SOUNDS OF THE CITY: THE EFFECTS OF URBANIZATION AND NOISE ON MOUNTAIN AND BLACK-CAPPED CHICKADEE COMMUNICATION

by

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Abstract

Urbanization leads to structural changes to habitats and introduction of anthropogenic noise, both of which can interfere with avian communication. While studies suggest that birds can adjust their vocal behaviour in response to urban noise, the relative effects of urban habitat structure vs. noise on avian communication are not well understood. Further, understanding which species can adjust to noise and the mechanisms they use to achieve this can help conservation efforts predict which species will be most negatively affected by increasing urbanization. Species that possess certain vocal attributes (e.g., repertoires or the ability to learn new songs types) may be more or less able to adjust to urban noise. Here, I investigate how two closely related species (mountain chickadees *Poecile gambeli* and black-capped chickadees *Poecile atricapillus*) adjust their vocalizations in response to noise. I look at relative effects of habitat structure and noise on signal transmission and transfer, how each species adjusts vocalizations in response to urbanization and noise (both naturally occuring and experimental), and whether these adjustments actually improve audibility in noise. I found that urban noise affects signal transmission and transfer more than habitat urbanization (Chapter 2), and both species adjust their vocalizations to noise by using mechanisms related to their natural vocalizing behaviour. Mountain chickadees change the proportion of time they spend singing vs. calling and spectrally adjust their songs to emphasize higher frequencies (Chapter 3). In contrast, black-capped chickadees use their natural pitch-shifting abilities to selectively sing higher-frequency songs in noisy conditions (Chapter 4). I also found evidence that these adjustments may improve audibility in noise. Among mountain chickadees, focal males from quiet areas responded more aggressively to playbacks of urban than rural songs when embedded in experimental noise (Chapter 5). Among black-capped chickadees, focal males responded more quickly to playbacks of high- than low-pitched songs, but only when high-pitched songs were played first, otherwise they did not differentiate (Chapter 6). In conclusion, I found that urban noise can have a large impact on the vocalizations of chickadees, but the two species experience different pressures from urbanization as a result of their natural vocalizing behaviour.

Anticipated Publications

As convention in a dissertation I use the first-person pronoun throughout this document. However, each chapter was conducted in collaboration with others who will be co-authors on resulting publications. These contributions are acknowledged here by indicating order of authorships by relative contributions to the works. In all instances, I was the primary researcher in designing, analyzing and writing the studies in this dissertation.

Chapter 2: LaZerte SE, Otter KA, and Slabbekoorn H. Relative effects of habitat transmission and noise interference on chickadee vocalizations. In prep for resubmission to *Bioacoustics*.

Chapter 3: LaZerte SE, Otter KA, and Slabbekoorn H. Mountain chickadees adjust chorus structure and signalling features in response to urban noise

Chapter 4: LaZerte SE, Otter KA, and Slabbekoorn H. Immediate vocal adjustment varies with local ambient noise in black-capped chickadees

Chapter 5: LaZerte SE, Otter KA, and Slabbekoorn H. Context-dependent response to Urban vs. Rural songs in a mountain chickadee playback study

Chapter 6: LaZerte SE, Otter KA, and Slabbekoorn H. Males respond faster to High- vs. Low-pitched black-capped chickadee songs in noise

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1 General Introduction

1.1 Urbanization

Humans have great potential for altering habitats. From urbanization to resource extraction, to the introduction of invasive species, we have changed the surface cover, structure, temperature, and species composition of the landscape. Urbanization is a problematic form of alteration, because the changes are both large and long term (McKinney, 2006). Urbanization can affect animals in a variety of ways, such as: habitat loss and fragmentation; increased competition from new species; increased predation; risk of collisions with vehicles and structures; and, environmental contaminants (Trombulak & Frissell, 2000; Chace & Walsh, 2006). However, less obvious influences of urbanization are its effects on animal communication systems. For example, we deliberately interfere with the chemical communication of insects by using synthetic pheromones to disrupt mating in pest species (Carde & Minks, 1995); we inadvertently interfere with the visual communication in fish by increasing water turbidity (Seehausen *et al.*, 1997); and, we mask vocal communication in frogs and birds with traffic noise (Slabbekoorn & Peet, 2003; Parris *et al.*, 2009). Altering or interfering with animal communication may have adverse effects on reproduction and fitness and, consequently, may affect population or species survival. Acoustic communication is a critical element involved in many different aspects of animal life, but especially so in avian systems, where it plays a key role in competition, mate attraction and reproduction (Collins, 2004). Because vocal communication is so important to avian fitness, human interference on signal transmission and perception is of paramount concern (Rabin & Greene, 2002; Patricelli & Blickley, 2006; Slabbekoorn & den Boer-Visser, 2006; Warren *et al.*, 2006; Luther & Gentry, 2013).

1.1.1 Noise

Anthropogenic noise is has the potential to compromise the environmental conditions and as such, has become an increasingly large problem for animal communication (Goines & Hagler, 2007; Slabbekoorn & Ripmeester, 2008). Anthropogenic noise in and around urban areas is mostly from traffic, but in non-urban areas it may arise from wind turbines, oil fields, all-terrain vehicles (ATVs), motorboats or snowmobiles (Chambers, 2005; Rabin *et al.*, 2006; Barber *et al.*, 2010). Consequently, the adverse effects of noise on avian stress (e.g., Reijnen *et al.*, 1995), perceived risk of predation (e.g., Quinn *et al.*, 2006), and avian communication (e.g., Slabbekoorn & Peet, 2003; Patricelli & Blickley, 2006) have been a focus of study.

Noise interferes with communication through masking, which occurs when signals of a given frequency are overlapped by background noise. This decreases the signal-to-noise ratio (SNR) of vocalizations and makes signals more difficult for the receiver to detect and discriminate from other possible signals (Wiley & Richards, 1978; Klump, 1996; Rabin & Greene, 2002; Barber *et al.*, 2010). Avian species respond to this interference in a variety of ways, such as avoiding areas of excess noise, either temporally (Fuller *et al.*, 2007) or spatially (Parris & Schneider, 2008), or by repeating signals (Brumm & Slater, 2006). Birds can also adjust their vocalizations (vocal adjustment) to increase the SNR in noisy conditions. A simple way of increasing SNR is to sing louder, which is generally known as the Lombard effect (e.g., Brumm, 2004; Brumm & Zollinger, 2011; Lowry *et al.*, 2012; Schuster *et al.*, 2012). Decreasing spectral (frequency) overlap between the signal and noise is an alternate mechanism for increasing the SNR, as it reduces masking from background noise (masking release). As urban noise tends to be low-frequency, a means by which birds can avoid noise interference is to sing at higher frequencies (spectral plasticity Slabbekoorn & Peet, 2003; Wood & Yezerinac, 2006; Hu & Cardoso, 2010; Verzijden *et al.*, 2010; Bermúdez-Cuamatzin *et al.*, 2011). Thus mechanisms exist which allow adjustment to the negative effects of noise on signal production and propagation, but the flexibility to make such behavioural adjustments may vary by species.

1.1.2 Habitat change

Another impact of urbanization on vocal propagation is through physical changes to the habitat, which in turn can alter signal transmission. Urban environments contain expanses of pavement and concrete, and areas with natural vegetation are often reduced to urban parks, backyards or small green spaces, which may or may not bear any resemblance to the native environment. Sound transmission may be directly altered by these structural changes, or may change as the result of altered micro-climate temperature shifts caused by open areas or asphalt (Rabin & Greene, 2002; Warren *et al.*, 2006). Urban habitats are typically open with few trees or shrubs; while this can result in less signal degradation (i.e. when signals are garbled) from sound scattering off small twigs and leaves, there may be an increase in signal degradation caused by wind (amplitude fluctuations; Richards & Wiley, 1980). Further, pavement and buildings present large reflective surfaces, which can distort sound through reverberations and echos (Slabbekoorn *et al.*, 2007).

Although noise pollution is pervasive, habitat structure also affects communication by changing signal transmission (Morton, 1975; Wiley & Richards, 1978; Brown & Handford, 2000; Warren *et al.*, 2006). Although the openness of urban areas, coupled with hard concrete surfaces, could create problems associated with sound fluctuations and/or echos (Richards & Wiley, 1980; Slabbekoorn *et al.*, 2007), pavement and buildings may also provide sound channels which could increase signal propagation distances (Gall *et al.*, 2012). However, many bird species are not found within the ”concrete jungle” of heavily urbanized centres, but rather occur in urban green spaces. These spaces typically contain trees and shrubs and few hard surfaces, but, structurally, are still more open than true rural forest habitat. Compared with rural areas, the specific habitat structure of urban green spaces could, therefore, still lead to more degradation from irregular amplitude fluctuations than occurs in native habitats with retained forest species, but less degradation from absorption and scattering by leaves, twigs and branches (Mockford *et al.*, 2011).

How birds should (and whether they do) adjust their songs in urban areas is less clear.

Reverberations and echos caused by hard surfaces in urban landscapes should favour pure-tone songs (e.g., Slabbekoorn *et al.*, 2002), songs with slowly repeated elements (Slabbekoorn *et al.*, 2007), or songs with lower frequencies (which are less affected by reverberations and barriers; Dowling *et al.*, 2012). However, increased amplitude fluctuations from wind (anticipated by the increased openness of urban landscapes) could favour repetition of song elements (signal redundancy; Brown & Handford, 2000). Open habitats would also generally favour lower frequencies to counter attenuation (amplitude loss), which is greater in high-frequency signals (Brown & Handford, 2000).

Over the past decade, scientists have started to investigate the effects of habitat urbanization on avian signal transmission (Slabbekoorn *et al.*, 2007; Nemeth & Brumm, 2010; Mockford *et al.*, 2011; Gall *et al.*, 2012), but few studies have investigated the relative effects of noise versus habitat change on avian communication (but see Dowling *et al.*, 2012; Gall *et al.*, 2012). Because noise and habitat change often occur congruently, they are difficult to tease apart. Studies looking at phantom roads (stretches of road noise broadcast to mimic the noise presence of a road without the physical disturbance; McClure *et al.*, 2013) and natural gas compressors (e.g., Habib *et al.*, 2007; Francis *et al.*, 2012) have shown that birds can be affected by noise independent of habitat disturbance. However, vocal adjustment in urban birds may be partially due to altered habitat structure as well as to urban noise. It is clear that both noise and habitat urbanization could affect animal communication, but the interplay between these two factors is still relatively unknown.

1.2 Why study vocal adjustment?

Behavioural plasticity can help species adapt to urban environments (Sol *et al.*, 2013). Vocal adjustment, and spectral flexibility in particular, are forms of behavioural plasticity which allow birds to cope with communication challenges in variable sound environments. However, not all species demonstrate vocal or spectral flexibility (Hu & Cardoso, 2010; Francis *et al.*, 2011*c*, 2012), and among those that do, not all have the same degree of flexibility (Francis *et al.*, 2011*a*). Understanding why some species demonstrate flexibility and others do not can help us understand which species are most likely to successfully colonize urban areas, and, more importantly, which species will be unable to do so (Slabbekoorn & Ripmeester, 2008).

Urban development is often fast-paced and species that take longer to adjust to the effects of noise pollution may be less successful (or completely unsuccessful) at persisting in urban spaces than those that demonstrate quick, plastic, vocal responses. By definition, species with high levels of within-individual variation in vocalizations should be capable of plastic responses. Additionally, in general, species that learn their songs appear able to adjust more to noise pollution than those that do not (Ríos-Chelén *et al.*, 2012). Another factor which may influence vocal plasticity in a species is the degree of vocal variability that naturally occurs among populations (Ríos-Chelén *et al.*, 2012). Therefore, species which show individual variation in signals, learn their songs, or which demonstrate regional variation in song characteristics, can be predisposed to vocal adjustment. Therefore, by assessing learning styles and vocal variability among and within individuals, we may be able to predict how quickly a species can adjust to noise and what mechanisms they might use. Despite the importance of vocal adjustment in determining which species are able to cope with human-altered environments, few studies examine the link between natural singing behaviour and why certain species are capable of vocal adjustment in urban landscapes.

Equally important to detecting vocal adjustment is determining whether the observed adjustments actually improve transmission and perception of signals. It has been fairly well established that many species do show vocal plasticity in urban habitats; however, it is less clear whether these vocal changes actually result in improved communication. Although there is evidence in support of vocal adjustment mitigating the effects of noise, adjustment may have costs or trade-offs (Patricelli & Blickley, 2006). In some cases, adjustments made to avoid masking or improve signal transmission may have maladaptive consequences, such as increasing energetic costs of signalling or altering the information contained by the signal (Fernández-Juricic *et al.*, 2005; Patricelli & Blickley, 2006; Slabbekoorn & Ripmeester, 2008;

Barber *et al.*, 2010). Knowing whether vocal adjustment represents a useful or detrimental behavioural change will help conservationists assess the sensitivity of a species to altered environments.

1.3 Chickadees

Chickadees are North American members of the Paridae family (chickadees and titmice) in the genus *Poecile* (Gill *et al.*, 2005). Two of the four common species in Canada, the mountain chickadee (*Poecile gambeli*) and the black-capped chickadee (*Poecile atricapillus*) form a sister-species clade and are both fairly common in British Columbia, Canada. In general they have three stereotypical vocalizations: a *chick-a-dee* call (Figure 1.1), a whistled song (Figure 1.2), and a gargle (Hailman & Ficken, 1996). Mountain chickadees are more restricted to western North America than black-capped chickadees and have been less intensively studied, but together these species present a useful model for comparison. Black-capped chickadees are ubiquitous throughout most of British Columbia (Foote *et al.*, 2010), use predominantly whistled songs (*fee-bee* songs) during dawn chorus signalling (a period of intense singing at dawn in the spring before and during the female fertile period) and are known to adjust the frequency of their songs during song matching with conspecifics (pitch-shifting; e.g., Ratcliffe & Weisman, 1985; Christie *et al.*, 2004). In contrast, mountain chickadees are found mostly in sub-boreal or Douglas-fir (*Pseudotsuga menziesii*) habitat in the more mountainous regions of southern British Columbia (McCallum *et al.*, 1999), use a mixture of both *fee-bee* songs and *chick-a-dee* calls during the dawn chorus (Grava *et al.*, 2013*a*), and do not demonstrate pitch-shifting. Further, while black-capped chickadees sing similar songs throughout their range, mountain chickadee songs vary substantially among populations (Grava *et al.*, 2013*a*). Therefore, both species have the potential to show vocal plasticity in response to noise; both species learn their songs, mountain chickadees show regional variation in songs as well as individual variation in the use of songs vs. calls, and black-capped chickadees show individual variation in frequency-use. That these two species

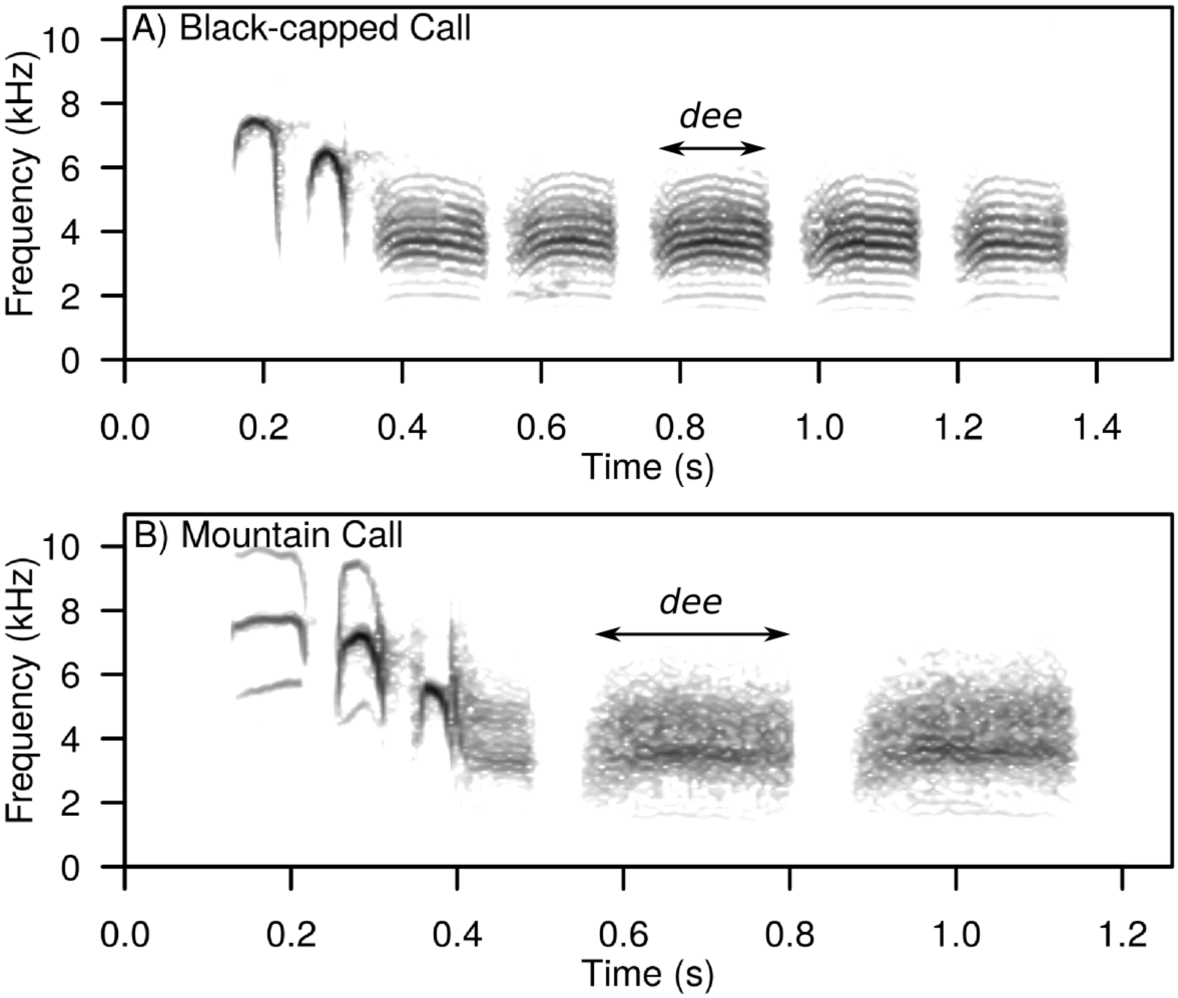

Figure 1.1: Spectrograms of chickadee *chick-a-dee* calls: (**A**) black-capped, (**B**) mountain chickadee. Arrows indicate an example of the *dee*-note in each case.

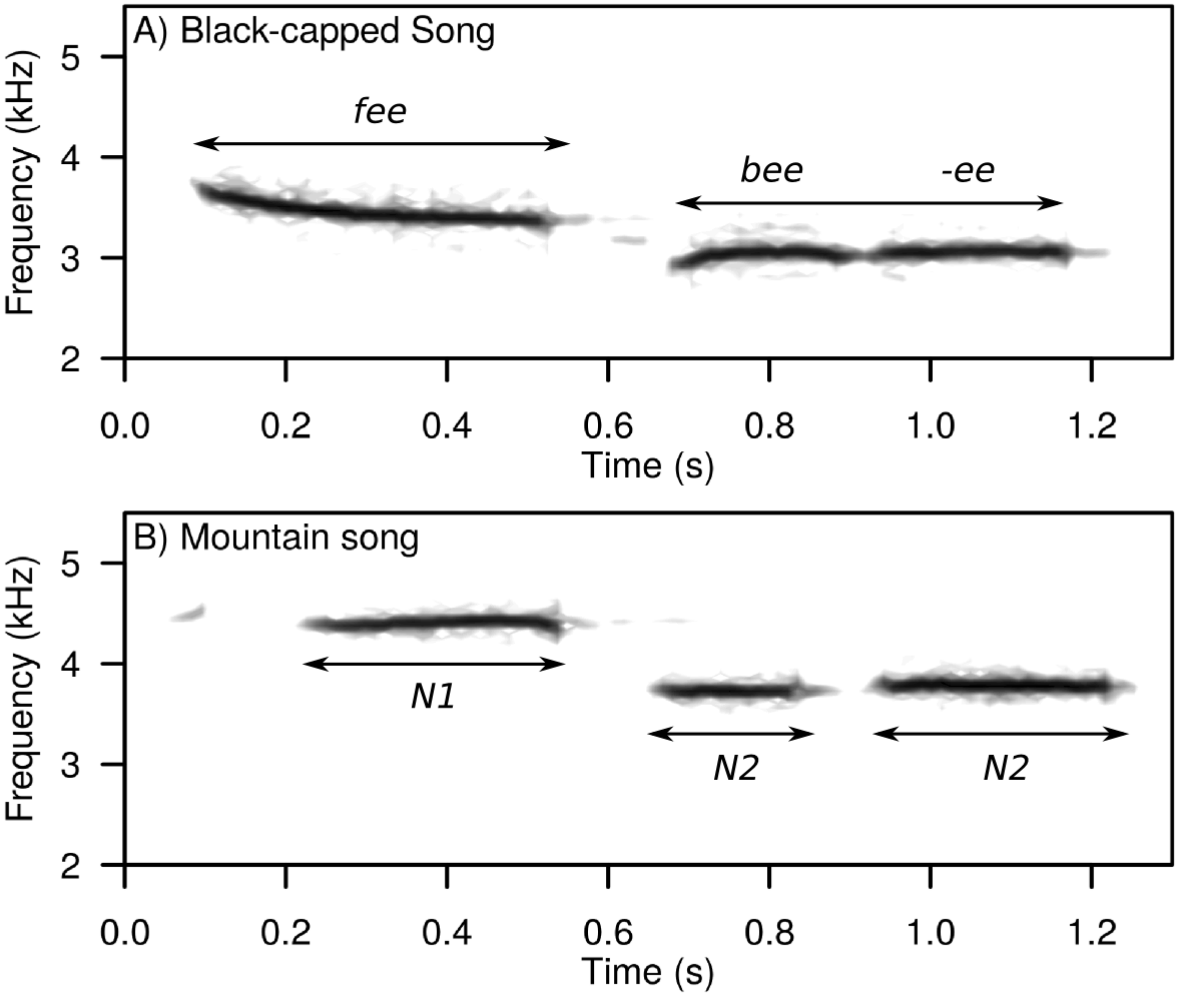

Figure 1.2: Spectrograms of chickadee whistled songs: (**A**) black-capped and (**B**) mountain chickadee. Arrows indicate standard note names for the *fee-bee* song of black-capped chickadees (**A**) or individual note-types assigned by frequency for the song of mountain chickadees (**B**; Chapter 3). The mountain chickadee song is preceded by a short introductory note.

are closely related phylogenetically, but still show many differences in singing style and variability, makes them a useful system for comparison.

These two species also differ in the relative degree of settlement in urban habitats, which suggests that their differences in behavioural traits may influence their tolerance towards urbanization. In western Canada, black-capped chickadees seem to invade farther into urban areas, and in greater numbers, than mountain chickadees. A brief analysis of birder observations submitted to E-Bird (Cornell Lab of Ornithology, 2014) supports this observation. I looked at all mountain chickadee observations within 20 km of three cities in British Columbia, Canada (Kelowna, Kamloops and Williams Lake; n = 54) and randomly selected 54 observations of black-capped chickadees within 20 km of Prince George, British Columbia. I had an independent observer qualitatively score the habitat type of each observation as either ’Urban’ or ’Rural’ at two different scales (~120 m^2, ~3.8 km^2). I omitted ambiguous observations (black-capped chickadees = 2, mountain chickadees = 5). At the scale of 120 m^2, there was no difference in the distribution of mountain and black-capped chickadees between urban and rural sites (Fisher Exact Test, $P = 1$; mountain = 59% rural, black-capped = 58% rural). However, at the scale of 3.8 km^2 black-capped chickadees were significantly more likely to be observed in urban areas than mountain chickadees (Fisher Exact Test, $P = 0.01$; mountain = 71% rural, black-capped = 44% rural). This suggests that mountain chickadees are not completely excluded from urbanized habitats, but are less well established in urban centres. Anecdotal evidence from local naturalists supports these findings as well, as many report having mountain chickadees in suburban backyards throughout the winter. In contrast, black-capped chickadees were almost as common in urban areas as in rural.

1.4 Sites

My studies were conducted in six cities throughout southern British Columbia. Mountain chickadees were recorded predominantly in parts of the province where natural habitat is drier and contains more Douglas-fir habitat, such as Williams Lake (52°07’N, 122°08’W; population 11,150), Kamloops (50°40’N, 120°20’W; population 85,678), and Kelowna (49°53’N, 119°29’W; population 117,312). Black-capped chickadees were recorded predominantly in Prince George (53°55′N, 122°44′W; population 88,043), Quesnel (52°58’N, 122°29’W; population 10,007), and Vancouver (49°15’N, 123°06’W; population 603,502). Both species were present in all cities with the exception of Vancouver (which had black-capped chickadees, but no mountain chickadees), although in each city one or the other species predominated (Figure 1.3).

1.5 Thesis Goals

In this thesis, I explore two overlapping general questions with respect to the effects of urbanization on avian communication. One question is in regard to the interaction between ambient noise and urban habitat. Although from recent studies it is clear that noise alone can affect avian communication, it is not clear how much of an additional effect urban habitat structure has. The second question focuses on the how different species adjust to noise and how natural singing behaviour might reveal behavioural mechanisms underlying vocal adjustments, predict noise impact, and explain species-specific distribution patterns.

I focused on these questions through a series of experiments outlined in five data chapters and one synthesis chapter. In **Chapter 2** I tested experimentally the relative effects of anthropogenic noise and habitat structure on signal transfer in chickadee calls and songs. In **Chapters 3 and 4** I recorded chickadees throughout southern British Columbia and experimentally exposed them to noise to investigate mechanisms of vocal plasticity used by mountain (Chapter 3) and black-capped chickadees (Chapter 4) in response to anthropogenic noise and urbanization. In **Chapters 5 and 6** I then used field playback trials to determine

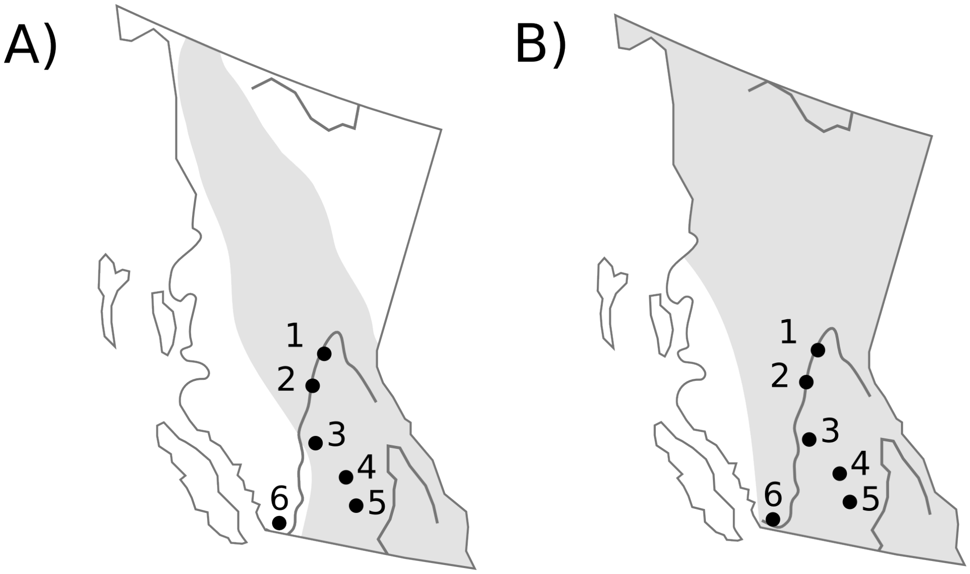

Figure 1.3: Distribution ranges of mountain chickadees (A) and black-capped chickadees (B) throughout British Columbia, Canada. Grey represents range. Numbered points represent locations of cities used in this dissertation. 1-Prince George, 2-Quesnel, 3-Williams Lake, 4-Kamloops, 5-Kelowna, 6-Vancouver. Distribution maps are reproduced with permission from from Birds of North America Online http:/bna.birds.cornell.edu/bna, maintained by the Cornell Lab of Ornithology.

whether changes to the vocalizations of mountain (Chapter 5) and black-capped chickadees (Chapter 6) imparted a communication advantage. Finally, in **Chapter 7** I presented the overall synthesis and conclusions of this thesis. This work was approved by the University of Northern British Columbia Animal Care and Use Committee (protocol No. 2011-05).

2 Relative effects of habitat transmission and noise interference on chickadee vocalizations

2.1 Introduction

Urbanization results in a variety of conservation issues, from habitat loss to invasive species and environmental pollutants (McKinney, 2002). However, urbanization also poses more subtle challenges by modifying animal interactions and interfering with animal communication. For example, light pollution can alter coastal fish communities (Becker *et al.*, 2013) and shift the timing of birdsong (Longcore & Rich, 2004), chemical pollution may affect availability of insect prey (Ciach & Fröhlich, 2013), and increased water turbidity can interfere with visual communication in fish (Seehausen *et al.*, 1997). Noise pollution can also negatively affect communication in many taxa that occur in urbanized areas and rely heavily on sound, such as birds, mammals, frogs, and insects (Patricelli & Blickley, 2006; Slabbekoorn & Ripmeester, 2008; Luther & Gentry, 2013; Naguib, 2013).

