. Predicted effect of three morphometrics collected from male chestnut-collared longspurs, male age, and brood size of their nest on offspring sex ratio allocation in Southern Alberta, 2016.

Female was used as the reference category.

<i>Predictors</i>	Log-odds of nestlings being male		
	<i>Log-Odds</i>	<i>CI</i>	<i>p</i>
(Intercept)	-6.01	-20.50 – 8.48	0.495
Male tarsus length (mm)	0.26	-0.45 – 0.97	0.546
Male mass (g)	-0.32	-0.96 – 0.32	0.411
Male tail length (mm)	0.10	-0.08 – 0.28	0.371
Male age [ASY] ¹	1.34	0.15 – 2.53	0.064
Brood size	0.19	-0.56 – 0.94	0.680
Random Effects			
σ^2	3.29		
$\tau_{00 \text{ nest_id}}$	0.34		
ICC	0.09		
$N_{\text{nest_id}}$	25		
Observations	96		
Marginal R^2 / Conditional R^2	0.094 / 0.179		

¹ ASY refers to after second year birds.

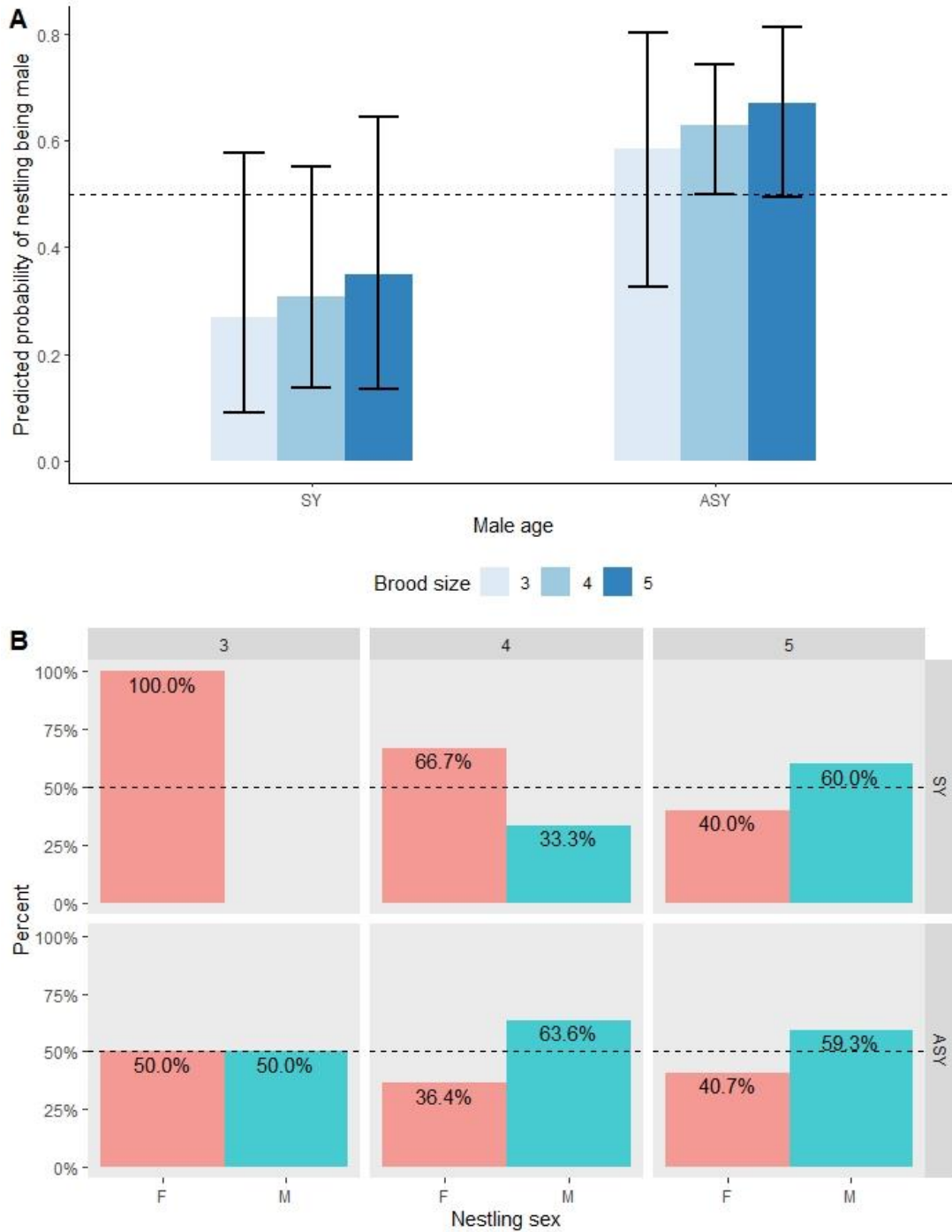


Figure 6. Correlation between nestling sex and male age ((second year [SY] and after second year [ASY]) as A) the probability of chestnut-collared longspur nestlings being male and B) the percentage estimated from the data of female and male nestlings in nests monitored in Southern Alberta, 2016. Bars indicate 90% confidence intervals. The dashed line indicates parity.

Effects of treatments on nestling sex ratio allocation

Nestling sex ratio allocation was more likely to be biased towards males at higher distances from silent playbacks and screwpumps (Table 7, Figure 7). However, when only considering nestlings with known social parents, I found that females with longer tails and longer tarsi, as well as older males, were more likely to have male offspring; treatment type had no significant effect within the subset of data available for this analysis (Table 8, Table 9).

Table 7. Predicted effects of treatments and distance from treatments (Log(m)) compared to controls on sex ratio allocation of chestnut-collared longspur nestlings, monitored in Alberta in 2016. Female was used as the reference category.

<i>Predictors</i>	Log-odds of nestlings being male		
	<i>Log-Odds</i>	<i>CI</i>	<i>p</i>
(Intercept)	1.34	-1.99 – 4.82	0.514
Active playback	-2.18	-6.50 – 2.06	0.400
Screwump	-4.67	-9.38 – -0.29	0.088
Silent playback	-4.44	-9.39 – 0.33	0.130
Distance from treatment (Log(m))	-0.51	-1.12 – 0.08	0.160
Brood size	0.29	-0.03 – 0.63	0.145
Active playback * Distance from treatment (Log(m))	0.46	-0.34 – 1.27	0.349
Screwump * Distance from treatment (Log(m))	0.95	0.13 – 1.83	0.063
Silent playback * Distance from treatment (Log(m))	0.95	0.05 – 1.88	0.086
Observations	233		
R ² Tjur	0.048		

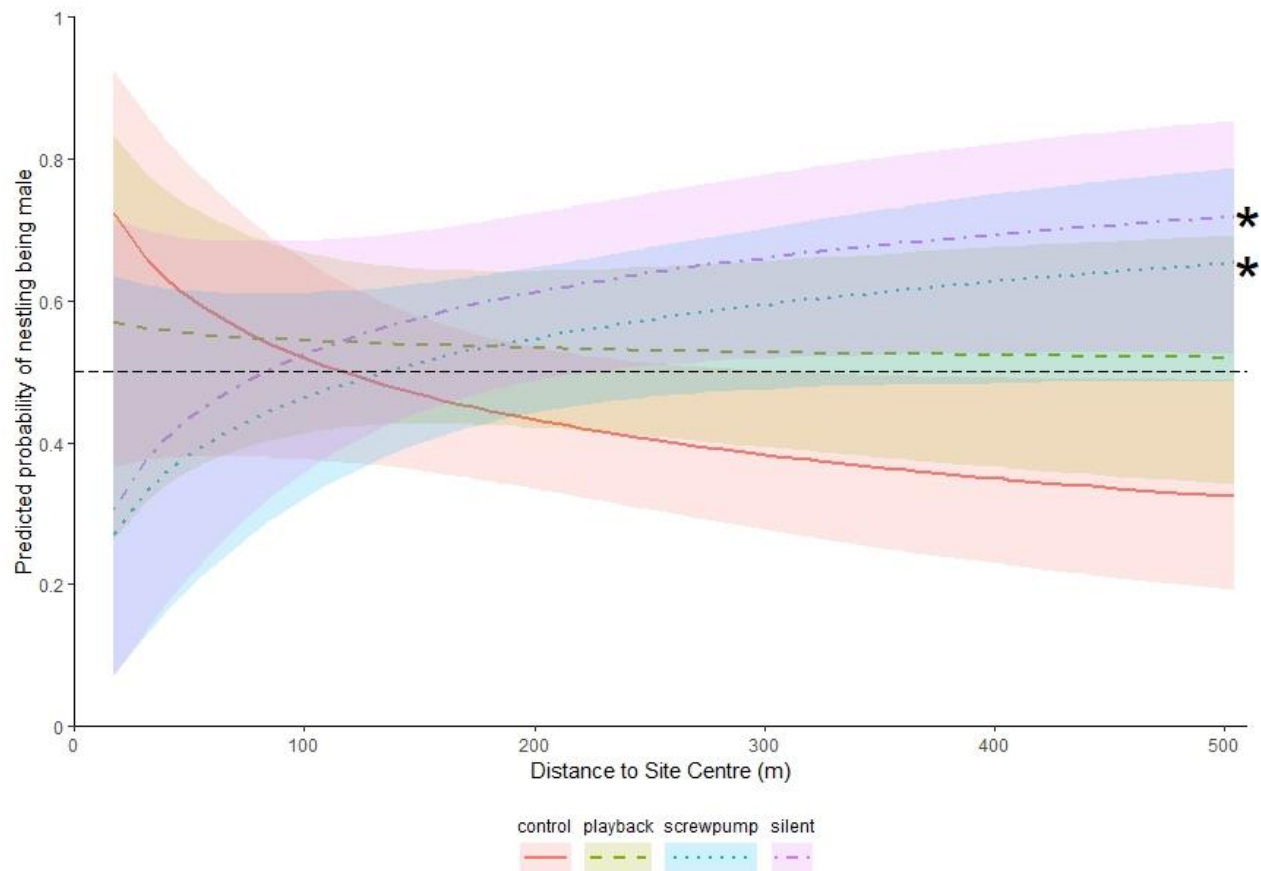


Figure 7. Probability of chestnut-collared longspur nestlings being male relative to treatment types (control, active playback, screw pump, and silent playback) and distance from treatments (m) in Southern Alberta, 2016. Asterix (*) represent significant interactions. The black dashed line indicates parity.

