

**AVIAN COMMUNICATION NETWORKS: HOW AUDIBLE ARE MOUNTAIN  
CHICKADEE MALES DURING DAWN SIGNALLING?**

by

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**ABSTRACT**

My thesis investigates how urban noise influences the relative audibility of songs to female Mountain Chickadees (*Poecile gambeli*), who assess male signalling at dawn while roosting within the nest cavity. Over two breeding seasons, I monitored Mountain Chickadees breeding on an urban/rural interface in Kamloops, BC, Canada. I broadcast typical Mountain Chickadee songs, with or without added noise, towards recently unoccupied nests while simultaneously re-recording these songs with microphones outside and inside the nest box to determine the relative audibility in relation to both distance and presence/absence of noise. I then tracked individual males' behaviour and movement during dawn signalling, while passively recording their songs with microphones — outside and inside the nest box — to determine the relative audibility of signals from the perspective of the roosting female. The relative audibility of songs decreased with increasing distance from the nest, which was compounded by increased urban noise. During dawn signalling, urban males respond to these effects by remaining closer to the nest, resulting in their songs being more audible within the nest than their rural counterparts. Overall, ambient noise and distance had an interactive effect on relative audibility of songs, suggesting complex dynamics of communication networks that may result in a trade-off, where males are forced to prioritize directing their signals to either their social mates or neighbours.

## **PREFACE**

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The design, execution, and analysis of all experiments in this thesis were directed by C. Snell, thus the thesis is written in first person singular. However, I would like to acknowledge the significant input received by the collaborators throughout the entirety of this Master of Science degree.

Research in 2020 occurred during the beginning of the COVID-19 pandemic, where BC/Kamloops guidelines highly recommended and encouraged individuals to stay home rather than venturing out into public spaces. Therefore, road traffic and foot traffic were drastically reduced.

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## CHAPTER 1: GENERAL INTRODUCTION

### 1.1 CHICKADEES AND SEXUAL SIGNALLING

The dawn chorus is a period of time prior to sunrise, where breeding and/or territorial birds sing at elevated rates (Welling et al. 1995). The dawn chorus occurs primarily in songbirds but has also been observed in non-passerines and non-avian species (Stacier et al. 1996; Burt & Vehrencamp 2005). The dawn chorus is used as a means of defending territories, attracting mates, and intra- and interspecific social communication (Collins 2004; Burt & Vehrencamp 2005). As song rates are often limited by physical condition, singing behaviour during the chorus acts as an honest advertisement of male fitness (Otter et al. 1997). Mating patterns often correlate with a male's performance during the dawn chorus (Kempnaers et al. 1997; Otter et al. 1997, 1998; Mennill et al. 2004; Foote et al. 2010) and suggests dawn signalling in chickadees functions as a communication network in which females assess the relative condition of their mates against other available males (Otter & Ratcliffe 2005). In chickadee species, the dawn chorus typically ends when the female emerges from the nest and the pair copulates (Otter and Ratcliffe 1993; Gammon 2004; McCallum et al. 2020). Female chickadees will often seek extra-pair copulations with neighbouring males soon after the dawn chorus if they deem their social mate as having lower individual quality compared to a higher quality neighbour (Smith 1988; Kempnaers et al. 1992; Otter et al. 1994; Mennill et al. 2003; Mennill & Ratcliffe 2004; Bonderud et al. 2018).

Previous studies in Great Tits (*Parus major*) hypothesized that acoustic signals during dawn singing are primarily intended for female receivers (Krebs et al. 1981; Mace 1986; Mace 1987; McGregor 1991), based upon observations that the intensity of dawn singing in

individual males peaks during the period of highest fertility of their mates (immediately before and during egg-laying; Mace 1987; Welling et al. 1995). In addition, male behaviour during the chorus is strongly influenced by both the presence and behaviour of his mate (Krebs et al. 1981; Mace 1986; Otter et al. 1993). The observation in several species within the Family Paridae that the cessation of dawn singing coincides with the emergence of the female from the nest cavity (Mace 1986; Otter et al. 1993; Gammon 2004) has led to suggestions that the chorus may be audible to the female from within the nest and has since been confirmed by placing microphones within the cavity (Otter & Ratcliffe 2005; Halfwerk et al. 2011). This demonstrates that not only is the female's mate audible, but often so too are neighbouring males. Halfwerk et al. (2011) also demonstrated that during dawn singing, females often call from within the cavity, and this can result in their mates altering their behaviour, suggesting that the males are also listening to the females within this signalling network.

The response of females to male singing suggests that there may be information embedded within the male's song, or in the pattern of singing, that is useful to females, which is likely based on evidence that dawn signalling has been shown to honestly reflect variation in male condition, dominance rank and/or age (Otter et al. 1997; Poesel et al. 2001; Ballentine et al. 2003). Further, studies show that song output is often limited by male somatic condition or access to food (see review in – Otter et al. 2021) and would therefore be an 'Index Trait' (Maynard-Smith & Harper 2003) — one that is essentially honest by design in that it can not easily be faked. For example, high-ranking Black-capped Chickadee (*Poecile atricapillus*) males sang earlier, sang for longer and at both higher average and

maximum song output (song/min) rates than their low-ranking flockmates during dawn signalling (Otter et al. 1997). Females could then simply assess the relative condition of their chosen mate against neighbouring males through relative song output during chorus singing. However, females can also gather information on their mates' abilities through eavesdropping on counter-singing interactions (Otter et al. 1999; Mennill et al. 2003; Burt & Vehrencamp 2005; Peake 2005; Mennill & Otter 2007) which do occur periodically between neighbours during the dawn chorus (Foote et al. 2008). As evidence suggests that female chickadees strategically adjust both nest placement (Ramsay et al. 1999) and entrance cavity orientation (Mennill & Ratcliffe 2004) to enhance acoustic properties within the cavity, they may be positioning themselves in an advantageous location to assess multiple males simultaneously (Murphy & Gerhardt 2002; Otter & Ratcliffe 2005). However, such network signalling of the dawn chorus can be disrupted by changes in inter-male spacing or signal transmission in different habitat types (Hansen et al. 2005).

## **1.2 CONSTRAINTS OF URBANIZATION**

One major contributor to habitat-induced effects on communication is global urbanization. Urbanization introduces excess noise (Slabbekoorn and Peet 2003) that can negatively affect vocal signals and reduce communication among individuals and between mates (Amrhein 2014). Bird species richness has been shown to decrease in areas with high anthropogenic noise, in part because noise can negatively affect breeding behaviour and predator detection (Manzanares 2008). Because birds use acoustic signals — in the form of songs or calls — to communicate with rivals and mates (Searcy and Nowicki 2000; Collins 2004), background noise can impede signalling. The signal structure of a species' song is shaped by both the habitat structure and typical distance through which sound must travel to receivers (Hunter &

Krebs 1979); in most passerine species, the structure of the notes and amplitude of the signal has evolved to transmit across typical inter-territory distances. Lower frequency whistled songs, like those of chickadees, have optimal transmission properties in forested habitats (Marten & Marler 1977), and allow the song to transmit larger inter-territory distances that are often seen in forest birds. However, because song notes are constrained to a narrow bandwidth, and selection favours notes in lower pitch ranges that tend to transmit farther, these notes can become obscured by other low-frequency sounds in the environment. Persistent low-frequency noise pollution common in urban environments can mask these acoustic signals (Slabbekoorn and Peet 2003); this then affects inter- and intraspecific communication, requiring birds to either adjust their vocalizations temporally or structurally to compensate or avoid urbanized regions as seen in “urban avoider” species (Blair 1996; Slabbekoorn and Peet 2003; Halfwerk and Slabbekoorn 2009; Nemeth et al. 2013; LaZerte et al. 2017; LaZerte et al. 2019).

Some species have begun to adjust to noise pollution by altering their vocal repertoire to consist of more calls and high-frequency songs (Slabbekoorn and Peet 2003; LaZerte et al. 2017), as songs that are of higher frequency are able to better transmit through urban noise pollution (Slabbekoorn and Peet 2003; Slabbekoorn 2004; LaZerte et al. 2017). Species have also adapted to noise by increasing song amplitude (Brumm 2004), emphasizing elements within the songs that have a higher pitch if unable to change the song type (LaZerte et al. 2017), or by singing more frequently or at times when noise pollution is lowest (e.g., while it is still dark; Fuller et al. 2007).

Urban singers may be forced into trade-offs between signals that counter noise pollution effects, versus those that convey information intended for receivers. High-frequency acoustic signals attenuate faster than low-frequencies; therefore, selection should favour songs that are lower in pitch to transmit further distances (Catchpole and Slater 1995). However, urban noise is predominately low-frequency — likely masking such songs — thus negatively effecting low-frequency vocalizers (Slabbekoorn and Peet 2003). As opposed to typical frequency patterns, intermediate or high-pitched acoustic signals are less likely to be masked in urban noise, but the sound waves are more easily scattered and reverberated off of impervious urban surfaces (Wiley and Richards 1982; Slabbekoorn et al. 2007) and are unable to travel as far as low-pitched signals (Catchpole and Slater 1995). Therefore, urban-settling vocalizers are forced to adopt signals that will not be masked but may compromise propagation distance to intended receivers (Luther et al. 2016).

When urban noise is alleviated, some species are able to rapidly shift back to what is sung in noiseless environments, indicating a trade-off had likely occurred when adapting to environments with urban noise. For example, new research has shown that within one breeding season some species can alter their behaviours to correspond with significantly lower ambient noise levels (e.g., during the COVID-19 pandemic; Derryberry et al. 2020; Gordo et al. 2021). This finding strongly suggests that the shifts adopted in urban areas represent a trade-off between transmission vs. optimal signal content, as birds shift away from ‘urban-adapted’ singing as soon as noise issues are alleviated.

### **1.3 STUDY SPECIES**

Mountain Chickadees (*Poecile gambeli*) are small, non-migratory songbirds that inhabit high elevation, montane coniferous forests of western North America (McCallum et al.

2020). This species has a life-history that is somewhat atypical of most urban-adapting birds; rather than being habitat generalists like most previously successful urban-adapting species (Blair 1996; Kozlovsky et al. 2017), they are considered habitat specialists (McCallum et al. 2020). Mountain Chickadees are, however, secondary cavity nesters largely reliant on cavities created by other species (McCallum et al. 2020), which means they can be attracted to nest boxes placed in urban landscapes. Similarly, as winter residents, supplemental food sources in the form of bird feeders may attract dispersing birds to settle in urban areas that neighbour natural habitats. Combined, nest box and bird feeder provisioning can help explain the invasion of suburban neighbourhoods on the periphery of cities by Mountain Chickadees, but more striking are recent studies that suggest not only are the birds occupying these landscapes, but they may also be adapting to urban environments. Marini et al. (2017a) found that urban Mountain Chickadees had similar reproductive output to their rural counterparts, but initiate nests earlier in the season. Further, nestlings had higher feather growth rates than rural birds (Marini et al. 2017a), possibly in response to differences in insect phenology between habitats (Hajdasz et al. 2019).

Urban Mountain Chickadees also appear able to adjust their dawn singing in high ambient noise areas; urban males start singing earlier in relation to dawn (Marini et al. 2017b) and tend to have more high-frequency song types compared to rural males (LaZerte et al. 2017). Urban males use more songs than *chick-a-dee* calls when vocalizing (Marini et al. 2017b), with songs known to have greater transmission range than calls, particularly in environments with high ambient noise (LaZerte et al. 2015). Adjusting to use more songs versus calls suggests Mountain Chickadees have some plasticity to respond to urban noise, but Marini et al. (2017b) also found that urban males have higher song output at dawn than their rural

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counterparts, suggesting they may also be in better physical condition, as song output during the dawn chorus is directly related to male condition (Cuthill & MacDonald 1990; Otter et al. 1997; Lucas et al. 1999; Poesel et al. 2004; Murphy et al. 2008; Grava et al. 2009). However, it is unknown whether these adjustments compensate sufficiently to still allow females and other males to assess dawn singing behaviour of males.

For chickadees, female assessment of dawn signalling during the nest lining/fertile period occurs most often while females roost within nest boxes. Studies on primary cavity-nesting Black-capped Chickadees, birds that excavate their own nest cavity, found that females mated to low-ranked mates chose nest cavities close to the borders of higher-ranking neighbours (Ramsay et al. 1999), and females tend to orient the entrance holes of natural cavity nests towards nearest neighbouring territories (Mennill and Ratcliffe 2004). Orientation of the entrance hole and location of the nest cavity would facilitate assessment by females, as songs of neighbouring males can be heard within the nest cavity alongside the songs of the female's mate (Mennill and Ratcliffe 2004). In Black-capped Chickadees, females are also known to eavesdrop on mate-vs-neighbour signaling at dawn to assess potential extra-pair mates (Mennill et al. 2003). Studies in related Great Tits found male choruses are not only audible from within nest boxes, but also that females call from within roost nests to their mates during dawn signalling (Halfwerk et al. 2011). As females rely on audibility to both communicate with and assess their mates, noise pollution may affect both female assessment and communication. While studies on signal modification and propagation have been conducted on Mountain Chickadees in urban landscapes, it is currently unknown whether these adjustments sufficiently compensate for signal-masking associated with urban noise pollution. Further, it is unknown whether these signal

adjustments in high ambient noise enable females to continue to monitor the relative signaling of their mate and neighbouring males. That will be the goal of this thesis.

Previous studies on the acoustic variables of nest boxes have been done on multiple edge species, those species that occur on the edges of forests beside openings and meadows, or that are predictably urban and may be considered generalists (Lampe et al. 2004; Mennill et al. 2004; Blumenrath et al. 2012; Grabarczyk and Gill 2019); however, to my knowledge this is the first study done on a primarily upper montane forest-dependent species that prefers habitats with high tree density. In addition, my study encompasses an urban-rural gradient of varying degrees of human development and habitat available to chickadees. Mountain Chickadees are an unlikely urban-adapting species, as they generally prefer continuous coniferous forests that are typically absent in urban landscapes. They are more widely spaced than Black-capped Chickadees and tend to remain within 100m of their nest site (C. Snell pers. obs), occurring in patches across a landscape. These patches can host a cluster of chickadee pairs, while being adjacent to an area with no pairs present. My study not only adds to a limited database of nest box acoustic studies, but adds a specialist, upper montane forest-dwelling species that has unpredictably become adaptable to certain characteristics of urban environments.