The ubiquitous nature of noise pollution can have especially serious implications for acoustic communication in birds (Slabbekoorn & Ripmeester, 2008) because of the importance of vocal communication in avian territoriality and reproduction (Collins, 2004). Ambient noise can mask vocal signals, which reduces their detectability (whether or not the signal is heard) and discriminability (whether or not the signal is distinguished from other possible signals; Klump, 1996; Rabin & Greene, 2002; Barber *et al.*, 2010). This is especially true for low-frequency vocalizations in urbanized areas, as the degree of frequency overlap between signal and noise determines the degree of masking (Klump, 1996; Brumm & Slabbekoorn, 2005) and urban noise is typically biased to low frequencies (Slabbekoorn & Ripmeester, 2008). Many species have changed the way they communicate in urban environments, which may yield perceptual advantages (Patricelli & Blickley, 2006). However, to date there is no direct evidence of the fitness benefits of altering signals (Slabbekoorn, 2013; Read *et al.*, 2013). Masking may be avoided or reduced by either altering the timing of singing (Fuller *et al.*, 2007; Arroyo-Solís *et al.*, 2013), converging on songs that are higher pitched (Slabbekoorn & Peet, 2003; Wood & Yezerinac, 2006; Parris & Schneider, 2008; Verzijden *et al.*, 2010), or increasing the amplitude of songs (Brumm, 2004; Nemeth *et al.*, 2013). However, while high-frequency songs are masked less by low-frequency noise, higher frequencies do not transmit as well as lower frequencies, especially in cluttered habitats with more obstruction (Marten & Marler, 1977; Wiley & Richards, 1978). Therefore, there may be a signal efficiency trade-off if song characteristics that reduce masking by anthropogenic noise also result in greater habitat-related signal degradation (Dowling *et al.*, 2012).

Although noise pollution is pervasive, habitat structure also affects communication by changing signal transmission (Morton, 1975; Wiley & Richards, 1978; Brown & Handford, 2000; Warren *et al.*, 2006). Urban areas are often more open than natural forests; this can lead to greater signal degradation due to increased amplitude fluctuations that result from wind interference (Richards & Wiley, 1980). Urban areas may also experience degradation caused by distinct echoes of signals reflecting off the surfaces of buildings and roads (Slabbekoorn *et al.*, 2007). Interestingly, pavement and buildings may also provide sound channels which could increase signal propagation distances (Gall *et al.*, 2012). However, many bird species are found only in urban green spaces, which typically contain trees and shrubs and fewer hard surfaces but are still more open than true rural forest habitat. Compared with rural areas, the specific habitat structure of urban green spaces could therefore lead to more degradation from irregular amplitude fluctuations, but less degradation from absorption and scattering by leaves, twigs, and branches (Mockford *et al.*, 2011).

Although both habitat structure and ambient noise can simultaneously affect efficient signal transfer in urban green spaces, these factors have received little attention in combination. Several studies compared urban signal transmission among different habitat-types but did not take noise levels into account (e.g., Slabbekoorn *et al.*, 2007; Mockford *et al.*, 2011). However, Nemeth & Brumm (2010) included both habitat and ambient noise in a theoretical study of urban signal transmission range. Their calculations suggested that the impacts of traffic noise may outweigh the impacts of habitat type as a selection pressure on acoustic communication in cities. Dowling *et al.* (2012) found opposing effects of urban noise and urban habitat structure, with low frequencies being affected by noise, and high frequencies by habitat structure. Furthermore, a recent analysis examined correlations between song variation in black-capped chickadees and both ambient noise interference and habitat structure (Proppe *et al.*, 2012). They found that variation in overall song frequency correlated with ambient noise levels, but not with habitat structure, while internal frequency ratios within songs showed habitat-dependent variation. These findings suggest a complex interaction between the effects of habitat structure and ambient noise levels on signal transfer and detection. Field studies addressing signal transfer under varying habitat and noise conditions may provide further insight into urban signalling conditions.

In addition to habitat structure and ambient noise, signal transfer and detectability can also depend on specific signal features. Species-specific acoustic features in calls or songs can influence signal efficiency and can determine whether some species are more predisposed than others to communicate and reproduce in urban green spaces. Two bird species which readily occupy urban green spaces are black-capped and mountain chickadees. They share two family-specific vocalizations: a *chick-a-dee* call and a whistled song (Hailman, 1989). *Chick-a-dee* calls are broadband with harmonics and little tonality (Lucas & Freeberg, 2007), suggesting they may have limited transmission. Behaviourally, these calls are relatively short-range signals probably used for flock cohesion, predator alerts and food advertisement (Lucas & Freeberg, 2007). However, mountain chickadees do use *chick-a-dee* calls during the dawn chorus, possibly for mate-attraction (McCallum *et al.*, 1999; Grava *et al.*, 2013*a*). Songs, on the other hand, are fairly high-pitched and tonal. The tonality suggests adaptation to forested habitats (Wiley & Richards, 1982; Brown & Handford, 2000) and to long-range transmission. Songs are used primarily for territorial defence and mate-attraction (Mennill & Otter, 2007). Because both species are adapted to forested habitats, but are also known to inhabit urban green spaces, they are a good system for examining how differences in habitat structure and noise challenge avian communication in urban green spaces.

In this chapter, I conducted transmission experiments in a replicated set of transects across gradients both in habitat structure and ambient noise so as to compare the relative effects of habitat-dependent transmission and ambient noise interference on signal transfer of chickadee vocalizations. I then used a subset of sites identified as either clearly urban or clearly rural to determine whether characteristics that negatively affected signal transfer were more common in urban green spaces than in rural forested areas. Finally, I discussed the implications these results may have for the settlement tendencies of chickadees in urban habitats.

2.2 Methods

2.2.1 Experimental design and sample sizes

I conducted transmission trials within 50 km of Prince George, British Columbia, Canada, between 4 May and 20 May, 2011 and between 26 April and 4 May, 2012. This corresponds with the peak period of spring vocalization in chickadees at this latitude, coinciding with the nest-building and egg-laying phase of reproduction, at which time full leaf-burst has not yet occurred. All trials were performed between 07:00 and 14:30, and all but 6 before 12:00. I did not perform trials on days with rain or high wind. To control for temporal effects, I conducted trials in sites of similar habitat on the same day, but which differed in ambient noise levels. Between 1 and 4 trials were performed per day, totalling 37 transmission trials across continuous gradients of both habitat structure and ambient noise.

For each transmission trial, I broadcast a sequence of stimuli with a Cowon iAudio 9 music player (Cowon Systems, Korea; Frequency response ~20 Hz - 20 kHz) attached to a 5W Roland Mobile Cube amplifier with two built-in loudspeakers (Roland Incorporation, USA; 'Full range audio' frequency response ~100 Hz - 20 kHz) fastened on top of a 3-m high extension pole. Stimuli were re-recorded onto a Marantz PMD 671 Digital Recorder (Marantz Canada, LLC) with a MKH70 Sennheiser microphone (frequency response 50 Hz - 20 kHz;

Sennheiser, Canada) fastened on top of a second, equivalent pole, 75m from the first (a distance corresponding the radius of a typical chickadee territory of 1.77 ha, *cf.* Mennill *et al.*, 2004). All transmission transects lines were across typical habitat for the area with few topographical changes (depressions or hills) between amplifier and microphone. If the transect line was on a slope, amplifier and microphone were angled to maintain a transmission path parallel to, and unimpeded by, the ground. Audio was recorded in WAVE format and digitized at a 16 bit 44.1 kHz sampling rate.

My emphasis in this study was to compare the relative effects of ambient noise and habitat openness on signal transfer over a variety of signal types. I therefore chose several stimuli for each of the two different vocalization types from two different species (e.g., Figures 1.1 and 1.2). The stimulus sequence played back at each transect was comprised of 11 unique stimuli including 2 black-capped chickadee calls (dominant frequencies: 3.60 - 3.68 kHz, repeated 2 times), 2 mountain chickadee calls (dominant frequencies: 3.59 - 3.76 kHz, repeated 2 times), 3 black-capped chickadee songs (*fee*-note 3.37 - 3.98 kHz, *bee*-note 3.02 - 3.48 kHz; population range *fee*-note 3.04 - 4.54 kHz, *bee*-note 2.80 - 3.71 kHz; repeated 2 times), and 4 mountain chickadee songs (highest note dominant frequencies 3.81 - 4.49 kHz, lowest note dominant frequencies 3.25 - 4.28; highest note population range 3.37 - 4.69 kHz, lowest note population range 3.04 - 4.08 kHz, repeated 1 time). The stimuli were combined into one WAVE file with 1-2s between each (1.5 min total). For each transmission trial, the sequence was broadcast 3-4 times to ensure at least one unfettered recording of each stimulus. If more than one replicate of a particular stimulus was discernible, I averaged measurements within and between sequences to obtain a single value per unique stimulus (11 in total per transect).

I obtained black-capped *chick-a-dee* calls from recordings made during previous studies on dawn vocalizations (van Oort *et al.*, 2006), and obtained mountain *chick-a-dee* calls from field recordings in a previous study (Grava *et al.*, 2013*a*). I obtained black-capped song stimuli from a previous study (Hansen *et al.*, 2005), and mountain songs from the Stokes field guide (Colver *et al.*, 1999). Amplitude of the transmission broadcast was set by the volume on the MP3 player and was consistent throughout the study. Calls and songs were broadcast at 63 ± 2 dB(Z) and 74 ± 2 dB(Z), respectively (mean ± standard deviation, measured at 5m). While these amplitudes are higher than natural levels, these differences in broadcast amplitude reflect natural differences between vocalization types. To control for speaker and microphone effects on frequency detection, we broadcast the sequence once over 5m with no vegetation between speaker and microphone, and low ambient noise; from this, we obtained the baseline control measure for comparison with the re-recorded transmission stimuli over the full 75m.

2.2.2 Measuring habitat structure and ambient noise

At each site, habitat structure was measured at approximately the midpoint between amplifier and microphone, centred on habitat representative of the transmission line. I recorded canopy cover and vegetation openness at heights of < 1 m, 1 - 2 m, and 2 - 3 m. Canopy cover was measured with a spherical (convex) densiometer in the four cardinal directions and averaged. Vegetation openness was quantified by photographing a 1 x 1 m board of yellow corrugated plastic held at a distance of 10m in 4 different directions and at heights of < 1 m, 1 - 2 m and 2 - 3 m. The mean percent area of the board unobscured by vegetation was determined by photo analysis, using ImageJ v1.46a (Schneider *et al.*, 2012). Average canopy cover ranged from 0.5 - 100% and average vegetation openness ranged from 15 to 99%. To reduce the number of variables and obtain a holistic measure of habitat structure for each site, I collapsed the variables with a principal components analysis (PCA) using R statistical software v3.1.0 (R Core Team, 2014). Kaiser-Meyer-Olkin (KMO) measures of sampling adequacy and Bartlett's sphericity were used to determine that my data had sufficient covariation for use in principal component analyses (KMO = 0.75; Bartlett's sphericity, $\chi^2 = 136.1$, df = 6, $P < 0.001$; McGregor, 1992). I retained the only principal component axis that accounted for greater variation than expected by chance using the broken stick model (PC1 = 76% Legendre & Legendre, 1998). This axis represented overall *habitat openness* with increasing canopy openness (loading = 0.35) and increasing habitat openness as measured by the vegetation board at each height (loadings = low 0.52, medium 0.55, high 0.54). All variables were easily interpretable and had loadings greater than 0.33 (Ho, 2006), therefore I did not apply any secondary rotations of the axes (Quinn & Keough, 2002).

Ambient noise levels were measured at the site of the microphone with a Pulsar 30 sound pressure meter (Pulsar Instruments plc., UK) as SPL dB in octave bands 125Hz through 4kHz (corresponding to a range of 88Hz to 5.68kHz). This frequency range was selected to match both the auditory range of chickadees (Henry & Lucas, 2010) and the dominant frequency range within which most calls and songs occur. Ambient noise measurements were taken multiple times, just before, during and/or after the transmission trial. Measures during the trial were taken between stimulus broadcasts. All measures for one site (range 2 - 5, median = 3) were averaged and ranged from 17.8 dB to 55.3 dB. All sites sampled included a broad gradient of ambient noise and *habitat openness* (Figure 2.1).

2.2.3 Measuring relative signal amplitude and degradation

Re-recorded stimuli were extracted using Avisoft-SASLab Pro v5.2.02 (Specht, 2012) and SoX v14.3.2 (Bagwell, 2011), and analysed with the R package seewave v1.6.7 (Sueur *et al.*, 2008). All re-recorded stimuli were checked visually and only those without sudden, overlapping background sounds were used (range 1 - 8, median = 3, repeats of each re-recorded stimulus per site). Spectrograms were created using a fast-fourier transform with a Hanning window length of 1024. Recordings were measured for relative signal amplitude (signal-to-noise ratios), detection of signal elements (minimum and maximum frequencies), and amplitude fluctuations.

Signal-to-noise ratios (SNR) were calculated from recordings as the ratio between root-mean-squared amplitudes of vocalization to background noise for each re-recorded stimulus (see Dabelsteen *et al.*, 1993; Proppe *et al.*, 2010). To obtain a less inflated measure of masking, re-recorded stimuli and background noise were band-pass filtered to the

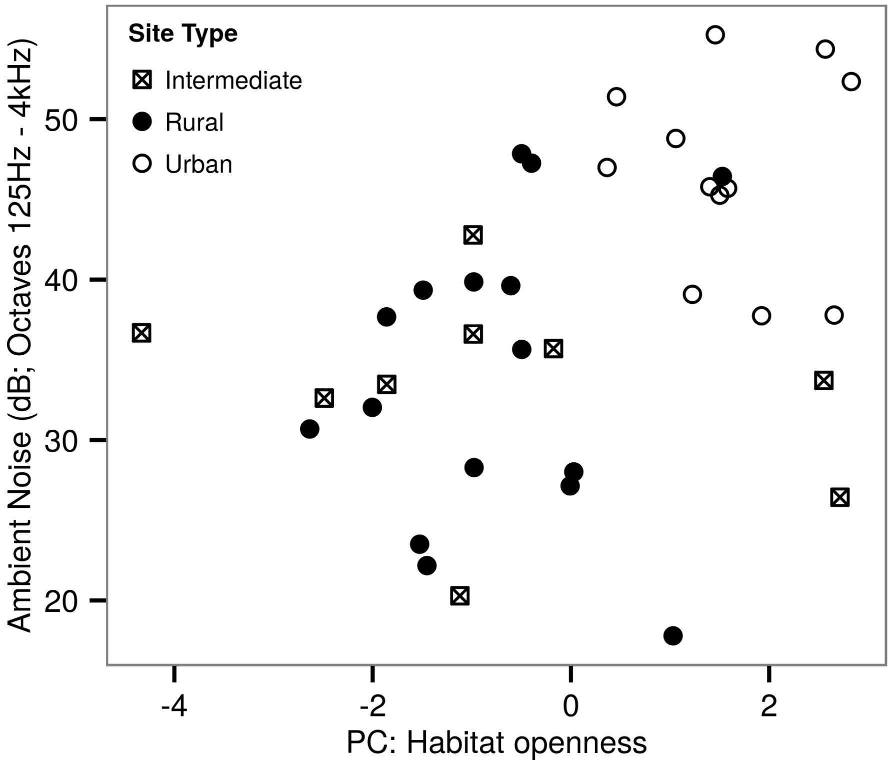

Figure 2.1: Transmission sites were sampled over continuous gradients of both *habitat openness* and *ambient noise*. Site type reflects the categorization of sites used in the assessment of the characteristics of urban green spaces.

minimum and maximum frequency limits of the original stimulus. Vocalization amplitude was obtained by subtracting the amplitude of background noise (E_n) from the amplitude of the re-recorded stimulus (E_y). Background noise amplitudes (E_n) were calculated as root-mean-squared amplitudes measured over a section of recording equal in length to the stimulus, in most cases just prior to the stimulus. However, if there was an overlapping sound at this point the background noise measurement was instead taken from a different part of the same recording (within 1.5 ± 4.8 min [mean ± SD] of the re-recorded stimulus) where there was a comparable level and distribution of background noise. The ratio was then converted to decibels by taking the log and multiplying by 10 using the formula:

$$\mathit{SNR} = 10 \log \frac{(E_y - E_n)}{E_n}$$

I measured detection of low- and high-frequency signal elements by calculating the loss of minimum and maximum frequencies of re-recorded stimuli compared with the original stimuli. The minimum and maximum detected frequencies of re-recorded stimuli were manually measured from a frequency power spectrum and were then compared with the mean value of the baseline control stimuli (stimuli re-recorded at 5m) resulting in a measure of frequency loss. Amplitude fluctuations were defined as the coefficient of variation of root-mean-squared amplitudes measured across each re-recorded stimulus song or call. Root-mean-squared amplitude was measured for the first, second and third ’thirds’ of each note in each re-recorded stimulus for songs and in each *dee*-note for calls (ranging from 0.06 to 0.15 s for songs and from 0.05 to 0.12 s for calls, depending on the length of the note).

2.2.4 Modelling the effects of habitat structure and ambient noise and on signal transmission

To determine how these 4 measures of signal transmission (SNR, loss of minimum and maximum frequencies, and amplitude fluctuations) were affected by habitat structure (*habitat* *openness*) and ambient noise (*ambient noise*), I used an information theoretic approach of model selection to evaluate a candidate set of five possible models for each measure (Burnham & Anderson, 2002). Because my goal was to examine signal transfer across different habitats, not necessarily within or between species, I had relatively few different stimuli exemplars for each vocalization type for each species. Therefore, I controlled for species by including it as a covariate. Because *chick-a-dee* calls and songs are structurally very different, they were analysed separately. This resulted in 8 separate sets of analyses (4 measures x 2 vocalization types).

In each set of analyses, I considered a candidate model set with 5 models to determine which variables might affect signal degradation. These included combinations of individual effects and interactions. Specifically, I analysed: 1) null model (intercept only), 2) null model (intercept and species only), 3) *ambient noise*, 4) *habitat openness*, and 5) *ambient noise* x *habitat openness* (main effects and interactions). Species was included as a covariate in all models except the first null model (model 1). In each analysis the global model (model 5) was assessed for goodness-of-fit (Symonds & Moussalli, 2011) by computing the marginal and conditional R^2s (Nakagawa & Schielzeth, 2013) with R package MuMIn v1.9.5 (Bartoń, 2013). I then ranked all models by small sample Akaike Information Criterion (AIC_c), and calculated differences in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c). From this, I calculated the normalized relative likelihood of each model (Akaike weights, w_i) to assess model selection uncertainty. In every analysis the best model had a $w_i < 0.9$. Thus model averaging was advised (Burnham & Anderson, 2002). The confidence set of candidate models included all models with a w_i greater than 10% of the maximum weight (relative likelihood approach; Burnham & Anderson, 2002; e.g., Turgeon *et al.*, 2010). For example, if the best model was w_{best} = 0.8, the confidence set of candidate models would include all models where $w_i > 0.08$. This cutoff also corresponds to a ΔAIC_c cutoff of < 4.61. Parameter estimates were averaged using weighted unconditional standard errors and are presented with 95% confidence intervals. Parameter estimates where zero was not in the

95% confidence interval are interpreted as being strongly correlated with the response variable (Mazerolle, 2006).

Each model evaluated was a linear mixed model (lme4 v1.1.5 package for R Bates *et al.*, 2014) with site and stimulus as crossed, random factors to control for pseudoreplication in those variables (Millar & Anderson, 2004). Where necessary, assumptions of normality were satisfied by transforming response variables by first anchoring the distribution at 1 and then using a Box-Cox transformation (Osborne, 2010). To allow for interpretation of main effects with significant interactions, I centred and standardized all explanatory variables (Schielzeth, 2010). To check for multiple collinearity, I confirmed that variance inflation factors (VIFs) were all < 10) and condition numbers were all < 30 for the global model (model 5) in each analysis (Quinn & Keough, 2002).

I illustrated relationships between strongly correlated explanatory variables (i.e. *habitat openness* and *ambient noise*) and the response variables (i.e. SNR, loss of minimum or maximum frequencies, or amplitude fluctuations) in figures showing both the model relationship (lines) and the raw data averaged for each site (points). Each relationship was plotted while holding all other variables constant. For better interpretation, response variables and the explanatory variable, *ambient noise*, were back-transformed to their original units. Figures were produced with the ggplot2 v0.9.3.1 package for R (Wickham, 2009).

2.2.5 Assessing characteristics of urban green spaces

Urban habitats are generally considered to be noisier and more open than rural habitats. To confirm this in my study, I categorized all transmission sites as either urban or rural based on proximity to the city of Prince George and degree of urbanization. Urban sites included parks, cemeteries, green corridors, backyards and road-side vegetation patches. Rural sites were all forests of varying ages and composition. Nine of the 37 sites were not clearly urban nor clearly rural and were therefore omitted. I then conducted two ANOVAs to determine whether habitat type (urban or rural) could predict *habitat openness* and/or *ambient noise*.

2.3 Results

2.3.1 Model selection

Overall, *ambient noise* had a clear effect on signal transfer in 6 of 8 analyses, *habitat openness* had no clear effects, and species correlated with the response in 3 analyses. In 6 analyses, model 3 (*ambient noise*) ranked highest, and model 5 (*ambient noise* x *habitat openness*) ranked second highest (see 2.5 Appendix). In the other 2 analyses (loss of maximum frequency in calls and amplitude fluctuations in songs) there was substantial model uncertainty resulting in all models (including both null models) being part of the confidence set of candidate models (see 2.5 Appendix). Therefore, the parameters did not clearly explain variation in the response variables and were not interpreted.

2.3.2 Effects of *habitat openness* and *ambient noise* on signal transfer

In *chick-a-dee* calls, *ambient noise* was associated with a decrease in SNR, a greater loss of minimum frequencies, and a decrease in amplitude fluctuations (Table 2.1; Figure 2.2). There was a trend for amplitude fluctuations to increase with *habitat openness* (CI90% did not overlap zero; Table 2.1. In contrast with the *chick-a-dee* calls of black-capped chickadees, calls of mountain chickadees had lower amplitude fluctuations (Table 2.1).

In whistled songs, *ambient noise* was associated with a decrease in SNR, a greater loss of minimum frequencies, and an increase in the loss of maximum frequencies (Table 2.2; Figure 2.3). There were no effects of *habitat openness*. Songs of mountain chickadees also lost more minimum and maximum frequencies than songs of black-capped chickadees (Table 2.2).

2.3.3 Assessing characteristics of urban green spaces

In sites identified as either distinctly urban or distinctly rural, urban noise sound pressure levels varied from a mean of 57.4 to 74.8 dB(Z) and rural noise levels varied between 51.2

Table 2.1: Calls: Model-averaged results on the effects of *habitat openness* and *ambient noise* on three measures of signal transfer and degradation. Species is a covariate reflecting how mountain chickadees differ from black-capped chickadees. Values are presented as regression slopes ± 95% confidence interval. Note that these are transformed values without relevant units. See figures for patterns with original units. Below the midrule are analysis information such as marginal and condition R^2s, the total number of models in the candidate set (No. models in candidate set), and the final number of models retained in the confidence set of candidate models (No. models in confidence set).

Parameter	Signal-to-noise ratio	Loss min freq	Amplitude fluctuations
(Intercept)	**17282 ± 13731** **	**0.754 ± 0.330** **	**0.193 ± 0.029** **
Species	5270 ± 18996	-0.031 ± 0.447	**-0.100 ± 0.037** **
Ambient Noise	**-6564 ± 3252** **	**0.313 ± 0.109** **	**-0.019 ± 0.015** **
Habitat openness	1552 ± 3207	-0.081 ± 0.104	0.013 ± 0.013 *
Ambient Noise x Habitat	2185 ± 3750	-0.043 ± 0.122	0.001 ± 0.016
R^2 (marg)	0.20	0.37	0.50
R^2 (cond)	0.78	0.82	0.72
No. models in candidate set	5	5	5
No. models in confidence set	2	2	3

** **bold** indicate 95% confidence intervals which do not overlap zero

* indicate 90% confidence intervals which do not overlap zero

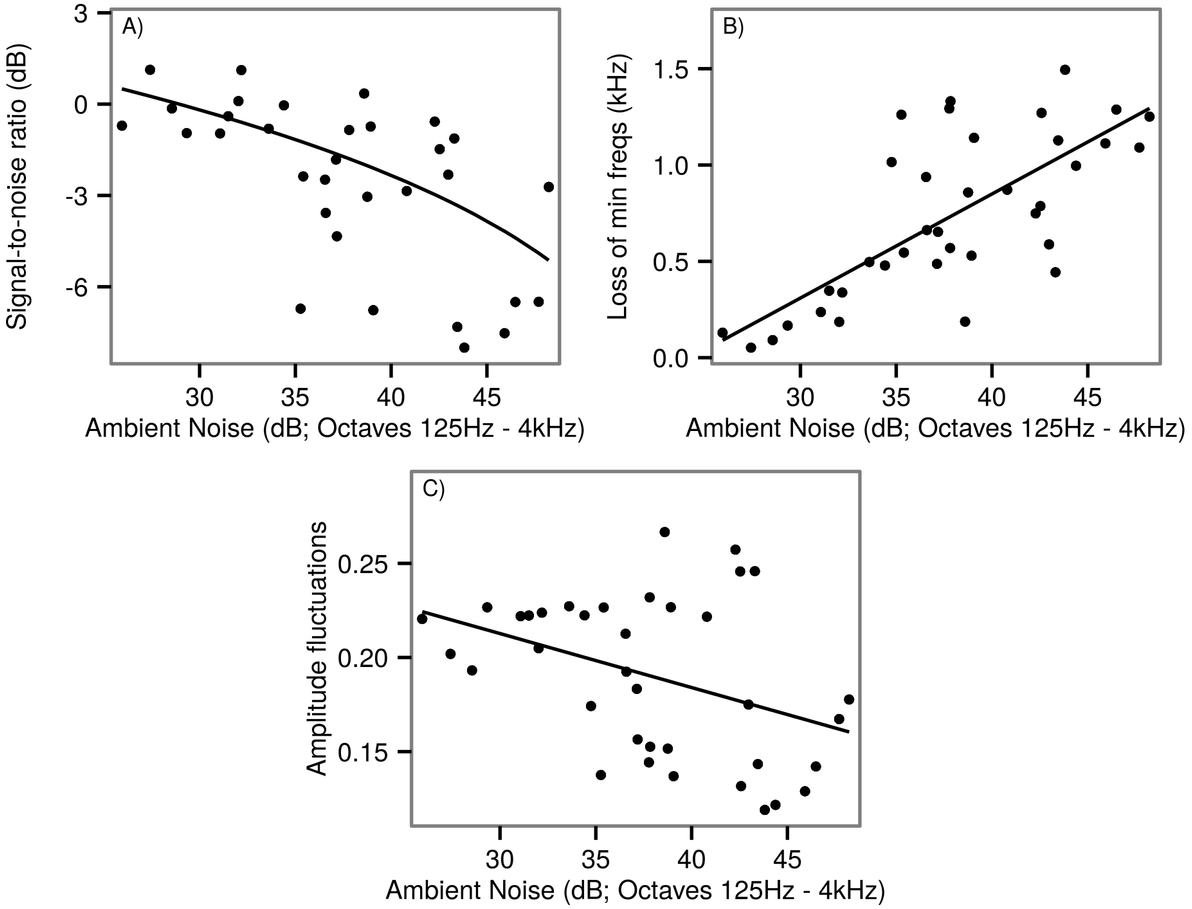

Figure 2.2: Among calls, *ambient noise* is associated with a reduction in signal-to-noise ratio (**A**), with increases in the loss of minimum frequencies (**B**) and with a reduction in amplitude fluctuations (**C**). Points are averaged raw values for each site. Lines represent model averaged relationships between the explanatory and the response variable.

Table 2.2: Songs: Model-averaged results on the effects of *habitat openness* and *ambient noise* on three measures of signal transfer and degradation. Species is a covariate reflecting how mountain chickadees differ from black-capped chickadees. Values are presented as regression slopes ± 95% confidence interval. Note that these are transformed values without relevant units. See figures for patterns with original units. Below the midrule are analysis information such as marginal and condition R^2s, the total number of models in the candidate set (No. models in candidate set), and the final number of models retained in the confidence set of candidate models (No. models in confidence set).