Table 8. Predicted effect of treatments, distance from treatments (Log(m)), brood size, and two morphometric measurements of females compared to controls on sex ratio allocation of chestnut-collared longspur nestling monitored in Alberta in 2016. Female was used as the reference category.

Log-odds of nestlings being male <i>Predictors</i>	Female tarsus length (mm)			Female tail length (mm)		
	<i>Log-Odds</i>	<i>CI</i>	<i>p</i>	<i>Log-Odds</i>	<i>CI</i>	<i>p</i>
(Intercept)	-21.90	-36.41 – -8.44	0.009	-10.53	-18.88 – -2.55	0.033
Active playback	-2.02	-7.82 – 3.74	0.561	-1.08	-6.75 – 4.63	0.752
Screwump	-2.72	-8.92 – 2.80	0.434	-1.89	-7.71 – 3.55	0.573
Silent playback	-1.86	-10.14 – 5.17	0.680	-4.05	-12.28 – 2.74	0.357
Distance from treatment	-0.08	-0.92 – 0.73	0.870	-0.03	-0.87 – 0.78	0.945
Female tarsus length (mm)	0.97	0.35 – 1.64	0.012			
Brood size	0.79	0.32 – 1.31	0.008	0.83	0.35 – 1.37	0.007
Active playback * Distance from treatment (Log(m))	0.48	-0.63 – 1.61	0.472	0.27	-0.82 – 1.36	0.679
Screwump * Distance from treatment (Log(m))	0.55	-0.49 – 1.69	0.399	0.33	-0.70 – 1.42	0.602
Silent playback * Distance from treatment (Log(m))	0.19	-1.15 – 1.72	0.824	0.62	-0.66 – 2.13	0.447
Female tail length (mm)				0.15	0.04 – 0.26	0.033
Observations	124			124		
R ² Tjur	0.148			0.131		

Table 9. Predicted effect of treatments, distance from treatments ($\text{Log}(m)$), brood size, and male age compared to controls on sex ratio allocation of chestnut-collared longspur nestling monitored in Alberta in 2016. Female was used as the reference category.

<i>Predictors</i>	Log-odds of nestlings being male		
	<i>Log-Odds</i>	<i>CI</i>	<i>p</i>
(Intercept)	1.49	-4.01 – 7.26	0.660
Active playback	1.39	-4.77 – 7.72	0.711
Screwump	12.00	-3.26 – 28.09	0.203
Silent playback	-29.75	-79.86 – 3.10	0.234
Distance from treatment	-0.75	-1.72 – 0.13	0.173
Male age [ASY] ¹	1.74	0.55 – 3.05	0.021
Brood size	0.24	-0.46 – 0.98	0.571
Active playback * Distance from treatment ($\text{Log}(m)$)	-0.31	-1.49 – 0.84	0.661
Screwump * Distance from treatment ($\text{Log}(m)$)	-2.01	-4.91 – 0.76	0.240
Silent playback * Distance from treatment ($\text{Log}(m)$)	5.41	-0.44 – 14.35	0.223
Observations	96		
R ² Tjur	0.163		

¹ ASY refers to after second year birds.

Effect of treatments on habitat selection by adult females and males

Since treatment and noise can mediate where individuals establish territories, I assessed whether parent morphometrics and age varied with treatment. Female tail length and tarsi were independent of treatments (Table 10).

Due to my small sample size of social males associated with sampled nests, I was unable to assess the effect of all four treatment types (control, silent playback, active playback, and screw pumps) on male age. I encountered complete separation and Hauck-Donner effect when trying to run this model. I monitored fewer nests close to screw pump infrastructures, which could limit model power. As an alternative, I grouped treatments in two categories: noiseless (control and silent playback) and noisy (active playback and screw pump). There was no significant correlation between treatment types (noisy and noiseless) distance from treatments and male age, indicating that noise did not impact the spatial distribution of social males around treatment (Table 11, Figure 8). Yet, older males tend to be closer to the center point of my sites, regardless of treatment type, indicating that older males might be avoiding other features on the landscape at the perimeter of sites, such as roads or bodies of water (Figure 8). There was also no effect of treatment on brood size (Table 12), indicating that the correlation between brood size and nestling sex allocation is not due to treatment type.

Table 10. Influence of treatments and distance from treatments (Log(m)) compared to controls on tarsus length (mm) and tail length (mm) of female chestnut-collared longspurs with known nests in Alberta in 2016.

<i>Predictors</i>	Female tarsus length (mm)			Female tail length (mm)		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	20.01	18.22 – 21.80	<0.001	51.03	41.39 – 60.68	<0.001
Active playback	0.07	-2.22 – 2.37	0.957	3.49	-8.90 – 15.88	0.638
Screwump	-0.16	-2.61 – 2.28	0.911	-4.52	-17.73 – 8.68	0.568
Silent playback	-2.04	-4.96 – 0.89	0.248	-4.93	-20.70 – 10.85	0.602
Distance from treatment	-0.07	-0.41 – 0.28	0.750	-0.11	-1.97 – 1.74	0.920
Active playback * Distance from treatment (Log(m))	-0.02	-0.45 – 0.42	0.951	-0.75	-3.10 – 1.61	0.597
Screwump * Distance from treatment (Log(m))	0.01	-0.45 – 0.48	0.958	0.98	-1.51 – 3.48	0.510
Silent playback * Distance from treatment (Log(m))	0.45	-0.10 – 1.00	0.176	1.02	-1.93 – 3.97	0.565
Observations	51			51		
R ² / R ² adjusted	0.146 / 0.007			0.080 / -0.070		

Table 11. Influence of noisy treatments and distance from treatments (Log(m)) compared to noiseless treatments on age of male chestnut-collared longspurs associated with nests in Alberta in 2016. Second year was used as the reference category.

Male age: ASY			
<i>Predictors</i>	<i>Log-Odds</i>	<i>CI</i>	<i>p</i>
(Intercept)	6.63	-2.54 – 17.50	0.244
Noisy treatment	1.24	-11.50 – 13.79	0.866
Distance from treatment	-1.47	-3.49 – 0.21	0.168
Distance from noise	-0.37	-2.80 – 2.05	0.791
Observations	35		
R ² Tjur	0.216		

** Noisy treatments include active playback and screwump infrastructure sites. Noiseless treatments include control and silent playback sites.*