#### **1.4 STUDY SITE**

I conducted this study in Kamloops, BC, Canada, during the 2019 and 2020 breeding seasons. Kamloops is situated within a valley at the junction of the Upper and Lower Thompson rivers, with biogeoclimatic zones of Bunchgrass at lower elevations, and Ponderosa Pine at higher elevations where Mountain Chickadees occur. I made use of a previously existing network of approximately 65 nest boxes in rural and 40 in urban



locations in the South Kamloops region (Marini et al. 2017b), which have been monitored annually since 2013. Due to this being a long-term chickadee study population, various box designs have been implemented throughout the years; however, box designs typically varied only by the material of the front face – ranging from cedar boards to PVC – while internal dimensions remained relatively consistent. In 2020, all boxes were replaced and standardized to one design, detailed in Chapter 3. Nest boxes were placed in two general areas: Kenna Cartwright Park, and several neighbourhoods in the upper urban areas of South Kamloops, including Thompson Rivers University campus (Figure 1.1). Kenna Cartwright Park, where most rural boxes were located, is an 800ha municipal park with over 40km of accessible trails and primarily consists of Ponderosa Pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) mixed forests, with grassland and sagebrush (*Artemisia* sp.) open areas and ground covering.

In most previous studies, urban and rural habitats are put into two dichotomous categories of ‘urban’ and ‘rural’; however, habitats within Kamloops are on more of an urban-rural gradient and are not two completely distinct categories. Therefore, for the purposes of my studies, I classified nest boxes as urban habitat if they were within 75 m of a human-made structure or road, or rural if there were no human-made structures or significant roadways or paths within 75 m of the nest box (Figure 1.2). Rural habitat classification excluded minor disturbances such as hiking or walking trails, like those throughout Kenna Cartwright Park. Rural sites consisted of native forests with high canopy closure interspersed with some open grassland meadows, whereas urban sites consisted of some forested areas and trees, grass lawns, and non-native vegetation typically found in urban areas and backyards. The canopy

is much sparser in urban habitats, and there are significantly more deciduous trees (largely ornamentals), compared to rural habitats (Marini 2016).

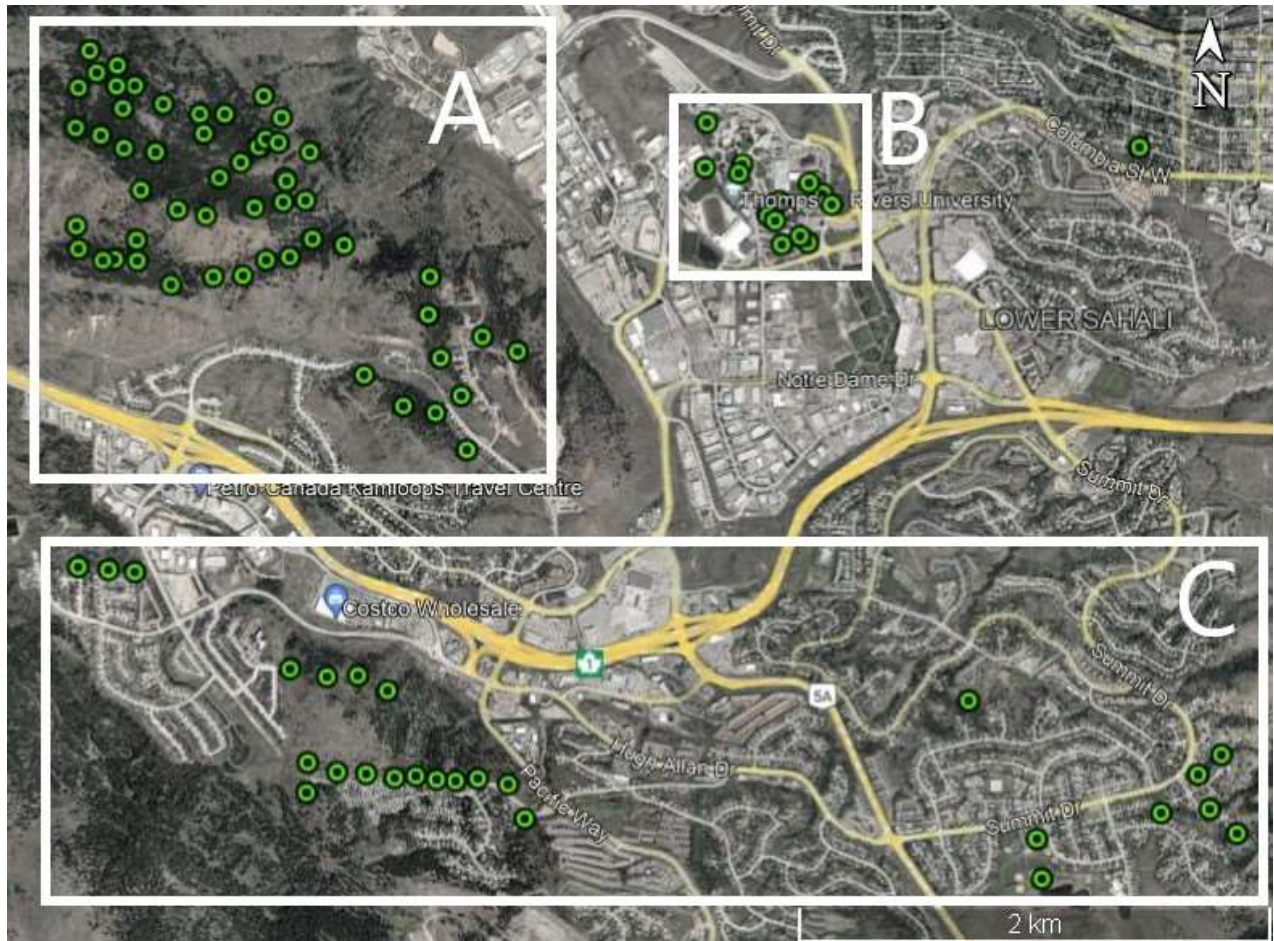


Figure 1.1 Mountain chickadee (*Poecile gambeli*) nest boxes were located throughout the southern area of Kamloops, BC, Canada. The Rural sites were mostly in Kenna Cartwright Park (A), while the Urban sites were mostly at Thompson Rivers University campus (B) and throughout several high elevation urban neighbourhoods (C). Photo Credit Google Earth Pro.



Figure 1.2. Google Earth image of a typical Rural Mountain Chickadee (*Poecile gambeli*) nest box site (top) and a typical Urban nest box site (bottom), in Kamloops, BC, Canada. The red circle shows the presence or absence of human-made structures, roadways, or large-scale trail systems within a 75m radius in which the habitat designation of each nest box site was based on.



## **1.5 THESIS OVERVIEW**

The goal of this thesis is to investigate urbanization effects on Mountain Chickadee communication, specifically, whether noise pollution affects signal structure, and female potential to assess male signalling. To determine this, I conducted audio recordings of male signalling from the perspective of the female – at and within the nest boxes where females roost overnight during the peak of the dawn chorusing period. In Chapter 2, I use playback broadcasts of male song at varying distances from the nest, and re-recorded these from within the nest boxes, to determine the relative audibility of male signals within the nest box, and how this is affected by distance of the signalling male. To simulate effects of noise pollution, I broadcast the songs with and without artificial noise, and determined how this feature of urban environments effects signalling. In Chapter 3, I tested how males respond to reduced signal audibility found in Chapter 2; using autonomous recording units (ARU) to passively record the chorus from the nest location, I simultaneously tracked individual singing males in urban and rural territories. This approach allowed me to observe how male chorusing is affected by ambient noise, its effect on signal audibility, and how males compensate. Finally, in Chapter 4, I synthesize my findings and compare these to current and past literature on female assessment in noisy environments and suggest potential future research directions.

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## **CHAPTER 2: URBAN LIVING: A FIELD TEST OF THE SIGNAL-TO-NOISE RATIO OF MOUNTAIN CHICKADEE SONGS IN NOISY ENVIRONMENTS**

### **2.1 INTRODUCTION**

Many temperate and tropical species of songbirds engage in intense bouts of singing in the period prior to, and extending through, sunrise. Known as the dawn chorus, singing during this period is hypothesized to function for territorial defense, mate attraction, and to facilitate social dynamics (Staicer et al. 1996; Collins 2004; Burt & Vehrencamp 2005). Early research on Great Tits (*Parus major*) suggested that one of the primary intended receivers of these vocal signals are female listeners (Krebs et al. 1981; Mace 1986; Mace 1987; McGregor 1991). In several species of cavity-nesting birds, males end their dawn signing when the mate female leaves the nest (Mace 1986; Pärt 1991; Otter & Ratcliffe 1993; Gammon 2004; McCallum et al. 2020), and peaks of dawn song output coincide with female fertility and/or commencement of egg-laying (Welling et al. 1995). In Black-capped Chickadees (*Poecile atricapillus*), male chorus behaviour such as movement patterns, distance from the nest, and song rates, were influenced by the fertility of their mate (Foote et al. 2008).

Differences in song output during dawn singing also correlate with male dominance/rank, extra-pair mating success and/or age (Welling et al. 1995; Kempenaers et al. 1997; Otter et al. 1997; Poesel et al. 2001; Ballentine et al. 2003), suggesting that dawn singing may be a means of honestly advertising the fitness or quality of a male (Otter & Ratcliffe 1993; Welling et al. 1995; Kempenaers et al. 1997; Otter et al. 1997). Females are thought to use dawn signalling as a means of assessing suitable mates, whether by eavesdropping to assess relative quality of interacting males (Otter et al. 1999; Mennill et al. 2003; Peake 2005;

Mennill & Otter 2007), or by evaluating song traits that may indicate overall fitness of males directly, such as age, dominance, or stamina (Otter et al. 1997; Burt & Vehrencamp 2005). Females can simultaneously sample and eliminate multiple territorial males by strategically positioning themselves within a communication network, or by cautiously sampling males from a distance while remaining undetected (Murphy & Gerhardt 2002; Otter & Ratcliffe 2005), especially if signal transmission is long-range (Otter & Ratcliffe 2005).

These vital communication networks can, though, be masked and disrupted by urban ambient noise (Patricelli & Blickley 2006; Naguib 2013; Slabbekoorn 2013), leading to a reduction in efficacy of intra- and interspecific signals, delayed responses, reduced information received, or increased risk of predation (Kern & Radford 2016; Grabarczyk & Gill 2019a). Anthropogenic noise is predominately low-frequency and can, for example, extend >300m from either side of roads (Forman & Deblinger 2000). This can decrease the area and distance that acoustic signals can be detected by animals (Barber et al. 2010), while differentially disrupting or overlapping low-frequency bird song or call notes (Halfwerk et al. 2011). In response to the daily flooding of low-frequency noise in urban areas, some animals have begun to adjust and adapt their behaviours and vocalizations. Some avian species shift their songs up in pitch or frequency so as not to be overlapped (Slabbekoorn & Peet 2003; Wood & Yezerinac 2006; Nemeth & Brumm 2009; Francis et al. 2011; Nemeth et al. 2013; Redondo et al. 2013; LaZerte et al. 2016; LaZerte et al. 2017a), while others may sing longer songs or sing at faster rates (Grabarczyk & Gill 2019b). Adjusting vocal amplitude may aid in compensating for noise (Nemeth et al. 2010); singing louder can help mitigate noise masking either in conjunction with pitch shifting, or when ability to pitch shift is limited. The

Lombard Effect – when animals increase their vocal amplitude in response to increased ambient noise – has been observed across many taxa, such as bats, birds, frogs, and fishes when in areas of high ambient noise (Brumm 2004; Zollinger & Brumm 2011; Schuster et al. 2012; Hage et al. 2013; Holt & Johnston 2014; Halfwerk et al. 2016; Dorado-Correa et al. 2017). Similarly, birds will adjust the temporal pattern of song timing to avoid peak anthropogenic noise periods, with some species singing hours before dawn (Fuller et al. 2007; Nordt & Klenke 2013; Dominoni et al. 2016). These adjustments to compensate for urban noise can result in birds singing atypical songs compared to rural counterparts (LaZerte et al. 2019a). However, not all vocal adjustments have proven successful and may even be less effective if the signal receiver is in an environment that may impede sound transmission, such as a nest cavity or amidst loud ambient noise.

Female chickadees typically roost within their nest cavity, and as such the acoustic properties of the cavity determine their ability to discern songs of their mates and prospective neighbouring males without having to leave the nest (Otter & Ratcliffe 2005). In Parid species, nest boxes generally do not impair female assessment of distant focal and neighbouring male chorus behaviour (Mennill & Otter 2007; Halfwerk et al. 2011), as females continue to respond to their social mates using calls from within the roost throughout dawn signalling (Halfwerk et al. 2011; C. Snell pers. obs.), and males moved closer to the nest if females delayed their vocal or emergence responses (Halfwerk & Slabbekoorn 2012). In Black-capped Chickadees, nest entrance holes were excavated to orient towards neighbouring males (Mennill & Ratcliffe 2004), and nest cavities themselves were often chosen in trees located close to territory boundaries, especially if neighbouring males were

higher ranked than their social partner (Ramsay et al. 1999). However, previous studies showed the signal-to-noise ratio (the level of the observed signal compared to the level of the background noise) of Great Tit and House Wren (*Troglodytes aedon*) songs were marginally reduced inside the nest box compared to outside (Blumenrath et al. 2004; Grabarczyk & Gill 2019a), and Pied Flycatcher (*Ficedula hypoleuca*) songs were found to have higher song degradation within the box than outside (Lampe et al. 2004).

As females rely on audibility to both communicate with and assess their mates relative to neighbouring males during dawn singing, noise pollution could affect female assessment and communication networks (Huet des Aunay et al. 2014; Grabarczyk & Gill 2019a) and can disrupt intraspecific communication networks (Quinn et al. 2006; Wood & Yezerinac 2006; Halfwerk & Slabbekoorn 2009; Nemeth & Brumm 2010; Halfwerk et al. 2011; Huet des Aunay et al. 2014). Some females prefer low-frequency songs, such as domestic canaries (*Serinus canaria*); however, with the addition of urban low-frequency noise, female responsiveness to these song types gradually decreased with increasing urban noise (Huet des Aunay et al. 2014). To the female roosting in the nest, the signal-to-noise-ratio of songs decreases with increasing distance of the male from the nest (Lampe et al. 2004; Blumenrath et al. 2004) and this is exacerbated with increasing noise around the nest (Halfwerk et al. 2012; Grabarczyk & Gill 2019a). Therefore, information gained from honest advertising of males during the dawn signalling period may be reduced for females in noisy environments (Halfwerk & Slabbekoorn 2012; Grabarczyk & Gill 2019a).

The objective of this study was to test the effect of distance and noise on signal-to-noise ratios of Mountain Chickadee songs (*Poecile gambeli*) by broadcasting songs from 25-75m

distances to previously used nest boxes in both urban and rural habitats. I placed a microphone outside and inside the nest box, and at each distance I broadcast Mountain Chickadee songs with and without added noise. I predicted that noise and distance would decrease the signal-to-noise ratio of chickadee songs and may differentially effect those recorded within the nest cavity, especially in urban habitats.