Parameter	Signal-to-noise ratio	Loss min freq	Loss max freq
(Intercept)	**1291** ± **547** **	**0.129** ± **0.033** **	**0.082** ± **0.021** **
Species	-96 ± 706	**0.042** ± **0.040** **	**0.038** ± **0.026** **
Ambient Noise	**-280** ± **136** **	**0.034** ± **0.016** **	**0.010** ± **0.006** **
Habitat openness	83 ± 137	-0.009 ± 0.016	-0.004 ± 0.006
Ambient Noise x Habitat	37 ± 160	-0.002 ± 0.019	-0.003 ± 0.007
R^2 (marg)	0.16	0.27	0.33
R^2 (cond)	0.78	0.64	0.68
No. models in candidate set	5	5	5
No. models in confidence set	2	2	2

** **bold** indicate 95% confidence intervals which do not overlap zero

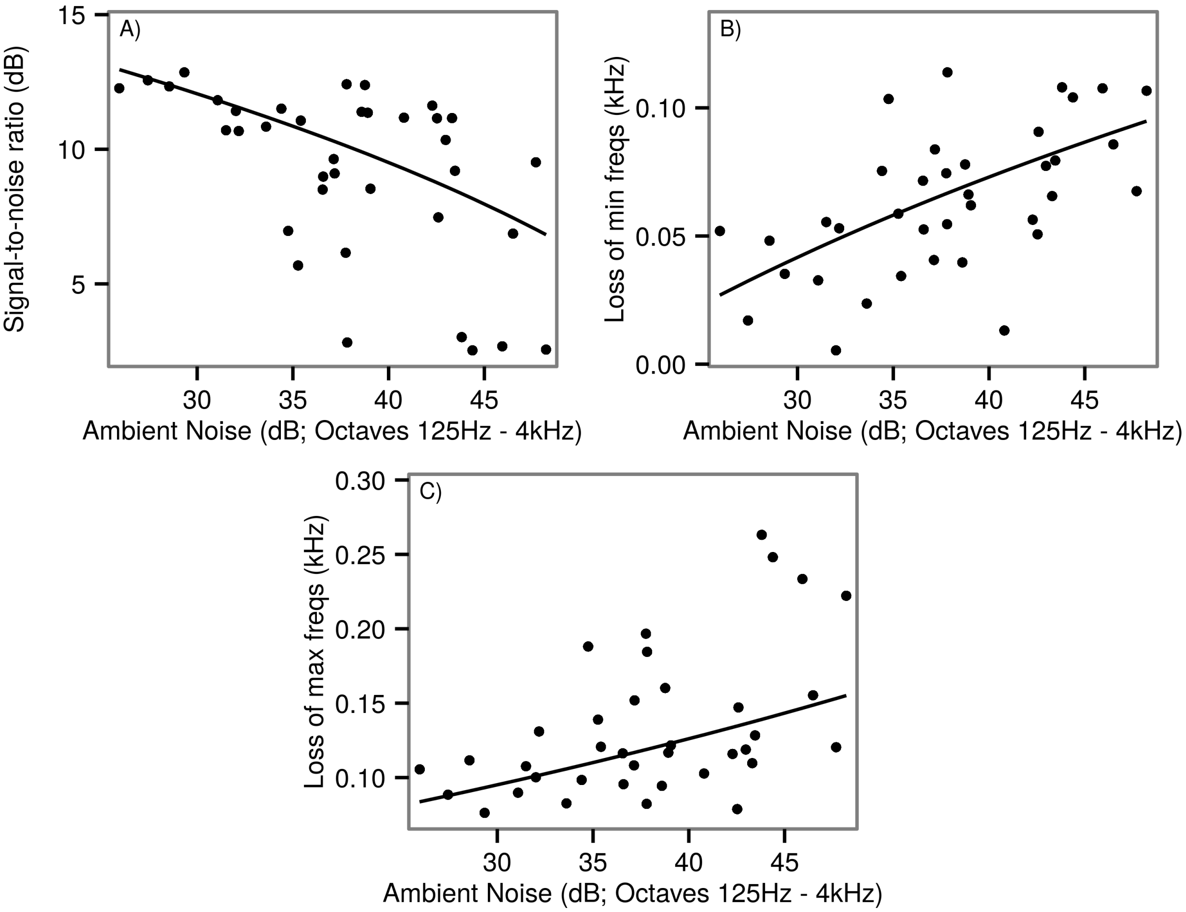

Figure 2.3: Among songs, *ambient noise* is associated with a reduction in signal-to-noise ratio (**A**), and with increases in the loss of minimum (**B**) and maximum (**C**) frequencies. Points are averaged raw values for each site. Lines represent model averaged relationships between the explanatory and the response variable.

and 65.7 dB(Z). Further, urban green spaces experienced significantly more ambient noise in the frequency range in which chickadees both vocalize and have highest auditory perception (0.088 kHz to 5.68 kHz; Slope Est ± CI95% = 12.8 ± 6.3 dB, $t = 4.15$, $P < 0.001$) and had greater *habitat openness* (Slope Est ± CI95% = 2.36 ± 0.77, $t = 6.31$, $P < 0.001$) than rural areas.

2.4 Discussion

Ambient noise had a greater negative effect on both signal-to-noise ratios and detection of signal features in transmitted chickadee vocalizations than *habitat openness*, and there were no interactions between the effects of *ambient noise* and *habitat openness*. *Ambient noise* reduced relative signal amplitude, and interfered with the detection of high and/or low frequency elements in all vocalizations. Models including *habitat openness* were retained in the confidence set of candidate models, suggesting it plays some role, but *habitat openness* did not show any clear patterns. These results, coupled with my finding that urban green spaces in Prince George are noisier than rural forested areas, suggest urban chickadees may have greater difficulties communicating than rural chickadees.

2.4.1 Signal masking and masking avoidance

As expected, ambient noise interfered with signal transfer and detection through masking. In addition to generally lowering signal-to-noise ratios, ambient noise selectively masked minimum and maximum frequencies. Consistent with masking theory, ambient noise masked the very low-frequency aspects more than high-frequency aspects (i.e. minimum frequencies in calls experienced greatest masking). Additionally, songs (which have lower maximum frequencies than calls) also had their maximum frequencies masked. Theoretical models suggest that in urban noise, both signal amplitude and frequency can increase communication distance (Nemeth & Brumm, 2010). Therefore, in chickadees, singing higher could increase potential communication distances by reducing the loss of signal features under noisy conditions. Furthermore, singing louder may be an effective way of increasing the range of vocalizations in noisy conditions and singing higher may allow birds to sing louder (Nemeth *et al.*, 2013). Other studies have also found that black-capped chickadees do sing higher frequency songs in noisy habitats (Proppe *et al.*, 2012), and will shift songs in response to experimental overlapping noise (Goodwin & Podos, 2013), but spectral flexibility has not been observed in mountain chickadees. This potential spectral constraints on mountain chickadee song may result in this species experiencing greater difficulties communicating in urban green spaces compared with black-capped chickadees.

Open habitat can affect the temporal structure signals by reducing scatter and increasing amplitude fluctuations from wind (Brown & Handford, 2000), but the influence of noise on the temporal structure of signals is relatively unknown. Here, I observed ambient noise reducing amplitude fluctuations in calls. It is unlikely that ambient noise actually affected the magnitude of amplitude fluctuations, but it may have filled in gaps of relatively low amplitude periods, thus reducing the range of amplitude fluctuations. The perceptual consequences of this are unknown, but ambient noise can have interactive effects with signal degradation that are not necessarily detrimental. An example of this would be the well-known and taxonomically widespread phenomenon of perceptual restoration (where missing signals are perceived as being heard when replaced with potentially masking noise; Warren, 1970; Braaten & Leary, 1999; Seeba *et al.*, 2010; Kobayasi *et al.*, 2012). It remains to be tested whether urban noise is merely overlaying a detrimental effect on top of signal degradation or whether it could actually counteract certain types of signal degradation related to air turbulence or reflective surfaces during propagation.

2.4.2 Sources of signal degradation and interference

Within the range of habitats tested, this study suggests that the effects of ambient noise outweigh habitat-dependent effects on signal transfer and detection, despite the fact that open habitats generally result in better signal transmission than closed habitats (Fotheringham &

Ratcliffe, 1995; Hansen *et al.*, 2005; Proppe *et al.*, 2010; Mockford *et al.*, 2011; but see Slabbekoorn *et al.*, 2007). These experimental results match theoretical findings that communication distances in urban areas are much smaller compared with forested rural sites when both habitat structure and ambient noise are considered (Nemeth & Brumm, 2010). My results also match field observations of black-capped chickadees (Proppe *et al.*, 2012). They found that the overall frequency of black-capped chickadee songs increased with ambient noise levels in a park as well as a city, but showed no relationship with canopy openness. However, in contrast with my findings, Gall *et al.* (2012) did find effects of habitat openness on signal transmission. They conducted a transmission study to calculate the active space (distance over which signal can be detected) of songs in brown-headed cowbirds (*Molothrus ater*) between urban and rural (which difference in noise), and open and closed habitats. They found evidence that habitat openness significantly influenced signal transfer despite considering noise. This difference may reflect the fact that I did not test transmission in highly urbanized areas with lots of pavement and large buildings, but could also highlight the potential influence of species-specific signal characteristics, such as signal frequency, on the relationship between ambient noise and habitat structure on signal transfer.

The general differences between signal transfer of calls and songs may also result in species-specific differences in the degree of noise interference experienced. For example, mountain chickadees utilize *chick-a-dee* calls to a far greater extent in their dawn signalling than do black-capped chickadees; the latter using song almost exclusively during this period (McCallum *et al.*, 1999; Grava *et al.*, 2013*a*). Because I found that calls were greatly masked by ambient noise (large reductions in SNR and large losses in minimum frequencies), mountain chickadees may experience a reduced ability to exploit urban habitat as a result of associated urban soundscapes. However, although I have evidence that signal transfer is altered by ambient noise, studies assessing the receiver side are necessary to confirm that this does indeed interfere with chickadee communication.

2.4.3 Conclusions

In summary, my transmission trials replicated in a large set of habitats have shown that vocalizations of two species of chickadee experience greater interference of signal transfer in urban green spaces compared with rural forests as a result of ambient noise. Ambient noise represented a large impediment to signal transfer, whereas differences in habitat structure between urban green spaces and rural areas had a relatively minor effect. As avian abundance and breeding success are known to decline as noise increases (Halfwerk *et al.*, 2011*b*; McClure *et al.*, 2013), these findings confirm that ambient noise should be matter of concern in species conservation. If management goals are to maximize the effectiveness of green spaces in attracting and retaining avian species, noise mitigation measures should be considered.

2.5 Appendix

2.5.1 Model Selection

All global models had adequate goodness-of-fit, measured as conditional R^2 (fixed and random effects) which ranged from 0.62 to 0.82. In 5 of the 8 analyses, model selection uncertainty was relatively low with 2 models being averaged (Tables A1-A2; A5-A7). In one analysis (amplitude fluctuations in calls; Table A4) model selection uncertainty was somewhat higher with 3 models being averaged. However, the remaining analyses (loss of maximum frequencies in calls and change in amplitude fluctuations in songs) had high levels of model uncertainty (Tables A3 and A8) and ranked all models (including both null models) in the candidate set. This suggests the parameters included did not adequately account for variation in the response variable.

Table A1: Model selection for signal-to-noise ratio (SNR) in calls. K represents the number of parameters including intercept and error. ΔAIC_c represent differences in AIC_c between the current model and the model with the lowest AIC_c. w_i represent Akaike weights. Greyed rows are models included in the confidence set of candidate models, which were model averaged.

	Model	Log-likelihood	K	AIC_c	ΔAIC_c	w_i
3	SNR ~ *Ambient Noise*	-1515.71	4	3044.05	0.00	0.77
5	SNR ~ *Ambient Noise* x *Habitat openness*	-1514.72	6	3046.51	2.47	0.22
4	SNR ~ *Habitat openness*	-1522.77	4	3058.15	14.10	0.00
2	SNR ~ null (only covariate)	-1523.03	3	3056.49	12.45	0.00
1	SNR ~ null (no parameters)	-1523.18	2	3054.65	10.60	0.00

Table A2: Model selection for loss of minimum frequencies in calls. K represents the number of parameters including intercept and error. ΔAIC$_c$ represent differences in AIC$_c$ between the current model and the model with the lowest AIC$_c$. w_i represent Akaike weights. Greyed rows are models included in the confidence set of candidate models, which were model averaged.

	Model	Log-likelihood	K	AIC$_c$	ΔAIC$_c$	w_i
3	Loss min freq (kHz) ~ *Ambient Noise*	-25.87	4	64.34	0.00	0.71
5	Loss min freq (kHz) ~ *Ambient Noise* x *Habitat openness*	-24.57	6	66.18	1.83	0.29
4	Loss min freq (kHz) ~ *Habitat openness*	-38.68	4	89.95	25.61	0.00
2	Loss min freq (kHz) ~ null (only covariate)	-38.93	3	88.28	23.94	0.00
1	Loss min freq (kHz) ~ null (no parameters)	-38.94	2	86.16	21.81	0.00

Table A3: Model selection for loss of maximum frequencies in calls. K represents the number of parameters including intercept and error. $\Delta\mathrm{AIC}_c$ represent differences in AIC_c between the current model and the model with the lowest AIC_c. w_i represent Akaike weights. Greyed rows are models included in the confidence set of candidate models, which were model averaged.

	Model	Log-likelihood	K	AIC_c	$\Delta\mathrm{AIC}_c$	w_i
2	Loss max freq (kHz) ~ null (only covariate)	383.93	3	-757.44	0.00	0.38
3	Loss max freq (kHz) ~ *Ambient Noise*	384.93	4	-757.26	0.17	0.34
4	Loss max freq (kHz) ~ *Habitat openness*	383.95	4	-755.30	2.14	0.13
5	Loss max freq (kHz) ~ *Ambient Noise* x *Habitat openness*	385.79	6	-754.54	2.90	0.09
1	Loss max freq (kHz) ~ null (no parameters)	381.06	2	-753.84	3.60	0.06

Table A4: Model selection for amplitude fluctuations in calls. K represents the number of parameters including intercept and error. ΔAIC$_c$ represent differences in AIC$_c$ between the current model and the model with the lowest AIC$_c$. w_i represent Akaike weights. Greyed rows are models included in the confidence set of candidate models, which were model averaged.

	Model	Log-likelihood	K	AIC$_c$	ΔAIC$_c$	w_i
3	Amp fluct ~ *Ambient Noise*	236.91	4	-461.21	0.00	0.56
5	Amp fluct ~ *Ambient Noise* x *Habitat openness*	238.61	6	-460.18	1.03	0.33
2	Amp fluct ~ null (only covariate)	233.83	3	-457.23	3.99	0.08
4	Amp fluct ~ *Habitat openness*	234.03	4	-455.46	5.76	0.03
1	Amp fluct ~ null (no parameters)	229.57	2	-450.86	10.36	0.00

Table A5: Model selection for signal-to-noise ratio (SNR) in songs. K represents the number of parameters including intercept and error. ΔAIC$_c$ represent differences in AIC$_c$ between the current model and the model with the lowest AIC$_c$. w_i represent Akaike weights. Greyed rows are models included in the confidence set of candidate models, which were model averaged.

	Model	Log-likelihood	K	AIC$_c$	ΔAIC$_c$	w_i
3	SNR ~ *Ambient Noise*	-1773.27	4	3558.91	0	0.79
5	SNR ~ *Ambient Noise* x *Habitat openness*	-1772.49	6	3561.61	2.70	0.20
4	SNR ~ *Habitat openness*	-1780.67	4	3573.71	14.80	0.00
2	SNR ~ null (only covariate)	-1780.78	3	3571.83	12.92	0.00
1	SNR ~ null (no parameters)	-1780.82	2	3569.81	10.91	0.00

Table A6: Model selection for loss of minimum frequencies in songs. K represents the number of parameters including intercept and error. ΔAIC_c represent differences in AIC_c between the current model and the model with the lowest AIC_c. w_i represent Akaike weights. Greyed rows are models included in the confidence set of candidate models, which were model averaged.

	Model	Log-likelihood	K	AIC_c	ΔAIC_c	w_i
3	Loss min freq (kHz) ~ *Ambient Noise*	353.26	4	-694.15	0.00	0.82
5	Loss min freq (kHz) ~ *Ambient Noise* x *Habitat openness*	353.89	6	-691.15	3	0.18
4	Loss min freq (kHz) ~ *Habitat openness*	345.43	4	-678.50	15.65	0.00
1	Loss min freq (kHz) ~ null (no parameters)	343.52	2	-678.87	15.28	0.00
2	Loss min freq (kHz) ~ null (only covariate)	345.28	3	-680.31	13.84	0.00

Table A7: Model selection for loss of maximum frequencies in songs. K represents the number of parameters including intercept and error. $\Delta\mathrm{AIC}_c$ represent differences in AIC_c between the current model and the model with the lowest AIC_c. w_i represent Akaike weights. Greyed rows are models included in the confidence set of candidate models, which were model averaged.

	Model	Log-likelihood	K	AIC_c	$\Delta\mathrm{AIC}_c$	w_i
3	Loss max freq (kHz) ~ *Ambient Noise*	541.88	4	-1071.39	0.00	0.74
5	Loss max freq (kHz) ~ *Ambient Noise* x *Habitat openness*	542.86	6	-1069.10	2.29	0.23
2	Loss max freq (kHz) ~ null (only covariate)	537.22	3	-1064.17	7.22	0.02
4	Loss max freq (kHz) ~ *Habitat openness*	537.23	4	-1062.09	9.30	0.01
1	Loss max freq (kHz) ~ null (no parameters)	534.45	2	-1060.74	10.65	0.00

Table A8: Model selection for amplitude fluctuations in songs. K represents the number of parameters including intercept and error. ΔAIC$_c$ represent differences in AIC$_c$ between the current model and the model with the lowest AIC$_c$. w_i represent Akaike weights. Greyed rows are models included in the confidence set of candidate models, which were model averaged.

	Model	Log-likelihood	K	AIC$_c$	ΔAIC$_c$	w_i
2	Amp fluct ~ null (only covariate)	314.18	3	-618.10	0.02	0.32
4	Amp fluct ~ *Habitat openness*	315.24	4	-618.12	0.00	0.32
5	Amp fluct ~ *Ambient Noise* x *Habitat openness*	316.86	6	-617.10	1.02	0.19
3	Amp fluct ~ *Ambient Noise*	314.22	4	-616.07	2.05	0.12
1	Amp fluct ~ null (no parameters)	311.37	2	-614.56	3.55	0.05

3 Mountain chickadees adjust chorus structure and signalling features in response to urban noise

3.1 Introduction

Increasing urbanization has led to wide-spread homogenization of avian communities as some species abandon urban areas while others colonize them (Clergeau *et al.*, 2006; McKinney, 2006). Variation in behavioural plasticity may partially explain why some species adapt more readily to these novel environments than others (Sol *et al.*, 2013). Vocal plasticity in particular may allow some avian species to overcome the masking effects of low-frequency urban noise pollution (Slabbekoorn, 2013; Francis *et al.*, 2011*c*). Some species of birds appear able to adjust by spatially or temporally avoiding noisy conditions (avoidance: Fuller *et al.*, 2007; McClure *et al.*, 2013), by singing higher (spectral plasticity: Slabbekoorn & Peet, 2003; Verzijden *et al.*, 2010; Luther & Derryberry, 2012), by singing longer (temporal plasticity: Hamao *et al.*, 2011; but see Yang *et al.*, 2014), and/or by singing louder (amplitude plasticity: Brumm, 2004). As the world's human population grows, predicting which species can use vocal adjustment to cope with noise pollution is a necessary part of assessing species' vulnerability to urbanization. Behavioural or morphological constraints may limit whether different species can make these vocal adjustments (Patricelli & Blickley, 2006).

Even species that are capable of vocal adjustment may be at a disadvantage in urban areas if there are constraints on plasticity, if plasticity develops slowly, or if it also brings along costs. Urban development is often fast-paced and species that take longer to adjust to the effects of noise pollution may be less successful compared with those that adjust quickly. There are several characteristics that may pre-dispose a species or population to more rapid vocal adjustment. First, species that learn their songs and those with more vocal variability among populations appear to adjust better to noise pollution than those that lack these characteristics (Ríos-Chelén *et al.*, 2012). Second, the ability to dynamically adjust vocalizations to immediate changes in the sound environment is another trait likely to benefit species in urban areas. Birds which demonstrate immediate flexibility may be more predisposed to colonize urban areas than those which require longer time periods to adjust.

Mountain chickadees have noticeable regional variation in songs (Lohr, 2008; Grava *et al.*, 2013*a*), but relatively little individual variation. Unlike their sister-species, the black-capped chickadee, male mountain chickadees sing a single song variant and do not pitch-shift entire songs, although they do occasionally adjust the number of repetitions of individual syllables within songs (McCallum *et al.*, 1999; personal observation). This suggests populations may show vocal adjustment over longer time periods, but individual males may have limitations on responding to immediate changes in local noise levels. Further, in contrast to black-capped chickadees, mountain chickadees use both songs and calls during the dawn chorus. As songs transmit better and are less masked than calls (see Chapter 2) individuals could benefit by switching to songs in more noisy conditions (similar to great tits *Parus major* switching to other song types dependent on the relative frequency overlap with experimental noise; Halfwerk & Slabbekoorn, 2009).

The goals of this chapter were to examine whether mountain chickadees show vocal adjustment in response to urbanization and/or ambient noise levels, and, if so, which mechanisms they use. I predicted mountain chickadees would show limited immediate plasticity in song structure in response to experimental noise, because they have little capacity for within-individual flexibility. However, I suspected they might switch between songs and calls in response to immediate noise conditions. To test these hypotheses, I compared mountain chickadee chorus structure and vocalization features among birds across gradients of anthropogenic noise and urbanization, in three cities in British Columbia, Canada. Because mountain chickadee songs vary among populations, I tested for population differences in vocal adjustment. I evaluated immediate plasticity by exposing individuals to 5-minute treatments of experimental noise during their dawn singing.

3.2 Methods

3.2.1 Field recordings

A total of 55 male mountain chickadees were recorded throughout the cities of Williams Lake (n = 17), Kamloops (n = 30) and Kelowna (n = 8) in British Columbia, Canada. I recorded males between 7 May and 22 May 2012, and between 5 May and 23 May 2013, which corresponds to the spring dawn-chorusing period. Because dominant males may also be the first singers (as with black-capped chickadees, see Otter *et al.*, 1997), I recorded the first 1-3 males to sing in a given area to minimize the effects of dominance on song structure. For each male, I recorded all vocalizations for at least 5 minutes (pre-treatment), then, if the individual was still chorusing, started 5 minutes of synthetic experimental noise (experimental noise treatment; see below) and continued to record the individual. I finished by recording for 5 minutes after the noise exposure was over (post-treatment). Experimental noise was broadcast from a Roland Mobile Cube amplifier (Roland Incorporation, USA) using a Philips GoGear Raga MP3 player (Philips Ltd., Canada). I calibrated the noise volume so that its amplitude at the location of the male would be approximately 67 dB(Z) (65 dB(A)). All recordings were made with MKH70 Sennheiser microphones (Sennheiser Inc., Canada) on to Marantz PMD671 Digital recorders (Marantz Canada, LLC; 22 bit and 44.1 kHz sampling frequency) at distances between 5 and 25m.

3.2.2 Synthetic experimental noise

While I could have used actual traffic recordings instead of synthetic experimental noise, this practice can lead to problems because any traffic recording could contain other sounds (e.g. biological signals) that could influence chickadee responses. Therefore, I instead chose to use a synthesized noise clip. This clip consisted of white noise adjusted to imitate an average traffic frequency-spectrum. Noise amplitude was reduced by 3 dB for every 500 Hz up to 10 kHz (Halfwerk & Slabbekoorn, 2009). The noise spectrum contained enough noise in the higher frequencies to at least partially mask chickadee vocalizations (Figure 3.1).

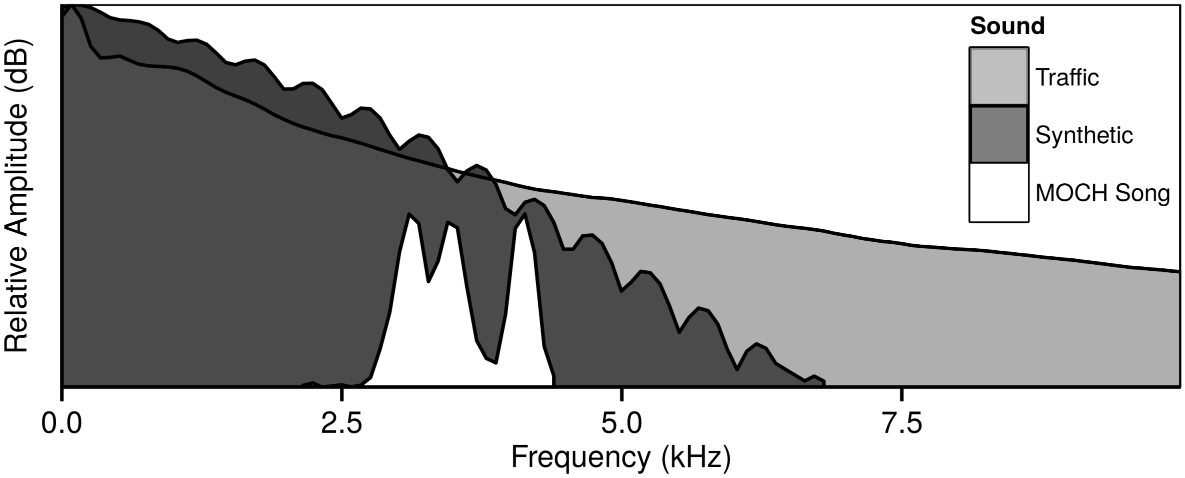

Figure 3.1: Frequency spectrum of traffic noise (pale grey; recorded in Prince George, British Columbia) and synthesized experimental noise (dark grey). White spectrum shows an example of a mountain chickadee song. The relative frequency distributions are comparable between sound clips, but absolute amplitude is not, as many factors contribute to the relative amplitudes.

3.2.3 Classifying noise and habitat urbanization

I recorded ambient noise levels before, during, and/or after each recording bout for a male using either a Pulsar 30 (Pulsar Instruments plc., UK) or a Gold Line SPL120L (Gold Line, USA) sound pressure level meter; if more than one reading was taken, I averaged multiple readings (1 - 3, median = 1). Habitat urbanization was measured as an ’Urbanization Index’ described below and was averaged within neighbourhoods (e.g. males recorded within the same sector or park in a city).

3.2.4 Urbanization index

Most studies contrasting urban and rural habitats use categories defined simply as ’Urban’ or ’Rural’ based on the investigator’s judgment. While this system is adequate for divergent habitats, it is less useful when intermediate habitats are considered. Further, urban habitats do not reflect either just noise or just habitat change, but a combination of the two. Here, I develop an urbanization index that reflects a continuous measure of habitat urbanization and show that it relates with both habitat features as well as cumulative noise measures.

Creating the urbanization index This index was developed by scoring habitat measures for various sites and using a principal components analysis (PCA) to collapse the measures into a holistic index of urbanization. Therefore, to have an urbanization index that could be comparable across all chapters in this dissertation, I included all sites in the creation of this index (Transmission sites, Chapter 2; sites of dawn recordings, Chapters 3 and 4; and playback sites, Chapters 5 and 6).

I identified habitat features of a circular area 150 m in diameter around a particular site. In the case of transmission sites, this was the midpoint of the transect. In the case of dawn recordings or playback experiments, it was the location of the singing male, or playback setup. I used Google Earth (Google Inc., 2012) to capture images of each site and to outline a 150m diameter circle around the centre point. I then developed a script for the GIMP photo editing software (The GIMP Team, 2013) which permitted me to identify and calculate the proportion of area covered by general vegetation (trees, bushes, natural grass, etc.), pavement, lawn, or buildings. I collapsed these measures using a PCA in R v3.0.2 (R Core Team, 2014). For this PCA, I retained one principal component axis (PC1 accounted for 70.1% of total variation), which was the only axis to account for more variation than expected by chance using the null broken stick model (Legendre & Legendre, 1998). All variables loaded were clearly interpretable with loadings greater than 0.33 (Ho, 2006); larger values of PC1 corresponded to decreasing overall vegetation, and increasing pavement, buildings, and lawn (PC loadings: vegetation = -0.573, pavement = 0.507, buildings = 0.456, lawn = 0.454). Thus, increasing PC1 values correspond to decreasing vegetation and increasing features associated with urban land use (e.g. pavement), thereby providing an index of urbanization.

Relating the urbanization index with habitat transmission and ambient noise To determine how the urbanization index varied with noise, I compared the index to long-term ambient noise recordings for a subset of 50 sites. To capture variation in noise, I mounted Olympus LS-7 digital voice recorders (Olympus Imaging America Inc., USA) in camouflaged, water-proof boxes 2-3 metres off the ground in a subset of sites (territories of both black-capped and mountain chickadees) studied in this dissertation. Internal timers were used to record ambient noise from 03:00 to 12:00. For each recording, I used SoX (Bagwell, 2011) to calculate the average sound power of five-minute segments of recording extracted at 15-minutes intervals. Because all units were set to record at the same level (gain), the sound power is comparable between recordings. Cumulative sound power was then calculated for each site over the 9-h period. I regressed the urbanization index against ambient noise accumulated until 10:00 (past 10:00 I had reduced sample sizes due to battery failure). To determine if the urbanization index accounted for a long-term effect of noise, independent of instantaneous noise measured at dawn, I included sound pressure levels measured at dawn in these sites as a covariate.

To investigate whether the urbanization index reflected habitat openness, a habitat-related transmission property common to urban areas (Chapter 2), I also ran a linear regression with the log of urbanization index against the log of habitat openness (a PCA measure calculated from vegetation in Chapter 2) for a subset of 37 sites.

3.2.5 Chorus and vocalization data

To quantify chorus structure, I examined between 5 and 10 minutes of recording for each individual for each treatment period (pre-treatment, experimental noise treatment, and post-treatment). Timing and type of vocalization (song or call) were extracted from recordings using Avisoft-SASLab Pro v5.2.02 (Specht, 2012). Chorus structure (the ratio of songs to calls) and the vocal output (vocalizations/minute) were calculated.