*** Distance from noise refers to distance from active playback and screwump infrastructure sites.*

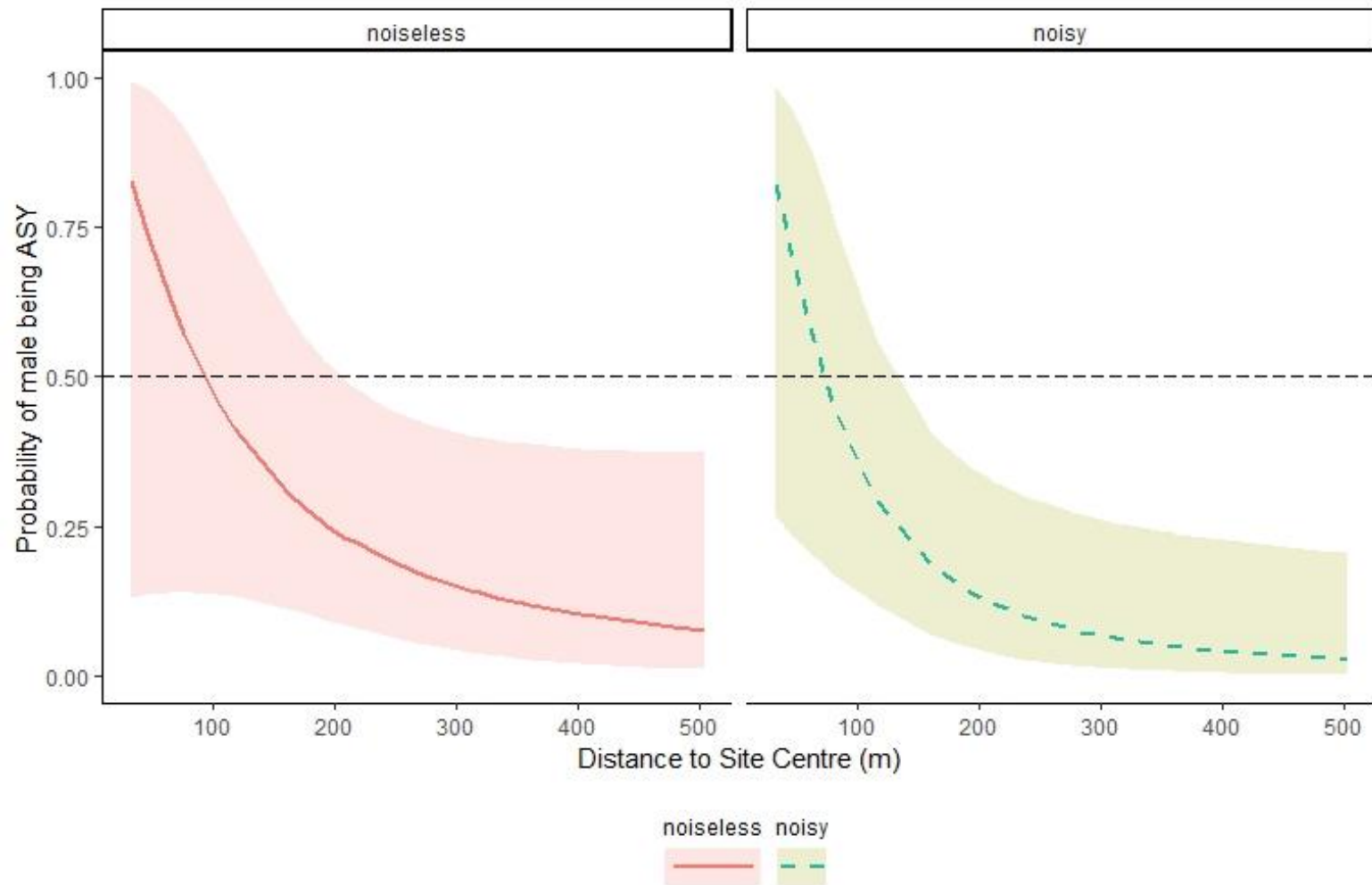


Figure 8. Age of all male chestnut-collared longspurs with associated nests relative to treatment types (noiseless and noisy) and distance from treatments (m) in Southern Alberta, 2016.

Table 12. Influence of treatments and distance from treatments (Log(m)) compared to controls on brood size of chestnut-collared longspurs in Alberta in 2016.

<i>Predictors</i>	Brood size		
	<i>Incidence Rate Ratios</i>	<i>CI</i>	<i>p</i>
(Intercept)	3.99	0.81 – 17.41	0.137
Active playback	1.12	0.15 – 8.41	0.927
Screwump	0.88	0.10 – 7.35	0.923
Silent playback	0.72	0.07 – 6.98	0.815
Distance from treatment	0.97	0.74 – 1.31	0.876
Active playback * Distance from treatment (Log(m))	1.01	0.69 – 1.47	0.979
Screwump * Distance from treatment (Log(m))	1.04	0.70 – 1.57	0.859
Silent playback * Distance from treatment (Log(m))	1.09	0.71 – 1.68	0.741
Observations	68		
R ² Nagelkerke	0.081		

DISCUSSION

While male and female nestling longspurs were morphologically and developmentally similar, sex ratio allocation was skewed towards males in large broods. Further, larger females and older social males reared more male chestnut-collared longspurs nestlings, suggesting that competitiveness and experience may be valuable traits contributing to successful breeding and greater fitness in adults (Freeman-Gallant et al. 1996, Oddie 2001, Velando et al. 2006, Benowitz et al. 2013, Niederhauser et al. 2021). Male nestlings were also more likely to be produced further from screw pump and silent playback treatments, suggesting that the presence of infrastructure altered habitat quality or its perception, possibly negatively, by social parents. Mitigation methods that reduce the footprint of oil infrastructure and landscape fragmentation (reviewed by Northrup and Wittemyer 2013) could reduce the potential consequences of altered nestling sex ratio on adult sex ratio and reproductive competition (Wilson and Pianka 1963, Clutton-Brock 2017, Kus et al. 2017).

Typically, the potential reproductive output of male nestlings exceeds that of females if they survive into adulthood and can secure mating opportunities, which is dependent on their quality and desirability as mates (Bowers et al. 2014, Trivers and Willard 1973, Whittingham and Dunn 2000). Due to competition for pair and extra-pair mating opportunities, there is more variation in reproductive output among males than females (Griffith et al. 2002), whereas females are limited in how many offspring they can produce but have greater certainty of rearing young (Griffith et al. 2002, Møller 2000). If parents were to produce small broods (four being an average sized brood, Yoo 2014) with more males, they may be at greater risk that none of them have any future reproductive output due to intraspecific competition. Hence, parents may benefit from

producing either larger broods with more males or smaller broods with more females, as found in my population of chestnut-collared longspurs. In some instances, large broods could produce the same number of females as small broods in addition to males (e.g. a large brood of five, while male-biased, could still produce two females, comparable to a small brood of two females). However, bigger broods result in greater food and care requirements, as well as greater sibling competition for those resources (Bowers et al. 2014), perhaps explaining why chestnut-collared longspur fledglings in my study area had lower survival rates if they were from larger broods (Carey 2021, unpublished data). This suggests that habitats with less risky environmental conditions should result in more males being reared as it would be a poor reproductive strategy to produce large broods of males where the necessary parental care cannot be provided. Thus, producing smaller broods with more females may be a lower-risk reproductive strategy that is appropriate for lower-quality female, less experienced male parents, and parents rearing young in risky environmental conditions. Older and larger parents, and parents rearing broods in safe habitats can benefit from the increased reproductive potential resulting from rearing more male offspring. Yet, the adaptability of brood size may depend on life history traits, population demographics, and biogeographical distribution of species (Skutch 1949, Skutch 1967, Lundblad and Conway 2021a). For instance, tropical birds tend to have small clutches that rarely vary in number regardless of whether parental care is provided by one or two parents (Skutch 1949). The relationship between clutch size and latitude might be due to differences in occurrence of extreme climatic events and environmental conditions (Skutch 1949), resource availability (Lundblad and Conway 2021a), and nest microclimate (Lundblad and Conway 2021b) among other hypotheses.

Rearing females may be a safer reproductive strategy, but my results suggest they require similar care as male nestlings. The nutritional requirements and parental care needed by one sex should be greater if it grows and develops faster (Fiala and Congdon 1983, Teather and Weatherhead 1989). For example, male nestling Eurasian treecreepers (*Certhia familiaris*) were bigger than their female counterparts; food availability and provisioning rate predicted sex ratio allocation in favor of males (Suorsa et al. 2003). However, morphometrics and body condition were similar between male and female nestlings in my study population, indicating that sex ratio bias should not be due to sexually dimorphic needs at the nestling stage that result in differential survival. This suggests that sex ratio allocation bias with brood size should result from the expected reproductive output mediated through parental and environmental effects instead.

No seasonal effect on sex ratio allocation was reported in my study population, perhaps because food is not limiting in the prairies (Wiens and Rotenberry 1979, Rotenberry and Wiens 1980). This differs from the results of other studies, which have found seasonal effects of temperature (Saino et al. 2008) and laying date (Rosivall et al. 2004) on sex ratio allocation. Temperature fluctuations and other weather events can decrease habitat quality, which can negatively affect the fitness of birds and require coping mechanisms (Whitehouse et al. 2013, Wingfield et al. 2017). Food availability can vary seasonally and become scarcer over the breeding period, affecting the body condition of birds (Kitaysky et al. 2002). Ultimately, seasonal changes in resource availability and habitat quality could cause females to adjust the sex ratio and size of their broods to maximize nestling number and survival (Husby et al. 2006, Trivers and Willard 1973) in some systems, but this may be unnecessary when food is superabundant.

Chestnut-collared longspur females with longer tails and tarsi were more likely to produce male offspring, perhaps because larger parents may have a competitive advantage and tend to be higher quality (see also Des Brisay 2018). Possibly, the larger size of females is indicative of their greater competitiveness for resources (Oddie 2001). For instance, larger individuals might have an increased ability to compete for high-quality territories (Ippi et al. 2018, Niederhouser et al. 2021). Individuals rearing young on high-quality territories and in safe environments should have greater reproductive success as determined by number and quality of offspring (Coulson and Porter 1985). If in Chestnut-collared longspurs, males have greater reproductive potential, high-quality adults should rear more males that might inherit their high-quality traits, such as larger size, that can provide them with a competitive advantage (Trivers and Willard 1973). My results show that larger size females can produce more male offspring, suggesting that large size may be a high-quality trait in adult female chestnut-collared longspurs.