## **2.2 METHODS**

### ***2.2.1 Field Protocol***

I describe habitat and study site details in Chapter 1. Nest boxes consisted of multiple design variants due to the gradual addition of boxes to the study site over time. This led to five slightly distinct box types in the population with similar internal dimensions, whereas the construction material differed slightly and could potentially affect acoustics. To account for this, I added box type as a random variable in statistical models.

I chose nest boxes in the long-term (established in 2013) Mountain Chickadee study population that were actively occupied during the 2019 field season (when the study was conducted) or had been occupied at least one time in the previous five years (indicating their potential suitability;  $N = 23$ ) across both urban ( $N = 11$ ) and rural ( $N = 12$ ) habitats. Two files were removed from analysis due to incomplete recordings or excess wind, leaving a total of 21 nest box trials for analysis. Once active nests had fledged and/or boxes were vacant, I mounted a Wildlife Acoustic SM4 Autonomous Recording Unit (ARU) above the nest box. The ARU unit recorded in stereo channels, with one channel having an external microphone recording outside the box, and the other channel recording from an internal microphone attached to a 3m cord placed inside the nest box. A small square piece of wood (~ 19mm x 19mm) was removed from the upper edge of a side wall of the nest box, where I



then affixed the external microphone, so the microphone was above the entrance hole and facing into the nest cavity. The ARU was set to record continuously until the speaker trials were completed (set on 16bit/44.1kHz digitization/sampling frequency). I used a retractable measuring tape to mark 25m, 50m, and 75m from the nest box, in the direction directly in front of the box entrance hole, as previous work has shown sounds from directly in front of the cavity entrance to be most audible (Mennill & Ratcliffe 2004).

Using the files created by LaZerte et al. (2017b), I used 40 different playback files on rotation that consisted of unique songs obtained from various geographic locations and from 13 different males (see LaZerte et al. 2019b for more details). At each distance interval, I broadcast two different playback stimulus types in succession: one stimulus consisted of only Mountain Chickadee songs broadcast from a single speaker at a typical volume of ~75dB (measured at 1m), and the second stimulus consisted of the same vocalizations from the same speaker as above, but with synthetic noise from actual traffic noise recordings simultaneously broadcast at ~68dB from the second speaker (LaZerte et al. 2017b; LaZerte et al. 2019b). Each “Noise-Added” sound file consisted of 60s of synthetic urban noise after slowly fading for the initial 20s, followed by 28 sequential Mountain Chickadee songs (14 songs/min) for 120s, and ending with 20s of synthetic urban noise slowly fading out, whereas “No-Noise” files were structurally the same but with no added urban noise (LaZerte et al. 2017b; LaZerte et al. 2019b). I used a Roland Mobile Cube amplifier with dual side-by-side 2.5W, 100mm diameter stereo speakers; this allowed me to broadcast the WAV song files from one speaker, and the noise files from a separate speaker simultaneously (LaZerte et al. 2017b; LaZerte et al. 2019b). The speaker system was attached to a Slik Able 300 DX tripod

to raise the speaker (1.6m above the ground) and to ensure the playback songs were not impeded by any low shrub vegetation.

I conducted this experiment on 23 nest boxes distributed across the Kamloops, BC, study sites between June 10<sup>th</sup> – July 2<sup>nd</sup>, 2019. Experiments were conducted early in the morning between 06:00-08:00 a.m., scheduled just after standard dawn chorus timing due to a concurrent experiment, the results of which are not reported here (see Chapter 3). Signal transmission quality has been shown to be significantly more consistent at dawn vs midday (Brown and Hadford 2003) with sounds transmitted over a longer distance at dawn than midday (Henwood and Fabrick 1979), however, other studies show that dawn conditions do not always constitute optimal conditions for long-range communications (Dabelsteen and Mathevon 2002). Therefore, starting times were cut off at 8:00 a.m. so as not to remain closer to dawn than midday. Each box was tested several days after the individual nest had been vacated. This approach allowed me to retain similar weather and climate characteristics of when the nests were active, to prevent the previous pair from being stressed, and to reduce the potential of interference or countersinging from the resident male during playbacks. I also made note of the status of neighbouring nests and whether they were still active, or in range of the speaker trial and would adjust my speaker trial date so that no known nests within audibility range were active during trials.

### **2.2.2 Data Analysis**

Mountain Chickadee songs typically contain two note types, “*fee*” and “*bee*” (McCallum et al. 2020), with a typical song structure in the population of two “*fee*” notes followed by two lower frequency “*bee*” notes. However, songs can often vary in frequency and number of

notes based on the individual, or habitat. Below, the “*fee*” notes are labelled as note one (N1) and “*bee*” notes are note two (N2).

Audio files from each speaker trial were loaded into Audacity v2.4.2 software (Audacity Team 2020). For each distance category (25m, 50m, and 75m), I examined the three clearest songs from each audio file, ensuring there was no other overlapping bird vocalizations, noises or heavy wind that would mask the song on the spectrogram. If it proved difficult to find three clear songs per distance category, I used a minimum of at least one song. Each song was then clipped and labelled into individual files, with the start of each note (N1 and N2) labelled (Figure 1; N = 466). In addition, I ensured that each song clipping had at least 0.5s of space prior to the start of the first note for background noise analysis (Figure 2.1; Figure 2.2).

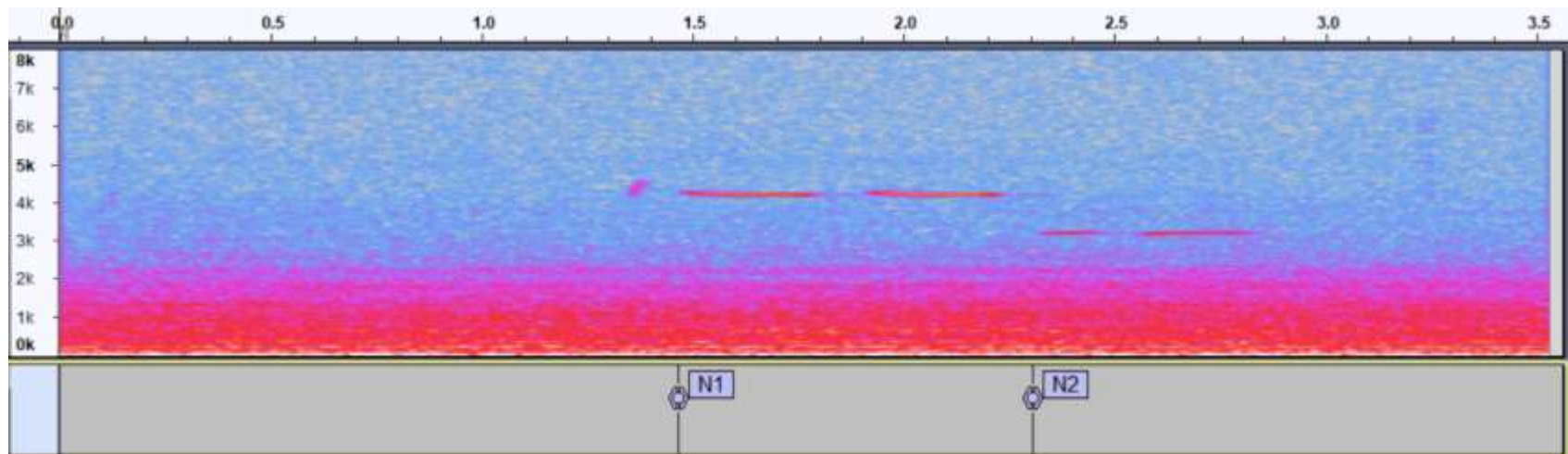


Figure 2.1. An example Audacity software (v2.4.2 Audacity Team 2020) spectrogram representing a typical Mountain Chickadee (*Poecile gambeli*) song clip from a playback trial, with associated labels for the start of each note type, N1 and N2. This example song playback clip is from a nest box in an Urban habitat in Kamloops, BC, Canada, using a No-Noise playback file. The speaker was 25m from the box and this song clip was recorded by the microphone placed inside the nest box.

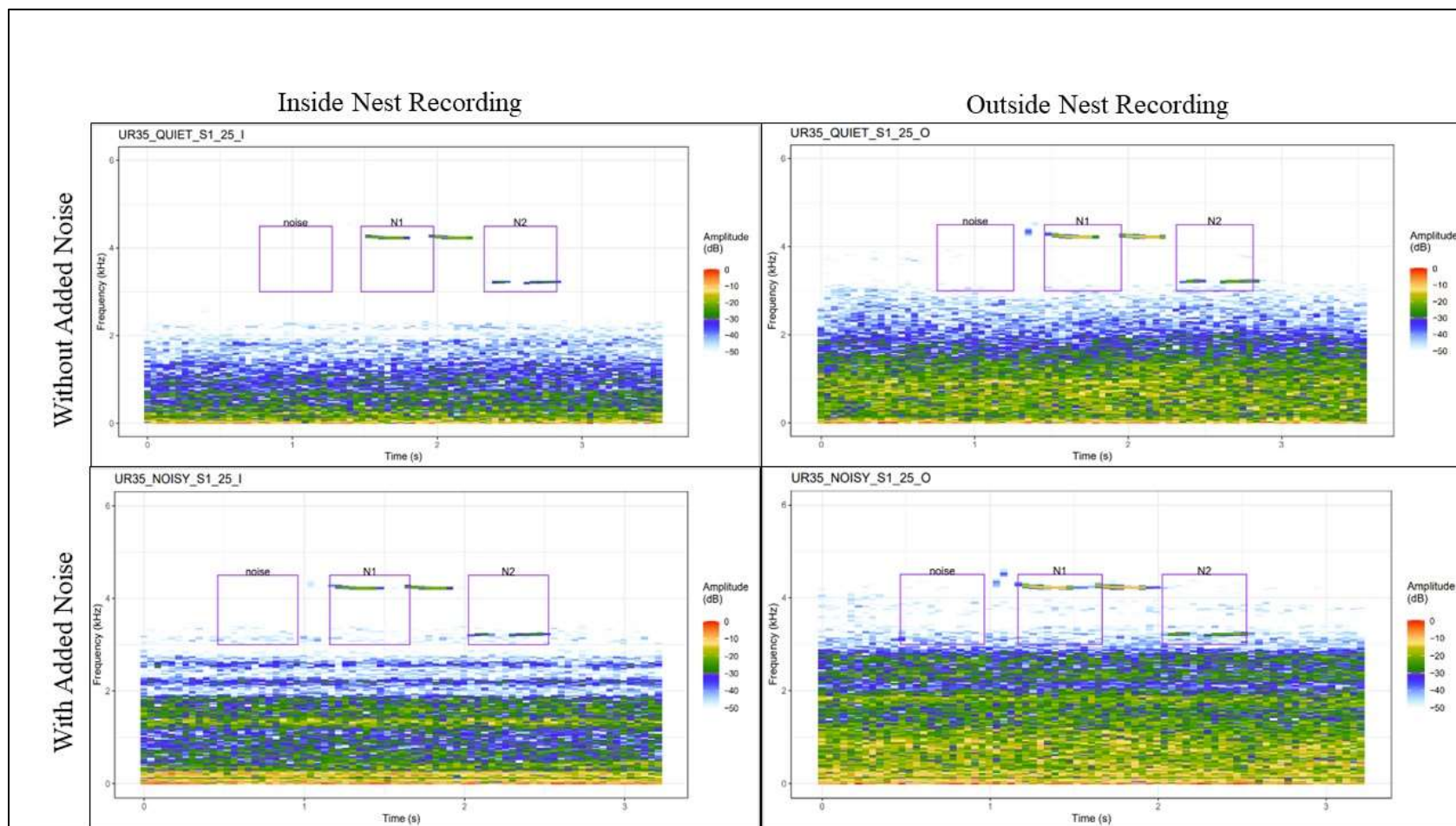
All analyses were conducted with R statistical software (v 4.0.3, 2020, R Development Core) through RStudio IDE (v 1.3.1093, 2020). R packages “tuneR” (Ligges et al. 2018), “glue” (Hester 2020), “kableExtra” (Zhu et al. 2021), “tidyverse” (Wickham et al. 2019), and “assertr” (Fischetti 2021) were used for general song data manipulation. First, I filtered by a frequency range of 3000-5000 Hz to approximate the entire song, and ensured no notes were out of this range. Using the R package “seewave” (v 2.1.6, Sueur et al. 2008), I extracted 0.5s of background noise before the first note and 0.5s of each note type to use for conducting root-mean-square (RMS) analysis (Figure 2.2). Any song clips that resulted in an RMS value lower than the background noise were checked and removed if the noise or overlap was too disruptive (N = 4). These RMS values were used to calculate signal-to-noise ratios (the level of the observed signal compared to the level of the background noise; SNR) in decibels using the following equation:

$$SNR = RMS \frac{note}{noise}$$

Then convert the signal-to-noise ratios to decibels using the following equation:

$$SNR (dB) = 10 * \log_{10}(SNR)$$

I then took the mean of the song clips to obtain one mean value per distance category (25m, 50m, 75m), nest box, treatment type (Noise-Added or No-Noise), microphone location (inside or outside). Next, I compared the signal-to-noise ratio of the songs between the inside and the outside of the nest box using Rstudio.



**Figure 2.2.** Example spectrograms of one Mountain Chickadee playback file song. All images are from one song broadcast from 25m away from the nest in the same Urban nest box in Kamloops, BC, Canada. The top two images were during a No-Noise playback trial, while the bottom two were from Added-Noise trials. The two images on the left were from the inside microphone and the two on the right are from the outside microphone.

I ran my analysis on each note type as chickadees have been known to adjust their songs, particularly the last few notes, in urban environments (LaZerte et al. 2017). A general linear mixed effects model was performed using the “lme4” (Bates et al. 2015) package for R, to assess associations between the signal-to-noise ratio of both note types and microphone position (inside or outside the nest box), distance from the box, treatment type (No-Noise and Noise-Added), and habitat type (Urban or Rural) and any interaction between treatment type and distance of the playback from the nest. Each model incorporated box design type as a random effect to account for the different box designs used in the trials. Figures were created using “ggplot2” (Wickham 2016) and “patchwork” (Pedersen 2020).

## **2.3 RESULTS**

Songs were broken into both note types, note 1 (N1) and note 2 (N2) for analysis. The signal-to-noise ratio (SNR) of N1: declined with increasing distance from the box; was lower in the Added-Noise treatment than the No-Noise treatment; and was slightly lower in Urban vs Rural habitat type. Microphone location (outside vs inside) did not significantly affect SNR. However, there was also an interaction effect between treatment type (No-Noise and Added-Noise) and distance of the playback from the nest (25m, 50m, 75m; Table 2.1; Figure 2.3); this indicated that the decline in SNR with increasing distance was greater in the No-Noise treatment than the Added-Noise treatment. This effect was largely due to the SNR already being fairly low even at short distances when noise was added, and so declining less overall with distance. By comparison, SNR was high at short distances in No-Noise treatments and only reach low levels at 75m in these trials.