To compare song and call features, I extracted 10 to 25 songs and 10 to 25 calls for each individual in each treatment period. Songs were extracted from recordings using SoX (Bagwell, 2011) and Avisoft-SASLab Pro v5.2.02 (Specht, 2012). Because mountain chickadee songs are variable among individuals, for each male I categorized all main notes (excluding introductory notes) into note-type using hierarchical cluster analysis of the note frequencies in R (Figure 3.2; these are not species-specific syllables, but are defined individually for each male). Males had between 1 and 4 note-types, which were numbered from highest to lowest frequency. For each song or call, I used the R bioacoustics analysis package, seewave v1.7.2 (Sueur *et al.*, 2008), to extract relevant note features. Start and stop times of each note were manually identified with a cursor from seewave spectrograms with Hanning window lengths of 256. I then applied bandpass filters of approximately 1kHz above and below the highest and lowest notes for songs and 2kHz above and below the highest and lowest notes for calls. Dominant frequencies of each note were automatically calculated using a Hanning window length of 1024 for songs and 4096 for calls. I analyzed two song features: (1) mean dominant frequency of the lowest pitched note-types (frequency of low-pitched note-type; Figure 3.2), and (2) the proportion of notes in a song which were the highest pitched note-type (proportion of high-pitched note-types; including individuals with only one

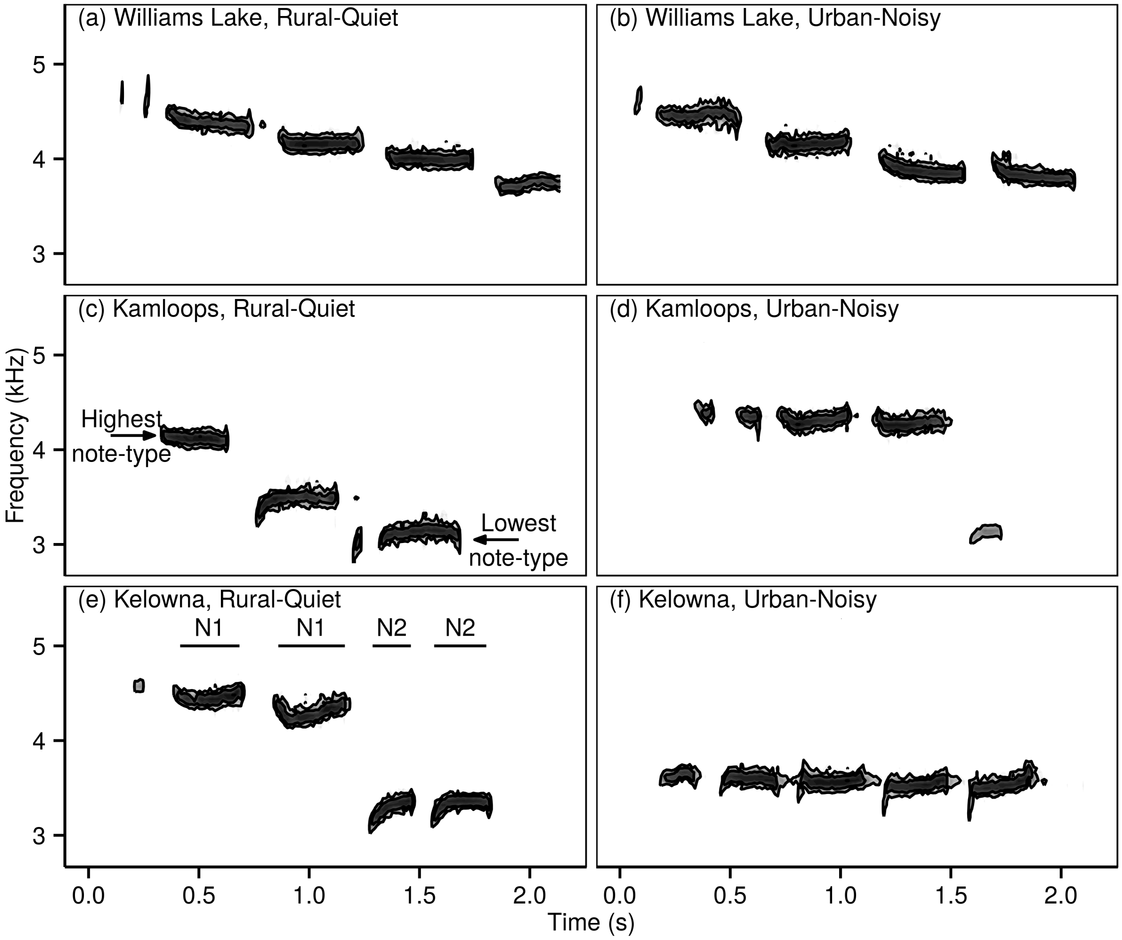

Figure 3.2: Songs of mountain chickadees are variable among and within populations [(a,b) Williams Lake, (c,d) Kamloops, (e,f) Kelowna]. The left panel shows examples of songs from relatively Rural-Quiet sites (a,c,e) and the right panel from Urban-Noisy sites (b,d,f). An example of note types (N1 and N2) are indicated in (e). These indicate different note-types (rather than syllables) assigned through cluster-analysis of frequencies. Rural-Quiet areas are defined as those with less than the median value for both urbanization index and ambient noise levels.

note-type). For calls, I examined the mean dominant frequency of the *dee*-note.

3.2.6 Analyses

Local conditions I used general linear mixed models to evaluate how chorus structure and vocalization features measured prior to experimental noise exposure were affected by the urbanization index (determined for the neighbourhood) and local ambient noise levels (recorded at the location of each singer). However, general differences in song features and frequencies among regions (Figure 3.3), suggested there may be regional effects as well. Therefore, I also included regional contrasts (Kamloops vs. Williams Lake and Kelowna vs. Williams Lake) as a parameter in the model and tested for interactions among these regional differences and both the urbanization index and ambient noise levels. All models were Gaussian linear mixed models (R package nlme v.3.1.117, Pinheiro *et al.*, 2013) with the exception of chorus composition (R package lme4 v.1.1.6, Bates *et al.*, 2014). To analyze chorus composition (the proportion of songs vs. calls in the chorus), I used a generalized linear model with the binomial family of errors and included an observation-level random effect to correct for over-dispersion (Browne *et al.*, 2005). To control for pseudoreplication caused by sampling individuals from nearby locations, I included neighbourhood (e.g. males recorded within the same sector or park in a city) as a random factor in all analyses. Regional contrasts were coded with sums contrasts (also called effect coding or deviant contrasts) so that parameter estimates reflect deviations from the overall regional mean (Wendorf, 2004). I only retained interactions where the interaction was significant at $\alpha = 0.10$ (backwards step-wise). Where there was an interaction with region, I conducted separate post-hoc analyses examining the effects of urbanization and ambient noise within each population.

I also noticed several individuals singing atypical songs. To determine whether there was a relationship between prevalence of such song types and either ambient noise or urbanization I conducted logistic regression (R statistical software v. 3.1.2, R Core Team, 2014). Individuals singing atypical songs (Figure 3.4) were defined as those with greater than

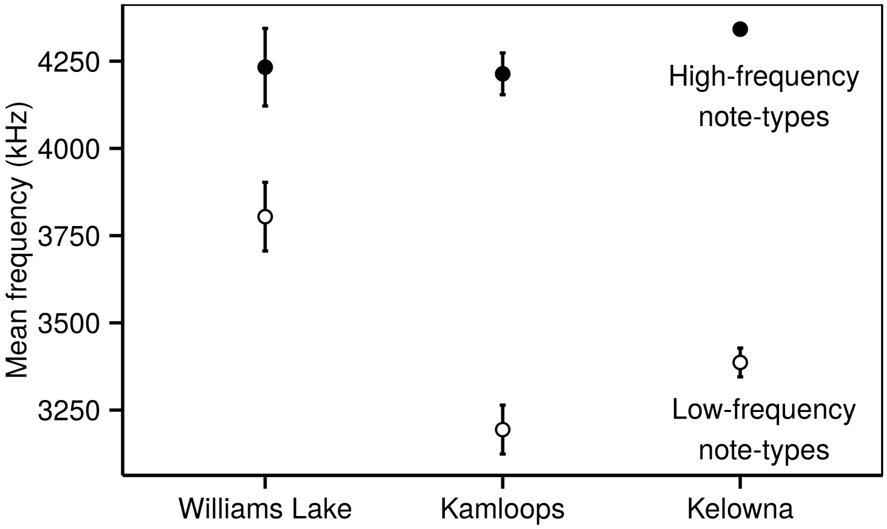

Figure 3.3: Populations show baseline differences in song frequencies, especially in low-pitched note-types. Mean baseline frequencies were calculated from mountain chickadee individuals in relatively Rural-Quiet areas (6 individuals from Williams Lake, 4 from Kamloops, and 2 from Kelowna). Bars denote standard errors. Rural-Quiet areas are defined as those with less than the median value for both urbanization index and ambient noise levels.

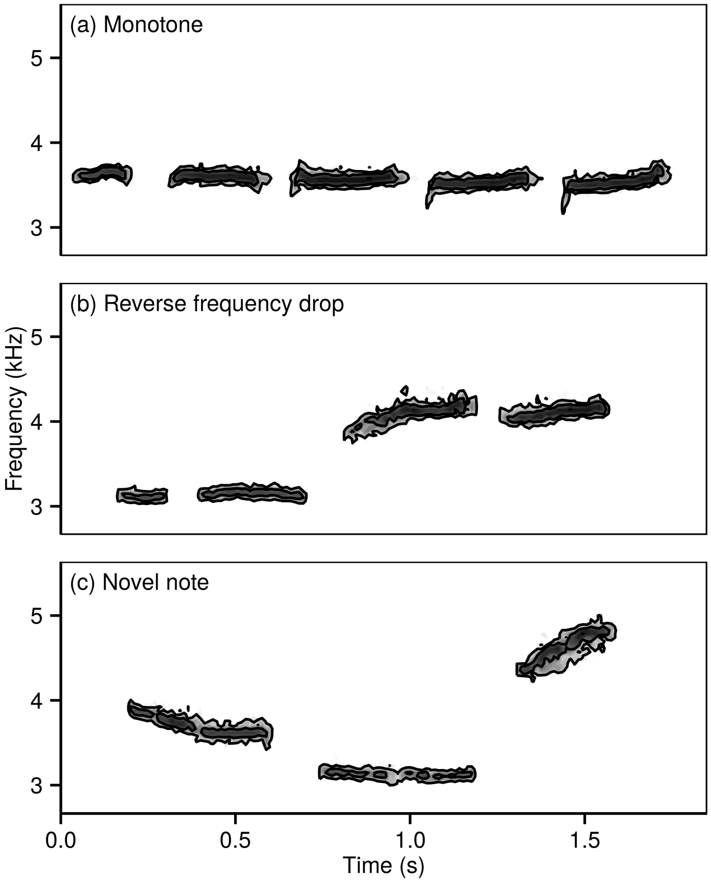

Figure 3.4: Atypical songs of mountain chickadees demonstrated either (a) a lack of frequency change between notes (monotone songs), (b) a reverse frequency drop, or (c) novel notes (e.g., notes with an extreme frequency sweep).

90% of all songs demonstrating any of the following: 1) a lack of frequency change between notes (monotone songs), 2) a reverse frequency drop (low-pitched note-types sung before high-pitched note-types), 3) novel notes (e.g. notes with an extreme frequency sweep).

Exposure to experimental noise I used general linear mixed models to investigate how chorus structure and vocalization features changed between the pre-treatment, experimental noise treatment, and post-treatment periods. As above, all were Gaussian models except the analysis of chorus structure which was modelled with binomial errors. To determine whether local conditions affected responses to experimental noise I also tested for interactions between experimental noise treatment and local ambient noise. I had lower sample sizes in this part of the study, particularly for song and call features, as many individuals either only sang or only called. I therefore had limited power and did not investigate interactions with either urbanization indices or region. To control for repeated measures within individuals and neighbourhoods, I included neighbourhood and individual ID as a nested random factor in all analyses, with the exception of song features (as only one individual per neighbourhood ended up in this analyses). As above, I only retained the interaction if it was significant at $\alpha = 0.10$.

Variable transformations and data presentation In all analyses, explanatory variables were centred to improve interpretation of main effects and interactions (Schielzeth, 2010). I transformed one variable (proportion of high-pitched note-types in the analysis of local ambient noise) to satisfy the assumptions of normality using a Box Cox transformation. I also checked all models for multiple collinearity (all Variance Inflation Factors < 7, condition numbers all < 30, Quinn & Keough, 2002; R statistical software v. 3.1.2, R Core Team, 2014)..

Results are presented as slope parameter estimates ± 95% confidence intervals. Confidence intervals are helpful metrics because they demonstrate the ’significance’ of a parameter (CI 95% which does not overlap zero corresponds to $P < 0.05$; CI 90% which does not overlap zero correspond to $P < 0.10$), the parameter estimate size (whether the effect is biologically meaningful), as well as the variability in the parameter estimate (Nakagawa & Cuthill, 2007). All figures were created with R package ggplot2 (v.0.9.3.1, Wickham, 2009) and are presented as untransformed data.

3.3 Results

3.3.1 Relating the urbanization index with habitat transmission and ambient noise

The total amount of noise exposure accumulated by 10:00 increased significantly with the urbanization index (slope ± CI 95%: 0.276 ± 0.238, t_{47} = 2.33, P = 0.024; Figure 3.5), even when controlling for instantaneous measures of noise levels at dawn (slope = 0.318 ± 0.240, t_{47} = 2.67, P = 0.01). Further, habitat openness significantly increased with the urbanization index (slope = 0.371 ± 0.132, t_{33} = 5.72, P < 0.001; Figure 3.6). Thus, the urbanization index reflects urbanized habitat as well as both urban habitat transmission characteristics, such as openness, and longer term, cumulative noise.

3.3.2 Local conditions

There were no effects of local ambient noise levels or urbanization indices on the ratio of songs to calls. Regional effects, however, suggest individuals in Williams Lake use fewer songs compared to calls than those from Kamloops ($z = -2.08$, $P = 0.037$; Table 3.1A), but there were no differences between Williams Lake and Kelowna ($z = 0.00$, $P = 0.998$). Vocal output did not vary with urbanization, local ambient noise, nor region.

On average, frequencies of the low-pitched note-type increased with local ambient noise (13.2 Hz per dB(Z), $t_{12} = 3.13$, $P = 0.009$; Figure 3.7; Table 3.1B), and an interaction between region and ambient noise suggested the magnitude of the effect differed among populations. The effect of ambient noise was lower in Kamloops than in Williams Lake ($t_{12} = -2.34$, $P = 0.038$), but there were no differences between Williams Lake and Kelowna ($t_{12} = 1.20$, $P = 0.254$; Table 3.1B). An individual from Williams Lake sang unusually low frequency low-pitched note-types (Figure 3.7, see circled outlier). Removal of

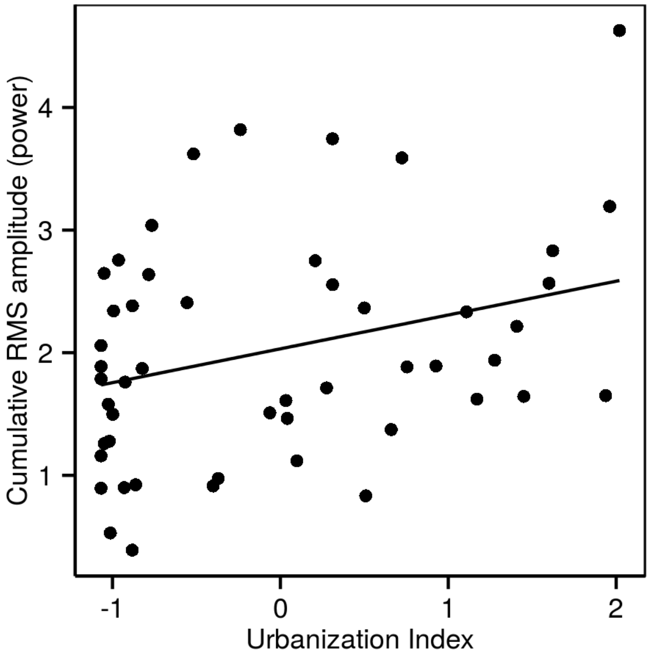

Figure 3.5: Noise exposure accumulated until 10:00 (cumulative sound power) increases as the urbanization index increases.

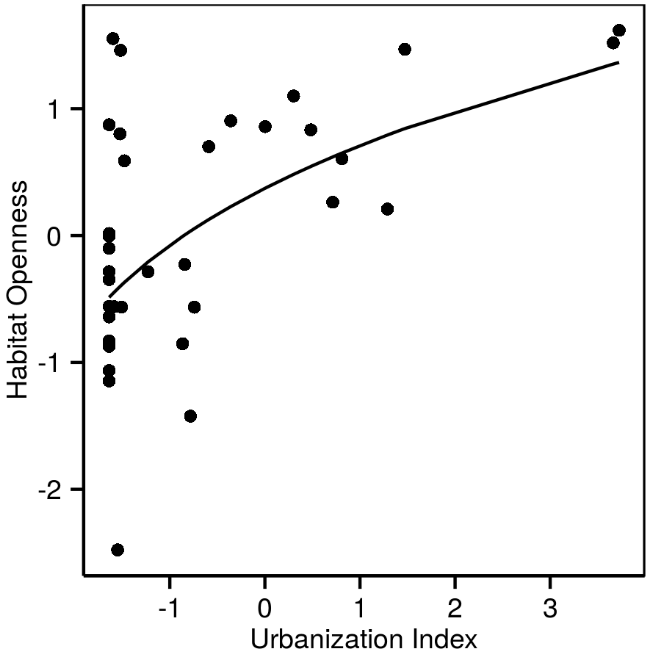

Figure 3.6: Habitat openness increases as the urbanization index increases.

Table 3.1: Local conditions: Results of mixed model analyses examining variation in Chorus Structure (A), Song Features (B), and Call Features (C) with urbanization indices (Urbanization) and ambient noise levels (Noise) in mountain chickadees. Significant regional main effects and interactions are either described or noted as NS (non-significant; see text for more details). Chorus comp refers to Chorus Composition, the ratio of songs to calls in the chorus. Kam refers to Kamloops, Wil to Williams Lake, Kam:Noise refers to the interaction between Region and Noise. Values are mixed model slope parameter estimates ± 95% confidence limits.

(A) Chorus Structure	n	Urbanization	Noise	Region
Chorus comp (Songs vs. Calls)	51	0.25 ± 0.63	0.10 ± 0.15	**Kam < Wil**
Vocal output	51	-0.17 ± 0.57	-0.03 ± 0.13	NS
(B) Song features				
Freq. low-pitched note-type (Hz)	40	19.5 ± 36.5	**13.2 ± 9.2** **	**Kam:Noise < Wil:Noise**
Prop. high-pitched note-type	40	0.02 ± 0.02 *	0.00 ± 0.00	NS
(C) Call features				
dee-note frequency	41	4.4 ± 19.4	0.3 ± 4.6	NS

** **bold** indicate 95% confidence intervals which do not overlap zero

* indicate 90% confidence intervals which do not overlap zero

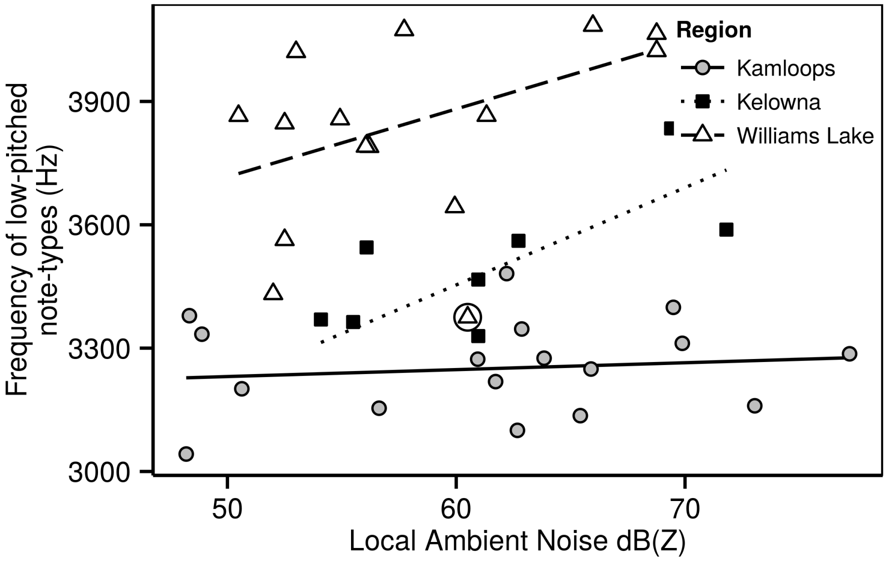

Figure 3.7: There was a relationship between frequency of low-pitched note-types and local ambient noise in mountain chickadees in Kelowna and Williams Lake, but not in Kamloops. The circled triangular point represents a bird from Williams Lake with unusually low frequency low-pitched note-type given the local ambient noise conditions.

this individual only strengthened the patterns observed.

To more closely examine the regional differences, I conducted post-hoc analyses of the relationship between frequency of low-pitched note-types and urbanization indices and ambient noise within each region. These analyses also supported the differences found among regions. Although all regions showed an increase in the frequency of low-pitched note-types with either urbanization or ambient noise, in Kamloops low-pitched note-types increased with urbanization indices (Slope Est. ± CI 95%: Urbanization = 37.8 ± 34.0 Hz, $t_{11} = 2.45$, $P = 0.032$; Ambient Noise = 0.7 ± 10.0 Hz, $t_3 = 0.21$, $P = 0.848$), while low-pitched note-types increased with local ambient noise levels in both Williams Lake (with removal of the outlier; Slope Est. ± CI 95%: Urbanization = 13.7 ± 94.0 Hz, $t_6 = 0.36$, $P = 0.734$; Ambient Noise = 16.9 ± 13.5 Hz, $t_5 = 3.22$, $P = 0.024$) and Kelowna (Slope Est. ± CI 95%: Urbanization = 58.3 ± 72.3 Hz, $t_2 = 3.47$, $P = 0.074$; Ambient Noise = 22.6 ± 14.5 Hz, $t_3 = 4.95$, $P = 0.016$).

The proportion of high-pitched note-types showed a non-significant trend for increasing with urbanization (2% per unit of Urbanization, $t_{21} = 1.87$, $P = 0.076$; Table 3.1). While the pattern seems suggestive, and is particularly suggestive with the removal of an outlier (resulting in regional patterns, Figure 3.8), these results are not robust. Presence of other outliers and influential observations reduces confidence in the analysis. Possibly this is the result of strong patterns in few individuals. Call features did not vary with urbanization, noise, nor region (Table 3.1C).

As urbanization indices increased, individuals were more likely to have atypical songs. Of 55 individuals, 5 sang atypical songs and all had urbanization indices of greater than 0.8. For every unit increase of urbanization, the odds of an individual having an atypical song increased by a multiple of 1.97 (CI 95% 1.10 - 4.58), but as ambient noise increased the odds were no different from 1.00 (0.87 - 1.12).

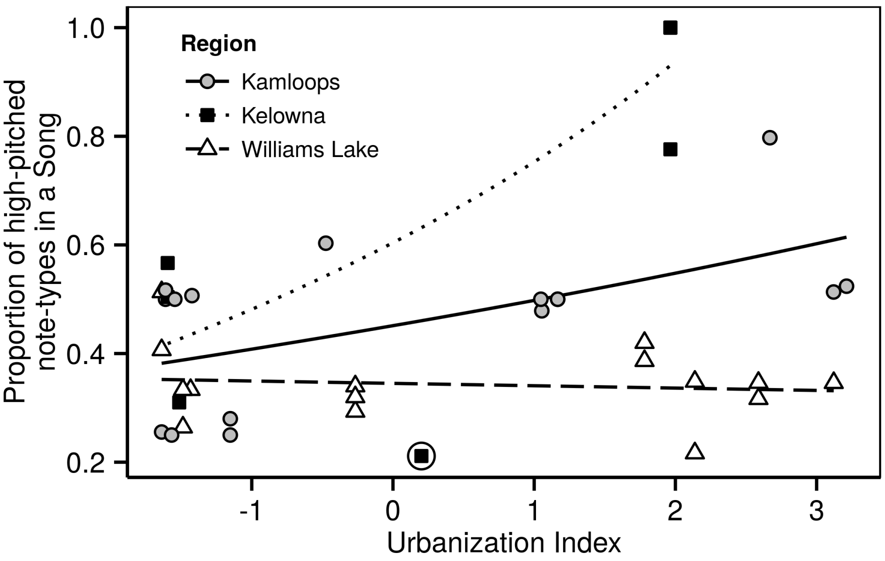

Figure 3.8: The proportion of high-pitched note-types in songs increased overall. With removal of an outlier, there was regional variation in this pattern. The circled square point represents an outlier bird from Kelowna with unusually low proportions of high-pitched note-types in its songs given the local urbanization index. Lines are modelled relationships with the outlier omitted.

3.3.3 Experimental noise exposure

Chorus structure and call features changed with exposure to experimental noise but song features showed little change. For chorus composition, there was an interaction between exposure to experimental noise and local ambient noise levels; compared with pre-exposure levels, males showed a non-significant trend of increasing the ratio of songs to calls during noise exposure as local ambient noise increased ($z = 1.77$, $P = 0.076$), which then became significant after noise exposure ($z = 2.30$, $P = 0.021$; Table 3.2A; Figure 3.9). There was a non-significant trend for vocalization rate to decrease after noise exposure (5-min after the treatment had ceased) compared with pre-exposure levels ($t_{55} = -1.80$, $P = 0.078$; Table 3.2A). As local ambient noise increased, the proportion of high-pitched note-types decreased after experimental noise ($t_{21} = -2.135$, $P = 0.045$; Table 3.2B), but only by 0.3% per dB(Z). The dominant *dee*-note frequency in calls increased by an average of 30.2 Hz during the experimental noise treatment compared with pre-exposure levels ($t_{30} = 2.22$, $P = 0.034$; Table 3.2C; Figure 3.10).

3.4 Discussion

Mountain chickadee vocalizations varied in response to local ambient noise conditions and also showed trends which varied with urbanization. Further, individuals adjusted their vocalizations in response to experimental noise exposure, and some of these adjustments also depended on local ambient noise levels.

3.4.1 Local conditions

Individuals occupying urbanized or noisy habitats sang songs that emphasized higher frequencies (higher low-pitched note-types, repeated high-pitched note-types) than those in quiet or rural habitats. This is a classic example of spectral adjustment, which would be expected to increase signal detection in urban noise (Patricelli & Blickley, 2006). Increasing the frequency of the lowest-pitched note-type is similar to increasing minimum frequencies

Table 3.2: Experimental noise exposure in mountain chickadees: Results of mixed model analyses comparing changes in Chorus Structure (A), Song Features (B), and Call Features (C) During or After exposure to experimental noise (Exp. Noise) compared with pre-exposure levels. Interactions between local ambient noise levels and experimental noise (Exp x Amb Noise) are reported where retained in the model. Non-significant interactions are reported as NS and were omitted from the models. Chorus composition refers to the ratio of songs to calls in the chorus. Values are mixed model slope parameter estimates ± 95% confidence limits.

(A) Chorus structure	n	Treatment	Exp. Noise	Exp x Amb Noise
Chorus composition (Songs vs. Calls)	31	During	-1.12 ± 2.07	0.26 ± 0.29 *
		After	-1.12 ± 2.16	**0.36 ± 0.30** **
Vocal output	31	During	-0.82 ± 1.09	NS
		After	-1.05 ± 1.13 *	NS
(B) Song features				
Freq. low-pitched note-types	16	During	19.4 ± 58.7	NS
		After	-10.5 ± 56.8	NS
Prop. high-pitched note-types	16	During	0.007 ± 0.023	0.001 ± 0.004
		After	-0.005 ± 0.021	**-0.003 ± 0.003** **
(C) Call features				
dee-note frequency	18	During	**30.2 ± 27.8** **	NS
		After	-7.6 ± 29.1	NS

** **bold** indicate 95% confidence intervals which do not overlap zero

* indicate 90% confidence intervals which do not overlap zero

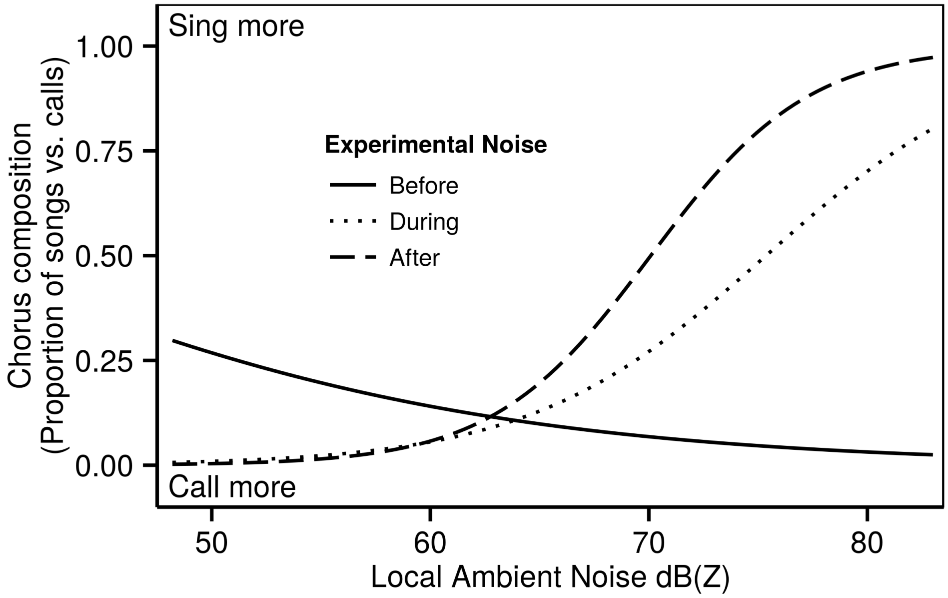

Figure 3.9: After experimental noise exposure, mountain chickadees in noisy areas switched to singing relatively more than calling. Lines represent logistic regression relationships between local ambient noise and the probability of singing vs. calling Before (solid), During (dotted), and After (dashed) experimental noise exposure.

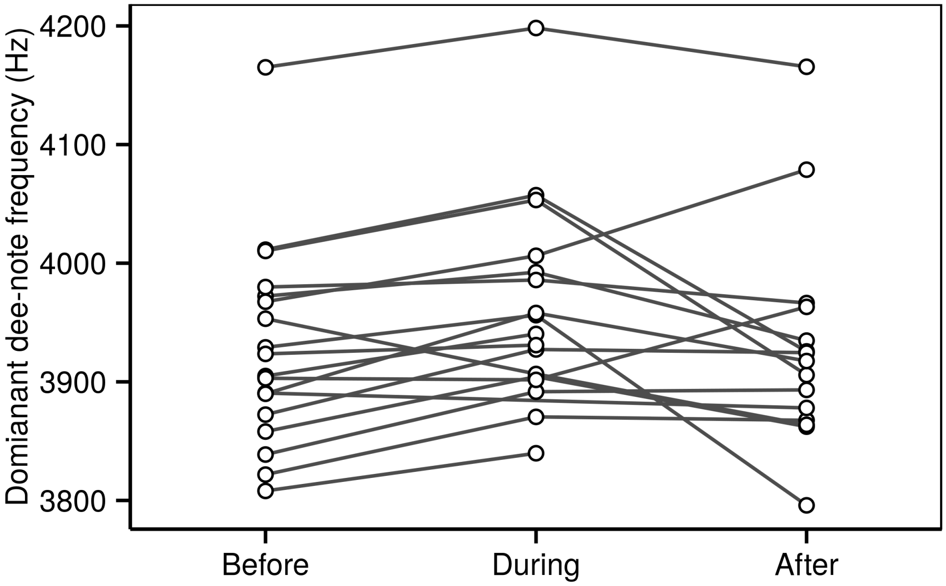

Figure 3.10: During experimental noise exposure the dominant frequency of *dee*-notes in the calls of mountain chickadees increased. Each set of lines represents the *dee*-note frequency of one individual Before, During, and After experimental noise exposure.

observed in many other species (Hu & Cardoso, 2010; Dowling *et al.*, 2012). In contrast, great tits (*Parus major*) increase frequency with local ambient noise levels (Slabbekoorn & Peet, 2003), but instead of shifting note frequencies higher, they sing different songs from a repertoire (Halfwerk & Slabbekoorn, 2009).