Older males were also likely to produce more male offspring. Older males might be higher quality because of greater resistance to oxidative stress (Bize et al. 2008), good genes for survival (Kokko and Lindström 1996), and access to better territories (Pärt 2001). Older adults have experience surviving and providing care that could make them good mates, especially social mates (Freeman-Gallant et al. 1996, Chuang-Dobbs et al. 2001, Velando et al. 2006, Schwagmeyer et al. 2012, Benowitz et al. 2013, Schroeder et al. 2016). In chestnut-collared longspurs, the contribution of males to parental care is imperative to nest survival (Lynn and Wingfield 2003). Adult age can also positively correlate with quality of parental care regardless of breeding experience and enhance nestling growth rate (Pittet et al. 2012). There are also other indicators of quality and attractiveness of older males that were not assessed in my study; for example, plumage and

ornamentation can vary with age (Freeman-Gallant et al. 2010). Older males might be more attractive than their younger counterparts and their attractive features could be perceived as desirable hereditary traits (Freeman-Gallant et al. 2010, Taff et al. 2011). Attractive features can also be proxy indicators of genetic quality (Kodric-Brown and Brown 1984). However, it is important to note that paternal effects on sex ratio allocation are divided between social and extra-pair males. The lack of significant effect of other male traits on sex ratio allocation could be because heritable characters with fitness benefits for nestlings can come from unidentified extra-pair males (Taff et al. 2011).

In addition to the influence of brood size and parental characteristics, I found effects of environmental factors from screwpumps and noise on nestling sex ratio allocation. Treatment type affected nestling sex ratio allocation, suggesting that the infrastructure resulted in gradients in environmental condition and habitat quality or perception of it. The probability of nestlings being males in sites with screwpumps and, surprisingly, silent playback sites was greater further from treatments and lower closer to them, while conversely, male nestlings were more likely to be produced near the centres of control sites, which is the point furthest from all sources of anthropogenic development, including roads, fencing, and other energy infrastructure. Taken together, this suggests that habitat farthest from anthropogenic development favours production of male nestlings, perhaps because it provides safer environmental conditions where producing more males can be a profitable reproductive strategy with perceived greater guarantee of nest success and offspring survival.

However, we found no effect of noise playback on sex ratio allocation, suggesting that noise is not the mechanism affecting sex ratio allocation; surprisingly, silent playback

infrastructure, but not noisy playback infrastructure, did affect sex ratio allocation. Anthropogenic development can have both positive and negative impacts on environmental quality, resulting in complex interactions and sometimes unpredictable outcomes. For example, infrastructure introduces perching opportunities that may not normally be available, particularly in natural open environments like the Canadian prairies, and perches might have both positive and negative impacts on songbirds. Perches may attract and increase predation rate (Andersson et al. 2009) and brood parasitism (Hauber and Russo 2000), but conversely, perches also present an opportunity for birds to sing at different heights, which can improve song propagation (Barker and Mennill 2009). Anthropogenic noise can also positively or negatively impact habitat quality, including predation risk. Noise can render prey and predator localisation more difficult (Francis et al. 2009, Siemers and Schaub 2010) and facilitate elusive approach by predators (Templeton et al. 2016) but might decrease predation by causing prey to be hypervigilant (Quinn et al. 2006) or if predators avoid noise (Francis et al. 2009). Predation risk may also vary with the population density of prey. In all likelihood the positive and negative effects of oil extraction infrastructure and noise are happening simultaneously, creating a dynamic landscape of variability in optimal decision making and life-history strategies around treatment types.

My results suggest that both biological and environmental characteristics interact to regulate sex ratio allocation in my study population of chestnut-collared longspurs. Effects of treatments could be explained in three ways: treatment effects may be mediated by characteristics of parents such that parents of different quality assort themselves differently across the landscapes relative to the presence of oil infrastructure; treatment effects may be mediated by parents but without affecting habitat selection; or treatments might alter the reproductive environment

resulting in production of more males. Treatments did not influence parental characteristics and brood size, indicating that effects of treatments on sex ratio allocation cannot be explained by measured morphometrics of parents. However, treatment might affect adult settlement on the landscape based on non-morphometric characteristics, such as hormone levels (Beletsky et al. 1989), or treatments may be redistributing birds on the landscape that would be there regardless. These birds might adjust to their surroundings, compensating as needed. Behavioural adjustments might function to mitigate the impacts from screw pumps and noise so that the resulting bias in nestling sex ratio allocation on the landscape is detectable. Female birds might be able to adjust the sex ratio of their broods regardless of their own body condition although breeding experience and size could make it more likely for individuals to rear larger, male-biased broods. On the other hand, the decreased effects of treatment when we included parental characteristics in models might be due to sample size. A small sample size might be insufficient to discriminate an effect of treatment and result in false positives (type I errors).

In conclusion, parent quality and perception of habitat quality by social parents can influence nestling sex ratio. Studies have found conflicting evidence of avoidance of energy development by chestnut-collared longspurs. Rosa (2019) found declines in abundance near noise from drilling rigs and power-grid pumpjacks but Nenninger and Koper (2018) did not find a significant difference in abundance around oil wells. My results indicate that adult settlement around treatments was not based on morphometric characteristics, indicating that parents may act as mitigators of effects of environmental conditions on their young. Adults might not consider environmental conditions on the landscape when selecting territories if they can behaviourally or physiologically compensate for negative impacts. Parents, particularly females, can influence

offspring physiology and development from the egg-laying to post-fledging stages through hormone deposition in their eggs (Romano et al. 2008) and parental care (Møller 2000). Alternatively, adults might not be able to discriminate quality of different habitats. The multitude of effects from anthropogenic noise and infrastructure, some conflicting with each other, present complex challenges for parents to assess threats, protect their broods, and coordinate care. Mitigation methods can be implemented to alleviate negative effects of oil development on birds and potential consequences of altered nestling sex ratio. Skewed nestling sex ratio can result in a bias in adult sex ratio and an increase in reproductive competition, which can have conservation implications, particularly for small populations (Wilson and Pianka 1963, Clutton-Brock 2017, Kus et al. 2017). For instance, small populations tend to be vulnerable to ecological events that negatively affect habitat quality, which can be disproportionately lethal for one sex and could be exacerbated by an already present sex ratio bias in the population (Clutton-Brock et al. 1985, Clutton-Brock 2017). In some rare cases, like that of the kakapo (*Strigops habroptilus*), small populations with biased sex ratios can benefit from conservation and species recovery programs focused on improving habitat quality, adjusting maternal condition, and altering nestling sex ratio in favor of the less produced sex (Clout et al. 2002, Robertson et al. 2006).

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Chapter 3. Variation in song structure of house wrens living in urban and rural areas in a Caribbean small island developing state

This chapter was published in October 2020 and was the result of a collaborative effort. Song recordings were collected by Andrew Horn, Kimberley Wetten, and me. I conducted all song measurements and statistical analyses. I wrote the first draft of this manuscript, which was then edited with the help of Nicola Koper and Miyako Warrington. We also received analytical and editorial advice and help from Claire Curry and Andrew Horn.

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CONNECTING TEXT

Anthropogenic noise can be chronic, like the one produced by oil infrastructure, but it can also be intermittent, which is the case of urban noise. Urbanization and urban noise are increasing threats throughout the world, particularly in the Global South. Countries of the Global South offer a very different tapestry of ecosystems, wildlife, and conservation challenges than countries of the Global North. Yet, the Global South is largely understudied and much of the Caribbean islands are underrepresented in the literature, making it difficult to assess conservation needs and determine appropriate mitigation methods. For instance, the urban landscape in low-income countries, such as Grenada, can differ from that of developed countries, so birds like the house wren (*Troglodytes aedon*) may require different acoustic adaptations to their urban environment, which, in turn, may have different conservation implications.

ABSTRACT

Most research on how birds adapt to urban environments has been conducted in cities in developed (Global North) countries, which differ structurally and acoustically from cities in developing (Global South) countries; therefore, optimal behavioural strategies of animals living in urban landscapes may also differ based on the economic status of the country in which they live. We studied Grenada's house wren population (*Troglodytes aedon grenadensis*) to investigate song plasticity of this subspecies in response to urbanisation. Grenada, a Small Island Developing State in the Caribbean, is under increasing pressure from tourism, urbanisation, and climate change, and little is known about its avian community. We recorded 33 Grenada house wrens at five urban and five rural sites across Grenada, and analysed effects of urbanisation using generalised estimating equations. Grenada house wrens used a mix of strategies to compensate for urbanisation. In urban habitats, Grenadian house wrens sang shorter introductions, faster trills, and increased the low frequencies of the introduction and the whole song. Grenada's house wrens use some unusual song alterations in urban environments, emphasising the importance of studying animal behaviour in Small Island Developing States to help us understand the unique anthropogenic pressures faced by species in these vulnerable regions.