Table 2.1. Results from a general linear mixed effects model using R software (v 4.0.3, R Development Core Team 2020), assessing the relationship between the signal-to-noise ratios of Mountain Chickadee (*Poecile gambeli*) playback song note 1 (N1) and treatment type (No-Noise, Added-Noise), distance of the playback from the nest (25m, 50m, 75m), and microphone location (outside, inside) with an interaction effect between treatment type and distance from the nest.

	<i>Estimate</i>	<i>Std. Error</i>	<i>df</i>	<i>t-value</i>	<i>Pr(&gt; t )</i>
Treatment Type	8.11	1.50	251.34	5.40	<0.00001***
Distance	-0.082	0.020	251.46	-4.05	<0.00001***
Microphone Location	-0.34	0.57	251.40	-0.59	0.55
Habitat Type	1.77	0.82	167.55	2.15	0.033*
Treatment:Distance	-0.090	0.028	251.41	-3.16	0.0018**

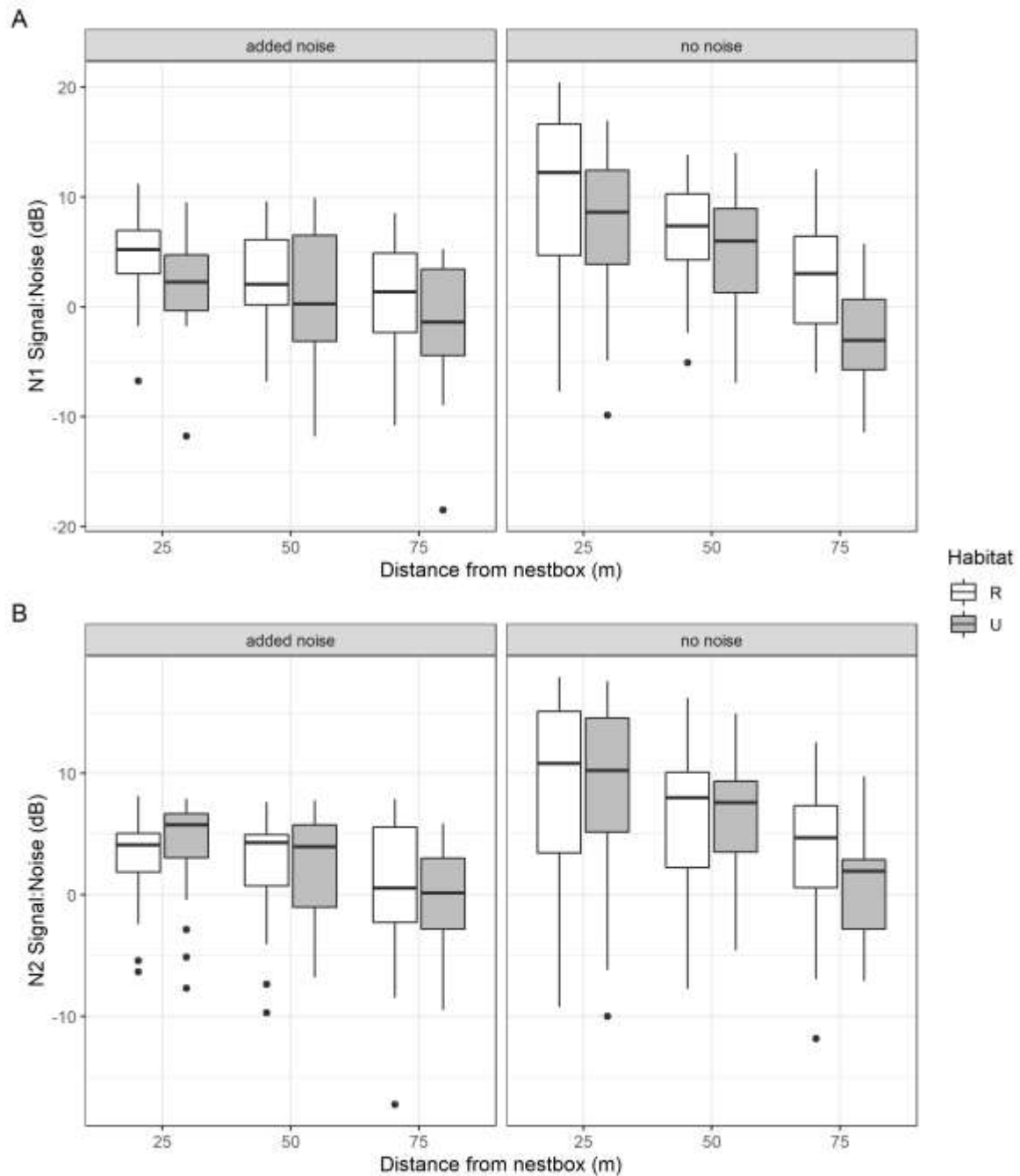
The signal-to-noise ratio (SNR) of N2 was lower in Added-Noise vs No Noise treatments, declined with increasing distance of the playback from the nest and was lower on the internal microphone than the external. There was no effect of habitat on SNR of the N2 note. There was, though, an interaction effect between treatment type (No-Noise and Added-Noise) and distance of the playback from the nest (25m, 50m, 75m; Table 2.2). This interaction is the same as with the N1 note – SNR of N2 decreases from a high value to low value with distance in No-Noise treatments, but already starts at a decreased value at 25m in the Added-Noise treatments and declines less with distance.

In contrast to N1 results above, N2 is affected by microphone location, indicating a difference in the SNR of songs based on whether the microphone was inside the nest box (internal) or outside the nest box (external; Table 2.2; Figure 2.4).

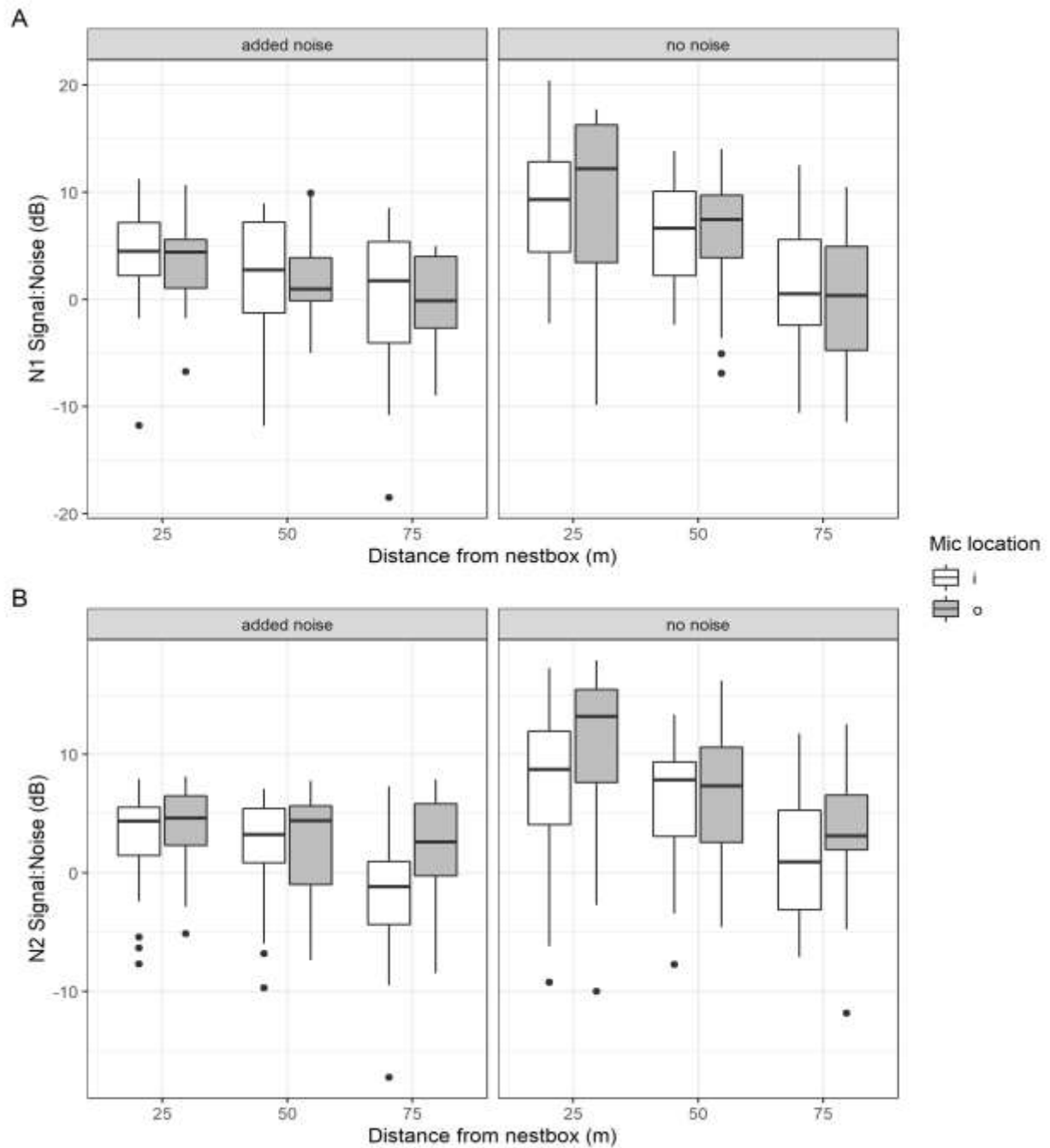


Table 2.2. Results from a general linear mixed effects model using R software (v 4.0.3, R Development Core Team 2020), assessing the relationship between the signal-to-noise ratios of Mountain Chickadee (*Poecile gambeli*) playback song note 1 (N2) and treatment type (No-Noise, Added-Noise), distance of the playback from the nest (25m, 50m, 75m), and microphone location (outside, inside) with an interaction effect between treatment type and distance from the nest.

	<i>Estimate</i>	<i>Std. Error</i>	<i>df</i>	<i>t-value</i>	<i>Pr(&gt; t )</i>
Treatment Type	7.04	1.41	249.27	4.99	<0.00001***
Distance	-0.080	0.019	249.29	-4.14	0.000047***
Microphone Location	1.89	0.54	249.27	3.48	0.00058***
Habitat Type	-1.19	0.79	230.38	-1.50	0.13
Treatment:Distance	-0.065	0.027	249.27	-2.45	0.015*



**Figure 2.3.** Signal-to-noise ratio (dB) of note one (N1; A) and note two (N2; B) of Mountain Chickadee playback songs at each distance interval (25m, 50m, 75m) for both Added-Noise and No-Noise treatments, while comparing the signal-to-noise ratio of notes at each habitat type (R = rural and U = urban) in Kamloops, BC, Canada. Trials with No-Noise exhibited a steeper decline in the signal-to-noise ratio of both note types as distance increased from the nest, regardless of habitat type. Whereas Added-Noise trials exhibited similar signal-to-noise ratios regardless of distance from the nest, habitat type or note type.



**Figure 2.4.** Signal-to-noise ratio (dB) of note one (N1; A) and note two (N2; B) of Mountain Chickadee playback songs in Kamloops, BC, Canada at each distance interval (25m, 50m, 75m) for both Added-Noise and No-Noise treatments, while comparing the signal-to-noise ratio of notes at the two microphone positions (I = inside the nest and o = outside the nest). As distance from the nest increased, both note types exhibited a steeper decline in signal-to-noise ratio in No-Noise trials compared to Added-Noise trials, regardless of microphone location.

## 2.4 DISCUSSION

As expected, songs had a higher signal-to-noise ratio in rural habitats, and in treatments with No-Noise. In addition, treatments with No-Noise had a higher signal-to-noise ratio at all distances (25-75m) and for both microphone positions (inside and outside the nest) compared to songs broadcast with added noise. The second note type, N2, had a lower signal-to-noise ratio inside versus outside of the nest in both treatment types, whereas the first note, N1, did not differ. There was an interaction between distance and treatment type for the signal-to-noise ratios of full songs, as well as the signal-to-noise ratio of N1 and N2 separately, suggesting that the signal-to-noise ratio decreased as distance of the speaker increased from the nest box, but that this decline was far more pronounced in songs broadcast without added noise. This pattern likely occurred because when noise was added to the playbacks, the signal-to-noise ratio for songs were already low, even close to the nest box (25m) – almost equivalent to songs broadcast at the maximum distance (75m) in the treatments without added noise. As I predicted, noise and distance resulted in a decrease in signal-to-noise ratios of chickadee songs, even when I provided optimal sound transmission parameters (i.e., optimal time of day, directly in line with nest entrance, and using previously successful nest cavities).

In this study, the signal-to-noise ratio was used as an indicator of relative audibility of songs. It was assumed that vocalizations picked up by the internal microphone would likely be heard by a female roosting within the nest, as previous studies have found positive correlations between the maximum frequency of songbird vocalizations and the high-frequency limit of sensitive hearing, suggesting coevolution of these characteristics (Henry and Lucas 2010). In addition, Mountain Chickadees have been observed singing from greater

distances than 75m (the furthest playback distance) and continue to elicit a response from the female within the nest from those greater distances (pers. obs. C. Snell), thus suggesting that any song played to the nest at maximum 75m would likely be heard by a female in the nest cavity.

Signal transmission is affected by both the medium through which it travels, such as shrubs vs. open space, and by the distance of the signaller to the receiver (Otter & Ratcliffe 2005). Because Mountain Chickadees inhabit large territories in open conifer forest areas, it is likely that songs become lost in transmission or degraded at greater distances, especially as this species transitions into urban environments where there are more physical and acoustic barriers impeding signal transmission. In some cases, Mountain Chickadees may be experiencing human-altered environments without having to shift into urban spaces; some rural habitats may remain rural in physical characteristics (e.g., open forests with no human-made structures in the vicinity) with minimal-to-no human presence but may have ambient noise levels like that of urban areas (C. Snell pers. obs.). These rural habitats with high ambient noise levels can occur in forests within 200-300m of major highways, such that the home territory of the birds can occupy habitat that resembles native forests of the region, while having acoustic spaces more akin to urban areas. This intrusion of noise pollution to otherwise suitable habitat can further mask and degrade signal transmission.

In response to ambient noise, urban Mountain Chickadees may use strategies to minimize the effects of masking. Previous studies have shown Mountain Chickadees in noisy environments adopt atypical songs compared to rural counterparts (composed of more repetition of N1 notes and omission or reduction of N2 notes; LaZerte et al. 2019b) or adjust

the pitch of their N2 notes up to reduce masking from ambient noise (LaZerte et al. 2017); the latter upward adjustment of N2 note pitch would reduce signal degradation in the nest cavity, as shown in this study. My results confirm that ambient noise dampens certain aspects of typical Mountain Chickadee songs, primarily the lower-frequency second note type, and song degradation increases as the signaller moves further from the nest. These results suggest that regardless of how optimal acoustic conditions are, songs will have a lower signal-to-noise ratio within the nest cavity, and primarily in environments with ambient anthropogenic noise.