I also found several small effects of urbanization in this study. In Kamloops, the frequency of low-pitched note-types increased with urbanization and there was a trend for the proportion of high-pitched note-types to increase with urbanization. It is possible that urbanization reflects habitat transmission properties (Warren *et al.*, 2006); however, I believe the effect of urbanization in this study reflects an aspect of noise that is in *addition* to that captured by instantaneous ambient noise readings made during the chorus itself. The urbanization index increases with cumulative ambient noise, even when controlling for instantaneous measures of local ambient noise. Further, the effects of urban noise interference can outweigh the effects of urban habitat transmission on signal transfer (see Chapter 2). The physical attributes of moderately urbanized habitats (e.g., urban green-spaces with large open areas, but lacking large concrete canyons resulting from tall buildings) would also be predicted to generally improve rather than degrade signal transmission (Mockford *et al.*, 2011; Gall *et al.*, 2012). If anything, urban habitat structure would be predicted to favour low-frequency aspects of signals to maximize transmission (Dowling *et al.*, 2012; Gall *et al.*, 2012). It is therefore unlikely that chickadees would emphasize higher frequencies in response to urban habitat structure.

I also found some evidence that atypical songs were more common in urban areas than in rural areas. This phenomena has also been observed in great tits (Slabbekoorn & den Boer-Visser, 2006), which demonstrated single-note songs (similar to my monotone songs) as well as songs with more than the usual number of note-types in urban areas compared with the normal 2-4 note songs in rural areas. Atypical songs could occur for several reasons. If urban areas are poorer quality habitats, mountain chickadees may be developmentally constrained and produce atypical songs as a result (e.g., black-capped chickadees in immature forests have lower song consistency than those from mature forests ; Grava *et al.*, 2013*b*). A related notion is that if urban habitats are of poor quality, poor-quality males (with poor-quality songs) may be more likely to settle in urban areas than high-quality males. Atypical songs may also be the result of poor learning (Gammon, 2007); ambient noise may be loud enough to mask parts of a neighbouring tutor's song, which could explain monotone songs (low-frequency notes were not heard, and thus not learned, properly). Alternatively, the prevalence of atypical songs could be an indication that vocal adjustment in these populations is still relatively recent and takes time. Individuals are adjusting their songs in different ways and the populations have not converged. Understanding the time frame of vocal adjustment in this species may help differentiate between these different hypotheses.

In this study, regional variation resulted in different patterns of vocal variability among populations. There are several potential explanations for this. First, baseline song frequencies differed regionally and would therefore experience different levels of masking from noise. Second, regions differed in the degree of urbanization (i.e. each city was of a different population size). Replication of sampling design within each population and releating this design across multiple populations - as conducted within this study - is necessary to identify general patterns of vocal adjustment (Slabbekoorn, 2013), but here we see that it can also highlight that there may be multiple ’solutions’ by which a species will adjust to local selection pressures on communication (*cf.* Grava *et al.*, 2013*a*).

3.4.2 Experimental noise

In response to experimental noise treatments, I observed immediate plasticity in chorus structure and call features, but not in song features. This contrasts with many studies which found evidence of spectral plasticity in songs (e.g., chaffinches *Phylloscopus collybita*, Verzijden *et al.*, 2010; house finches *Carpodacus mexicanus*, Bermúdez-Cuamatzin *et al.*, 2011; reed buntings *Emberiza schoeniclus*, Gross *et al.*, 2010). With chorus composition, only male mountain chickadees in noisy habitats demonstrated the most appropriate response of switching from calls to song during noise exposure. Although great tits switch between songs in a repertoire (Halfwerk & Slabbekoorn, 2009), to my knowledge this is the first study to identify a species which switches between vocalization types as a mechanism to reduce masking. Individuals from noisy areas may have learned to sing through noise to maximize transmission, reflecting a long-term learned response, rather than a short-term immediate response. However, shifting the composition of the chorus from songs to calls may affect the signal value of dawn vocalizing, resulting in a functional compromise between signal information and masking-release (Read *et al.*, 2013; Slabbekoorn, 2013). This would particularly be true if songs and calls are intended for different recipients (McCallum *et al.*, 1999). However, a better understanding of the purpose of calls in mountain chickadee dawn choruses is needed to clearly interpret these patterns.

With vocal output, there was a trend for decreasing rate of vocalization after experimental noise exposure, possibly resulting from temporal masking-avoidance (wait until the noise goes away). Although there was only a non-significant trend, the suggestion of a decline in vocalization rate after a rise in experimental noise level seems worthwhile to explore in future studies.

During experimental noise, mountain chickadees also increased the frequency of *dee*-notes by an average of 30 Hz. While calls are generally considered static, chickadees are capable of adjusting *dee*-note frequencies, as seen by convergence in frequency characteristics in winter flocks of black-capped chickadees (Mammen & Nowicki, 1981). However, in Carolina chickadees (*Parus carolinensis*, a close relative of mountain chickadees) Grace & Anderson (2014) observed no relationship between the minimum frequency of *dee*-notes and local levels of traffic noise. As I also observed no change in dominant *dee*-note frequencies with local ambient noise levels, this difference is unlikely due to differences in the type of frequency measurement. In my experimental noise treatment, the frequency of *dee*-notes increased only during noise exposure and were back to pre-exposure levels in the 5-min period after experimental noise exposure, and there was no relationship with local ambient noise conditions. This suggests that mountain chickadees show immediate plasticity in call features when noise becomes *relatively* louder. That there is no relationship with local ambient noise levels suggests that these shifts are not sustainable in the long term, and individuals living in noisy habitats may habituate to the noise. Potentially this increase in frequency may correlate with an increase in amplitude (Lombard effect, a reflexive increase in amplitude in response to noisy conditions), as the Lombard effect is often accompanied by a small upwards shift in frequency (Brumm & Zollinger, 2011). Further studies examining chickadee call amplitude changes in a laboratory setting may help clarify this, but these findings highlight the importance of experimental noise exposure when investigating vocal plasticity.

3.4.3 Conclusions

Variability among populations and species vocalization behaviour can be used to predict how well a species can adjust to anthropogenic noise. In this study I found evidence that song features in mountain chickadees vary with local ambient noise levels and habitat urbanization. Mountain chickadees show population-level song variability, and these findings confirm that these regional differences may affect how different populations respond to noise. I did not observe immediate spectral plasticity of song features, which is unsurprising, as mountain chickadees show little within-individual variation. However, I found that mountain chickadees do use a novel mechanism of switching between calls and songs when exposed to experimental noise, but that only males in noisy habitats do this. Chickadees also demonstrated short-term shifts in the *dee*-note frequency of their calls. Taken together this suggests that mountain chickadees do show vocal adjustment to anthropogenic noise. However, they are unable to spectrally adjust their songs in the short-term. Although individuals can switch between songs and calls, birds cannot sing more than 100% of the time. This mechanism is therefore somewhat constrained. In addition, switching between calls and songs in response to noise may result in trade-offs with signal function. Mountain chickadees may therefore be slower to invade urban areas than species that demonstrate, quicker, or more appropriate spectral plasticity.

4 Immediate vocal plasticity varies with local ambient noise in black-capped chickadees

4.1 Introduction

Masking of animal vocalizations occurs when noise overlaps the same frequency domain as a signal, making the signal difficult to detect (Klump, 1996; Brumm & Slabbekoorn, 2005). Anthropogenic noise is often low-frequency and the degree of spectral overlap with animal vocalizations depends largely on the natural frequency of a species' signals and the capacity of those species to alter these frequencies. By avoiding overlap with anthropogenic noise (spectral avoidance), species can achieve masking release, which may alleviate some of the communication challenges associated with increased noise pollution common to urban areas (Rabin & Greene, 2002; Patricelli & Blickley, 2006; Slabbekoorn, 2013). There is evidence that bird species with naturally high-frequency vocalizations may be less affected by urban noise (Hu & Cardoso, 2009; Francis *et al.*, 2011*b*; Proppe *et al.*, 2013), and masking release through spectral plasticity (the ability to dynamically alter signal frequency) has been observed across various species (e.g., Verzijden *et al.*, 2010; Bermúdez-Cuamatzin *et al.*, 2011). Although evidence of direct fitness benefits resulting from this spectral avoidance is still lacking, the widespread occurrence suggests it may mitigate the effects of noise at least for some species (Halfwerk *et al.*, 2011*a*, but see des Aunay *et al.*, 2014).

Mechanisms of spectral plasticity differ among species (Slabbekoorn, 2013). Some species can shift individual notes or syllables within their songs to higher frequencies (Chapter 3; Bermúdez-Cuamatzin *et al.*, 2011). Species with vocal repertoires can selectively sing higher-frequency notes or syllables (Ripmeester *et al.*, 2010*b*), or higher-frequency song types (Halfwerk & Slabbekoorn, 2009). Different mechanisms may permit quicker reaction times, and presumably, the more quickly an individual can react, the more capable they will be at compensating for anthropogenic noise. Species which demonstrate natural spectral plasticity may be able to mount an immediate plastic response to noise exposure, such as immediately singing higher-frequency songs from within their repertoire (Halfwerk & Slabbekoorn, 2009, e.g.,). Prolonged exposure to ambient noise could also result in longer-term effects (either through evolution or behavioural plasticity), such as actually changing repertoires to drop songs with low-frequency elements in favour of songs that are higher frequency (e.g., Ríos-Chelén *et al.*, 2012; Slabbekoorn & den Boer-Visser, 2006). However, prolonged exposure to ambient noise could also result in immediate spectral plasticity being developed as a trait in itself. If so, I would expect that immediate spectral changes in response to experimental noise would minimize the effects of masking on signals (e.g., be adaptive) and that their prevalence would be associated with increased local ambient noise levels.

Most studies have not addressed the role of local ambient noise (or familiarity with noise) in immediate plasticity. For example, shifts in repertoire use in immediate response to experimental noise have been observed in great tits (*Parus major*; Halfwerk & Slabbekoorn, 2009), but individuals in this study were tested during quiet times of day, birds were familiar with anthropogenic noise, and differences in local ambient noise levels were not accounted for. My studies on mountain chickadees (Chapter 3), however, suggest that exposure to ambient noise can influence immediate plasticity in the use of songs vs. calls. While I observed no immediate spectral plasticity in the songs of mountain chickadees, this is not unexpected, as mountain chickadees do not show within-individual variability in songs. Black-capped chickadees, however, may possess an advantage in spectral plasticity responses to urban noise not seen in their sister species.

Black-capped chickadees exhibit noise-dependent spectral variation (Proppe *et al.*, 2012) and naturally ’pitch-shift’ songs upwards or downwards by 80Hz or more during male-male territorial interactions (Otter *et al.*, 2002). Each male typically has a frequency range of several hundred Hz over which it can produce these pitch-shifted renditions of their songs (Horn *et al.*, 1992). Further, it has been experimentally shown that they can use this ability to spectrally shift their songs away from overlapping noise (Goodwin & Podos, 2013;

Proppe *et al.*, 2011). Although this species is considered to have only a single-song repertoire, this ability to pitch-shift may enable individuals to use these pitch-shifted songs as a 'pseudo-repertoire' (Mennill & Otter, 2007), providing black-capped chickadees with a unique mechanism for spectral flexibility. Black-capped chickadees in noisy habitats do show immediate spectral plasticity with fluctuating noise (Proppe *et al.*, 2011), but it is unclear whether the expression of this trait varies among birds in different habitats, or with different prior levels of noise exposure.

If chickadees are exposed to persistent, long-term noise, they may respond by generally choosing to sing more high-pitched songs and fewer low-pitched songs within their frequency range, or they may drop their lowest-pitched songs altogether. However, exposure to sudden noise that masks the lower part of a bird's frequency range may result in an immediate plastic response, with chickadees responding by switching to sing fewer low-pitched songs (*cf.* Halfwerk & Slabbekoorn, 2009). Individuals having prior experience with noise may be more familiar with noise and may make faster or more appropriate adjustments (*cf.* Chapter 3). Therefore, I investigated whether black-capped chickadees showed a relationship between frequency-use and local ambient noise conditions (*cf.* Proppe *et al.*, 2012). I also used experimental noise exposure to test for a relationship between immediate spectral plasticity in response to experimental noise and those same local noise levels.

4.2 Methods

4.2.1 Field recordings and noise exposure

Fifty-three male black-capped chickadees were recorded in and around the cities of Prince George, Quesnel, Kelowna, and Vancouver, British Columbia, Canada (Figure 4.1). Of these, 42 recordings were used to determine how frequency use correlated with ambient noise levels, and 28 were used to determine how males respond to experimental noise (recordings of 17 males were used in both analyses). All sites were chosen over a variety of habitat types (rural through urban). Recordings were performed between 27-March and 15-May during the spring

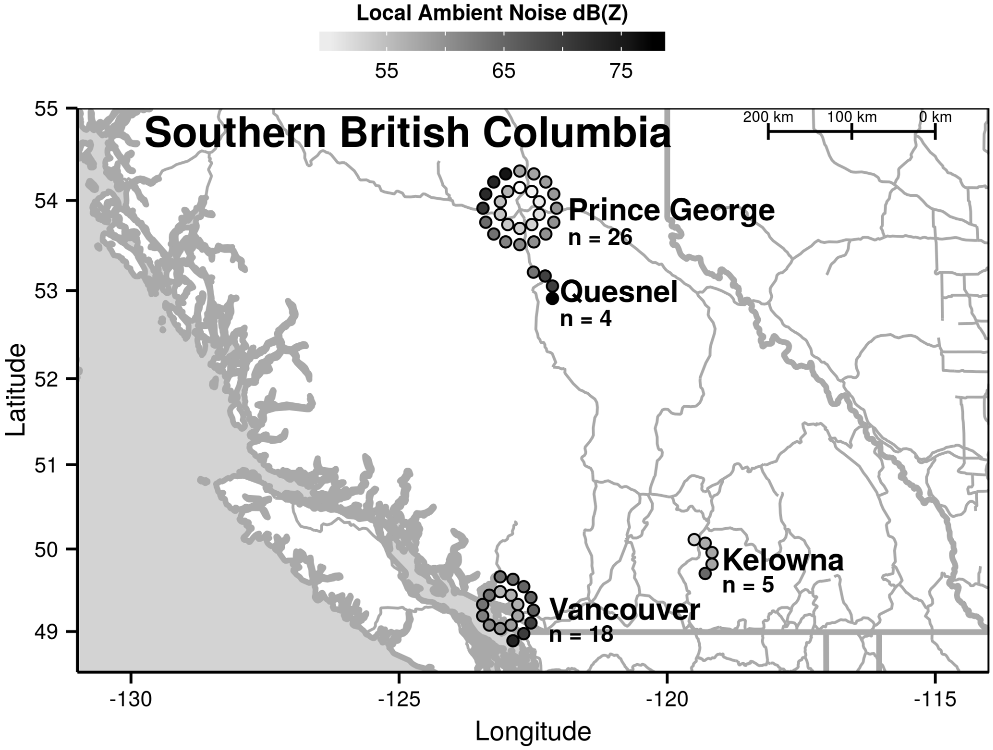

Figure 4.1: Sampling occurred in central and southern British Columbia, Canada. Each point represents an individual black-capped chickadee sampled. The scale of this map does not permit detailed depiction of sites within each region, therefore sites have been arranged in a ring around each region. The colour of each point represents the amplitude of the local ambient noise of each site. Note, however, that in reality, neighbouring sites will not necessarily have similar noise level as urban noise patterns are typically heterogeneous. Sampling was a question of logistics, availability of urban parks (e.g., Quesnel is a small city) and the relative abundance of black-capped chickadees to other chickadee species (e.g., Kelowna contains predominantly habitat suitable for mountain chickadees).

dawn-chorusing periods of 2011, 2012 and 2013. Because dominant males start singing earlier than sub-dominants (Otter *et al.*, 1997), I recorded the first chickadees to sing in a given area to minimize any effects of dominance. Once located, I recorded singing males for a minimum of 5 minutes prior to experimental noise exposure. I continued to record males during the 5-minute experimental noise treatment.

Experimental noise was a synthesized noise imitating the frequency-spectrum of traffic (see Section 3.2.2; Figure 4.2), and was broadcast from a Roland Mobile Cube amplifier (Roland Incorporation, USA) connected to a Philips GoGear Raga MP3 player (Philips Ltd., Canada). The volume of experimental noise faded in over 20s at the start of the recording and was then maintained at approximately 67 dB(Z) (65 dB(A)) at the location of the chickadee throughout the 5-min trial; it then faded out over 20s at the end of the trial. All recordings of focal males were made with MKH70 Sennheiser microphones (Sennheiser Inc., Canada) on to Marantz PMD671 Digital recorders (Marantz Canada, LLC; 22 bit and 44.1 kHz sampling frequency) between a distance of 5 and 20 m. I measured local, naturally present, ambient noise levels (dB(Z)) before, during, and/or after the recording of each male using either a Pulsar 30 (Pulsar Instruments plc., UK) or a Gold Line SPL120L (Gold Line, USA) sound pressure level meter and averaged multiple readings (range 1-3, median 1). Habitat urbanization was measured using the ’Urbanization Index’, described in Section 3.2.4, and was averaged within neighbourhoods (e.g., males recorded within the same sector or park in a city).

4.2.2 Sound analysis

Songs were extracted from recordings using SoX (Bagwell, 2011) and Avisoft-SASLab Pro v5.2.02 (Specht, 2012). All sound analysis was performed with the R bioacoustics analysis package, seewave v1.7.2 (Sueur *et al.*, 2008) in R v.3.1.0 (R Core Team, 2014). I applied a bandpass filter from 1.25kHz below the lowest note to 1.25kHz above the highest note and used an Hanning window length of 1024 for all frequency measurements and a length of 256

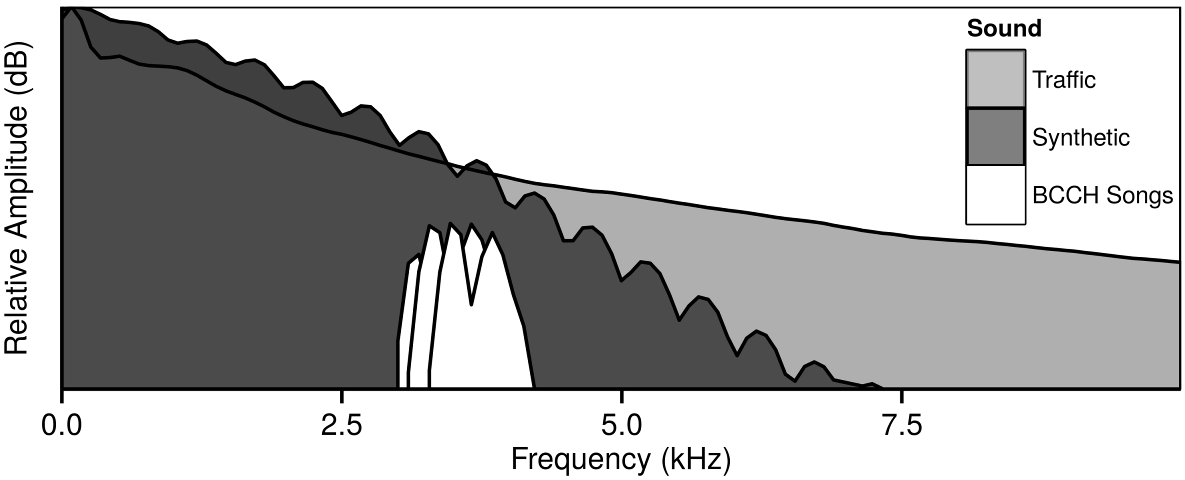

Figure 4.2: Frequency spectrum of traffic noise (pale grey; recorded in Prince George, British Columbia) and synthesized experimental noise (dark grey). White spectrums show examples of three black-capped chickadee songs shifted to different frequencies. The relative frequency distributions are comparable between sound clips, but absolute amplitude is not, as many factors contribute to the relative amplitudes.

for all temporal measurements. The start and stop of each note was manually identified on a seewave spectrogram with a mouse cursor. I measured the dominant frequency of the *bee*-note and used this to classify song frequency throughout this study (Figure 1.2A). This is the typical metric for representing frequency of shifted songs in black-capped chickadees (e.g., Otter *et al.*, 2002; Christie *et al.*, 2004). As the birds maintain consistent frequency ratios within pitch-shifted songs (Weisman *et al.*, 1990), a single reference frequency can be used to classify the whole song.

Because black-capped chickadees naturally shift song frequency up and down throughout the chorus, it was necessary to analyze and compare frequency use within periods of chorus, rather than simply analyzing a random sample of songs. Therefore, for all analyses I quantified overall song frequency use through five measures (Figure 4.3): (1) the overall mean song frequency, (2) the mean highest- and (3) lowest-pitched song frequencies, calculated from songs sung in the top and bottom 25% bandwidths, and the proportions of total songs sung from the (4) upper and (5) lower 25% bandwidths.

For local ambient noise analyses, I quantified frequency use for each male in the 10-min period of chorus prior to experimental noise or in the middle of the recording, if there was no experimental noise exposure. Bandwidths were calculated for each individual as the upper and lower 25% of that individual's song frequencies in the 10-min period.

For experimental noise analyses, I quantified two 5-min periods of chorus just before and during experimental noise exposure. The bandwidths used to define highest- and lowest-pitched song frequencies were calculated individually for each 5-min period (i.e. not overall bandwidth). In contrast, the bandwidths used to calculate the proportion of songs sung from the upper and lower bandwidths was calculated from all detected song frequencies across both 5-min periods (Figure 4.3).

In all analyses, I omitted outlier songs before bandwidth calculations. Outliers were defined as groups of ≤ 4 songs with frequencies above or below the 1.5 x Interquartile frequency range. I also removed individuals with fewer than 20 songs per 10- or 5-min period

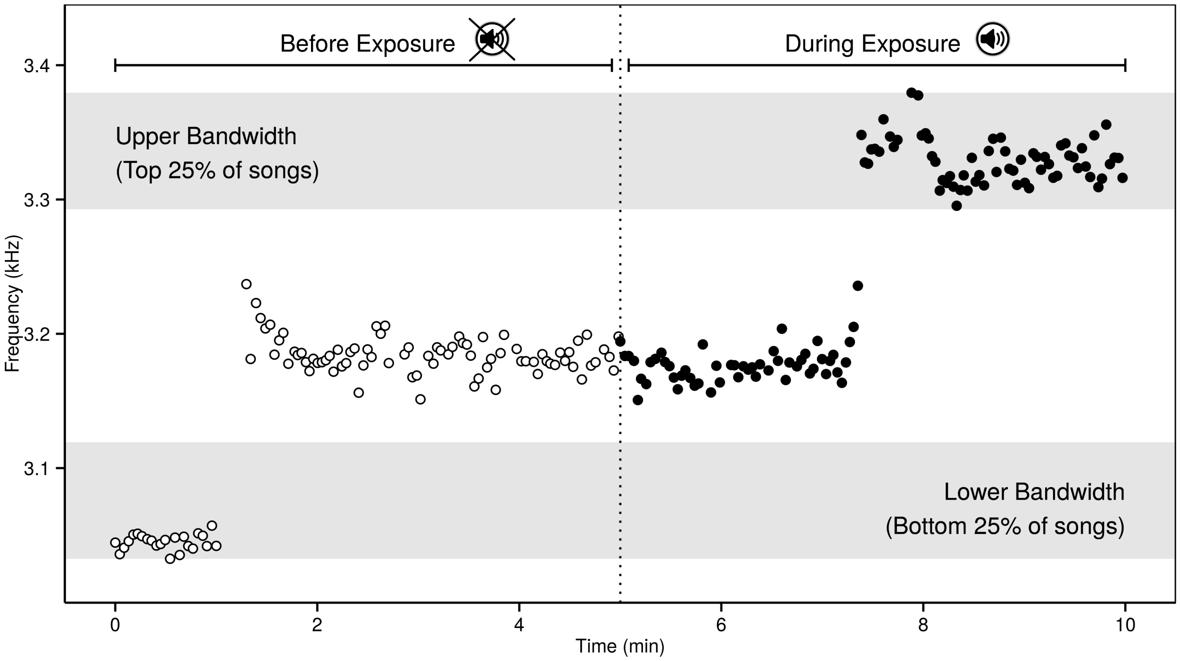

Figure 4.3: An example of 219 successive songs sung during 10 minutes of dawn singing by an individual male black-capped chickadee before and during experimental noise exposure. Points represent the frequencies of individual songs (defined by the dominant frequency of the *bee*-note). This individual shows clear pitch-shifting through three distinct frequency clusters ranging from just over 3000 Hz to just over 3300 Hz. The grey bands represent the upper and lower 25% frequency bandwidths of this 10-min chorus recording. The vertical dotted line represents the start of the experimental noise treatment. White circles represent songs sung before experimental noise exposure, black represent those sung during experimental noise exposure. Five measures of frequency use are calculated for each section (before and during) of this chorus. (1) Overall (mean) song frequency (before 3.15 kHz; during 3.26 kHz); (2) Mean frequency of highest-pitched songs (before 3.19 kHz; during 3.34 kHz); (3) Mean frequency of lowest-pitched songs (before 3.04 kHz; during 3.18 kHz); 4) Proportion of songs sung from the upper 25% bandwidth (before 0%; during 57%); 5) Proportion of songs sung from the lower 25% bandwidth (before 23%; during 0%).

or when I was unable to calculate song frequencies for more than 15% of songs due to poor recording quality.

4.2.3 Statistical analysis

I used linear mixed models (LMM; R package nlme v. 3.1.117 Pinheiro *et al.*, 2013) for all analyses with neighbourhood as a random factor to account for pseudoreplication. Although other studies have found minor regional differences in black-capped chickadee songs (Hahn *et al.*, 2013), there were so few regional differences in the measures used in this study that region was omitted as a random factor. Urbanization may confound the effect of local ambient noise. Therefore I included the index of urbanization as a covariate in all analyses (at the level of the neighbourhood).

To determine how local ambient noise correlated with frequency use in chickadees, I used local ambient noise (at the level of the individual) as my explanatory variable. To analyze changes in frequency use due to experimental noise exposure, I calculated my response variables as individual *changes* in frequency use from before to during experimental noise exposure. Local ambient noise (at the level of the individual) was included as an explanatory variable. I centred, but did not scale, all explanatory variables. Therefore, significant intercept estimates would reflect significant overall changes in the response to experimental noise, and significant slope estimates of local ambient noise would reflect an effect of local ambient noise on *change* in frequency use during experimental noise exposure.

Where necessary, response variables were transformed to satisfy normality. For all analyses assumptions of normality and constant variance were confirmed. Multiple collinearity was assessed and found to be negligible (all Variance Inflation Factors < 10, condition numbers all < 30, Quinn & Keough, 2002; R statistical software v. 3.1.2, R Core Team, 2014). Figures were created with R packacke ggplot2 v. 1.0.0 (Wickham, 2009) and show model predictions which demonstrate the relationship between response and explanatory variables while controlling for random effects.

4.3 Results

4.3.1 Prior to experimental noise exposure: Frequency use and local ambient noise

During natural singing prior to experimental noise exposure, there were no effects of ambient noise on the mean song frequency, the highest-pitched song frequency, or the proportion of songs sung from the lower bandwidth (Table 4.1). However, the mean frequency of the lowest-pitched songs did increase by 9.8 Hz per dB(Z) increase in local ambient noise (Figure 4.4; Table 4.1) and the proportion of songs sung from the upper bandwidth decreased by 0.1% for every dB(Z) increase in local ambient noise (Figure 4.5; Table 4.1). The urbanization index was not a significant covariate in any analysis, but did show trends in two cases (CI 90% did not include zero; $P < 0.1$; Table 4.1).

4.3.2 Experimental noise exposure: Immediate spectral plasticity

Exposure to experimental noise did not result in any overall changes in frequency use before vs. during experimental noise exposure (all intercepts $P > 0.05$; Table 4.2). However, changes to frequency use during exposure to experimental noise did correlate with local ambient noise (Table 4.2). The change in frequency of the lowest-pitched songs increased by 10.2 Hz per dB(Z) increase in local ambient noise levels (Figure 4.6; Table 4.2C) and there was a non-significant trend for the change in frequency of the highest-pitched songs to increase by 9.5 Hz per dB(Z) (Table 4.2B).

There was no change in the proportion of songs sung from the upper bandwidth in general, nor was this change in proportion affected by local ambient noise levels. In contrast, while there was no overall change in the proportion of songs sung from the lower bandwidth, there was a non-significant trend for this change in proportion to decrease by 2.8% for every dB(Z) increase in local ambient noise levels (Table 4.2E).

Both non-significant trends should be treated with caution, as each case was affected by different influential observations. The urbanization index was never a significant covariate (CI 95% did not include zero; $P > 0.05$).

Table 4.1: Prior to experimental noise exposure: Results of linear mixed models testing for correlations between frequency use in black-capped chickadees and local ambient noise. Urbanization indices were included as covariates. In these analyses, significant intercept estimates indicate values different from zero, but are not of biological significance. Units of each response variable were either hertz (Hz) or proportions (Prop). Transformed response variables are indicated (Trans). Slope Est ± CI 95% refers to slope parameter estimates ± the 95% confidence intervals. The slope estimate indicates how much the response variable changes for every unit of change in the explanatory parameter. DF refers to degrees of freedom.