INTRODUCTION

Urbanisation presents a challenge for birds by creating a new structural and acoustic environment, resulting in increased risks of frequency masking and distraction from fitness-related tasks (Ortega 2012; Rosa and Koper 2018). A large body of literature has attributed the success or failure of various avian species in urban habitats to their ability to adapt to changes in the acoustic landscape (Hu and Cardoso 2009; Francis et al. 2011a; Proppe et al. 2013). Birds are highly reliant

on songs and calls to defend their territories, find mates, and maintain social bonds, and thus altered acoustic environments can interfere with key biological needs of birds (Francis 2015). Frequency masking of these songs by urban noise can alter signal detectability, discrimination, and information content of vocalisations, which in turn can negatively impact fitness (Lohr et al. 2003; Slabbekoorn and Ripmeester 2008).

However, negative impacts of anthropogenic noise on birds may be mitigated through behavioural alterations. Birds can avoid temporal overlap with noise if amount of noise varies predictably with time of day (Arroyo-Solís et al. 2013), or birds may avoid areas closer to noise sources (e.g. Fahrig and Rytwinski 2009, Ortega 2012, CJW et al. 2013). Alternatively, birds may cope with noise by employing strategies that rely on the plasticity of their singing behaviours to minimise frequency masking (Barber et al. 2010). One frequently documented strategy to minimise frequency masking by anthropogenic noise is to sing all (*Parus major*, Slabbekoorn and Peet 2003; *Melospiza melodia*, Wood and Yezerinac 2006; *Junco hyemalis*, Slabbekoorn et al. 2007; house wrens, Redondo et al. 2013) or part of songs, such as syllables or sections (Redondo et al. 2013; Curry et al. 2017, Warrington et al. 2018), at a higher frequency. However, different strategies may be used depending on the noise source and acoustic characteristics (Warrington et al. 2018). Song adjustment strategies are not mutually exclusive, and individuals may change multiple signal features independently (Potvin and Mulder 2013). Song plasticity is species-specific and appears to be an important indicator of a species' ability to thrive in an urban environment (Proppe et al. 2013, Slabbekoorn 2013, Francis 2015). Context-dependent vocal modulations for improved communication in noisy urban habitats falls under the acoustic

adaptation hypothesis, which was developed under the theory that vocalisations are adapted to propagate well in environments in which species evolved (Morton 1975).

In addition to introducing anthropogenic noise, the built environment of urban landscapes affects how sound propagates (Warren et al. 2006). Reverberation against vertical structures tends to cause song degradation and is a common problem that birds deal within human-altered and natural habitats (Richards and Wiley 1980, Slabbekoorn et al. 2007). Therefore, birds may also adjust songs to minimise reverberation in some urban environments (Dowling et al. 2011). Trill rate, singing frequency, signal duration, and distance from receiver affect the intensity of reverberation (Naguib 2003). Trills are particularly susceptible to degradation by reverberation because all elements are produced in the same frequency bandwidth (Naguib 2003). Increased trill rate and trill duration can amplify reverberation and have an accumulative effect, which can be beneficial or detrimental depending on habitat (Naguib 2003). Signal duration may also be increased in noisy conditions to improve detectability by receiver, as found in king penguins, *Aptenodytes patagonicus* (Lengagne et al. 1999); Japanese quails, *Coturnix japonica* (Potash 1972); and great tits, *Parus major* (Hamao et al. 2011).

However, the extent to which behavioural strategies such as these are necessary and effective varies regionally, as urban environments are geographically and locally heterogeneous. Urban areas usually include a patchwork of parks, gardens, roads, buildings and other structures, but the proportion and size of these differs significantly among urban areas, and particularly between cities in low-middle income (developing/Global South¹) and high-income

¹ In this paper we use the term ‘developing’ and ‘developed’ country, to correspond with the term ‘Small Island Developing State’, which is widely used by Caribbean governments to describe themselves. However, we recognise that ‘Global North/South’ is preferred in many contexts (Mitlin and Satterthwaite 2013).

(developed/Global North) countries. In developed countries, the most highly urbanised areas are characterised by high densities of tall buildings and little greenspace, which are associated with loud and unpredictable noise, high rates of reverberation, and other altered sound propagation patterns (Warren et al. 2006). However, this is not always the case in low- and middle-income countries in general, and in Small Island Developing States in particular.

Small Island Developing States are faced with unique economic and environmental challenges, including a narrow resource base, high development costs, vulnerability to natural disasters, and fragile ecosystems that include small populations of evolutionarily distinct plants and animals (UN-OHRLS 2011). The socioeconomic characteristics of Small Island Developing States result in structural differences between their urban centres and those in developed countries, and this may result in different ecological impacts of urbanisation as well. In comparison with their counterparts in developed countries, many urban environments of Small Island Developing States have narrower roads, slower traffic, and shorter buildings, interspersed with small public greenspaces. For example, in the Small Island Developing State of Grenada in the Caribbean, few buildings are taller than four stories, few roads have more than two lanes, and urban areas are surrounded by diverse mixed-wood forest. Its largest city, St. George's, has a population of under 34,000 (2012 census; [FCO] Foreign and Commonwealth Office (UK)) and its developed area covers just 0.575 square km. This type of urbanisation results in more openness and fewer and smaller reflective surfaces than cities in developed countries, so birds here may require different acoustic adaptations to their urban environment. However, this has yet to be quantified as most bioacoustics research has taken place in developed countries. This limits our ability to understand animal behaviour and make conservation and management decisions necessary for protecting

wildlife in Small Island Developing States (Blumstein and Turner 2005). This is problematic because the small populations present on Small Island Developing States are at significant risk from environmental change, and the evolutionarily unique populations found on many islands may have developed different adaptations in response to anthropogenic pressures in comparison with related taxa on mainlands (Lande 1998; Siliceo and Díaz 2010).

House wrens (*Troglodytes aedon*) are found throughout Grenada but behaviour of the island's endemic subspecies (*T. a. grenadensis*) has never been described in academic journals; indeed, little is known about the Central and South American subspecies in comparison with those in North America (Rendall and Kaluthota 2013, Dos Santos et al. 2016). House wrens elsewhere have long been used to study emerging patterns in vocalisations among its many populations, subspecies, and related species (Kroodsma 1977, Sosa-López and Mennill 2014, Kaluthota et al. 2016). House wrens appear to have readily adapted to urban environments, suggesting biological and behavioural mechanisms that enable the species to persist in sympatry with humans (Slabbekoorn and Peet 2003).

House wrens have complex songs and large repertoires, which may contribute to their ability to adapt to a wide variety of habitats (Platt and Ficken 1987, Redondo et al. 2013, Brumm and Bee 2006). The introduction section of the song is composed of a series of soft notes, whereas the terminal section is composed of distinct syllables and notes, including a trill (Rendall and Kaluthota 2013, Dos Santos et al. 2016, Kaluthota et al. 2016). The function of each section of house wren song is not well understood because of the complexity of their singing and extensive song repertoire (Rendall and Kaluthota 2013, Dos Santos et al. 2016). The introduction may be used mainly by paired males for nesting activities and pair-bonding (Johnson and Kermott 1991,

Dos Santos et al. 2016). The terminal section might communicate information regarding male quality, mating behaviour, and territoriality (Catchpole 1987). Without information on the mating system and much of the life history of Grenada's house wren population, it is difficult to predict the functionality of each song section in our endemic population (LaBarbera et al. 2012, Llambías et al. 2012, Dos Santos et al. 2016); however, it seems likely that the introduction section is designed for short-distance communication, whereas the terminal section is used for long-distance communication, as in other house wren populations (Johnson and Kermott 1991, Dos Santos et al. 2016). Trills are thought to be an honest signal of male quality because they are demanding to produce and limited by biomechanics (Podos 1997, Podos et al. 2004, Cramer 2013). Trill characteristics have been correlated with reproductive success in some species (Ballentine 2004, Caro et al. 2010), although not in house wrens in New York (Cramer 2012, 2013).

We investigated the effects of anthropogenic noise on the song structure of Grenada's house wren population by comparing song characteristics in urban and rural populations. We hypothesised that because introduction and terminal components of house wren songs differ in biological function, house wrens may use different compensatory strategies for each section. We predicted that Grenadian house wrens would adjust all parts of their song – introduction section, terminal section, and trill – in urban (noisier) environments by increasing minimum frequency to avoid frequency masking, preserve short- and long-distance communication, and ensure acoustic signals of mating quality are received. We also predicted that Grenadian house wrens in urban areas would use slower trills to reduce the risk of reverberation and maintain trill performance (Warren et al. 2006) as an indicator of quality as a mate. We predicted that Grenadian house wrens

in urban areas would sing longer songs and have longer terminal sections to increase detectability and ensure communication with long-distance receivers.

METHODS

Study site

The island of Grenada, in the Lesser Antilles, is of volcanic origin and has relatively low avian biodiversity (Groome 1970). It has approximately 50% forest cover (primarily secondary growth), 29% agroforestry (e.g. nutmeg, cocoa, citrus, mango, breadfruit, avocado), and 6% other cultivated land (Niles 2013). Grenada's avian biodiversity is estimated to include 160 different species, including many occasional visitors. It has only one known avian endemic species, the Grenada dove (*Leptotila wellsi*) (Groome 1970, Rusk 2009), but has several near-endemic species, such as the Lesser Antillean tanager (*Tangara cucullata*) and Grenada flycatcher (*Myiarchus nugator*), and endemic subspecies, such as the Grenada hook-billed kite (*Chondrohierax uncinatus mirus*). Our surveys suggest that the Grenada house wren is almost entirely restricted to the largest island, Grenada, but some individuals can be found on the other smaller islands that are part of the country of Grenada (Williams, Koper and Warrington, unpublished data).