Previous research in other avian species has shown that nest boxes alter signal transmission (Lampe et al. 2004; Kight et al. 2012), particularly as distance increases. Similar to my results, Pied Flycatcher (Lampe et al. 2004), Great Tit (Blumenrath et al. 2012) and House Wren (Grabarczyk & Gill 2019) vocalizations were found to be marginally degraded within the nest box. LaZerte et al. (2016) showed pitch shifts in many urban Mountain Chickadee songs, where individuals would often repeat the high note (N1) more and reduce the number of low notes (N2) they sing, likely as an adaptation for low-frequency ambient noise that can mask typical low pitch song notes. I demonstrate here that the lower pitch note, N2, does in fact become marginally degraded within the nest box, especially in environments with increased ambient noise, which may explain LaZerte et al.'s (2016) result that males in noisy environments reduce their use of this note type.

Given that these results suggest noise and distance interact to decrease signal audibility, I would predict that urban males in typically noisier environments may be more constrained to chorus close to the cavity than rural males. That may then constrain their ability to signal to

more than just their mate, which could impede their ability to defend their entire territory from competing males. This limitation could potentially reduce the size of territory they can maintain, as well as effecting the likelihood of mating with neighbouring females assessing potential extra-pair mates (cf. Kempenaers et al. 1997). In addition, by being constrained to the area nearest the nest box, individuals may miss important warning signals or presence of predators. By understanding how specialist cavity-nesting species signal transmission is affected by urban ambient noise, we may become better suited to understand the large-scale ecological outcomes of these urban noise pressures and can better prioritize mitigation of these pressures on surrounding biodiversity.

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## **CHAPTER 3: NETWORKS AND NOISE FOR MOUNTAIN CHICKADEES: URBAN MALES ARE MORE AUDIBLE TO NESTING FEMALES THAN RURAL MALES**

### **3.1 INTRODUCTION**

Urban noise pollution can mask avian communication networks (Patricelli and Blickley 2006; Naguib 2013) and result in delayed responses from receivers, reduced information received through acoustic signals, disruption of intra- and interspecific signals, and increased risk of predation (Kern and Radford 2016; Grabarczyk and Gill 2019a). Urban noise is primarily low frequency, such as traffic or construction noise, and can transmit more than 300m on either side of roadways (Forman and Deblinger 2000). These low-frequency sounds reduce the distance and area that animals can detect acoustic signals (Barber et al. 2010), while differentially masking or overlapping bird song or call notes that are low-frequency (Halfwerk et al 2011).

Birds reliant on dawn signalling amidst high ambient noise may be required to compensate by singing closer to the nest (Halfwerk et al. 2012), or by adjusting their vocalizations. Some species shift songs up in pitch (Slabbekoorn and Peet 2003; Wood and Yezerinac 2006; Nemeth and Brumm 2009; Francis et al. 2011; Nemeth et al. 2013; Redondo et al. 2013; LaZerte et al. 2016; LaZerte et al. 2017; Grabarczyk and Gill 2019b), shift song timing to avoid peak urban noise (Fuller et al. 2007; Nordt and Klenke 2013; Dominoni et al. 2016), increase vocal amplitude in response to increased ambient noise (the Lombard Effect; Brumm 2004; Zollinger and Brumm 2011; Schuster et al 2012; Hage et al. 2013; Holt & Johnston 2014; Halfwerk et al. 2016; Dorado-Correa et al. 2017), or sing atypical songs that may decrease frequency overlap with noise (LaZerte et al. 2019). In Mountain Chickadees (*Poecile gambeli*), the signal-to-noise ratio of songs decreased with increasing distance from

the nest, especially in urban habitats with added noise (Chapter 2). This finding would suggest that a female receiver located at the nest site may have difficulty discerning her mate and neighbouring males as both distance of the signaller from the nest and noise within the environment increase.

Early research in Great Tits (*Parus major*) suggest that females are one of the primary intended receivers of these dawn vocalizations of chickadee and titmice species (Krebs et al. 1981; Mace 1986; Mace 1987; McGregor 1991). Females are known to eavesdrop on signalling interactions between their mates and neighbouring males (Otter et al. 1999; Mennill et al. 2003; Peake 2005; Mennill & Otter 2007), as well as evaluating song traits (e.g., song rates) that are honest advertisements of male fitness, dominance, age, or stamina (Burt & Vehrencamp 2005; Chapter 1). As songs typically have long-range transmission, a female can position themselves within a communication network that allows them to sample multiple males while remaining undetected (Murphy & Gerhardt 2002; Otter & Ratcliffe 2005); however, changes in inter-male spacing and singing in different habitats can disrupt the network signalling of the dawn chorus (Hansen et al. 2005). However, not all vocal adjustments have proven successful, and may be even less so if the signal receiver is within a cavity that can further degrade signal transmission, or if the ambient noise is too loud and thus impedes the transmission of these vocal signals.

Female chickadees rely on the acoustic properties of their chosen nest cavity to hear signals of their social mates and neighbouring males, as they remain within their nest during dawn signalling (Otter and Ratcliffe 2005). Female emergence causes a shift in male behaviour; the male stops vocalizing, the pair copulate, and then they begin foraging together



(Otter and Ratcliffe 1993; Gammon 2004; McCallum et al. 2020). Female chickadees tend to select cavities that are located close to territory boundaries, especially if the neighbours are higher ranked than social mates (Ramsay et al. 1999), and females excavate entrance holes that orient towards neighbouring male territories (Mennill and Ratcliffe 2004), suggesting that cavities may be selected partially for their acoustic properties. Studies, though, have shown that nest cavities can marginally degrade sound (Lampe et al. 2004), resulting in a lower signal-to-noise ratio of vocalizations within the cavity compared to outside (Blumenrath et al. 2004; Grabarczyk and Gill 2019a; Chapter 2), and this effect is intensified with increasing ambient noise around the nest (Halfwerk et al. 2012; Grabarczyk and Gill 2019a) as studies have found females to be less responsive to low-frequency songs as urban noise gradually increased (Huet des Aunay et al. 2014). However, previous studies of Parids found nest boxes generally do not impair female assessment of distant acoustic signals (Halfwerk et al. 2011). Further, females vocalize to their mate from within the nest during the dawn chorus (Halfwerk et al. 2011), and males will move closer to the nest if high noise levels delay these signals being produced by females (Halfwerk and Slabbekoorn 2012). This suggests that high noise levels associated with increased urbanization could impede female perception, as well as modify male behaviour in an attempt to compensate for these noise levels, and to ensure the female is present at the nest.

To test the effect of distance and noise on Mountain Chickadee dawn signalling, I recorded the dawn signalling of 50 males over two breeding seasons in an urban/rural habitat gradient. I used an Autonomous Recording Unit (ARU) placed above nest boxes, with a microphone both outside and inside the boxes, to record male signals from the perspective of

listening females. I then tracked and recorded male behaviour, vocalizations, and distance from nests during the dawn chorus, while also recording ambient noise levels in territories. Based on the results of Chapter 2, I predicted that during the dawn signalling period, distance and noise would reduce the probability of recording male songs from within the cavity compared to outside, especially in urban environments. I also predicted that males in noisy environments would attempt to compensate by remaining closer to the nest during dawn signalling.

## **3.2 METHODS**

### ***3.2.1 Field Protocol***

I describe habitat and study site details in Chapter 1. Due to the continuous integration of boxes over time, there were multiple nest box designs throughout the study site. Within the study site, there were a total of five box designs with similar internal dimensions; however, some consisted of differing construction material that may potentially affect acoustics. To account for this, I added box type as a random variable in the models. In 2020, I replaced all boxes with a common design for standardization. New boxes were constructed of 25.4 mm x 152.4 mm cedar fence boards, with an internal dimension of 100 mm length x 100 mm width x 254 mm height. All nest boxes were placed randomly within likely or confirmed chickadee habitat, with no particular entrance hole orientation and at least 1-2m off the ground.

I monitored nest boxes every 4-5 days starting in mid-April, making note of nest and clutch initiation date, number of eggs, number of hatchlings, and fledge date. If nests appeared to be active (signs of excavation or presence of nest lining, chickadees, etc.) then I monitored them every 2-3 days, recording nest status, presence and/or number of eggs, and

whether the pair was previously banded. I monitored inactive boxes once every seven days for late-nesting pairs. I used nest box traps to catch chickadees at their nest cavity at the beginning of nest-initiation (before the onset of egg-laying) and measured and banded adults with numbered USGS (US Geological Survey) bands. If adults were not captured prior to incubation, I used nest box traps to capture the adults one to three days after eggs hatched.

Once Mountain Chickadee pairs began using nest cavities and were in late nest building/early egg-laying phase, I attached a Wildlife Acoustics SM4 (ARU) on each nest tree. The ARUs were mounted approximately 300mm above the nest box and placed the day before dawn chorus recording to allow for the birds to acclimate to the presence of the ARU unit. Each ARU device had two microphones which allowed the use of stereo channels to record dawn choruses. One microphone (directly fixed onto the ARU device) recorded signals outside the nest box, while a second microphone, on a 3m cord, was placed into the nest via a small hole in the upper, back corner of the nest box. The hole created to insert the internal microphone was small enough to simulate natural holes in trees and did not disrupt the chickadees. This internal microphone allowed me to record sound from within the nest box, approximating what a female roosting within the box would hear of males during the dawn singing period. Using both microphones enabled me to assess the number and audibility of males in the area from both outside and inside the nest box.

I pre-set the ARUs to begin recording 45 min prior to dawn (set on 16bit/44.1kHz digitization/sampling frequency), based on civil twilight, in both urban and rural areas, ensuring that I recorded the initiation, and entire bout of, dawn singing by the focal male associated with the nest box. Two observers also arrived on the focal male's territory prior to

the onset of dawn singing and one observer manually recorded the male's dawn singing (Audiotechnica AT8015 microphones attached to either a Marantz PMD 561 or 661 recorders, set on 16bit/44.1kHz digitization/sampling frequency), while also tracking the movements of the focal male throughout the chorus. Actively recording the focal male using hand-held recorders allowed me to confirm the ARU's external microphone detected the start and end of the chorus. A second observer simultaneously collected sound pressure levels (SPL) at the start of the chorus (see details below), every 5 min during the chorus, and at the end of the chorus. This observer also flagged each new singing location of the male (greater than 10m from previous song post), as observer 1 recorded the male. Once the chorus had finished (cessation of singing for 5 consecutive minutes), I returned to each marked song post to take GPS coordinates (accuracy +/- 5m; Garmin GPSmap 60CSx). Using these coordinates, I measured the distance of these locations to the nest box and averaged these distances to get the average focal male distance from nest during each dawn singing.

To measure ambient noise level on the male's territory, I used either a Pulsar 30 or Goldline SPL in 2019, or a REED R8080 Data Logging Sound Level Meter in 2020. All SPL meters used were set for flat response in A-weighting. The SPL observer would watch the SPL meter for 10s and note the highest and lowest value on the meter. After the chorus, I took the average of the high and low values per reading, and then averaged those values for one final average SPL reading per dawn chorus. I switched to REED SPL meters in 2020 for consistency between multiple chorus field crews. To account for variation in sound level readings of the different SPL devices, I conducted a calibration comparison analysis. I visited 20 locations post-field season (July 2020) ranging on a continuous scale from high to low ambient noise, and used all four units (1 Goldline, 1 Pulsar and 2 REED SPLs)

simultaneously and recorded their average SPL reading over 30s. I performed linear regressions between each pairwise combination (two REED against one another, Average REED vs Goldline, Average REED vs Pulsar, Goldline vs Pulsar). The SPL calibration resulted in the REEDs being highly correlated ( $R^2 = 0.99$ ; Appendix A1a). I then corrected values from the other two meters to those of the REEDs for standardization. I adjusted the readings on the Goldline ( $R^2 = 0.79$ ; Appendix A1b) and Pulsar ( $R^2 = 0.41$ ; Appendix A1c) to be comparable to the REEDs by multiplying the values by the slope and intercept of the relationship.

I tracked males' behaviour both during and after the chorus – specifically whether he returned to his nest box upon the emergence of the female and whether the pair copulated, as is typical of chickadees. I recorded two males per day throughout the dawn chorus period — nest initiation to early egg-laying — which is spread over 2-3 weeks in late-April through mid-May due to the differential timing of breeding onset in the rural/urban sites.

All field work for this project was conducted under Canadian Wildlife Service (CWS) permit number 10940 and Animal Care and Use Committee (ACUC) numbers: UNBC-2017-01 and UNBC-2020-01.

### **3.2.2 Data Analysis**

I collected a total of 54 dawn chorus ARU recordings from the 2019 ( $N = 24$ ) and 2020 ( $N = 30$ ) field seasons, from 26 urban and 24 rural sites; however, 4 recordings were lost due to excess noise or corrupt files. Each ARU recording had two channels, one for each microphone (within and outside of the nest box). These recordings varied in length based on each individual male's dawn singing bout and ranged from 10 to 106 minutes. The

recordings were broken into 120s clips and were individually annotated using Avisoft-SASLab Pro v5.2.15 software (Specht 2019). Annotations included noting calls, songs, or “other” vocalizations (e.g., gargles, seets, contact calls) of the focal male, focal female, and any neighbouring chickadees. I visualized all spectrograms in Avisoft (*parameters*), and made note of whether the vocalization could be visualized on the spectrograms for the external microphone (outside the nest box), the internal microphone (inside the nest box), or both. I determined the total number of vocalizations visible on the spectrograms at the nest location (outside microphone) and the number visible from the female’s location within the nest (inside microphone). For the purpose of this study, vocalizations visible on the spectrograms were considered audible, or able to be heard by the female within the nest or outside of it. For each chorus, I then determined the average male distance from the nest during the chorus and average ambient noise levels.

Analyses were conducted in R (v 4.0.3, R Development Core Team 2020) using RStudio (v 1.3.1093, 2020). To investigate the degree of noise pollution birds are contending with, I first examined whether ambient noise levels (dB; after standardizing readings from different devices) differed by habitat (urban vs rural) and/or year (2019 and 2020) using a general linear model. I initially tested the full model with interaction terms between fixed effects, then removed non-significant interactions using a backwards stepwise approach ( $p$  to remove  $> 0.1$ ) until only significant interactions ( $p < 0.05$ ) and/or the main effects remained in the model.

To determine relative audibility of vocalizations, I first conducted a linear regression of the number of songs detected within the nest (recorded on the internal microphone) against

the total number of songs in the chorus (recorded on the outside microphone). I took the residual values for each male to create a relative audibility score; this gave an index of whether the male's vocalizations were more or less audible than the expected value, corrected for differences between the total number of vocalizations the males produced. I repeated this step but with number of *chick-a-dee* calls audible within the nest compared to the total number of calls to create a residual calls variable.