Response Variable	Parameter	Slope Est.	±	CI 95%	DF	t	P
(A) Overall frequency (Hz)	(Intercept)	**3135.8**	±	**293.3**	23	22.12	< 0.001 **
	Ambient Noise (dB)	1.9	±	4.8	16	0.83	0.417
	Urbanization index	5.6	±	36.0	23	0.32	0.750
(B) Highest-pitched frequencies (Hz)	(Intercept)	**3233.9**	±	**316.1**	23	21.17	< 0.001 **
	Ambient Noise (dB)	2.4	±	5.2	16	0.98	0.342
	Urbanization index	16.6	±	37.2	23	0.92	0.367
(C) Lowest-pitched frequencies (Hz)	(Intercept)	**2514.3**	±	**316.5**	23	16.43	< 0.001 **
	Ambient Noise (dB)	**9.8**	±	**5.2**	16	4.03	0.001 **
	Urbanization index	-26.2	±	29.5	23	-1.83	0.080 *
(D) Proportion sung from upper bandwidth (Trans)	(Intercept)	**1.01**	±	**0.65**	23	3.23	0.004 **
	Ambient Noise (dB)	**-0.01**	±	**0.01**	16	-2.14	0.048 **
	Urbanization index	0.06	±	0.06	23	2.03	0.054 *
(E) Proportion sung from lower bandwidth (Prop)	(Intercept)	0.14	±	0.70	23	0.42	0.676
	Ambient Noise (dB)	0.00	±	0.01	16	0.65	0.525
	Urbanization index	-0.01	±	0.07	23	-0.28	0.784

** **bold** indicate 95% confidence intervals which do not overlap zero (correspond to $P < 0.05$)

* indicate 90% confidence intervals which do not overlap zero (correspond to $P < 0.10$)

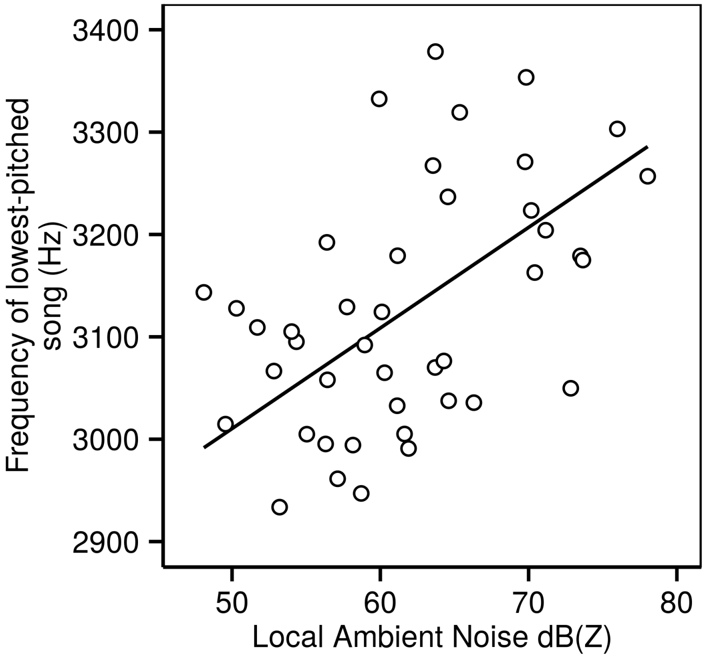

Figure 4.4: Prior to experimental noise exposure, mean frequency of lowest-pitched songs in black-capped chickadees increased with local ambient noise levels (dB(Z); $P = 0.001$). Points are raw data values. Line represents model relationship.

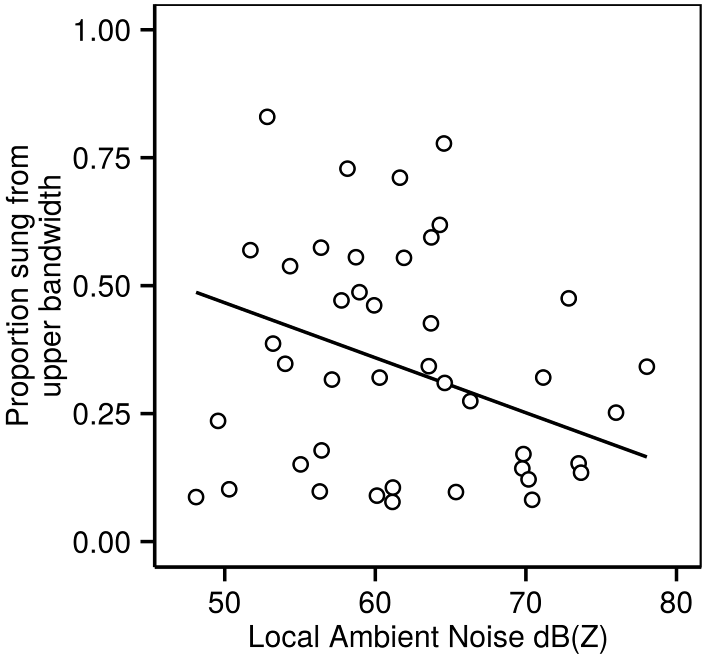

Figure 4.5: Prior to experimental noise exposure, proportion of songs sung by black-capped chickadees from the upper bandwidth decreased with local ambient noise levels (dB(Z); $P = 0.048$). Points are raw data values. Line represents model relationship.

Table 4.2: Experimental noise exposure: Results of linear mixed models testing for changes in frequency use in black-capped chickadees during exposure to experimental noise. The response variables are calculated as differences (before vs. during noise exposure) and the explanatory variables have been centred. Therefore significant intercept estimates can be interpreted as overall positive or negative changes in the response variable as a result of experimental noise (see text for more details). Ambient Noise reflects the relationship between changes in frequency use and local noise conditions. Urbanization Index is a covariate included to control for the frequency sung prior to experimental noise exposure as well as local levels of urbanization. Units of each response variable were either hertz (Hz) or proportions (Prop). Slope Est ± CI 95% refers to slope parameter estimates ± the 95% confidence intervals. The slope estimate indicates how much the response variable changes for every unit of change in the explanatory parameter. DF refers to degrees of freedom.

Response Variable	Parameter	Slope Est.	±	CI 95%	DF	*t*	*P*
(A) Change in overall frequency (Hz)	(Intercept)	-4.0	±	67.0	14	-0.13	0.900
	Ambient Noise (dB)	7.7	±	11.2	11	1.51	0.158
	Urbanization index	25.8	±	49.1	14	1.13	0.278
(B) Change in highest-pitched frequencies (Hz)	(Intercept)	-23.5	±	65.9	14	0.77	0.457
	Ambient Noise (dB)	9.5	±	11.1	11	1.89	0.085 *
	Urbanization Index	8.3	±	48.3	14	0.37	0.716
(C) Change in lowest-pitched frequencies (Hz)	(Intercept)	-13.8	±	63.2	14	-0.47	0.646
	Ambient Noise (dB)	**10.2**	±	**10.0**	11	2.25	0.046 **
	Urbanization Index	14.0	±	46.9	14	0.64	0.531
(D) Change in proportion sung from upper bandwidth (Prop)	(Intercept)	0.014	±	0.192	14	0.15	0.880
	Ambient Noise (dB)	0.014	±	0.032	11	1.01	0.335
	Urbanization Index	0.079	±	0.141	14	1.20	0.249
(E) Change in proportion sung from lower bandwidth (Prop)	(Intercept)	-0.064	±	0.169	14	-0.82	0.428
	Ambient Noise (dB)	-0.028	±	0.028	11	-2.17	0.053 *
	Urbanization Index	-0.057	±	0.124	14	-0.99	0.338

** **bold** indicate 95% confidence intervals which do not overlap zero (correspond to $P < 0.05$)

* **bold** indicate 90% confidence intervals which do not overlap zero (correspond to $P < 0.10$)

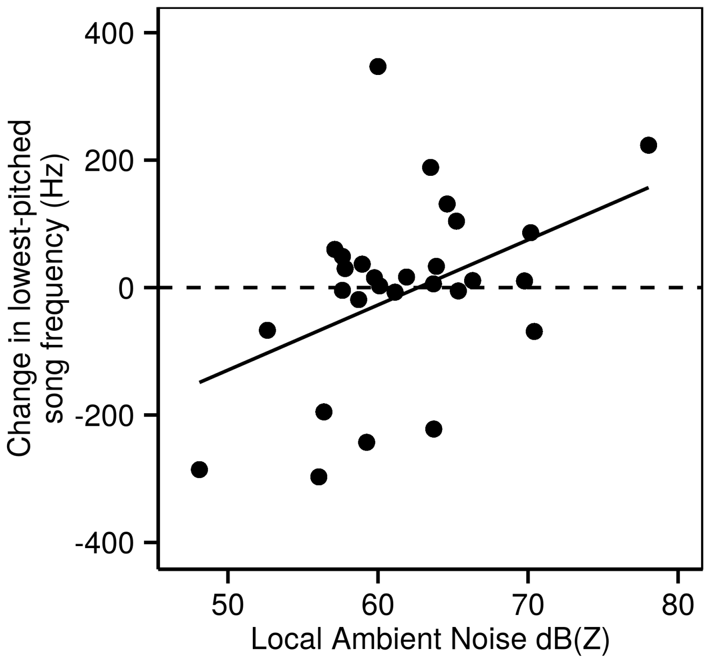

Figure 4.6: During experimental noise exposure, there was a positive correlation with change in lowest-pitched song frequencies of black-capped chickadees and local ambient noise (dB(Z); $P = 0.046$). Points are raw data. Solid line represents model relationship. Horizontal dashed line represents point of no change from before experimental noise: points below the line reflect a downward change in frequency, points above the line reflect an upward change in frequency.

4.4 Discussion

There was a general pattern among male black-capped chickadees recorded across a broad geographic region in British Columbia; males residing in areas with high levels of ambient noise sang their lowest-pitched songs at higher frequencies than those residing in areas with low levels of ambient noise. Further, responses of males to playbacks of experimental noise depended on local noise levels. When I broadcast experimental noise in already noisy areas, the lowest-pitched songs males sang were higher in frequency, and showed trends of utilizing a lower proportion of low-pitched songs from their repertoire.

These findings suggest several conclusions. First, consistent with previous studies, black-capped chickadees do show spectral changes with increasing anthropogenic noise (Proppe *et al.*, 2011, 2012) and they use pitch-shifting as a mechanism for masking avoidance (Goodwin & Podos, 2013). Second, my experimental noise component revealed a novel discovery that the magnitude and direction of the immediate spectral response varies with local ambient noise conditions, and that individuals in noisier areas respond in a manner most likely to result in masking release.

4.4.1 Spectral Avoidance

I found that black-capped chickadees sing higher frequencies in noisy habitats. However, I only looked at singing during these noisy conditions, and I do not know how chickadees would have sung in quiet conditions (*cf.* Hanna *et al.*, 2011). I therefore cannot say definitively whether the correlation between frequency use and ambient noise levels arose over long or short time frames. However, my study does offer insights into the mechanism used in black-capped chickadees to avoid masking by noise. My findings support those of Proppe *et al.* (2012), although in my study, this increase in frequency resulted from an upward shift in the lowest-pitched songs only, not in songs overall. Coupled with the observation that when exposed to experimental noise, individuals in noisy habitats sang higher lowest-pitched songs and proportionally fewer songs from the lowest bandwidth, these results suggest black-capped chickadees use their pre-existing pitch-shifting abilities as a mechanism for avoiding masking by selectively dropping their lowest-pitched songs during noisy conditions. Other tits also use similar mechanisms to avoid masking: great tits switch to higher-frequency song types from a repertoire (Halfwerk & Slabbekoorn, 2009), and mountain chickadees switch between songs and calls (Chapter 3). However, in black-capped chickadees pitch-shifting is a unique mechanism in that it results in changes to frequency alone (as opposed to whole songs or vocalization types).

There is little evidence that absolute song pitch (within normal species limits) is important in chickadee communication; rather it appears to be pitch-matching between competitors that is important (Otter *et al.*, 2002). However, social dominance in black-capped chickadees correlates with both relative note amplitude and consistency in relative frequency ratios between the *fee* and *bee* notes (Christie *et al.*, 2004; Hoeschele *et al.*, 2010). To assess dominance based on consistent frequency ratios, multiple songs and pitch-shifting must be heard and the best (but not the only) discrimination between high- and low-ranking males is observed at low frequencies (Christie *et al.*, 2004). If males in noisy areas are avoiding or increasing the frequency of their lowest-pitched songs, this will result in a contraction of the bandwidth within which individual males can pitch-shift. Further, I also observed that individuals sang fewer songs from the top 25% of their bandwidth as local ambient noise increased, suggesting they may tend to converge on mid-pitched songs. Potentially intermediate frequencies may be easier to produce (see Cardoso, 2012), but ultimately this suggests anthropogenic noise may result in a loss of information in vocal messages that are broadcast during vocal interactions. In particular, the restrictions on matching frequencies of male counterparts may result in a functional compromise (Slabbekoorn, 2013), such that masking may be reduced but at the expense of communication with conspecific males (Luther & Magnotti, 2014) or females (Halfwerk *et al.*, 2011*a*). Studies show that male black-capped chickadees use both frequency matching and song overlap in contests (Otter *et al.*, 2002) and that dominant males which are overlapped and frequency-matched lose paternity in their nests

(Mennill *et al.*, 2002). Ambient noise may therefore constrain a male's ability to avoid being frequency-matched by rivals, which could have consequences on reproductive output.

4.4.2 Immediate plasticity and local ambient noise

Immediate spectral plasticity may in itself be a trait that is developed over time. I found that the immediate spectral response to experimental noise had a positive correlation with local ambient noise levels. As ambient noise increased, males responding to experimental noise sang higher-frequency songs and sang proportionally fewer of their low-frequency songs. Although immediate spectral plasticity has been observed in other tit species (e.g., Halfwerk & Slabbekoorn, 2009), this is the first time it has been shown to depend on local ambient noise conditions (but see Chapter 3).

One explanation for my results is that the experimental noise acted synergistically with local noise levels to create a compounding effect and that both loud ambient noise and loud experimental noise were required before individuals would react. However, in response to experimental noise, not only did individuals in noisy areas sing fewer low-pitched songs, but individuals in quieter areas actually sang more low-pitched songs, suggesting that additive noise is not a sufficient explanation. Another explanation is that prolonged noise exposure leads males to adopt more appropriate spectral responses during peak noise bursts, resulting in better masking release among urban black-capped chickadees.

Living in noisy areas could lead to appropriate immediate spectral plasticity for a variety of reasons. It is feasible that immediate spectral plasticity confers fitness benefits, although we currently lack empirical evidence for this. Immediate spectral plasticity may have evolved in birds living in noisy areas, or individuals with predisposed genetic characteristics may preferentially disperse to noisy areas. However, noise varies considerably across short distances in my study, while juvenile chickadees disperse over fairly large distances (median distance ~1.1 km but up to 11 km; Weise & Meyer, 1979). It therefore seems highly unlikely that the patterns I detected are the result of a direct genetic difference between individuals from noisy and quiet habitats. On the other hand, the patterns may well be related to individual learning or habituation.

Males may require experience with singing in noise to learn the appropriate response to reduce masking. Goodwin & Podos (2013) found that black-capped chickadees in rural (and presumably quiet) parks pitch-shift more quickly in response to narrow bands of overlapping noise, but shifts were equally likely to be higher or lower than the frequency of the masking noise. This demonstrates that black-capped chickadees do show noise-dependent immediate spectral plasticity without much prior experience. Perhaps the ability to pitch-shift in response to noise is an innate response, whereas pitch-shifting to maximize masking release requires experience with the nature of noisy conditions. Birds which are unfamiliar with low-frequency urban noise may find it stressful or distracting and may shift songs in response, but not necessarily in a manner that reduces masking (e.g., shifting downwards in response to low-frequency noise). Alternatively, black-capped chickadees may need to hear themselves being masked for some time before they can shift to the most appropriate song frequency. Studies examining stress levels between birds from different habitats after being exposed to noise may help distinguish between these two explanations. Another approach would be to measure changes in immediate plasticity over increasing periods of sustained experimental noise exposure, in order to determine how quickly chickadees learn adaptive responses to noise.

Goodwin & Podos, 2013 observed no directionality in pitch-shifting response to narrow frequency bands of overlapping noise. If male black-capped chickadees are accustomed to avoiding escalated contests resulting from frequency-matching (Otter *et al.*, 2002; Fitzsimmons *et al.*, 2008), shifting downwards is as appropriate as shifting upwards and may explain the lack of directionality. However, in response to experimental noise in quiet areas, I observed downward shifts in frequency as opposed to merely random shifts. Shifting to lower frequencies could be an appropriate response when noise is uncommon, typically occupies a narrow bandwidth, or arises from more natural sources. For example, if noise experienced in quiet areas is generally bird song from other species, it might be more appropriate to shift down to avoid high-frequency inter-specific masking (Pohl *et al.*, 2009; Yang *et al.*, 2014).

4.4.3 Conclusions

This study presents evidence of black-capped chickadees using pitch-shifting as a novel mechanism for avoiding masking from anthropogenic noise, and suggests that immediate spectral plasticity itself is associated with longer-term exposure to local ambient noise. Provided noise-dependent frequency use in black-capped chickadees does in fact lead to better signal perception in noisy habitats, and consequently to increased fitness, this would suggest that black-capped chickadees are relatively well suited to the communication challenges posed by urbanization. However, my results also suggest that immediate plasticity may not be as quick a response as it appears. Further, individuals responding to noise by avoiding lower-frequency songs may limit their available frequency bandwidth. This may compromise other aspects of signalling (e.g., avoidance of pitch-matching during contests) and consequently other aspects of reproductive strategies in urban landscapes.

5 Context-dependent response to urban vs. rural songs in a mountain chickadee playback study

5.1 Introduction

Anthropogenic noise has the potential to interfere with vocal communication in birds (e.g., Slabbekoorn & Peet, 2003; Patricelli & Blickley, 2006). Noise results in increased masking of vocal signals and consequently reduced active space (the distance over which a signal can be heard, Lohr *et al.*, 2003). In birds, studies have found that many species adjust their vocalizations in noise (e.g., Ripmeester *et al.*, 2010*a*; Verzijden *et al.*, 2010; Bermúdez-Cuamatzin *et al.*, 2011; Chapter 3; Chapter 4). Yet it is often untested whether such vocal adjustments actually improve audibility.

While playback studies have investigated whether receivers differentiate between normal and adjusted signals, it is difficult to determine whether these differences reflect audibility or other factors. For example, Ripmeester *et al.* (2010*b*) investigated populations of urban and rural European blackbirds (*Turdus merula*) and found that individuals responded more strongly to songs from their own habitat type or from their own population. Similarly, Mockford & Marshall (2009) exposed urban and rural great tits (*Parus major*) to urban and rural playback songs and found that individuals responded more strongly to songs from the same habitat type. Although individuals differentiated between signal types, it is unclear how much these differences relate to relative audibility of the signals compared with other signal characteristics.

Vocal adjustments may result from responses to other phenomena rather than simply from noise, particularly as long-term exposure to noise often correlates with urban-rural gradients. Variable song characteristics could also reflect differences in individual characteristics (e.g., aggression or dominance) which may vary along urban-rural gradients. For example, a series of broadly replicated studies shows that urban song sparrows (*Melospiza melodia*) are both more bold and more aggressive than their rural counter-parts (Evans *et al.*, 2010; Scales *et al.*, 2011). Noisy miners (*Manorina melanocephala*, Lowry *et al.*, 2011) may also show this pattern, but this study only considered one pair of urban/rural populations. In contrast, an urban population of dark-eyed juncos (*Junco hyemalis thurberi*) was found to be less aggressive than a nearby rural population, possibly due to a milder climate (Newman *et al.*, 2006). As a result of these underlying differences, individuals in urban areas may produce songs with elements or patterns which both signal individual levels of aggression as well as improve audibility in noisy conditions (*cf.* Ripmeester *et al.*, 2010*a*; Hamao *et al.*, 2011).

Even if birds adjust their vocalizations in direct response to noise, these adjustment may not always result in greater audibility due to trade-offs between increasing signal-to-noise ratios and signal information (Halfwerk *et al.*, 2011*a*). Vocal adjustments could result in better signal detection, but at the cost of reduced discrimination. Luther & Magnotti (2014) found that northern cardinals (*Cardinalis cardinalis*) differentiate between playbacks of synthetic songs of average frequency and synthetic signals adjusted to a high frequency, but average-frequency signals elicit stronger reactions overall. Vocal adjustments could thus result in better transmission but not necessarily increased perception by focal males.

Mountain chickadees sing whistled multi-note songs which vary considerably among populations (Grava *et al.*, 2013*a*; Chapter 3), and can be severely masked by urban noise (Chapter 2). Individuals in noisy (and sometimes urban) areas have low-pitched note-types that are higher in overall frequency than those in quite areas (Chapter 3). There was also a non-significant trend for urban birds repeating the highest-pitched note-types more than rural birds (Chapter 3). However, it is unknown whether these adjustments actually improve audibility of these signals to receivers in noisy conditions.

I performed paired playback trials in sites across a continuous gradient of urbanization to determine if mountain chickadees detect and respond more to urban songs than rural songs when either is embedded in noise. I initiated playbacks with songs from either locality (urban or rural) embedded in synthetic noise, to differentiate between habitat effects and audibility in noise. Songs increased from low to high amplitude relative to background noise to determine at what point signals were detected, and how strong the response to these signals was. I hypothesized that songs which are more audible in noise would be detected earlier and at lower relative amplitudes and would therefore elicit faster initial responses. However, if initial detection does not differ, songs that are better discriminated overall may be perceived as a greater threat and may elicit more overall aggression.

Therefore I asked two main questions: when stimuli are embedded in experimental noise, (1) do mountain chickadees respond more quickly to urban songs than to rural songs? and (2) do mountain chickadees respond more aggressively to urban songs than to rural songs?

5.2 Methods

5.2.1 Site and timing

Playback trials were conducted throughout south-central British Columbia in the cities of Kelowna, Kamloops and Williams Lake. Twenty-one male mountain chickadees were successfully exposed to two playback trials each between 8 May and 21 May 2012 and 5 May and 20 May 2013. I used a paired design, so that both playback stimuli (Urban and Rural) were presented to each focal male. The two stimuli were presented between 7am and 11am, separated by a median of 1.5 hours. If birds failed to respond to the 2nd stimuli (see Section 5.2.3 for criteria) we returned the following day to reattempt the trial (n = 4). A maximum of 3 days separated trials for an individual. The order of playback trials (Urban/Rural vs. Rural/Urban) alternated between focal males, and neighbours were never tested on the same day. In total, I had 10 males who received Urban/Rural order of presentation and 11 males with Rural/Urban order. To avoid pseudoreplication of playback stimuli, I used 16 unique stimuli sets and played each set to a maximum of two focal males (once ordered Urban/Rural, and once Rural/Urban).

5.2.2 Playback files

All songs used in playbacks were unique and obtained from dawn chorus recordings of 13 male mountain chickadees from Kelowna, Kamloops and Williams Lake in 2012 and 2013 (Chapter 3), or in Riske Creek in 2010 (a small community ~50km west of Williams Lake; (Grava *et al.*, 2013*a*)). All songs were from individuals unfamiliar to the focal male. Any background noises were removed and songs were normalized to a constant volume prior to use. Songs recorded in habitats with positive urbanization indices (see Section 3.2.4) were designated 'Urban', while those recorded in habitats with negative urbanization indices were designated 'Rural' (Figure 5.1).

For each playback broadcast, a WAV file with two channels was created. The left channel consisted of synthetic noise with a frequency spectrum similar to traffic noise (see Chapter 3.2.2). The right channel contained mountain chickadee songs. There were four unique songs spaced approximately once every 4s. This sequence was repeated seven times over 2 min (rate of 14 songs/min to a total of 28 songs over two minutes). With each repeat of the four songs, I increased the amplitude of the stimuli so that over the course of a trial the signal-to-noise ratios of the songs compared to the background noise in the left channel ranged from -16 dB at the start to -1 dB at the end of the playback. Broadcasts of each session were initiated by gradually fading in the background noise in the right channel to full volume over 20s. Males were then exposed to 40s of background noise to acclimate. At this point, the stimuli (Urban vs. Rural songs) were initiated on the left channel, from which they increased in relative volume over the two minute trial as described. After the stimuli finished, noise faded out over 20s to complete the session (Figure 5.2). The playback was broadcast from a Roland Mobile Cube amplifier (Roland Incorporation, USA; 'Full range audio' frequency response ~100 Hz – 20 kHz)) connected to a Philips GoGear Raga MP3 player (Philips Ltd., Canada) at a volume so that background noise was ~68 dB(Z) (63 dB(A)) at 5m and the loudest song (without background noise) was ~67 dB(Z) (64 dB(A)) at 5m. As the left and right channels correspond to the two side-by-side speakers in these amplifiers, noise and

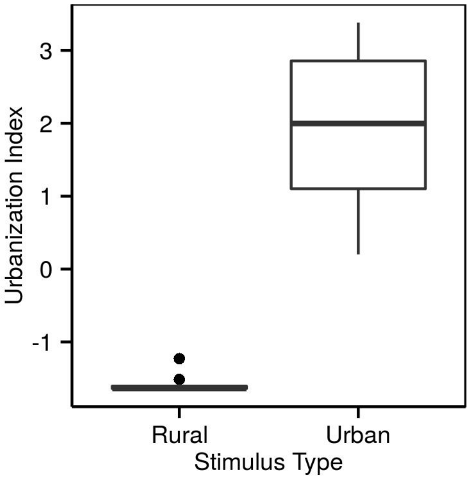

Figure 5.1: Distribution of urbanization indices associated with the stimuli songs in each playback. ’Urban’ stimuli used only songs recorded at sites with an urbanization index > 0; ’Rural’ from sites < 0. Boxplots reflect distribution of data. Boxes show 25th, 50th and 75th percentiles, ’whiskers’ are to the minimum and maximum values within 1.5 x the inter-quartile range (IQR). Points are values outside of 1.5 x IQR.

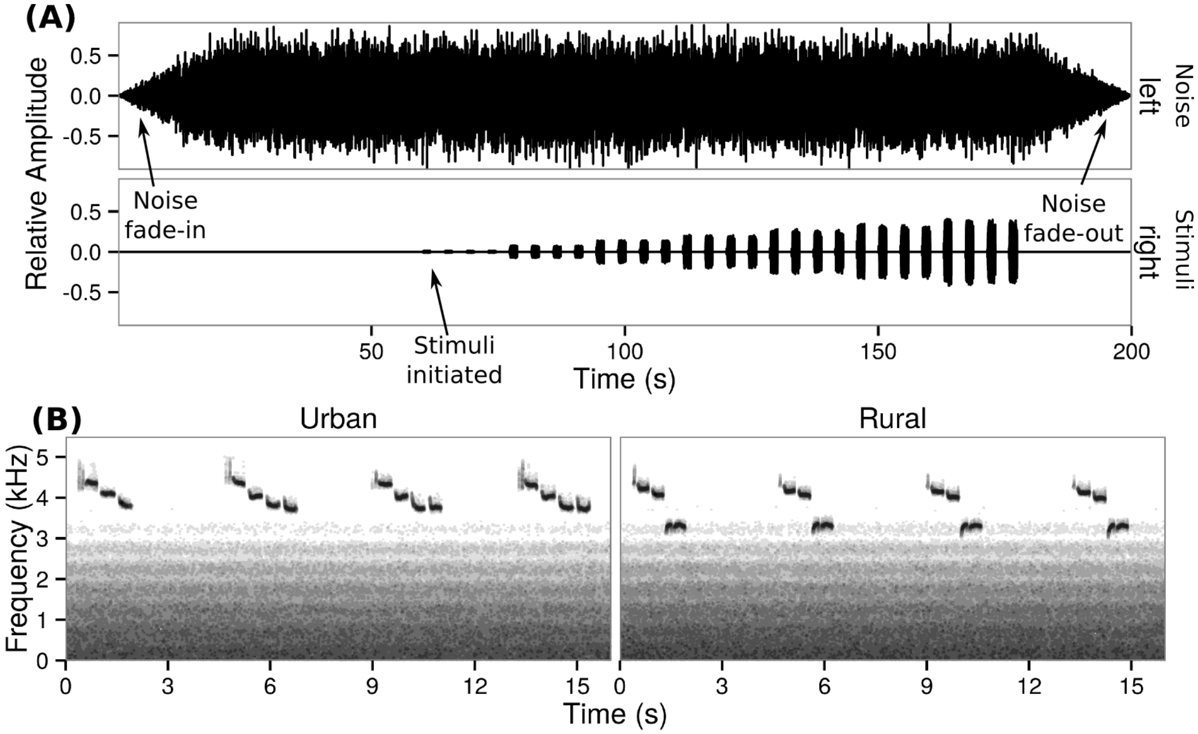

Figure 5.2: Mountain chickadee playback trials consisted of a WAV file with one channel of noise and one channel of songs repeated at increasing amplitudes. The oscillogram (A) shows the increasing song amplitude as well as the noise fade-in and fade-out. Spectrograms (B) show examples of the two types of songs used: Urban (left) and Rural (right).

stimuli were broadcast from the same direction with respect to the focal male.

5.2.3 Playback trials

To ensure the focal male was within auditory range, all playback trials started with a series of mountain and/or black-capped chickadee *chick-a-dee* calls (Grava *et al.*, 2013*b*). I presented 12 calls over 30s; if the focal male responded within 25m of the playback speaker, I stopped the calls and initiated the playback sequence (above). If there was no response from the focal male after 30s of priming calls, I gave 2min of silence and restarted priming calls. If males failed to respond to a second and a third sequence of priming, trials were aborted until at least the following day. Conversely, if males were detected within 25 m of the speaker prior to initiating priming calls, I still played at least two priming calls. In this manner, all males received at least two calls to ensure that motivation and priming was similar between trials. As there was at least a 1-minute delay between the last priming call and the first stimuli broadcast, it was not possible to standardize focal male position. Focal males that were either too close (< 5m) and so could have easily perceived faint stimuli, or too far (> 25m) and so might not have heard the stimuli were omitted from analysis.