We recorded 33 birds at five urban and five rural sites (Figure 9). Urban and rural sites differed in the amount of vegetation, man-made infrastructure (mainly roads and low buildings), traffic, and anthropogenic noise. Urban sites were characterised by dense buildings, higher population density, and relatively heavy traffic on paved roads with few natural greenspaces. Rural sites were characterised by the predominance of mixed forest, usually gravel or dirt roads rather than paved roads, light traffic, and low population density. As approximately 75–80% of the native

vegetation on the island was cleared by European colonists for agricultural purposes by the 1800s (Beckles 1992), much of the forest vegetation is secondary growth, frequently including exotic plant species of South American or Asian origin. Therefore, rural sites were defined not by species composition, but based on cover of greenspace relative to built environment. Sites such as orchards that are human-altered but plant-dominated were classified as rural because of the low densities of structures built from impermeable materials. To quantify differences between urban and rural sites, using aerial imagery, we estimated surface cover of greenspace and built environment, and identified road type within a 50 m radius of each bird recording location. At urban sites, the built environment made up $63 \pm 15\%$ at each bird recording location, whereas greenspace covered $37 \pm 15\%$ of each location, and all adjacent roads were paved. At rural sites, the built environment made up $18 \pm 14\%$ of the location, whereas greenspace covered $82 \pm 14\%$ of the area, and road types were gravel or dirt roads, or trails.

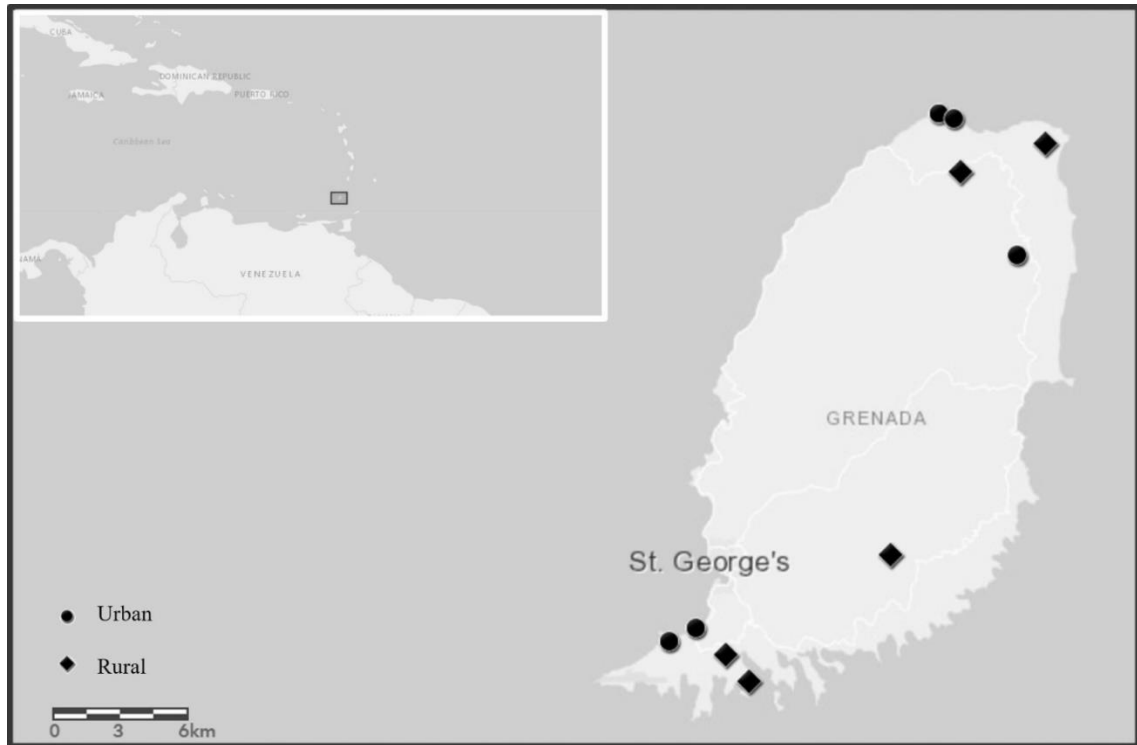


Figure 9. Map of Grenada, its position in the Caribbean, and the location of the rural ($n = 5$) and urban ($n = 5$) sites used for Grenadian house wren (*Troglodytes aedon grenadensis*) song recordings.

House wren songs could be heard at distances of at least 100 m, depending on perch height of receiver and sender, background noise, and song elements, but signal-to-noise ratio significantly decreases beyond 50 m, regardless of those factors (Holland et al. 1998).

Song recordings

We recorded free-living unbanded individuals from 16 April – 8 May 2016, 23 February – 3 March 2017, and 17–27 August 2017. All individuals were assumed to be males as we know of no evidence of female singing in this species. We recorded songs as uncompressed WAV files (bit depth 16 and sampling rate 44.1 kHz) using a Zoom H4N handheld digital recorder with built-in 90° stereo microphones or Rode NTG-2 directional microphone to record songs from close distance. Although it is possible that recorder type impacted our recordings, we believe that it is unlikely to have significantly altered our conclusions, for several reasons: (1) both microphone systems record high-quality sound, (2) the H4N handheld digital recorder's microphone is designed to remove the stereo effect generally associated with omnidirectional microphones, (3) we recorded both urban and rural songs using both types of recorders, and (4) we used song parameters known to be relatively robust and repeatable (see below). We recorded songs between 06:30 h – 11:00 h (32 individuals), although one individual was opportunistically recorded at 16:45 h.

We recorded songs in similar conditions: low wind, clear days, and no rain. To ensure we did not record the same individual more than once, birds recorded within 2 km of each other were only ever recorded during the same period and by the same observer, to ensure that different individuals could be identified with certainty. Most individuals were at least 50 m apart. We were

unable to measure distance between recorders and vocalising birds, but distances did not vary systematically between treatments.

Song measurements

We manually selected songs in Raven Pro 1.4 (Charif et al. 2010). Raven Pro's settings were standardised for all recordings with Hann window size = 512 samples, frequency grid resolution discrete Fournier transform (DFT) = 512 samples, grid spacing = 93.8 Hz, time grid 50% overlap, and hop size = 256 samples. We used Raven Pro's standard 3 dB filter bandwidth of 135 Hz (short-term Fournier transform) for spectrogram display.

We selected every distinguishable song and section in our recordings, choosing from the channel with highest signal-to-noise ratio. We also avoided songs that overlapped with other sounds following the 'threshold' protocol outlined by Podos (1997) to avoid unwanted background noise and limit human bias during the selection process. We selected whole songs, introduction sections, terminal sections, and trills. We considered songs as 'whole songs' if they had introduction and terminal sections and the beginning of the introduction section was clear on the spectrogram. We excluded songs without clear introduction sections from our analyses of whole songs to limit human bias during selection.

We measured five song parameters for the whole songs and the different sections within songs. We measured the 90% frequency bandwidth (Hz; henceforth referred to as 'bandwidth'), 5% low frequency (Hz; 'lowest frequency'), 95% high frequency (Hz; 'highest frequency'), and 90% duration (s; 'duration') of whole songs, introduction sections, terminal sections, and trills. We also measure the trill rate (s^{-1}) as the number of trill notes per second using the 90% duration

of the trill. We chose these frequency variables because they are relatively robust, are least likely to show bias during manual selection, and include built-in measurements in Raven Pro (Charif et al. 2010).

Statistical analyses

For each section of the song, we used generalised estimating equations (GEE) within a generalised linear model, using the package ‘geepack’ (Halekoh et al. 2006) in R version 3.4.4 (R core Team 2018), to investigate the effects of habitat type on each of the above song parameters. We included habitat type as an explanatory variable. Data were normally distributed and homoscedastic, so we used a Gaussian error structure and identity link. We assumed an exchangeable correlation structure (similar to including bird ID as a random variable in a linear mixed model) to control for sampling several songs for each individual. We treated all birds as coming from the same population, as the island of Grenada is only 344 km² (Eyre 1989). Sites were no more than 28 km apart. We used α of 0.1 to determine significance to reduce the risk of Type II error, which can have serious consequences in conservation biology (Taylor and Gerrodette 1993).

When we analysed effects of habitat type on trill rate we included bandwidth and song frequency in the model, as trill rate is influenced by those song parameters (Podos 1997). We used the quasiliikelihood under the independence model criterion (QICu), a variation of Akaike’s Information Criterion (AIC) suitable for generalised estimating equations (Pan 2001), to determine which biological variables should be included in the model. The model with the smallest QICu value was considered the best model (Pan 2001), but any model with a $\Delta \text{QICu} \leq 2$ was considered competitive (Burnham and Anderson 2002). We compared models that included habitat type,

bandwidth, lowest frequency, and highest frequency as explanatory variables, with and without interactions with habitat type. After using QICu value to determine which song parameters were biologically important and should be included as independent variables, we used a null hypothesis significance testing approach to assess the influence of habitat on trill rate, to be consistent with our analyses for other response variables (Mundry 2011).