I used my relative audibility score as my dependent variable and a general linear mixed-effect models in the package “lme4” (Bates et al., 2015) in conjunction with “lmerTest” (Kuznetsova et al., 2017) to test for relationships between relative audibility of focal male songs and calls against habitat (urban vs rural), average distance of the focal male from nest during the chorus, and ambient noise levels. Each model incorporated chorus ID and box type as a random effect to account for individual boxes being occupied in both years and various box designs used in 2019. I first ran the whole model with all fixed effects and all interaction terms between fixed effects, and then sequentially removed any non-significant interactions ( $p$  to remove  $> 0.1$ ), in a backwards stepwise fashion until only significant interactions and/or the main effects remained in the model. I used “ggplot2” (Wickham, 2016) and “patchwork” (Pedersen, 2020) to create the figures.

### **3.3 RESULTS**

#### ***3.3.1 Ambient noise***

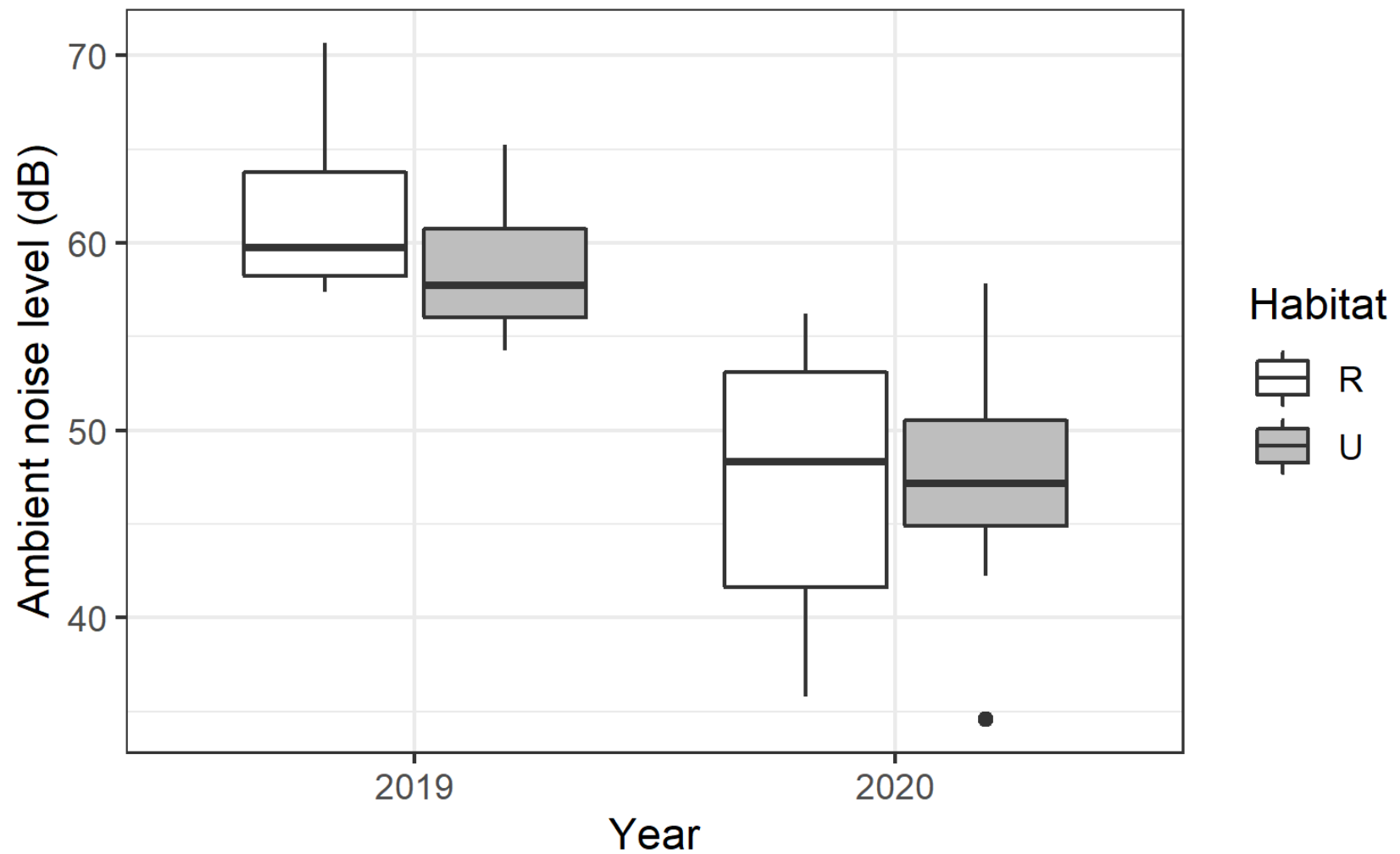
Ambient noise levels (dB) were not associated with habitat type (Urban or Rural); however, ambient noise was associated with year of study (Table 3.1). The 2020 field season had significantly lower sound pressure level readings than 2019, but the ambient noise levels

were similar between habitats within each year (Figure 3.1). The interaction term was not significant ( $P = 0.3$ ) so was removed from the final model.

Table 3.1. A Linear model using R software (v 4.0.3, R Development Core Team 2020) of the relationship between ambient noise levels (average dB) during Mountain Chickadee (*Poecile gambeli*) dawn choruses in Kamloops, BC, Canada, and habitat type (Urban and Rural) and year of study (2019 and 2020).

	<i>Estimate</i>	<i>Std. Error</i>	<i>df</i>	<i>t-value</i>	<i>Pr(&gt; t )</i>
Habitat Type	-1.45	1.53	1	-0.95	0.35
Year	-12.76	1.53	1	-8.36	<0.0000000001***





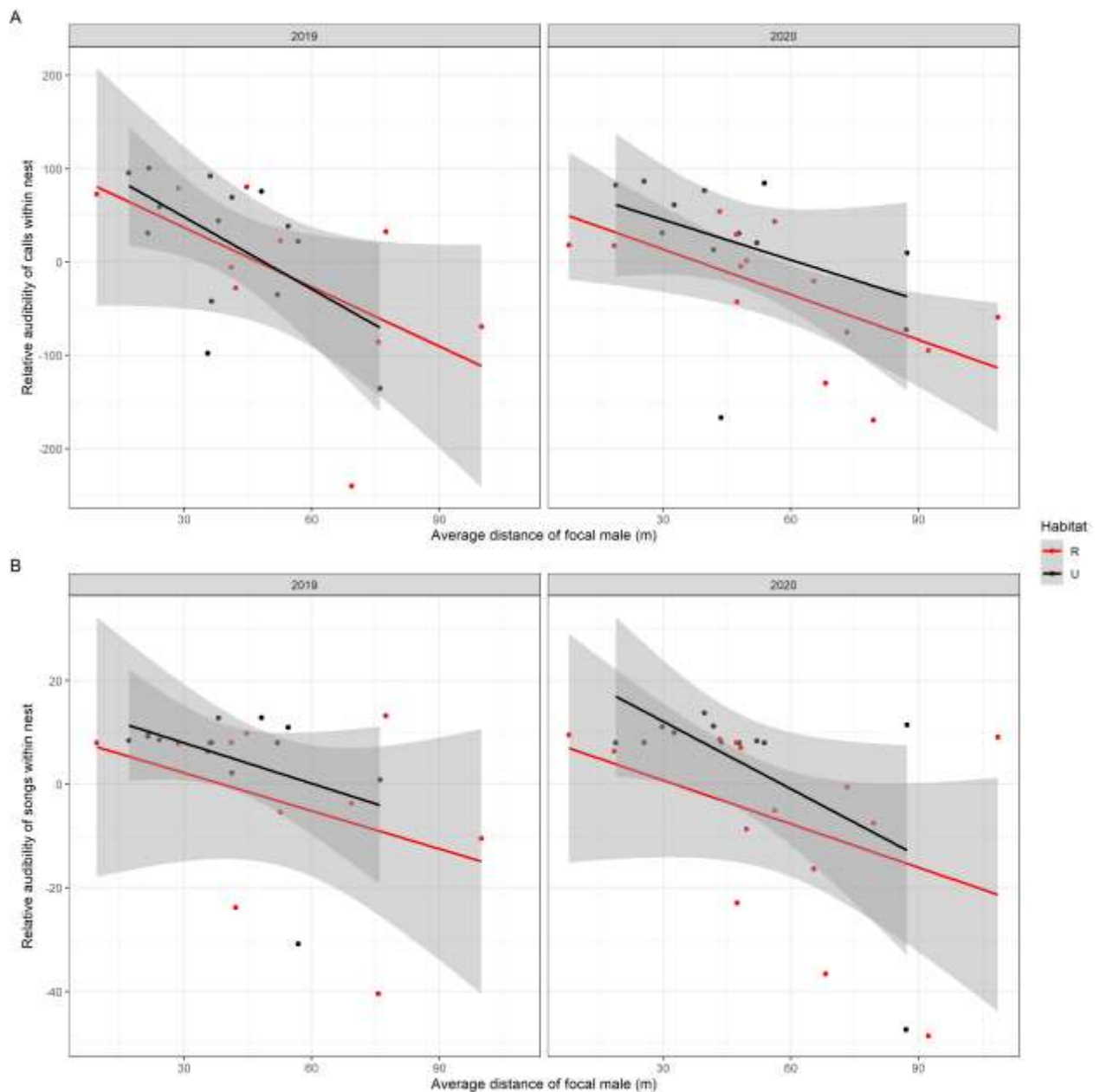
**Figure 3.1.** Average ambient noise levels during Mountain Chickadee dawn chorus in 2019 and 2020 field seasons in Kamloops, BC, Canada, based on habitat types (U = Urban and R = Rural). The 2020 field season had significantly lower average ambient noise levels than 2019, regardless of habitat type.

### 3.3.2 Relative call audibility within the nest

I examined relative audibility of *chick-a-dee* calls (residual scores for each male from number of calls audible within the nest relative to total calls recorded) against habitat type, ambient noise levels, and average distance of the male from the nest during the chorus. None of the interactions were significant (all  $p > 0.90$ ), so they were subsequently removed from the model; the final model retained only the main effects. Ambient noise levels (average dB), and habitat (Urban and Rural) were not associated with the relative audibility of *chick-a-dee* calls during the chorus. However, relative audibility of *chick-a-dee* calls decreased the further the male was from the nest (Table 3.2; Figure 3.2).

Table 3.2. Results from a general linear mixed effects model using R software (v 4.0.3, R Development Core Team 2020), assessing the relationship between the relative audibility of Mountain Chickadee (*Poecile gambeli*) calls and average distance of the male from the nest box, habitat type (urban and rural) and ambient noise levels (average dB).

	<i>Estimate</i>	<i>Std. Error</i>	<i>df</i>	<i>t-value</i>	<i>Pr(&gt; t )</i>
Average Distance	-2.00	0.39	38.90	-5.07	0.00001***
Habitat Type	26.17	20.35	36.24	1.29	0.21
Average dB	0.73	1.11	26.14	0.66	0.51



**Figure 3.2.** Relative audibility of Mountain Chickadee (*Poecile gambeli*) chick-a-dee calls (residual values of male calls audible within the nest relative to total male calls recorded; A) and songs (B) in relation to average distance of focal males from the nest, with respect to year of study and habitat (U = Urban and R = Rural) in which they occur. Both years exhibit a decline in relative call audibility as distance of the male from the nest increases. Shown with a 95% C.I.

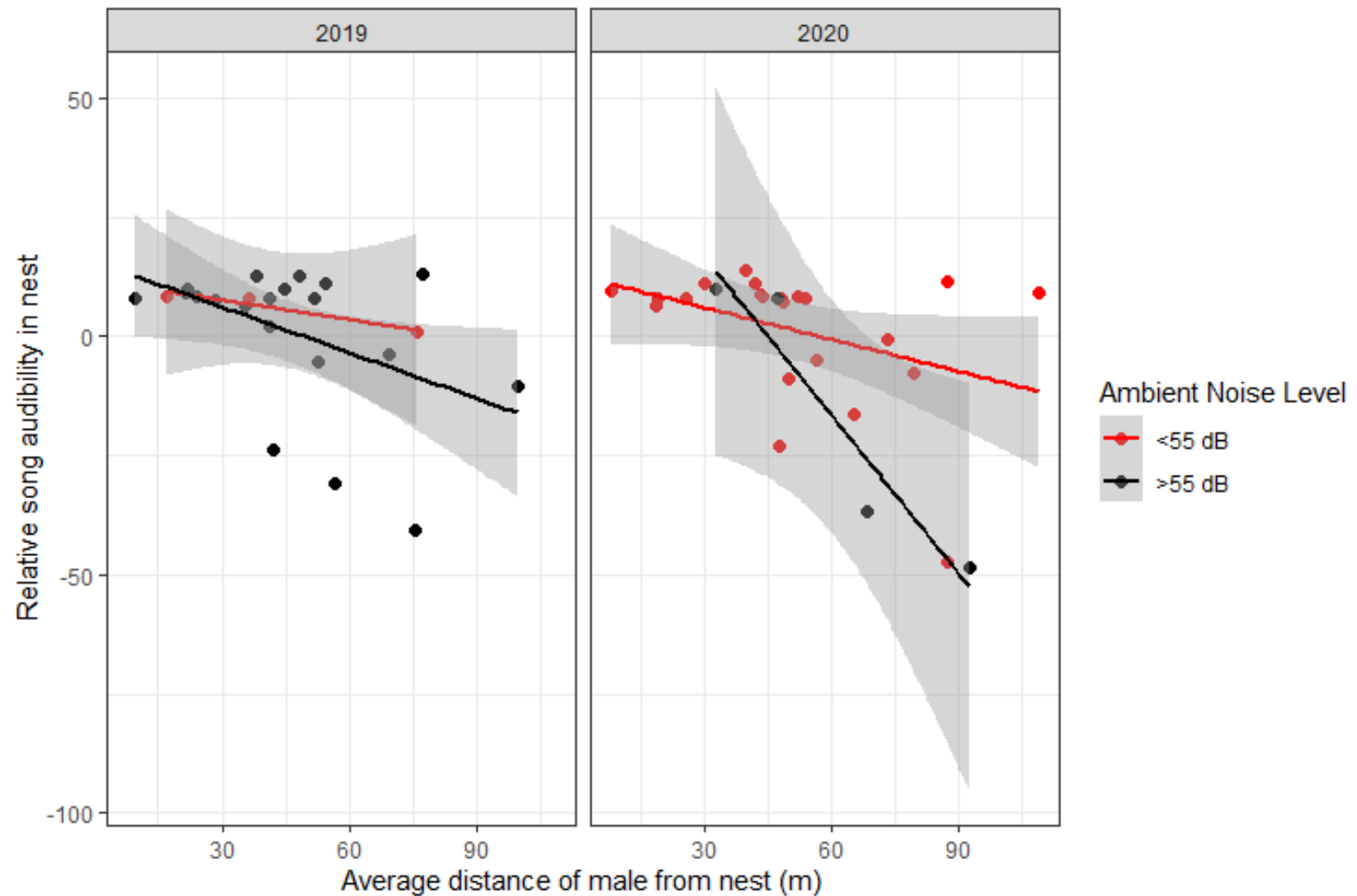
### 3.3.3 Relative song audibility within the nest

I examined relative audibility of songs (residual values for total songs audible within the nest vs all songs recorded for each male) against habitat type, ambient noise levels and distance of the male from the nest. The relative audibility of focal male songs tended to decline with average distance of the male from the nest, but did not vary by habitat type, or ambient noise levels (dB; Table 3.3).