Throughout the trial I dictated all the focal male's movements and recorded their vocalizations onto a MKH70 Sennheiser microphone (Sennheiser Inc., Canada) onto a Marantz PMD671 Digital recorder (Marantz Canada, LLC; 22 bit and 44.1 kHz sampling frequency). Distances were measured by eye by the same observer (SEL) in all trials. Ropes marked at 5m and 10m distances were stretched away from the speaker in four directions and were used to aid distance estimates. Laser range finders were used during and/or after the trial to confirm perch heights. Ambient noise was measured after each trial with a Pulsar 30 sound Pressure level meter (Pulsar Instruments plc., UK) and averaged to obtain a measure of the general site noise levels experienced by the focal male. Ambient noise varied from 50 to 72 (median 64) dB(Z) for Urban/Rural pairs and 52 to 74 (median 62) dB(Z) for Rural/Urban pairs. In this study, ambient noise levels were significantly correlated with the focal male's urbanization index ($r = 0.55$, $P < 0.001$), indicating that for sites surveyed in this study, noisy sites were also more urbanized.

5.2.4 Focal male responses

I tracked when vocalizations and movements were made, and the distance to the speaker each time the focal male moved. From these observations I defined three measures of focal male response to the playback. (1) Latency to first reaction, defined as the time it took (in seconds) for the focal male to either start singing or fly more than 2m towards the speaker; (2) A holistic index of aggression with respect to time spent close to the speaker; and (3) a holistic index of aggression with respect to focal male singing. The two indices of aggression were calculated with a principal component analysis (v3.1.2, R Core Team, 2014) using measures of time spent at various distance classes (s), latency to the closest approach to the speaker (s), the closest approach (m), and the total number of songs sung (Grava *et al.*, 2013*b*). I evaluated only principal component axes which had more total variance explained than the broken stick model given the number of variables measured (Legendre & Legendre, 1998), and I only interpreted contributions which were greater than 0.33 (Ho, 2006). Higher scores on the first axis (PC1) reflected the individual spending more time close to the speaker (within 5m), spending less time far from the speaker (15-25m), taking more time to get to the closest distance, but getting closer to the speaker overall (*Approach and stay close*; Table 5.1; Figure 5.3). Higher scores on the second axis (PC2) were indicative of individuals spending time close to the speaker (within 5m), spending less time at intermediate distances (5-15m) and singing more (*Approach and sing*; Table 5.1; Figure 5.3).

5.2.5 Statistical analysis

To determine how the three responses differed between Urban and Rural playback trials, I conducted linear mixed models using focal male ID as a random factor (v3.1.118, Pinheiro *et al.*, 2014; R v3.1.2). My explanatory variables were stimuli type (within subject; Urban vs.

Table 5.1: Principal component analysis of mountain chickadee response to playback stimuli. Bold values reflect variables with contributions of greater than 0.33.

Parameter	PC1	PC2
Time < 5m	**0.43**	**0.49**
Time 5-15m	0.20	**-0.69**
Time 15-25m	**-0.54**	0.24
Latency to min dist.	**0.37**	0.09
Min Distance	**-0.58**	-0.11
Total songs sung	-0.08	**0.45**
Total Variance explained	0.43	0.26

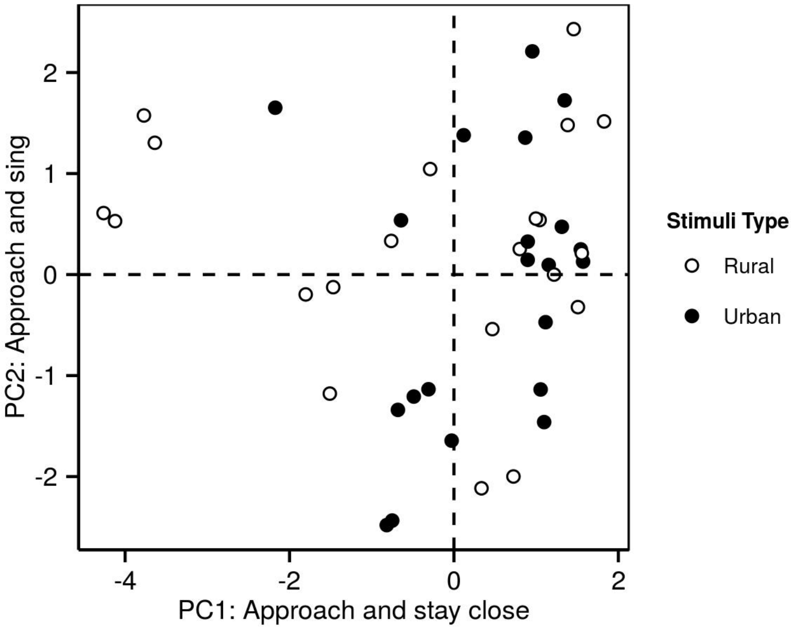

Figure 5.3: Biplot of PC1 (*Approach and stay close*) and PC2 (*Approach and sing*), the first two axes of the Principal Component Analysis. White points represent reactions by focal males to Rural stimuli, black points represent reactions to Urban stimuli.

Rural), centred local ambient noise (between subject; in dB(Z)) and playback order (between subject; Urban/Rural vs. Rural/Urban). I also investigated interactions between stimuli type and each of the other two variables to see whether differential responses were related to playback order or local noise conditions. I retained interactions in models where $P < 0.10$, but omitted interactions from the final analysis where $P > 0.10$. To control for differences in starting location, I included the distance the focal male was from the speaker at the start of the playback trial as a covariate in all analyses. As it became clear that familiarity may explain the results of PC1, I performed a linear mixed model post-hoc analysis examining the relationship between PC1 and whether or not the stimuli originated in the focal male's region (local vs. foreign). I confirmed that multiple collinearity was negligible (all Variance Inflation Factors < 7, condition numbers all < 30, Quinn & Keough, 2002; R statistical software v. 3.1.2, R Core Team, 2014). Where necessary I used Box-Cox transformations to satisfy the assumptions of normality. All categorical variable contrasts (stimuli type and playback order) were coded with sums contrasts (also called effect coding or deviant contrasts) so that parameter estimates reflect deviations from the overall mean (Wendorf, 2004). All figures were produced with the R package ggplot2 (v1.0.0 Wickham, 2009). Spectrograms and oscillograms were produced with the R package seewave (v1.7.3 Sueur *et al.*, 2008) with an Hanning window length of 1024.

5.3 Results

Overall, focal males responded on average 26 seconds into the playback (0.04s to 1.8min). Focal males showed a non-significant trend for reacting more slowly to Urban stimuli (latency to first response, Table 5.2), and there were no effects of playback order, ambient noise, or starting distance on latency to first reaction (Table 5.2).

For PC1 (*Approach and stay close*), focal males showed a non-significant trend for responding on average more to Urban playbacks than to Rural playbacks (Table 5.2). However, there was an interaction between stimuli type and local ambient noise, indicating

Table 5.2: Results of linear mixed models in mountain chickadees testing how Latency to first reaction, PC1 (*Approach and stay close*), and PC2 (*Approach and sing*) vary with Stimuli Type (Urban vs. Rural), Playback Order (Urban/Rural vs. Rural/Urban), Local ambient noise levels (dB(Z)) and interactions. All response variables are either transformed (Trans) or are unitless. Slope Est ± CI 95% refers to slope parameter estimates ± the 95% Confidence intervals. Slope estimates indicate how much the response variable changes for every unit of change in the explanatory parameter. DF represents degrees of freedom.

Response variable	Parameter	Slope Est.	±	CI 95%	DF	*t*	*P*
Latency to first reaction (Trans) (n = 21)	(Intercept)	**3.61**	±	**1.57**	19	4.81	< 0.001 **
	Stimuli Type	0.47	±	0.56	19	1.75	0.097 *
	Playback Order	-0.09	±	0.59	18	-0.32	0.750
	Local ambient noise (dB)	0.02	±	0.10	18	0.47	0.641
	Starting distance (m)	0.04	±	0.12	19	0.73	0.473
PC1 *(Approach and stay close*) (n = 21)	(Intercept)	0.99	±	1.24	18	1.68	0.111
	Stimuli Type	0.34	±	0.41	17	1.75	0.098 *
	Playback Order	0.15	±	0.50	18	0.63	0.537
	Local ambient noise (dB)	0.07	±	0.08	18	1.84	0.082 *
	Starting distance (m)	-0.08	±	0.09	17	1.82	0.086 *
	PB Hab. x PB Order	0.35	±	0.40	17	1.84	0.083 *
	PB Hab. x Amb noise	**-0.06**	±	**0.06**	17	-2.11	0.050 **
PC2 *(Approach and sing*) (n = 21)	(Intercept)	-0.11	±	1.04	19	-0.22	0.827
	Stimuli Type	-0.20	±	0.30	19	-1.40	0.177
	Playback Order	0.00	±	0.53	18	-0.01	0.994
	Local ambient noise (dB)	0.00	±	0.09	18	0.07	0.943
	Starting distance (m)	0.01	±	0.07	19	0.42	0.682

** **bold** indicate 95% confidence intervals which do not overlap zero (correspond to $P < 0.05$)

* indicate 90% confidence intervals which do not overlap zero (correspond to $P < 0.10$)

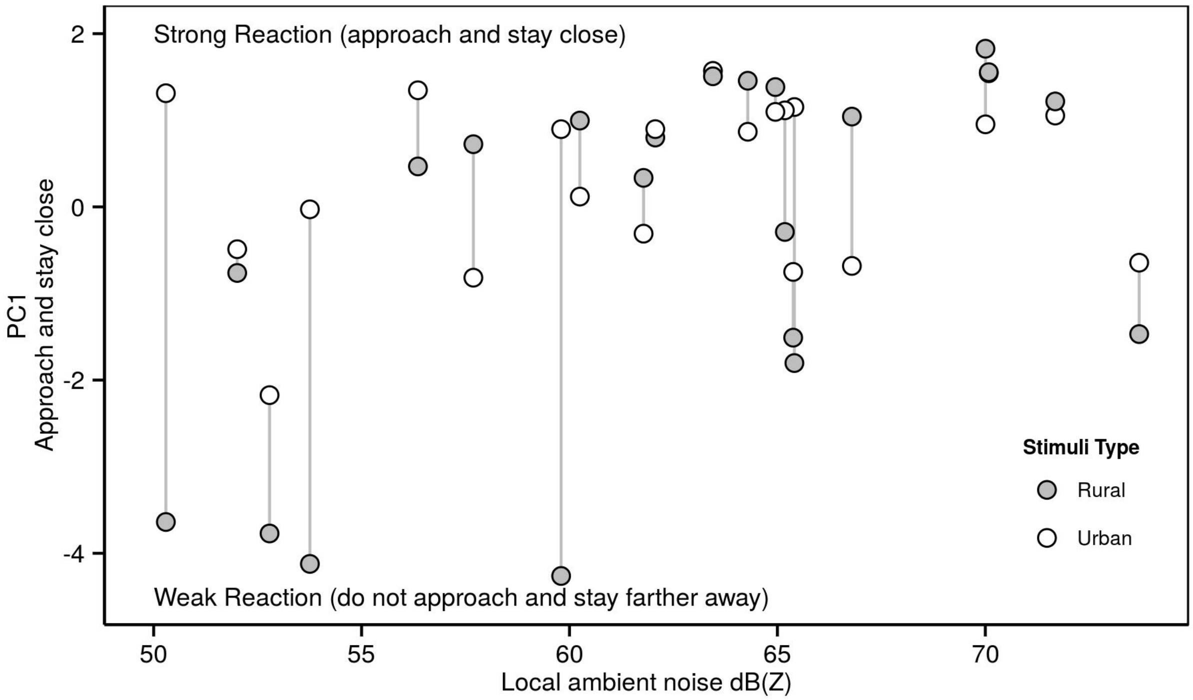

Figure 5.4: Focal male mountain chickadees differ in their response to PC1 (*Approach and stay close*) as ambient noise increases. Focal males from quiet areas approached and stayed closer to Urban playbacks than to Rural playbacks, whereas males from noisy areas did not differentiate strongly between the stimuli types. Each set of points connected with a line represents one focal male. The grey points represent responses to Rural stimuli, the White points represent responses to Urban stimuli.

that the difference in these approach reactions between Urban and Rural playbacks decreased as ambient noise increased (Table 5.2; Figure 5.4). Consequently, the greatest differentiation between stimuli types occurred among males in quiet neighbourhoods, who had stronger reactions to Urban vs. Rural stimuli. As ambient noise levels increased, focal males had an overall higher response level to stimuli, but did not differentiate between stimuli types. There was also a non-significant interaction between stimuli type and playback order (differences between responses to Urban vs. Rural stimuli were greatest when Urban stimuli were presented first), and a non-significant trend in starting distance (”approach” scores were lower among males that were already close to the speaker at the start of the playback). There was also a non-significant, overall trend for ”approach” scores to increase as local ambient noise increased (Table 5.2). A post-hoc analysis was performed to test for differences in PC1 between regions (local vs. foreign; Slope Est. ± CI 95%; 10.40 ± 65.65, $t_{17} = 0.33$, $P = 0.74$).

For PC2 (*Approach and sing*), there were no significant effects. Focal males did not sing more to stimuli of one habitat type over the other, and there were no effects of playback order, ambient noise or starting distance (Table 5.2).

5.4 Discussion

I found no support for my first hypothesis; there was only a non-significant trend for a difference in latency to first response between stimuli type, providing little indication that stimuli recorded in urban areas were inherently better at being detected in noise than stimuli recorded in rural areas. My second hypothesis, that better discrimination of Urban songs would lead to greater aggression compared with Rural songs, was partially supported; I did see greater overall aggression, as measured by approach scores, towards Urban vs. Rural stimuli, but this relationship changed with local ambient noise levels.

There are several potential explanations for the patterns I observed. Males in quiet areas may have reacted more to Urban than to Rural stimuli because the males perceived these signals as ”foreign”, whereas males in noisy areas were unable (or unwilling) to differentiate (and thus discriminate) between local and foreign signals. However, other playback studies comparing urban and rural habitat types found that males reacted more strongly to playbacks from similar habitats rather than from different habitats (Ripmeester *et al.*, 2010*b*; Mockford & Marshall, 2009), and there is no *a priori* reason to suspect mountain chickadees would differ in this regard. Further, a post-hoc analysis in this study shows that there were no among-male differences in aggression (PC1: *Approach and stay close*) shown to playbacks from local vs. foreign regions, differences which I would expect if individuals were responding more to unfamiliar stimuli. Therefore, it seems unlikely that differentiation between local and foreign songs explains the patterns seen in my study.

Three other explanations may be more illuminating. First, receivers may better detect and differentiate signals with characteristics which minimize masking by background noise. Second, receivers familiar with anthropogenic noise may have an improved ability to perceive all signals in noise. Finally, there is evidence that urban birds may exhibit greater aggression and boldness, which could result in different motivation to react among the focal males, as well as affect the relative motivation signalled in the stimuli I broadcast.

5.4.1 Stimuli characteristics and masking

I predicted that urban mountain chickadees would adjust their songs to improve detection and discrimination in noise. Because all stimulus songs were embedded in experimental noise, this may explain why males in quiet areas reacted more strongly to Urban than to Rural playbacks. If local ambient noise levels further masked signals, I would have expected that as ambient noise increased, relative discrimination would favour Urban stimuli over Rural stimuli. In fact I saw the opposite; males in areas of loud ambient noise had high levels of aggression towards, and little discrimination between, either stimuli, whereas focal males in quiet neighbourhoods showed low levels of aggression towards Rural stimuli and high levels towards Urban stimuli. This could indicate that differences in audibility between stimuli result in a differential response among males unfamiliar with ambient noise, whereas males familiar with noise do not differentiate as they have improved signal perception in noise.

5.4.2 Familiarity with noise

There is some evidence that zebra finches (*Taeniopygia guttata*) can learn to correctly discriminate among songs that have been degraded by distance (Mouterde *et al.*, 2014). Potentially, birds could do the same for noise-related interference. Males in noisy areas may be better at discriminating songs in noise overall, so they do not differentiate between the stimuli types, but react quickly and aggressively to all signals. In Chapter 4, I found evidence that black-capped chickadees from noisy areas exhibited immediate plasticity by adjusting signals to minimize masking better than those from quiet areas, suggesting that familiarity with long-term noise exposure may result in signallers learning how to effectively signal in noise; this playback study could be evidence that receivers can also learn to better discriminate signals in noise.

5.4.3 Increased aggression

Finally, as local ambient noise was correlated with urbanization in this study, different levels of aggression and boldness between birds from urban vs. rural habitats may explain both why Urban playbacks received more aggression overall, and why focal males from noisier areas did not differentiate between playbacks. Studies show that urban birds tend to be bolder and more aggressive than their rural counterparts (Evans *et al.*, 2010; Scales *et al.*, 2011; Lowry *et al.*, 2011). Further, these differences in aggression can result in changes to song characteristics (e.g., Ripmeester *et al.*, 2007, 2010*a*; Hamao *et al.*, 2011). There is some evidence that mountain chickadees in harsher environments are less dominant to those in milder environments (Kozlovsky *et al.*, 2014). Therefore if urban habitats could be considered milder (due to easier food access, etc.), they might attract more dominant individuals. Black-capped chickadees signal motivation and aggression through frequency-matching and song-overlapping (Otter *et al.*, 2002), but little is know about how mountain chickadees signal aggression. If urban mountain chickadees are generally more aggressive, Urban stimuli may carry cues to this effect and could therefore be perceived as a greater threat. Focal males from quieter areas could have responded more aggressively to Urban playbacks as a result of this greater perceived threat. Further, focal males from noisier (more urban) habitats might have shown high levels of aggression to both playbacks, due to greater innate aggression. However, a better understanding of aggression and urbanization in mountain chickadees is required before either hypothesis can be confirmed

5.4.4 Context-dependent responses to playback

The relationship between urbanization, aggression and communication is potentially complex (Slabbekoorn, 2013). Increased aggression and increased discrimination due to either signal adjustment or receiver perception are three hypotheses which may account for the patterns of response I observed, but they are not mutually exclusive. It is possible that any one is acting on the receiver or sender side, or that they are influencing both in tandem. The responses I witnessed in this study may have depended on the context in which playbacks were conducted (Luther & Magnotti, 2014). In quiet habitats, the higher discrimination I observed may reflect stronger propagation properties of urban stimuli compared with rural stimuli. This would have improved discriminability of urban signals when embedded in noise and could have led to greater responses from focal males. In contrast, focal males in typically-noisy habitats may have either higher aggression levels (Evans *et al.*, 2010; Scales *et al.*, 2011; Lowry *et al.*, 2011), or improved perception of signals in noise; either explanation could explain the lack of discrimination between the stimuli and the high responsiveness overall in these focal sites.

5.4.5 Conclusions

I found evidence of context-dependent discrimination between Urban and Rural stimuli in mountain chickadees. This discrimination may be the result of a combination of different factors. Further lab and field studies of receiver detection and discrimination are needed to help determine whether this is the result of increased aggression in urban habitats or from improved communication in noisy habitats by urban signallers and receivers, or some combination of the two. In mountain chickadees, however, there are clearly differences between urban and rural signallers and/or receivers. Further studies investigating the effects of these differences on social interactions, settlement, and breeding success could help determine whether individuals in urban areas are successful with high-quality territories, or stuck in ecological traps. It is interesting to note that had I only used focal males from quiet areas (in an attempt to control background noise levels), I would have concluded that mountain chickadees clearly discriminated between Urban and Rural stimuli in experimental noise. This highlights the importance of considering context and the effect that long-term familiarity with noise may have on studies of this nature.

6 Males respond faster to high- vs. low-pitched black-capped chickadee songs in noise

6.1 Introduction

Low-frequency anthropogenic noise can interfere with avian communication through masking of overlapping frequencies Rabin & Greene (2002); Brumm & Slabbekoorn (2005); Barber *et al.* (2010). Vocalizing at higher frequencies could, theoretically, improve detection and discrimination in noise, and both modelling and laboratory studies support this idea (Nemeth & Brumm, 2010; Pohl *et al.*, 2012). Further, there are numerous examples of bird species demonstrating spectral adjustment in response to noise (e.g., Slabbekoorn & Peet, 2003; Wood & Yezerinac, 2006; Verzijden *et al.*, 2010; Bermúdez-Cuamatzin *et al.*, 2011; Chapters 3 and 4). While the numerous examples of noise-dependent spectral plasticity in birds suggest this feature must be somehow adaptive, field studies have yet to demonstrate that spectrally-adjusted songs actually improve detection and discrimination over unadjusted songs (Luther & Magnotti, 2014).

One possibility is that spectrally-adjusted songs do not, independently, improve detection and discrimination, as birds may adjust to sing higher as a byproduct of singing louder (Nemeth *et al.*, 2013). Another possibility is that spectral adjustment may come at a cost in terms of the perceived quality of the signal (functional compromise hypothesis, Slabbekoorn & Ripmeester, 2008; Gross *et al.*, 2010; Slabbekoorn, 2013). For example, the southern brown tree frog (*Litoria ewingii*; Parris *et al.*, 2009) adjusts to vocalize at higher frequencies, but low frequencies are associated with greater reproductive potential. In playback studies, receivers may be less motivated to respond to perceived low-quality songs, even if they are easier to detect (des Aunay *et al.*, 2014; but see Halfwerk *et al.*, 2011*a*). Finally, as anthropogenic noise tends to correlate with urbanization, it is possible that spectral adjustments are responses to other urban factors, such as aggression and density (e.g., Ripmeester *et al.*, 2010*a*).

Playback studies on great tits (*Parus major*), European blackbirds (*Turdus merula*), and northern cardinals (*Cardinalis cardinalis*) show that birds can differentiate between noise-adjusted and -unadjusted songs (Mockford & Marshall, 2009; Ripmeester *et al.*, 2010*b*; Luther & Magnotti, 2014). However, the role of noise on differentiation is ambiguous; in each study noise was not experimental, but was associated with the habitat of the focal male tested. It is therefore unclear whether differentiation between signal types is the result of better detection or discrimination in noisy conditions, or whether it is the result of habitat-related effects. In Chapter 5, I found evidence that mountain chickadees from noisy habitats did not differentiate between urban and rural stimuli when embedded in experimental background noise. In contrast, individuals from quiet habitats did differentiate, further suggesting that local ambient noise can result in more than signal-masking. Therefore, playback studies attempting to determine whether adjusted signals improve audibility in noise should account for the habitat context of focal males.

Black-capped chickadees have a single song type (*fee-bee* whistled song) but individual males are capable of pitch-shifting their songs up and down in frequency during male-male interactions (Otter *et al.*, 2002). Black-capped chickadees also use pitch-shifting to spectrally adjust their vocalizations to sing higher frequencies in noisy conditions (Proppe *et al.*, 2012; Chapter 4) or to shift away from narrow bands of masking noise (Goodwin & Podos, 2013). However, it is unknown whether high-frequency songs are actually more audible in noise. Potentially, black-capped chickadees switch to higher frequency songs because they are easier to sing loudly, but the high frequencies themselves are not sufficiently high for masking release.

Here I tested black-capped chickadees for differences in response to high- vs. low-frequency songs in a playback experiment combining song and experimental noise. I normalized high- and low-frequency songs and played the songs embedded in noise, starting with quiet songs and gradually increasing in song amplitude. I hypothesized that songs which are more audible in noise will be detected earlier at lower amplitudes and will therefore elicit quicker reactions. I also examined relative aggression directed at the two song frequencies for two reasons. First, if initial response time does not differ, songs that are better discriminated overall may be perceived as a greater threat and may elicit more overall aggression. Second, if initial response time does differ, it is important to know whether this is related to overall aggression and perceived threat rather than detection. Therefore I asked two main questions: When stimuli are embedded in experimental noise, do black-capped chickadees respond (1) more quickly or (2) more aggressively to high- vs. low-frequency songs?

6.2 Methods

General methodologies closely follow those of Chapter 5, so I focus here on specifics associated with this study, particularly where methods diverge.

6.2.1 Site and timing

I performed playback trials in Prince George, Quesnel and Vancouver, British Columbia, Canada, between 5 April and 18 April 2012, and between 27 April and 3 May 2013. Paired trials were conducted across a variety of landscapes from highly urbanized to completely undisturbed rural, as well as across a gradient of ambient noise. Twenty-four male black-capped chickadees were successfully exposed to matched stimuli playback trials (dyads). Each focal male was presented with one trial containing low-pitched stimulus-songs and one containing high-pitched stimulus-songs embedded in background noise. The playbacks for each male were presented between 7am and 12pm, and dyadic stimuli were separated by a median of 1 hour (range 40 min to 4.4 hours). Neighbours were never tested on the same day. Playback order (High/Low vs. Low/High) alternated between focal males, and in total I exposed 13 males to the High/Low order of stimuli and 11 males to the Low/High order. To avoid pseudoreplication of playback stimuli, I used 17 unique stimuli sets and played each set to a maximum of two focal males (once ordered High/Low, and once Low/High).

6.2.2 Playback files

All songs used in playbacks were unique and obtained from dawn chorus recordings of 11 male black-capped chickadees from Prince George, Kamloops, Kelowna and Vancouver in 2011 and 2012 (Chapter 4). All songs were from individuals unfamiliar to the focal male. Song frequencies were defined as the dominant frequency of the second ’*bee*’-note (Christie *et al.*, 2004). Because black-capped chickadees routinely pitch-shift their songs, it was possible to get both low- and high-frequency songs from recordings of a single individual. Therefore, all stimuli dyads were created from low-frequency (2.99 - 3.21 kHz) and high-frequency (3.34 - 3.50 kHz) songs recorded from a single male black-capped chickadee (Figure 6.1). By pairing trials so that each focal male only heard songs from a single individual, I control for effects of dominance or song consistency (Grava *et al.*, 2013*b*). Hereafter, I refer to playbacks with high-frequency songs as ’High-pitched stimuli’ and those with low-frequency songs as ’Low-pitched stimuli’. Background noises were removed from songs and songs were normalized to a constant volume prior to use.

As in Chapter 5, for each playback trial a WAV file with two channels was created. The left channel broadcast synthetic noise with a frequency spectrum similar to traffic noise (see Section 3.2.2), while the right channel broadcast the stimulus songs with increasing amplitude as the trial progressed (Figure 6.2). See Chapter 5 for further details.

6.2.3 Playback trials

To ensure the focal male was within range and responsive, I started all playback trials by priming with a series of black-capped chickadee *chick-a-dee* calls (as in Chapter 5; Grava *et al.*, 2013*b*). As in Chapter 5, I omitted focal males which were either too close (< 5m) and so could have easily perceived faint stimuli, or too far (> 25m) and so might not have heard the stimuli.

A MKH70 Sennheiser microphone (Sennheiser Inc., Canada) was used to record dictated focal male movements and vocalizations during the trial. Distances were measured

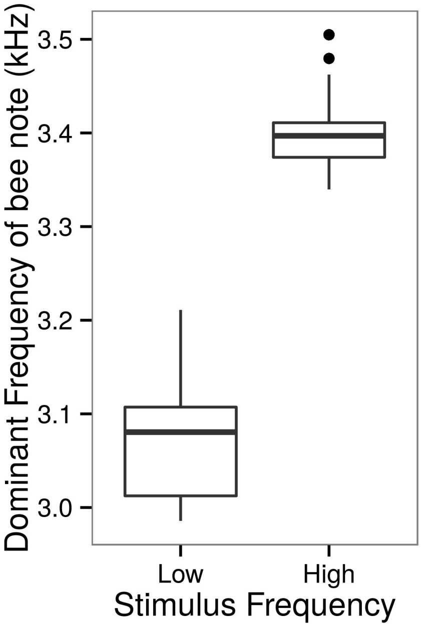

Figure 6.1: Playback stimuli for black-capped chickadees were designated either ’Low-pitched’ or ’High-pitched’ depending on the frequency of the *bee*-note of the songs from which they were comprised. Boxplots reflect distribution of data. Boxes show 25th, 50th and 75th percentiles, ’whiskers’ are to the minimum and maximum values within 1.5 x the inter-quartile range (IQR). Points are values outside of 1.5 x IQR.

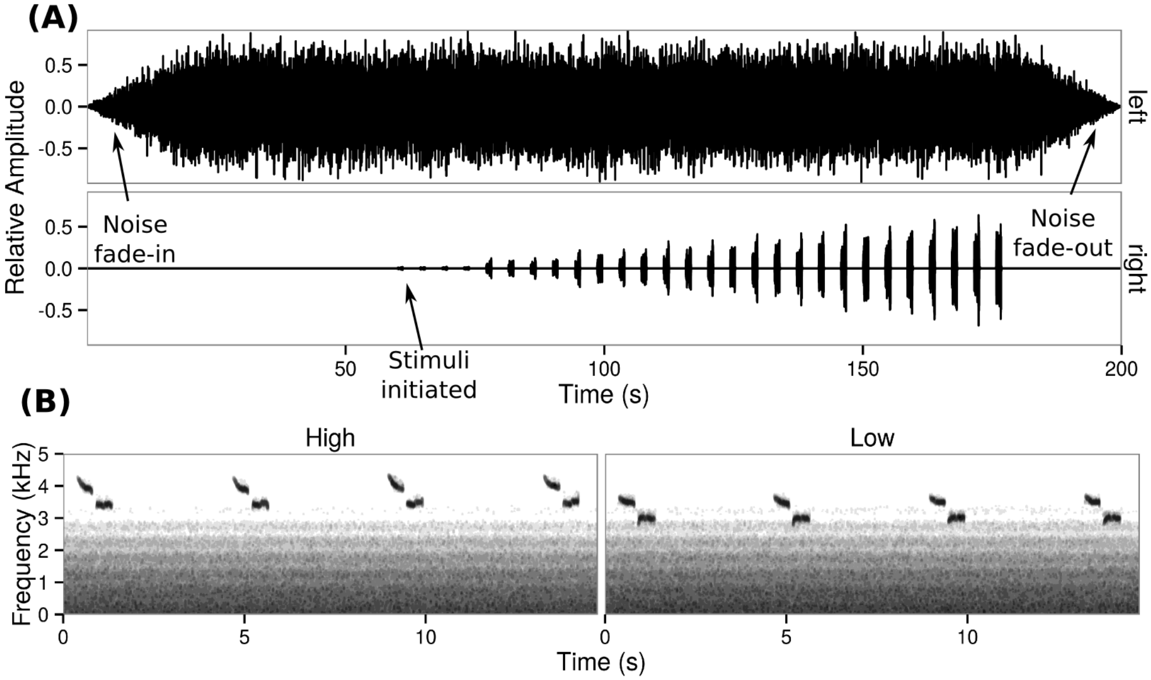

Figure 6.2: Playback trials for black-capped chickadees consisted of a WAV file with one channel of noise and one channel of songs repeated at increasing amplitudes. The oscillogram (A) shows the increasing song amplitude as well as the noise fade-in and fade-out. Spectrograms (B) show examples of the two types of songs used: High-pitched (left) and Low-pitched (right).

by eye by the same observer (SEL) in all trials. Ropes marked at 5m and 10m distances were stretched away from the speaker in four directions and were used to aid distance estimates. A laser range finder was used during and/or after the trial to confirm perch heights.