RESULTS

We recorded 33 individuals, and included every song and section that met our requirements in our analyses. We recorded 285 whole songs from 27 birds, including 134 from rural sites from 14 birds and 151 from urban sites from 13 birds. We had sufficient information to analyse 281 introduction sections (135 rural, 146 urban) from 27 birds (14 rural, 13 urban), 519 terminal sections (304 rural, 215 urban) from 32 birds (18 rural, 14 urban), and 237 trills (126 rural, 111 urban) from 20 birds (10 rural, 10 urban). We recorded an average of 16 songs per bird, ranging between 1 and 72 songs recorded for individual birds.

Whole songs of Grenada's house wrens differed between urban and rural populations, and the internal structure of the song also varied with habitat type (Figure 10). The wrens adjusted both introduction sections and trills in urban areas. Introduction sections had significantly higher lowest frequencies ($\beta = 197.7 \text{ Hz} \pm 99.7 \text{ SE}$, Wald Statistic = 3.93, $P = 0.047$; Table 13) and had a significant but small decrease in duration ($\beta = -0.1368 \text{ s} \pm 0.0823 \text{ SE}$, Wald Statistic = 2.77, $P = 0.096$; Table 13) in urban areas compared to rural areas; other song parameters did not vary significantly between habitat types. Trill rate was significantly faster in urban areas ($\beta = 5.48 \text{ s}^{-1} \pm 1.40 \text{ SE}$, Wald Statistic = 15.2, $P < 0.001$; Table 13), even after controlling for effects of trill frequency. Trill rate increased significantly with minimum frequency ($\beta = 0.0031 \pm 0.0008 \text{ SE}$,

Wald Statistic = 14.61, $P < 0.001$) and, to a lesser extent, highest frequency ($\beta = 0.0011 \pm 0.0006$ SE, Wald Statistic = 3.24, $P = 0.072$). QICu values indicated trill rate was best explained as a function of lowest frequency, highest frequency, and habitat type without interaction terms (Table 14).

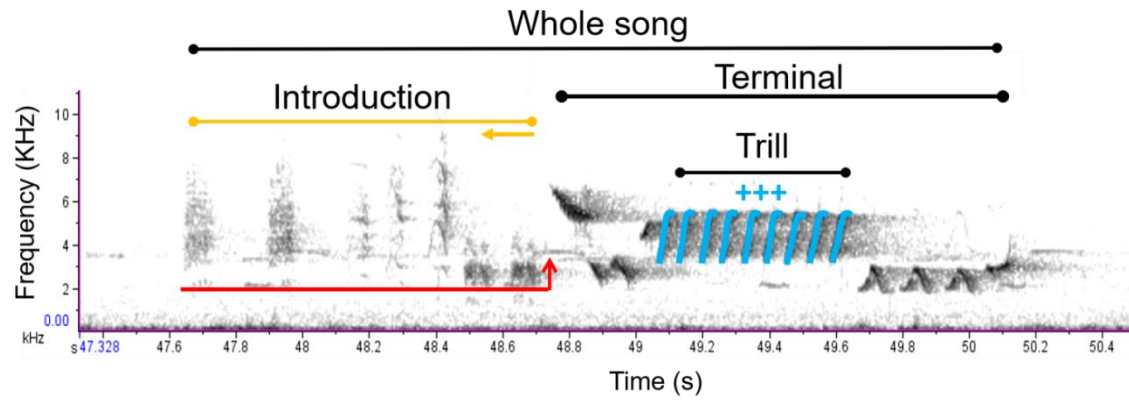


Figure 10. Representation of adjustments to introduction and trills of Grenadian house wren songs in urban compared with rural habitats. The lower frequency of the introduction is shown in red; it was higher in urban habitats compared with rural habitats as indicated by red arrows. Blue represents trill rate and its increase in songs of urban birds. Orange indicates the duration of the introduction section, which was shorter in urban sites.

Table 13. Means and standard deviations of sound parameters measured for whole songs, terminal sections, and trills of Grenada's house wrens (*Troglodytes aedon grenadensis*) recorded in urban and rural habitats across 10 sites in Grenada, West Indies (5 urban and 5 rural). Measurements are reported as mean \pm SD.

Sound parameters	Rural	Urban
Whole song		
90% frequency bandwidth (Hz)	2959.43 \pm 1142.49	2959.46 \pm 718.16
5% low frequency (Hz)	2501.86 \pm 206.45	2476.39 \pm 167.14
95% high frequency (Hz)	5461.29 \pm 1125.47	5435.83 \pm 700.81
90% duration (s)	1.11 \pm 0.29	1.18 \pm 0.28
Introduction		
90% frequency bandwidth (Hz)	4385.96 \pm 915.21	4086.41 \pm 721.71
5% low frequency (Hz) *	2300.09 \pm 324.64	2533.11 \pm 335.35
95% high frequency (Hz)	6686.04 \pm 789.50	6619.52 \pm 706.37
90% duration (s) •	0.63 \pm 0.31	0.62 \pm 0.33
Terminal		
90% frequency bandwidth (Hz)	2801.59 \pm 973.46	2879.53 \pm 785.58
5% low frequency (Hz)	2429.39 \pm 217.77	2463.11 \pm 197.43
95% high frequency (Hz)	5230.98 \pm 966.14	5342.63 \pm 791.67
90% duration (s)	1.02 \pm 0.30	1.06 \pm 0.23
Trill		
90% frequency bandwidth (Hz)	1338.44 \pm 546.39	1342.35 \pm 376.95
5% low frequency (Hz)	2868.25 \pm 637.13	3302.08 \pm 589.41
95% high frequency (Hz)	4206.67 \pm 1089.81	4644.43 \pm 846.80
90% duration (s)	0.40 \pm 0.13	0.39 \pm 0.14
Trill rate (s ⁻¹) ***	13.40 \pm 3.96	19.08 \pm 3.82

• P between 0.05 and 0.1

* $P \leq 0.05$

** $P \leq 0.01$

*** $P \leq 0.001$

Table 14. Ranking of the generalized estimating equation models investigating the effect of habitat and song parameters on trill rate with and without interaction terms.

Model	QIC_u	ΔQIC_u	Model weight
Habitat + 5% frequency + 95% frequency	237	0.00	0.452
Habitat x 5% frequency + 95% frequency	239	2.06	0.161
Habitat + 5% frequency	240	2.84	0.110
Habitat	241	3.50	0.079
Habitat x 95% frequency + 5% frequency	241	3.76	0.069
Habitat x 5% frequency	241	4.13	0.057
Habitat + 95% frequency	241	4.14	0.057
Habitat x 95% frequency	244	6.82	0.015

DISCUSSION

Grenada's house wrens used a combination of strategies to compensate for noise and other alterations of the acoustic environment in urban habitats. Notably, in contrast to our predictions, Grenada's house wrens had significantly faster trills at urban than rural sites. Although fast trills are more likely to degrade through reverberation in the presence of vertical structures (Naguib 2003), they can increase the distance sounds are transmitted (Slabbekoorn et al. 2002, Naguib 2003) or elicit stronger responses from conspecifics (Slabbekoorn et al. 2002). Our result is somewhat surprising because in developed countries, fast trills can be a disadvantage in urban areas (Wong et al. 2010). However, in many Small Island Developing States, such as Grenada, most urban buildings are shorter than surrounding trees, perhaps allowing songs to propagate above or between buildings. Further, some secondary forest in our rural areas may be less open than urban areas, where buildings are separated by roads and gardens. This highlights the fact that effective vocal adaptations to urban environments may differ between developed countries and Small Island Developing States.

The lower frequencies of the introduction section were higher in urban songs, perhaps to reduce frequency masking by anthropogenic noise, which is generally dominated by low frequencies (Patricelli and Blickey 2006, Hasselquist and Bensch 2008, Kaluthota et al. 2016). Birds may sing at higher frequencies in urban environments because birds select higher frequency notes or songs from their repertoires (Bermúdez-Cuamatzin et al. 2009, Nemeth et al. 2013), and repertoire selectivity is particularly likely in species with large repertoires like the house wren (Bermúdez-Cuamatzin et al. 2009). However, raising the lowest frequencies might result from other mechanisms, such as biomechanical responses to singing at higher amplitudes in noisier sites

(Brumm and Bee 2006, Roca et al. 2016). The Lombard effect is known to happen when individuals - or birds - attempt to avoid masking by producing higher amplitude sounds to increase signal-to-noise ratio (Brumm and Bee 2006). Increased amplitude has been correlated with higher frequency, possibly because of the interconnectedness of biological structure involved in sound production (Brumm and Bee 2006, Zollinger et al. 2012). The introduction notes of the house wren songs attenuate faster over a shorter distance in comparison with the trill (Dabelsteen et al. 1993), perhaps making this portion of the song particularly sensitive to this issue, and to challenges with recording songs under field conditions. Further research focused on Grenada house wren vocalisations could clarify the mechanisms behind this frequency shift.