Table 3.3. Results from a general linear mixed effects model using R software (v 4.0.3, R Development Core Team 2020), assessing the relationship between the relative audibility of Mountain Chickadee (*Poecile gambeli*) songs and average distance of the male from the nest box, habitat type (Urban and Rural) and ambient noise levels (average dB).

	<i>Estimate</i>	<i>Std. Error</i>	<i>df</i>	<i>t-value</i>	<i>Pr(&gt; t )</i>
Average Distance	-0.32	0.093	41.48	-3.47	0.0012**
Habitat Type	7.49	4.47	37.40	1.68	0.10
Average dB	-0.18	0.25	41.11	-0.71	0.48

Due to the large difference in ambient noise between years, I also investigated choruses based on year. I classified choruses with average noise levels above 55 dB (N = 25) as occurring within noisy habitats, and those with below 55 dB (N = 25) as occurring within quieter habitats. In 2019, most males were in noisier habitats and song declined with distance, but the few males that were in quieter habitat this year had a slightly lower decline in audibility with distance (2019 in Figure 3.3). In 2020, which was quieter overall, there were more males singing in quieter habitat (< 55 dB) and their relative audibility did not decline as sharply with distance as the few males who were singing in noisier habitats in 2020 (2020 in Figure 3.3).



**Figure 3.3.** The relative audibility of Mountain Chickadee (*Poecile gambeli*) songs within the nest (residual values of male songs audible within the nest relative to total male songs recorded) declined with increasing distance of the focal male from the nest during the chorus in both 2019 and 2020, but the decline was sharper in noisier habitats (ambient noise > 55 dB) than in quieter habitats (ambient noise < 55 dB). Shown with a 95% C.I.

### 3.3.4 Distance vs ambient noise

As relative audibility of both songs and calls was primarily associated with distance of the male from the nest, I explored what factors affected male location during the dawn chorus. Due to the large difference in ambient noise levels between years, I analyzed male distance in relation to noise levels and habitat individually for 2019 and 2020. I used male distance from the nest as the dependent variable with ambient noise and habitat as fixed-effects. In 2019, there was a significant interaction between habitat and ambient noise levels on the distance males travelled from their nests during the chorus (Table 3.4; Figure 3.4). Rural males moved further from the nest when exposed to higher ambient noise; however, urban males moved slightly closer when exposed to higher ambient noise.

Table 3.4. Results from a linear model using R software (v 4.0.3, R Development Core Team 2020), assessing the relationship between the average distance of Mountain Chickadee (*Poecile gambeli*) males from the nest box and both habitat type (Urban and Rural) and ambient noise levels (average dB) in 2019.

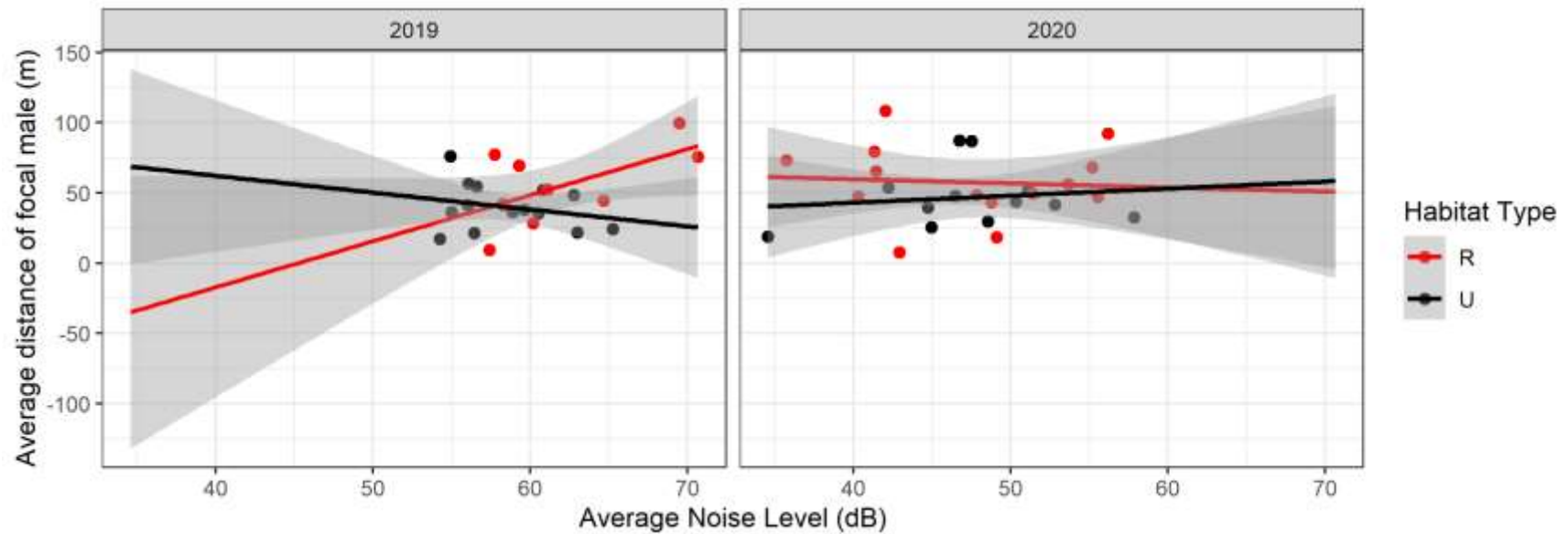
	2019	Estimate	Std. Error	df	t-value	Pr(> t )
Habitat Type		258.50	120.31	1	2.15	0.044*
Average dB		3.28	1.30	1	2.52	0.020*
Habitat:Avg_dB		-4.48	2.00	1	-2.24	0.037*

In 2020, the interaction between ambient noise and habitat was not significant; therefore, it was subsequently removed from the model. In contrast to 2019, there was no association of ambient noise level or habitat type (Table 3.5; Figure 3.5) on the distance of the male from the nest during his singing bout in 2020. As 2020 was quieter than 2019, it appears that male

distance from the nest was no longer explained by ambient noise levels and did not differ based on habitat type.

Table 3.5. Results from a linear model using R software (v 4.0.3, R Development Core Team 2020), assessing the relationship between the average distance of Mountain Chickadee (*Poecile gambeli*) males from the nest box and both habitat type (urban and rural) and ambient noise levels (average dB) in 2020.

	2020	Estimate	Std. Error	df	t-value	Pr(> t )
Habitat Type		-10.87	9.84	1	-1.10	0.28
Average dB		0.017	0.82	1	0.02	0.98



**Figure 3.4.** The average distance of male Mountain Chickadees (*Poecile gambeli*) from the nest during the dawn chorus varied based on habitat type (U = urban and R = rural), ambient noise levels and year of study. In 2019, rural males moved farther away from their nest as noise levels increased, whereas urban males tended to move closer. However, in 2020 during the COVID-19 pandemic, rural males tended to move closer to their nest with increasing ambient noise, though only slightly, whereas urban males tended to move farther away. Shown with a 95% C.I.



### 3.4 DISCUSSION

Ambient noise was significantly lower in 2020, during the COVID-19 pandemic, compared to 2019; interestingly, though, habitat type (urban or rural) did not differ in average ambient noise level in either year. This lack of difference between habitat types likely reflects the fact that the urban and rural sites lie near a major highway traversing the south side of Kamloops, so even though habitat within the male's territory may be fully vegetated with native habitat, it may still have significant noise pollution. Further, some of the highly urban habitats were set back from this highway and major roads, so could be relatively quiet. This unexpected global pandemic could, though, explain the major drop in noise levels in 2020, as the data was gathered approximately one month after the international COVID-19 pandemic shut down, and travel restrictions during this time resulted in major reductions in noise from car traffic.

The most predominant effect on relative audibility of both calls and songs in the nest box was the distance of the male from the nest. As both urban and rural males moved further from the nest, their calls and songs became less audible within the nest cavity; this decline was slightly less pronounced in urban birds in lower ambient noise than when in higher ambient noise. In 2020, with lower noise levels, chorusing males that were maintaining higher distance from the nest did not compromise their song audibility compared to birds chorusing in 2019. When I looked at male behaviour in relation to noise, I found a curious effect in the louder 2019 year. As ambient noise levels increased, urban males moved slightly closer to the nest and became more audible in the nest box, whereas rural males moved further away and became less audible. In contrast, during the 2020 year with reduced ambient noise levels, urban and rural males did not differ in their distance from the nest in

relation to ambient sound levels. Thus, with lower ambient noise in 2020, both rural and urban males did not appear to use ambient noise levels to adjust their distance from the nest to compensate for relative song/call audibility.

These results suggest that amidst normal ambient noise levels, urban Mountain Chickadees may be constrained to remain closer to their nest to ensure their social mate can hear their vocalizations, but simultaneously this would reduce their ability to hear or communicate with rivals and neighbours. Prioritizing mates over neighbours may constitute a trade-off for urban chickadees, where males are required to remain closer to the nest during dawn signalling bouts, but risk reduced communication with neighbours. However, urban male chickadees appear to have adjusted to urban ambient noise by reducing the distance they sing from the nest during dawn signalling periods, likely as a reaction to reduced female responses or difficulty in hearing female responses in noisy conditions.

The response of rural males in higher levels of ambient noise, though, seems counter-intuitive – my data show these males roam farther from the nest during dawn signalling bouts when noise levels are high. These males may be moving in these high noise conditions to interact vocally with neighbours (Foote et al. 2010), especially if those neighbours may be further away than urban neighbours, but the consequence may be reducing their audibility to the female within the nest cavity.

Many studies have shown that birds can adapt to urban noise in various ways, whether by altering their song structure or by adjusting their behaviour and daily routines. Precautionary guidelines during the COVID-19 pandemic reduced motor vehicle and human foot traffic and excess construction noise in urban settings, potentially alleviating some of the adverse effects

of urban noise on surrounding biodiversity. Birds responded to the considerably lower ambient noise during COVID-19 by exhibiting greater vocal performance by singing at lower amplitudes and frequencies (Derryberry et al. 2020), or by being more detectable, primarily in the mornings during typical peak dawn chorus, illustrating a seemingly rapid change in daily routines (Gordo et al. 2021). Similarly, Mountain Chickadees appeared to alter their dawn signalling behaviour by adjusting their average distance from the nest box when the quieter 2020 season alleviated ambient noise, allowing urban males to stray further from the nest cavity yet still remain audible.

My results suggest that urban males may have more experience adjusting to persistently high ambient noise, as these males remained closer to their nest than their rural counterparts in response to higher noise levels. However, that could lead to a trade-off for urban males; by remaining closer to the nest, it would ensure their social mate can hear them but might reduce their ability to communicate with neighbouring males and potential eavesdropping females. Staying close to the nest may also functionally reduce their territory size due to inadequate territorial defense. Although, differences in territory density or breeding synchrony between habitats could also be a driver of urban males remaining slightly closer to the nest, while rural males move further away amidst higher ambient noise levels.

Rural males, however, do not seem well-equipped to overcome increasing ambient noise. Males in the noisiest environments spent a greater amount of their dawn chorus signalling further from the nest than the few rural males in quiet habitats. This behaviour may lead to a trade-off of their social mate not being able to hear them as well, while ensuring neighbours and other breeding females can. If the male's social mate cannot hear them adequately during

dawn signalling, this may lead to the female evaluating the social mate as less fit and may seek neighbouring males for copulatory events. Males could try to compensate for this increased distance by shifting their signalling to a greater proportion of songs relative to *chick-a-dee* calls, the former of which transmit farther in noisy conditions (LaZerte et al. 2015), and there is evidence that chickadees in noisier habitats do adjust to songs that compensate for low-frequency noise levels (Proppe et al. 2012; LaZerte et al. 2017). However, the extent that these adjustments fully compensate still awaits further study. The fact that alleviation of noise during the COVID-19 lockdown in 2020 resulted in both urban and rural males displaying similar behaviour during dawn signalling would suggest, though, that urban noise does create constraints on males.

My study found significantly lower ambient noise levels within both urban and rural habitats of Kamloops, BC, during 2020, which aligns with Derryberry et al. (2020) and Gordo et al. (2021). Lower ambient noise levels led to behavioural changes in Mountain Chickadees, with this species exhibiting rapid adjustment to reduced noise levels. Urban Mountain Chickadees in the pre-COVID-19 field season remained closer to the nest – where the female resides during dawn signalling – as ambient noise levels increased; this behavioural adjustment has also been observed in confamilial Great Tits, where males moved closer to the nest to increase their signal-to-noise ratio when females were exposed to noise and thus reduced their response rates (Halfwerk et al. 2012). During the quieter 2020 COVID-19 field season, this response seemed to be reduced and the need to remain closer to the nest diminished – noise levels in 2020 never reached the levels seen in 2019, and distance from the nest during dawn signalling did not differ between males in rural and urban habitats

that year. As the world human population begins to resume activity in a post-COVID era, this will likely lead the chickadees to revert to behaviour seen in typical noise levels (e.g., 2019). It is encouraging, though, that if we can move towards reducing noise constraints, species seem to exhibit high behavioural plasticity to quickly re-adjust to quieter conditions.

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## CHAPTER 4: CONCLUSIONS AND FUTURE DIRECTIONS

### 4.1 DISCUSSION

Ambient noise due to anthropogenic activity can mask and disrupt avian communication networks and acoustic signalling (Slabbekoorn and Peet 2003; Patricelli and Blickley 2006; Halfwerk et al. 2011; Naguib 2013; Amerhein 2014). The goal of this thesis was to assess the signal-to-noise ratio (SNR) and relative audibility of Mountain Chickadee songs with regards to ambient noise levels. Specifically, I asked how audible chickadee songs were to females roosting within the nest box during dawn signalling events. I found that distance of the male from the nest box affected the signal-to-noise ratio of songs, where increasing distance of the male from the nest box resulted in decreasing SNR within the nest box. I then tested these results in a natural context of dawn signalling. I also took advantage of an inadvertent ‘experiment’ in my thesis – the significant alleviation in ambient noise levels in 2020 due to the COVID-19 pandemic, to see how this affected male behavioural response. In 2019, a year with typical noise levels, urban males were more audible to females than rural males, due to their behaviour of remaining closer to the nest box during dawn singing. With increasing ambient noise levels, urban males moved slightly closer to the nest, whereas rural males moved farther away; however, in unusually quiet ambient noise levels (2020), urban and rural males did not differ in either their distance from the nest box or the relative audibility of their vocal signals in the nest box.

Mountain Chickadee acoustic signals are masked by ambient noise – songs are less audible within the nest amidst high noise levels and at greater distances. In Chapter 2, I showed that songs had lower signal-to-noise ratios within the nest at greater distances and this effect was amplified when signals were broadcast with added low-frequency noise.

Similarly, in Chapter 3 I found that songs and calls were also less audible with increasing distance, and again this effect was slightly amplified in noisier conditions. Urban males, who may have greater prior experience dealing with elevated noise levels, appeared to compensate by remaining slightly closer to the nest. However, this may have created a constraint on their ability to signal to neighbours. In response to the major reduction of noise pollution in 2020 in both habitats, males showed dynamic shifts in behaviour; urban males and rural males did not differ in relative audibility or in distance from the nest. These results suggest behavioural plasticity to rapidly adjust to the reduction in ambient noise due to COVID-19 protocols, which in turn suggests that pre-COVID behaviour was influenced by the presence of noise pollution. Urban males were no longer constrained to remain close to their nest box and moved further from the nest during signalling events. Rural males in noisier habitats frequently moved away from the nest during pre-COVID signalling, perhaps to respond to obscured songs of neighbours — these males were now able to shift closer to the nest box during dawn signalling when noise was alleviated. These results suggest a trade-off for the focal male of being audible to neighbouring males and females or being audible to the social mate within the nest box. With elevated noise levels, males must choose whether they dedicate their time and energy into courting and communicating with their social mate or straying further from the nest to defend their territory from other males or engage with neighbouring females. Urban males appear to adjust to increased ambient noise by opting to not stray far from the nest during dawn signalling bouts (Chapter 2 and 3); therefore, urban males have been constrained to remain closer to the nest to better communicate with their mate while likely risking losing their territory or resources to competing intruders. Rural males must also accept a trade-off between remaining close to the nest for their mate to hear

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them or straying further to adequately defend their territory. It appears that rural males in high noise environments opted to venture much further from the nest than urban counterparts, but this may compromise their ability to be heard by their mate. If their social mate cannot perceive their signals, she may assume the male is of low quality and this could affect mating decisions (Mennill et al. 2004).

These results, specifically Chapter 3 with the dynamic shift in behaviour and distance of the male, coincide with recent literature looking at rapid adjustment of bird behaviour due to the COVID-19 pandemic and reduction in ambient noise. With the alleviation of urban ambient noise levels due to stay-at-home restrictions, some bird species were able to rapidly adapt and alter their song characteristics to exhibit greater vocal performance by singing at lower amplitudes and frequencies (Derryberry et al. 2020), or were able to adjust their daily routines, becoming more detectable, especially during the early morning (Gordo et al. 2021). Previous studies on this Mountain Chickadee population have shown adjustments in their vocalizations due to urban noise. They tend to sing atypical songs in urban habitats (LaZerte et al. 2019) or increase song frequency and sing more songs than calls in elevated noise conditions (LaZerte et al. 2017), while also singing earlier than rural counterparts with a higher song output (Marini et al. 2017). These previous findings align with my results showing that ambient noise reduces the relative audibility of songs, especially the low notes (N2) or low-frequency calls. Therefore, it appears likely that these chickadees have already begun compensating for this masking of N2 notes by adjusting their song notes when amidst urban noise. Studies have begun to assess the audibility of vocalizations within nest boxes and have found birds to be less audible within the nest box as distance from the nest

increases (Lampe et al. 2004; Blumenrath et al. 2012), while being further exacerbated by increasing ambient noise at the nest site (Halfwerk et al. 2012; Grabarczyk and Gill 2019). These constraints could act in concert to suggest that in noisy conditions males must either choose between remaining close to the nest to increase their audibility to their mate, or roam farther from the nest to make songs more audible to neighbouring birds. With the reduction of noise pollution constraints in 2020, males in rural and urban habitats assumed similar behaviour and had similar audibility within the nest, suggesting that noise pollution does add constraints to dawn signalling in this species.

## **4.2 FUTURE DIRECTIONS**

After observing dynamic shifts in male behaviour, particularly their position from the nest during dawn signalling, it would be enlightening to assess whether the female displays any changes in behaviour based on noise levels around or in the nest. Studies rarely assess the female role in communication networks and the behaviour of the male, especially cavity-nesting females that remain in the roost during dawn signalling events. Future studies could conduct a noise manipulation study on females within the nest, similar to studies by (Halfwerk et al. 2016) on Great Tits (*Parus major*) and Blue Tits (*Cyanistes caeruleus*), to assess whether alterations to female behaviour or responses to males may also cause large shifts in male behaviour, regardless of ambient noise levels. Other future research could assess whether males respond to experimental noise by decreasing the area they cover during the chorus and remaining closer to the nest. This could be tested by recording male behaviour one day, and then placing a speaker near the nest broadcasting noise the second day. Recording the same male for two choruses, one with added noise and one without, could show whether males are aware that their mates may have difficulty hearing them, and may

result in the male compensating by remaining closer to the nest and covering less distance. In addition, further research on territory sizes and clustering/dispersal of Mountain Chickadees could help explain differences in behaviours between habitat types.

### **4.3 CONCLUSIONS**

Mountain chickadees are a unique species to study in relation to success in urban environments, as they have been able to successfully cope with habitat urbanization, which is considered unusual for a specialist species. Relatively little research has been conducted on Mountain Chickadee life history, and to my knowledge, little is currently known about female mate-assessment and response to male acoustic signals in urban environments, particularly with the introduction of urban noise. Although Mountain Chickadees have been successful in urban areas, several other songbird species have not. Further understanding of Mountain Chickadee behaviour and signal transmission in urban and rural areas should help better understand the life history of this specialist songbird, as well as the behaviour and signal success of other birds having to cope with urban encroachment.

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<https://doi.org/10.1093/auk/123.3.639>.
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**APPENDIX A**

1. A)

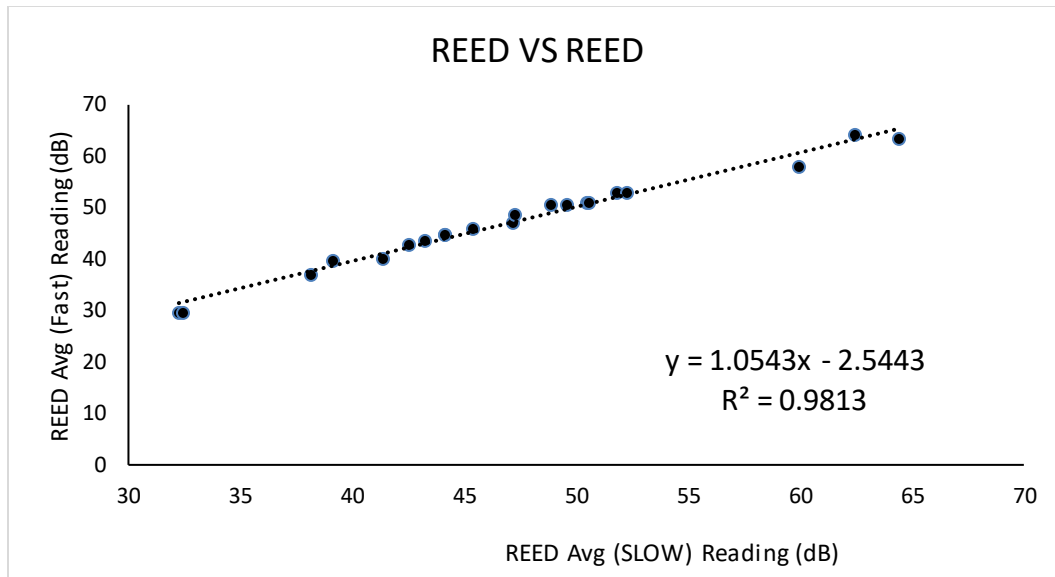


Figure A1A. Linear regression of sound pressure level meter readings, comparing both REED models.

B)

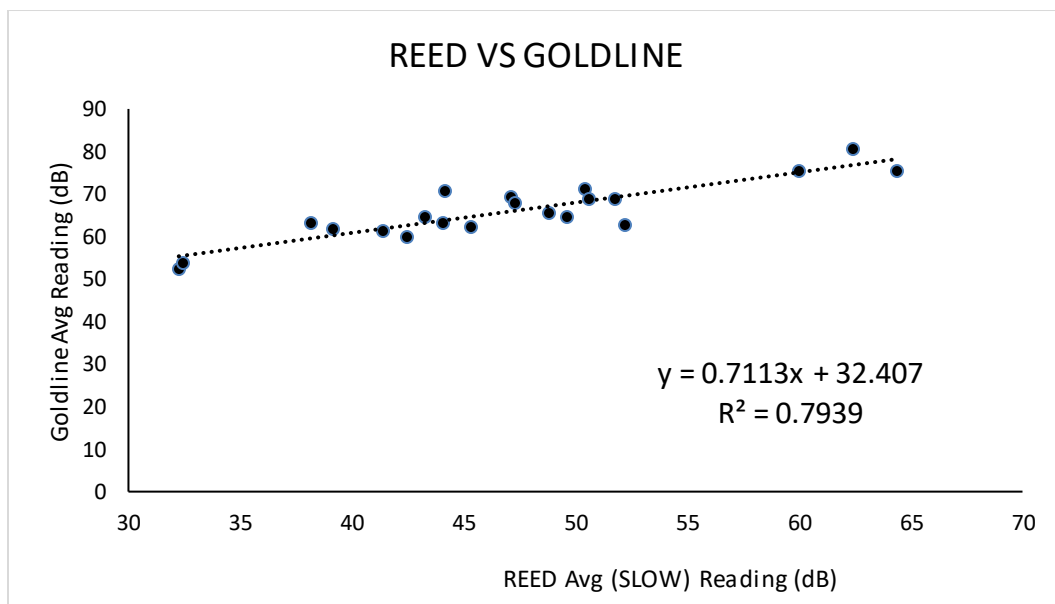


Figure A1B. Linear regression of sound pressure level meter readings, comparing the REEDs with the Goldline model.

C)

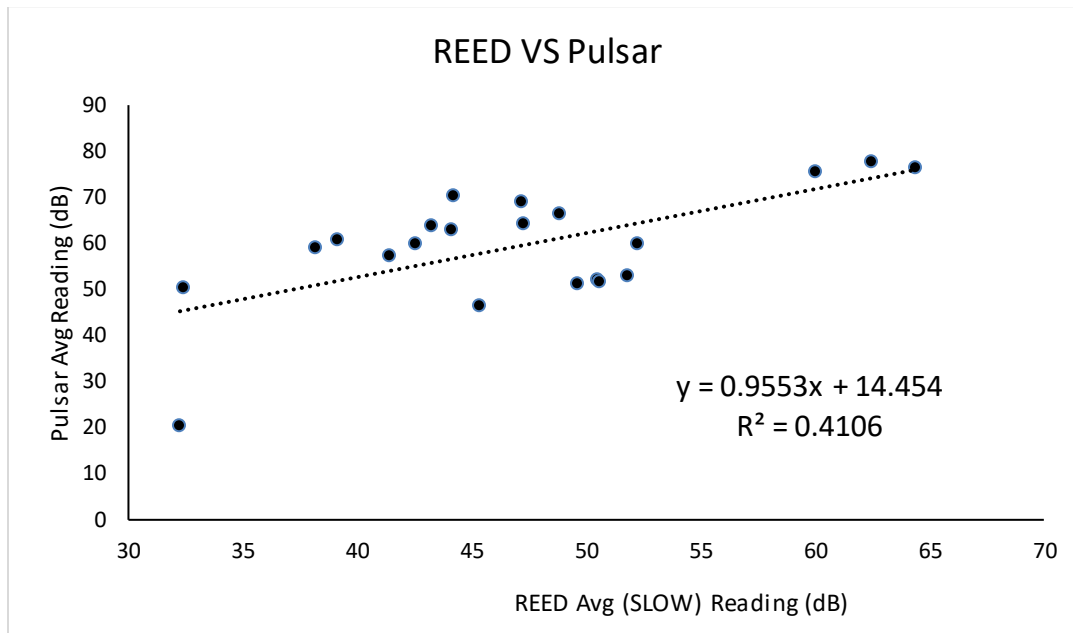


Figure A1C. Linear regression of sound pressure level meter readings, comparing the REEDs with the Pulsar model.

D)

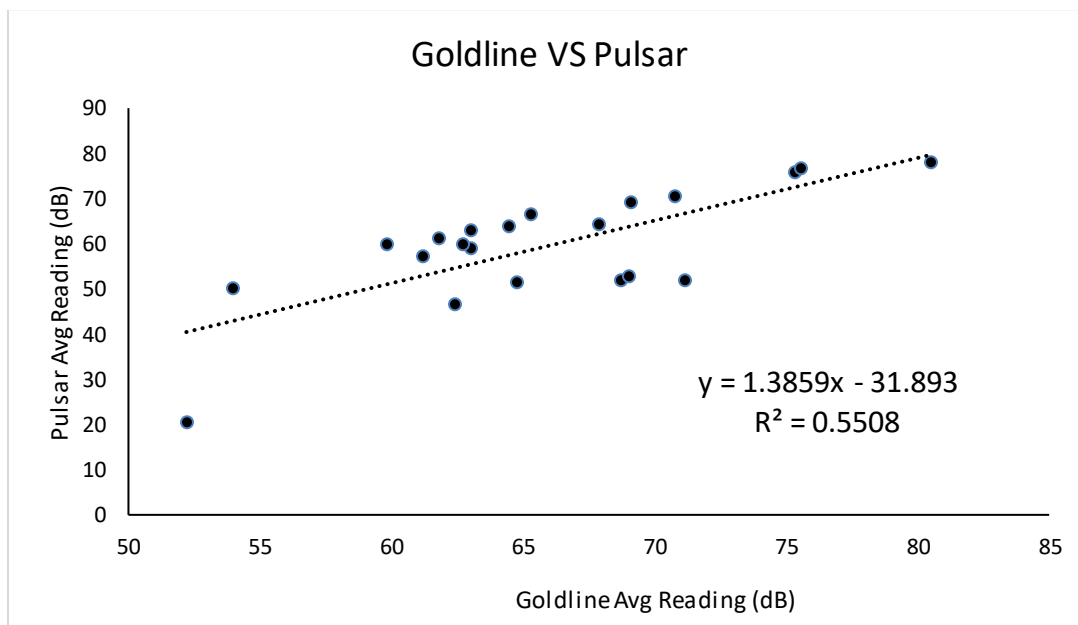


Figure A1D. Linear regression of sound pressure level meter readings, comparing the Goldline with the Pulsar model.