In urban habitats, Grenada's house wrens also slightly but significantly decreased the duration of the introduction section of the songs, contrary to what we expected. Song production can be costly in terms of energy and time (Lambrechts and Dhondt 1988, Hasselquist and Bensch 2008, but see Ward et al. 2004); a previous study found that songs with faster trills were sung in shorter bouts in a noisy environment, suggesting energetic and motor constraints of song production (Brumm and Slater 2006). Previous studies have observed both decreases (Slabbekoorn and den Boer-visser 2006, Francis et al. 2011b) and increases in song duration (Potvin and Macdougall-Shackleton 2015) in response to noise, indicating that a variety of mechanisms are at play. Additional research on conspecific responses to urban Grenadian house wren songs is necessary to assess whether decreasing the duration of the introduction section negatively affects communication (Patricelli and Blickey 2006).

The presence of compensatory behaviours in urban environments can be indicative of a species' ability to thrive in human-disturbed environments (Francis 2015, Brumm and Bee 2006),

perhaps helping to explain the abundance of this unique subspecies across its tiny island range. Some frequency shifts in songs we observed in Grenada are consistent with acoustic adaptations to urban environments commonly seen in developed countries (Roca et al. 2016), but the faster trill rates and decreased introduction durations are more unusual. This suggests that Grenada's house wrens may use unique strategies to communicate relative to their mainland cousins; clearly, more research is needed to better understand the particular challenges posed by urban environments in Small Island Developing States to the wildlife sharing these environments.

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Chapter 4. Management implications and conclusions

CONNECTING TEXT

I investigated the impact of noise produced by industrial machinery and urban activities in two drastically different contexts and found effects with potential negative consequences for bird populations. While not necessarily harmful to populations, changes in nestling sex ratio allocation of chestnut-collared longspurs in the Canadian prairies and song structure of house wrens in Grenada both invite caution about the effects of anthropogenic disturbances and suggest the need for future research. Regardless of the long-term and population-level outcomes, conservation measures can be implemented to mitigate risks and monitor populations. However, management implications and the implementation of conservation measures vary between the high-income countries of the Global North, and the low- and middle-income countries of the Global South.

CANADIAN PRAIRIES AND INDUSTRIAL NOISE MANAGEMENT

Noise management for wildlife conservation in Canada benefits from legal requirements already in place and financial means of industries. The Species at Risk Act (SARA), in place since 2002, aims to prevent species extinction through legal means. It recognizes at risk species (endangered, threatened, special concern and extirpated) and ensures their legal protection and monitoring. Harming, killing, capturing, possessing, collecting, selling, and trading of extirpated, endangered, and threatened species are prohibited under the Species at Risk Act (2002). The habitats and rearing sites of extirpated, endangered, and threatened species are also given protection. Hence, the nests of threatened birds, such as chestnut-collared longspurs, are protected and the potential impacts of industrial activities on them need to be determined by Environmental

assessment. Any effect found must be relayed to the proper federal agency and management measures need to be approved. The Migratory Birds Convention Act 1994 offers additional legal protection to migratory birds and their nests, prohibiting their possession and commercial use.

Although many previous studies have focused on single species, their management recommendations might benefit many other co-existing species (Bernath-Plaisted et al. 2017, Des Brisay 2018, Rosa 2019). Effects of infrastructure and noise can be managed and mitigated through planning, noise barriers, and restoration. Improved planning could limit landscape fragmentation and reduce the acoustic footprint of oil extraction, which may be particularly beneficial to chestnut-collared longspurs. Extraction infrastructures can be centralized, powerlines can be buried, number of roads can be limited, and horizontal drilling can be favored when building new wells (Allred et al. 2015, Thompson et al. 2015). Noise barriers can be used to dampen noise but should be treated with caution because they could further fragment the landscape and alter acoustic signals from wildlife (Parris and Schneider 2009, Francis et al. 2011). Post-extraction restoration would also benefit various species. Above-ground infrastructures, such as oil wells and roads, that are no longer in use should be decommissioned and vegetation restored using native species (Rosa 2019).

CONSERVATION MANAGEMENT IN THE CARIBBEAN

The Caribbean and the Global South face conservation challenges that are likely to accrue with the increase in population growth in the upcoming decades and solutions need to be community-based. Without neglecting the importance of conservation areas and national parks, a North American protective approach of ecosystems can be harmful in mid- and low-income countries and areas used by Indigenous communities (Montgomery et al. 2020). The creation of protected areas barring humans can cause relocation of populations, loss of traditional indigenous

knowledge, loss of livelihood, lack of adherence to regulations and laws, and violence (Montgomery et al. 2020). Community-based conservation can result in long-term, inclusive, and successful programs.

In the Caribbean, conservation biologists should focus their efforts on education, public outreach, national pride, enforcement of legislation, and better governance (Raffaele 2004, UNEP 2010). Training and education through universities and local organizations can help promote local expertise and build on local existing knowledge. Public outreach is needed to engage local communities and build on existing national pride by bringing awareness to local indigenous and endemic species that need protection. Anecdotally, many Grenadians know of the endemic and critically endangered Grenada dove (BirdLife International 2021) and demonstrate pride towards it but do not differentiate the species from other dove species inhabiting the island, giving the incorrect impression that the species is common on the island. Public outreach can also promote citizen science (Bergen 2020) and political interest (Raffaele 2004). Public outreach can help highlight ways conservation goals can align with other political issues like housing, food, and employment through ecotourism (Raffaele 2004, Koens et al. 2009). Lastly, gaps in legislation and regulations, and poor enforcement of existing laws are common challenges in the Caribbean, including in Grenada, that need to be addressed through better governance as they threatened the success of any conservation effort (Raffaele 2004, UNEP 2010).

FUTURE RESEARCH

Mating and breeding strategies of birds can be affected by oil development and anthropogenic noise in various ways, including by altering nestling sex ratio allocation, but little is known on the matter. More research is needed to understand how changes in nestling sex ratio

allocation can affect nestling and fledgling survival (Nicolaus et al. 2009) and population trends (Maness et al. 2007). Extra-pair reproduction, another known component of avian breeding strategies, should be studied as it also could be influenced by anthropogenic activities (Pipoly et al. 2019). Extra-pair paternity rates, resulting from extra-pair copulations, could also correlate with nestling sex ratio allocation (Johnson et al. 2009). Future research could also assess the benefits of different mitigation methods for oil development and noise on wildlife (Northrup and Wittemyer 2013). Conservation managers could prioritize mitigation measures based on effects on taxa of concern and available funds, advising industries on best management practices.

More research regarding the impacts of altered communication from human activities and urbanization could also benefit birds and conservationists. Many species of birds, such as house wrens in Grenada, demonstrate changes in song signalling in presences of noise. However, information is sparse on the effects of receiver interpretation of altered signals and should be investigated in future studies (Halfwerk et al. 2011). Studies should assess signal perception by conspecifics (Antze and Koper 2018), such as mates (Halfwerk et al. 2011) and intraspecific competitors (Grabarczyk et al. 2018). Also, researchers may want to focus on avian species with limited song repertoires and plasticity. Song repertoire size and song plasticity are species-specific and have been related to the capacity to adjust to urban areas (Francis 2015). I also encourage studies to focus on lesser-known species, species with small habitat range, unique sub-populations, species found in mid- and low-income countries, and species or populations residing in areas subject to high levels of anthropogenic activities and urbanization. Much of the current literature available focuses on a restricted number of well-studied species primarily found in high-income countries.

Understanding the effects of anthropogenic disturbances on the breeding grounds of birds has obvious conservation implications but conditions on the wintering grounds can also have long-term impacts. A growing body of literature demonstrates that what happens on the wintering grounds of birds can significantly impact behaviours and fitness during the subsequent breeding season (Goodenough et al. 2017). Worldwide, future research should investigate the yearly cycles of bird species, understanding migrations patterns, habitat requirements, and threats throughout their range (Marra et al. 2015). Understanding the interconnectedness of the environmental conditions that birds are reared in and live through will help implement more impactful conservation measures and will require international efforts.

CONCLUSIONS

Anthropogenic noise, intermittent and chronic, from human activities can affect wildlife in a variety of ways, including by altering communication of house wrens and breeding behaviours of chestnut-collared longspurs. Although the conservation consequences for house wrens and chestnut-collared longspurs are unknown, anthropogenic noise remains a potential threat. Means to manage environmental threats are dependent on context and may not translate to direct actions, such as sound barriers around oil and gas infrastructures, but instead focus on education, monitoring, and advocacy for improved governance. Socioeconomic limitations need to be considered when making conservation management and policy recommendations. Proper recommendations require a shift to increase research in medium- and low-income countries where urban development is projected to greatly affect critical areas for biodiversity (Angel et al. 2011, Organisation for Economic Co-operation and Development 2019). With better research throughout

ecosystems and species habitat range, conservation managers could focus their effort on measures benefiting species globally.

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