Each site was characterized by urbanization and noise levels. Urbanization was quantified via an urbanization index (see Section 3.2.4). Urbanization indices ranged from -1.4 to 3.1 (median -0.22) for sites where I played High/Low playback pairs and from -1.6 to 2.2 (median 0.72) for those where I played Low/High pairs. Local ambient noise was measured after each trial with a Pulsar 30 sound pressure level meter (Pulsar Instruments plc., UK) and averaged to obtain a measure of the general site noise levels experienced by the focal male. The general noise levels experienced by focal males at each site (Local Ambient Noise) ranged from 56 to 71 (median 65) dB(Z) for sites where I played High/Low playback pairs and from 53 to 71 (median 64) dB(Z) where I played Low/High playback pairs. Urbanization indices and noise levels were not correlated ($r = 0.20$, $P = 0.17$).

6.2.4 Focal male responses

I tracked when vocalizations and movements were made, and the distance to the speaker each time the focal male moved. From these observations I defined three measures of focal male response to the playback. (1) Latency to first reaction (s), reflecting the time a focal male took to either start singing or fly more than 2m towards the speaker; (2) An index of aggression reflecting greater time spent close to the speaker; (3) An index of aggression reflecting more focal male singing. These two measures of aggression are commonly used metrics among playback studies in black-capped chickadees (e.g., Grava *et al.*, 2013*b*). I used principal component analysis (v3.1.2, R Core Team, 2014) to calculate the two indices of aggression. Variables included were: time spent within various distance categories (s), latency to the closest approach to the speaker (s), the closest approach (m), and the total number of songs sung. I evaluated only principal component (PC) axes with greater total variance explained than the broken stick model, given the number of variables (Legendre & Legendre, 1998). I only interpreted contributions which were greater than 0.33 (Ho, 2006). High scores on the first principal component axis (PC1) reflected birds spending more time close to the speaker (< 10m), spending less time far from the speaker (> 20m), taking longer to get to the closest distance, but getting closer to the speaker overall (PC1: *Approach and stay close*; Table 6.1). High scores on the second principal component axis (PC2) reflected birds spending less time at intermediate distances (10 - 20m), spending more time far from the speaker (> 20m), and singing less (Table 6.1; Figure 6.3). I multiplied PC2 loadings by -1 in order to create an index reflecting greater time spent at intermediate distances, less time spent farther away, and more songs sung (PC2: *Sing more*).

6.2.5 Statistical analysis

I analyzed focal male responses to High vs. Low playbacks with linear mixed models using focal male ID as a random factor with R statistical software v3.1.2 using the nlme package (v3.1.118, Pinheiro *et al.*, 2014). Previous work showed that black-capped chickadees adjusted their vocalizations in response to ambient noise but not to urbanization indices (Chapter 4), therefore I also examined the effect of local ambient noise levels. My explanatory variables were Stimuli Frequency (within subject; High-pitched vs. Low-pitched), centred Local Ambient Noise (between subject; in dB(Z)) and Playback Order (between subject; High/Low vs. Low/High stimuli presentation). I also investigated interactions between Stimuli Frequency and each of the other two variables to see whether Playback Order or Local Ambient Noise influenced responses. I kept interactions with $P < 0.10$ in models, but omitted interactions where $P > 0.10$ from the final analysis. Because audibility can also be affected by distance, I included the Starting Distance of each focal male to the speaker as a covariate. I confirmed that multicollinearity was not a problem (all Variance Inflation Factors < 7, condition numbers all < 30, Quinn & Keough, 2002; R statistical software v. 3.1.2, R Core Team, 2014) and, where necessary, used Box-Cox transformations to satisfy the assumptions of normality. Contrasts for categorical variables

Table 6.1: Principal component analysis of black-capped chickadee responses to playback stimuli. Bold values reflect variables with contributions of greater than 0.33.

Parameter	PC1	PC2
Time < 10m	**0.54**	0.26
Time 10-20m	-0.16	**-0.75**
Time > 20m	**-0.48**	**0.39**
Latency to min dist.	**0.38**	-0.12
Min Distance	**-0.53**	-0.11
Total songs sung	0.19	**-0.44**
Total Variance explained	0.45	0.25

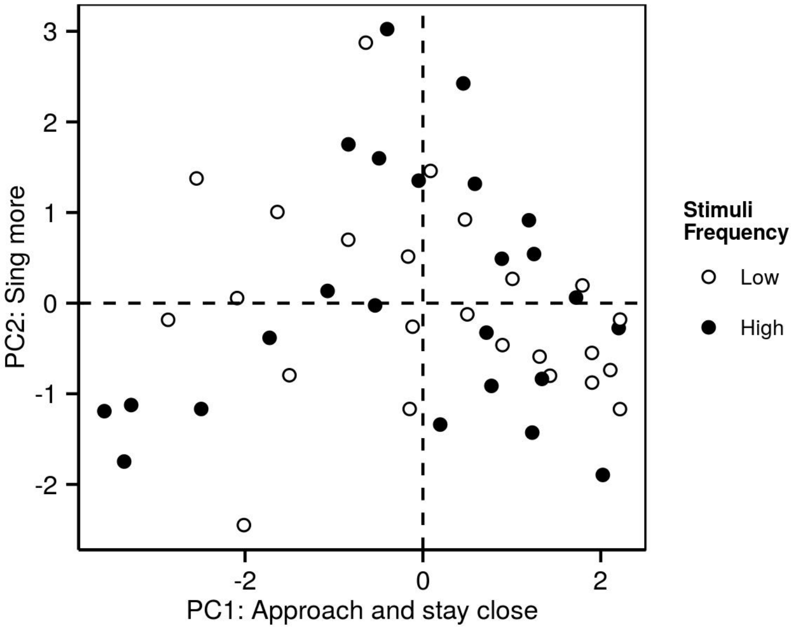

Figure 6.3: Biplot of PC1 (*Approach and stay close*) and PC2 (*Sing more*), the first two axes of the Principal Component Analysis of responses of black-capped chickadees. White points represent reactions by focal males to Low-pitched stimuli, black points represent reactions to High-pitched stimuli.

(Stimuli Frequency and Playback Order) were coded with sums contrasts (also called effect coding or deviant contrasts) so that parameter estimates reflect deviations from the overall mean of that variable (Wendorf, 2004). All figures were produced with the R package ggplot2 (v1.0.0 Wickham, 2009). Spectrograms and oscillograms were produced with the R package seewave (Sueur *et al.*, 2008, v1.7.3) with a Hanning window length of 1024.

6.3 Results

For latency to first reaction, there was a significant interaction between Stimuli Frequency and Playback Order (Table 6.2); males responded more quickly to High-pitched vs. Low-pitched stimuli when Playback Order was High/Low than when Playback Order was Low/High (Figure 6.4). Post-hoc analysis revealed these differences to be significant: when Playback Order was High/Low, focal males responded significantly faster ($t_9 = 2.26$, $P = 0.05$) to High-pitched vs. Low-pitched stimuli, but when Playback Order was Low/High there was no difference in latency to first response ($t_{11} = -1.08$, $P = 0.30$).

Focal males did not differentiate between Stimuli Frequency with respect to approaching the speaker PC1 (*Approach and stay close*; Table 6.2). However, there was a significant negative effect of Starting Distance on PC1 (Table 6.2), indicating that as Starting Distance decreased, PC1 increased (individuals approached and spent more time near the speaker). For PC2 (*Sing more*), there were no effects of Stimuli Frequency (Table 6.2; Figure 6.5), but there was an overall effect of Playback Order (Table 6.2; Figure 6.5). Focal males sang more to both playbacks if the first one they were exposed to was a Low-pitched playback.

Table 6.2: Results of linear mixed models in black-capped chickadees testing how Latency to first reaction, PC1 (*Approach and stay close*), and PC2 (*Sing more*) vary with Stimuli Frequency (High vs. Low), Playback Order (High/Low vs. Low/High), Local Ambient Noise (dB(Z)) and interactions. All response variables are either transformed (Trans) or are unitless. Slope Est ± CI 95% refers to slope parameter estimates ± the 95% Confidence intervals. Slope estimates indicate how much the response variable changes for every unit of change in the explanatory parameter. DF represents degrees of freedom.

Analysis	Parameter	Slope Est.	±	CI 95%	DF	t	P
Latency to first reaction (s) (Trans) (n = 21)	(Intercept)	**12.55**	±	**5.51**	21	0.02	< 0.001 **
	Stimuli Frequency	1.07	±	1.73	21	1.29	0.210
	Playback Order	0.22	±	2.02	21	0.23	0.822
	Local Ambient Noise	0.19	±	0.46	21	0.87	0.394
	Starting Distance	-0.12	±	0.38	21	-0.64	0.527
	Stimuli Freq x PB Order	**2.01**	±	**1.71**	21	2.45	0.023 **
PC1 (*Approach and stay close*) (n = 21)	(Intercept)	**1.61**	±	**1.39**	22	2.40	0.025 **
	Stimuli Frequency	0.06	±	0.41	22	0.32	0.750
	Playback Order	-0.01	±	0.55	21	-0.03	0.973
	Local Ambient Noise	-0.07	±	0.12	21	-1.19	0.246
	Starting Distance	**-0.12**	±	**0.09**	22	-2.61	0.016 **
PC2 (*Sing more*) (n = 21)	(Intercept)	-0.05	±	0.97	22	-0.10	0.922
	Stimuli Frequency	-0.04	±	0.28	22	-0.29	0.772
	Playback Order	**-0.52**	±	**0.39**	21	-2.76	0.012 **
	Local Ambient Noise	0.04	±	0.09	21	0.99	0.333
	Starting Distance	0.00	±	0.07	22	0.01	0.995

** **bold** indicate 95% confidence intervals which do not overlap zero (correspond to $P < 0.05$)

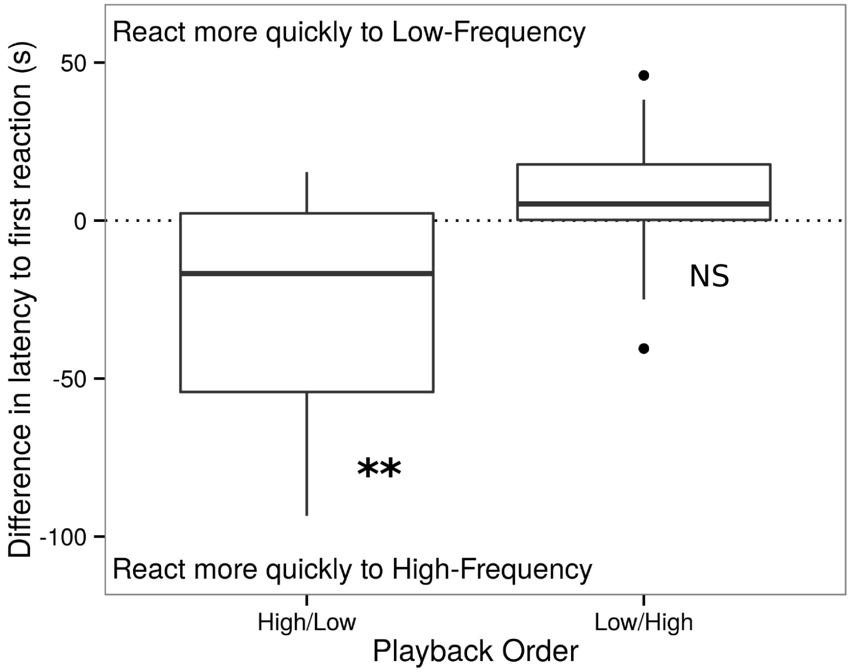

Figure 6.4: Male black-capped chickadees reacted more quickly to High- vs. Low-pitched stimuli, but only when High-pitched stimuli were presented first in paired trials. The dotted line reflects no difference between trials. Positive values above the dotted line reflect a greater latency to High- vs. Low-pitched stimuli, resulting in a quicker reaction during playbacks with Low-pitched stimuli. Negative values therefore reflect a quicker reaction during playbacks with High-pitched stimuli. Differences in latency from High- vs. Low-pitched stimuli were tested for each playback ordering in post-hoc tests. ** indicates significant differences, NS non-significant differences. Dots on the boxplots represent outliers (greater than 1.5 x inter-quartile range). Boxplots reflect distribution of data. Boxes show 25th, 50th and 75th percentiles, 'whiskers' are to the minimum and maximum values within 1.5 x the inter-quartile range (IQR). Points are values outside of 1.5 x IQR.

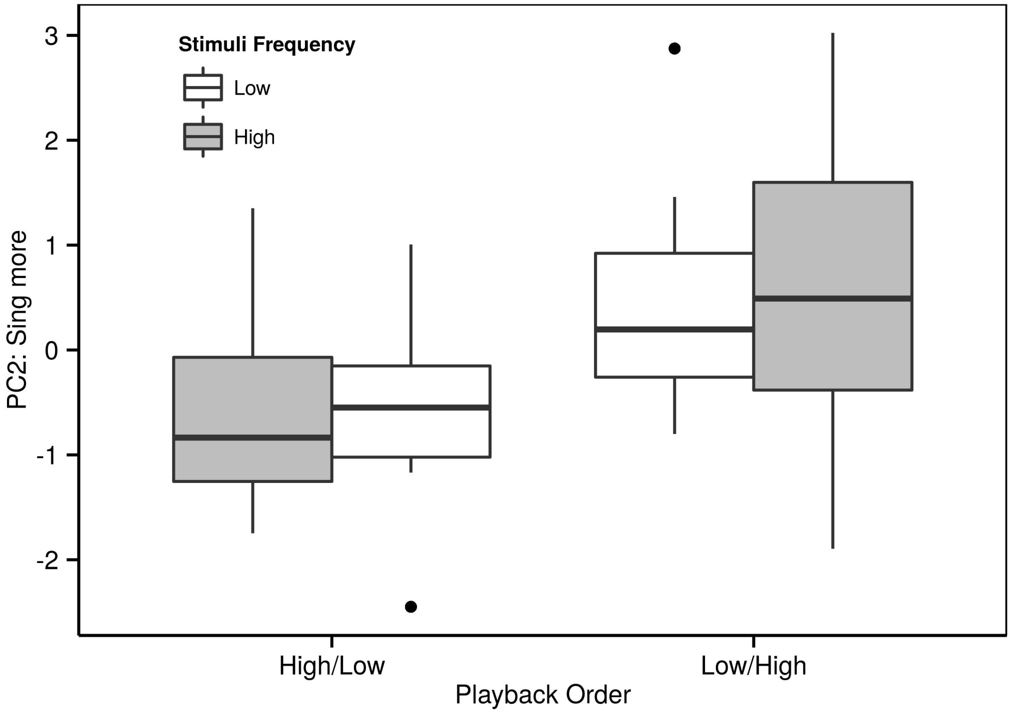

Figure 6.5: While there were no differences in *PC2: Sing more* between playbacks of High- and Low-pitched stimuli, focal black-capped chickdadees sang more in response to both of the matched stimuli when Low-pitched stimuli were presented first. Boxplots reflect distribution of data. Boxes show 25th, 50th and 75th percentiles, 'whiskers' are to the minimum and maximum values within 1.5 x the inter-quartile range (IQR). Points are values outside of 1.5 x IQR.

6.4 Discussion

I found that black-capped chickadees responded faster to High- vs. Low-pitched stimuli embedded in noise, but only when playback order of stimuli presented was High/Low. I found no evidence that black-capped chickadees respond more aggressively to High- vs. Low-pitched songs, suggesting that any differences in latency are unlikely to be the result of perceived threat. This suggests that in black-capped chickadees at least, high-frequency songs may have better detection in noise than low-frequency songs, independent of amplitude. In contrast, I found no evidence of discrimination between signals, and, interestingly, ambient noise had no effect on relative responses to High- vs. Low-pitched stimuli.

6.4.1 The role of frequency in signal detection

Focal males may have responded more quickly to High- than to Low-pitched stimuli either because High-pitched stimuli were more audible, or because High-pitched stimuli were perceived as being a greater threat. However, in this study, paired playback stimuli (High- vs. Low-pitched) originated from the same recording of a single black-capped chickadee. As such, variation among years, seasons, habitats, times of day, and individual motivation were largely consistent within stimuli pairs. The only other feature which may have been perceived as a greater threat is high song frequency.

Frequency-matching during intra-sexual singing bouts indicates a male black-capped's willingness to escalate contests (Horn *et al.*, 1992; Otter *et al.*, 2002; Mennill & Ratcliffe, 2004; Fitzsimmons *et al.*, 2008; Foote *et al.*, 2008). If high-frequency songs were also used to communicate increased aggression, I would have expected to see significantly closer approaches to the speaker during playbacks of High- compared with Low-pitched stimuli and I would have expected High-pitched stimuli to elicit more singing than Low-pitched stimuli, neither of which occurred. I did see an overall effect of Playback Order on *PC2 (Sing more)*, suggesting that Low-pitched stimuli might have some sort of priming effect, resulting in more songs being sung in response to High-pitched stimuli, but only when they were preceded by

Low-pitched stimuli. However, this would suggest Low-pitched stimuli were perceived as more aggressive than High-pitched stimuli. Although high frequencies correlate with density and potentially aggression in some species (Ripmeester *et al.*, 2010*a*; Hamao *et al.*, 2011), to my knowledge, only one study has tentatively suggested absolute frequency itself may reflect aggression in black-capped chickadees (Hill & Lein, 1987); In their study, lower-pitched songs were suggested to be the more aggressive signal. Subsequent playback studies, however, suggest that it is pitch-matching rather than pitch itself that appears more important (Mennill & Otter, 2007). Therefore, there is little evidence that differences in frequency between the stimuli would in themselves have motivated focal males to quicker responses.

As found in other studies, playback order can influence how individuals react to the stimuli (e.g., priming; Naguib, 1999). In my study, the effect of Playback Order on latency to first response may be related to habituation. Slower responses to the Low-pitched stimuli when the order was High/Low but no difference in latency of response to either stimuli when the order was Low/High could be explained by the combined effects of detecting High-pitched stimuli more rapidly, but simultaneously responding more slowly to the second playback due to habituation.

6.4.2 No effect of local ambient noise

In this study I found no effect of local ambient noise on either detection or discrimination of High- vs. Low-pitched stimuli. In contrast, in Chapter 5 I found that local ambient noise affected signal discrimination, but not detection. Other studies have also found differences in discrimination between adjusted and unadjusted signals among individuals from different habitats (Ripmeester *et al.*, 2010*b*; Mockford & Marshall, 2009; Luther & Magnotti, 2014). This seemed to suggest that discrimination between signals may be influenced by habitat differences in how receivers perceive both signaller motivation and signal adjustment. In the current study, however, habitat-related differences in receiver perception do not seem to be a factor. This may be due to the fact that black-capped chickadees naturally produce both high-and low-frequency songs. High-frequency songs are not adjusted songs, rather it is the use of different naturally-occurring frequencies that reflects adjustment to noise in this species (Chapter 4). Thus high-frequency songs would be familiar to focal males in different habitats, and are unlikely to represent a trade off between signal audibility and signal content. However, in other species, adjusted songs may be quite different from ’natural’ songs. In these species, adjusted songs may reflect trade-offs between signal audibility and signal content (functional compromise hypothesis), which would then result in differential discrimination depending on receiver perception.

6.4.3 Conclusions

Although playback order has a strong effect on response, I found evidence that black-capped chickadees can detect high-frequency songs more quickly than low-frequency songs embedded in experimental noise. Although some of these findings contrast those of other playback studies, my work supports the findings of laboratory studies on great tits, which showed greater detection of high- vs. low-frequency signals in urban noise conditions (Pohl *et al.*, 2009, 2012). Although in previous chapters I found evidence that familiarity with noisy environments may affect black-capped chickadee signalling (Chapter 4) as well as mountain chickadee receiver perception (Chapter 5), in this study I found no evidence that familiarity with noise influences receivers responses towards signals. Due to the strong effect of playback order, lab studies regarding actual perception in black-capped chickadees, rather than desire to respond, may help confirm whether black-capped chickadees’ high-frequency songs are indeed more audible in noise than low-frequency songs.

7 Conclusion and Synthesis

There were two broad purposes to this dissertation. First, I wished to compare the relative effects of urban habitat change and urban noise on avian communication. Second I wanted to determine whether species-specific singing behaviours could be used to predict how species deal with these urban communication challenges. To fulfill these goals I examined transmission of black-capped and mountain chickadee vocalizations through different habitats with different noise levels (Chapter 2), the abilities of these two species to adjust their vocalizations in the face of noise and habitat change (Chapters 3 and 4), and finally I used playback studies to determine the degree to which signal detection and discrimination was improved by these vocal changes (Chapters 5 and 6).

7.1 Relative effects of urban habitat and urban noise

My study focused on the urban habitats used by chickadees, which were predominantly green spaces. Although many urban areas contain very little vegetation, urban green spaces are more important to chickadees and many other retained species in urban areas than other urban areas. It is therefore important to maintain communication in these areas.

The results of the transmission experiments in Chapter 2 suggest that anthropogenic noise may be more problematic than the altered habitat, with respect to signal loss and degradation, in urban green spaces. I also determined that chickadee songs propagated better than calls, and were less affected by noise. While there were slight differences between species, these overall patterns held true. Further, while urban noise influenced vocal adjustment in chickadees, I observed only a few effects of urbanization indices on vocal adjustment in mountain chickadees (Chapter 3) and none at all in black-capped chickadees (Chapter 4). In the mountain chickadee chorus chapter (Chapter 3), I also considered long-term noise levels across different habitats and found that despite often similar ambient noise levels at dawn, urban sites accumulated more noise over the course of the morning than rural sites. It therefore seems as if the impact of urban habitat on avian communication corresponds to increased noise overall, not merely an immediate measure of noise.

While changes in the physical structure of habitats that accompany habitat urbanization did influence communication to some degree, I found anthropogenic noise to be the dominant factor influencing transmission in urban green spaces. However, in other types of urban habitats, where buildings and pavement are more common, habitat structure may lead to more negative effects on communication such as reverberation and echos in urban canyons (Warren *et al.*, 2006). Further, structural changes may affect other species in different ways, depending on the structure of their vocalizations (e.g., Dowling *et al.*, 2012; Gall *et al.*, 2012). While urbanization may have less of an impact on communication in green spaces, it still has the potential to greatly affect other aspects of avian survival and reproduction (Chace & Walsh, 2006).

7.2 Differences between mountain and black-capped chickadees

I chose to compare mountain and black-capped chickadees because they are closely related, yet have different vocalization behaviour. Mountain chickadees show little song variability within individuals, but high regional variation among populations. This suggests it may take time to adjust their vocalizations to noise. However, mountain chickadees use two types of vocalizations during the dawn chorus, suggesting they may be able to deliberately switch between the two to improve signal-to-noise ratios (SNR) in noisy situations. Black-capped chickadees only sing during the dawn chorus, but they do utilize ’pitch-shifting’ to create variability in this signal.

7.2.1 Vocal adjustment and local ambient noise levels

Mountain chickadees changed several aspects of their vocalizations as noise and/or urbanization increased (Chapter 3). The frequency of the lowest notes used in their songs increased and the highest notes tended to be repeated more often. In black-capped chickadees, frequency of the lowest-pitched songs positively correlated with local ambient noise. Although, spectral adjustments correlating with local ambient noise levels are not novel findings (e.g., Slabbekoorn & Peet, 2003; Hu & Cardoso, 2010; Proppe *et al.*, 2012), it is interesting that such closely related species adjusted their songs in different ways. This supports other recent findings that phylogenetic relatedness is not a good predictor of abilities and mechanisms of vocal adjustment (Francis *et al.*, 2011*a*,*c*).

7.2.2 Immediate Plasticity

Both species also showed immediate plasticity in response to experimental noise exposure. Mountain chickadees increased the frequency of the *dee*-note in their calls and changed to singing more than calling. Interestingly, we observed no correlation between *dee*-note frequency and ambient conditions, matching findings that *dee*-note frequency in Carolina chickadees (*Poecile carolinensis*) was also not correlated with local ambient traffic noise (Grace & Anderson, 2014). This suggests that *dee*-note plasticity in mountain chickadees may be a very short-term response. Switching between calls and songs has the dual function of increasing tonality of vocalizations (e.g., red-winged blackbirds *Agelaius phoeniceus*, Hanna *et al.*, 2011), as well as increasing minimum frequencies (e.g., chaffinches *Fringilla coelebs*, Verzijden *et al.*, 2010, and house finches *Carpodacus mexicanus*, Bermúdez-Cuamatzin *et al.*, 2011). In contrast, black-capped chickadees used a completely different mechanism of adjusting to ambient noise. Immediate plasticity in black-capped chickadees has been observed in response to fluctuating traffic noise (Proppe *et al.*, 2011), but here I found evidence that black-capped chickadees used their natural ’pitch-shifting’ ability as a mechanism to adjust overall frequency use during the chorus (Chapter 4). Rather than shifting all individual songs to higher frequencies, they selectively sang fewer low-frequency songs within their normal range of variation. While other species may selectively sing higher-frequency song types from their repertoires (Halfwerk & Slabbekoorn, 2009; Luther & Baptista, 2010), to my knowledge, black-capped chickadees are the only species to use pitch-shifting as a mechanism to avoid masking.

A novel finding in these studies is that immediate plasticity in both mountain and black-capped chickadees correlated with local ambient noise levels. In noisy areas, individuals adjusted their vocalizations in a manner that could reduce masking, whereas in quiet areas they did not. This suggests that appropriate vocal plasticity may either be learned or may evolve as a result of longer-term exposure to high levels of ambient noise (longer than my 5-min exposure, at least). Assuming this is not the result of evolved differences (as the cities I have studied are mostly small and dispersal between rural and urban environments is likely to be high), these findings suggest that learning may play a large role in the ability of avian species to reduce masking in anthropogenic noise (*cf.* Ríos-Chelén *et al.*, 2012). Future studies addressing the time-scale of these changes would be useful for confirming whether these patterns result from developmental plasticity (i.e. learned during song crystallization), or an intermediate period of familiarization (i.e. learned as an adult over hours, days, weeks, etc.).

7.2.3 Detection and Discrimination

Playback studies showed that while there is some evidence for greater detection and discrimination of adjusted songs, the patterns are not straightforward (Chapters 5 and 6). In mountain chickadees, there was evidence that urban songs were less masked than rural songs and that mountain chickadees discriminated between these two signal types. However, discrimination depended on local ambient noise conditions; males in quieter sites discriminated between, and responded more aggressively to, urban stimuli, while birds in noisy neighbourhoods showed high levels of aggression to both stimuli types. This suggests audibility may be confounded with other traits such as perceived aggression. In black-capped chickadees, I found evidence that high-frequency songs were less masked and were detected earlier than low-frequency songs; however, a strong effect of playback order complicated interpretations. Male black-capped chickadees showed faster response to high-pitched stimuli, but only when they were the first stimuli presented.

7.3 Consequences for mountain and black-capped chickadees

7.3.1 Implications for colonization of urban areas

Despite their relatedness, mountain and black-capped chickadees clearly have different mechanisms for adjusting their vocalizations to noise and they react to noise in different ways. Black-capped chickadees can use pitch-shifting to adjust their songs during noisy conditions, and seem extremely well suited to urban noise. In contrast, while mountain chickadees do adjust to noise, their mechanisms seem unlikely to be as effective (switching between songs and calls can only go so far) or as quick (spectral adjustment in songs was not immediate). These differences may partially explain why black-capped chickadees are more common in urban environments than mountain chickadees (Chapter 1), although habitat is likely influential as well.

Despite these drawbacks, however, mountain chickadees are able to adjust their vocalizations, and do invade into the edges of urban areas. In contrast, some species do not adjust their vocalizations, but instead avoid noise altogether. For example, grey flycatchers (*Empidonax wrightii*) avoid noise by leaving noisy habitats (Francis *et al.*, 2011*c*), and European robins (*Erithacus rubecula*) increase the amount of time spent singing at night, when urban noise is low (Fuller *et al.*, 2007). The ability to adjust vocalizations in mountain chickadees may permit them to colonize urban areas, even if not as effectively as black-capped chickadees. That mountain and black-capped chickadees are so closely related, yet show very different abilities and mechanism of vocal adjustment, suggests that learning styles and signalling behaviour are better predictors of vocal adjustment than phylogenetic relatedness.

7.3.2 Potential fitness consequences

Colonization of urban areas, however, is not evidence that populations are healthy. Often urban areas may result in ecological traps (Schlaepfer *et al.*, 2002). For example, birds may be attracted to urban landscapes by temporally-available resources, such as bird feeders. However, once settled, they may face deficits of other resources (e.g., nest sites, food with which to provision young) or impediments to mechanisms of mate choice. For example, vocal adjustment in chickadees may accommodate urban noise, but may also counter signals that evolved for female assessment of males. To date there is little evidence that vocal adjustments actually result in fitness benefits, and it is entirely possible that they result in trade-offs or even in fitness costs (Read *et al.*, 2013). Shifts in signal features which decrease masking by noise may also eliminate features that females are attending to. For example, southern brown tree frogs (*Litoria ewingii*) increase the frequency of their calls in traffic noise. Females, however, prefer low-frequency calls, as call frequency is negatively correlated with male size in many amphibians (Parris *et al.*, 2009). Thus, increasing call frequency in response to noise may render males unattractive to females, or may reduce the ability of females to differentiate and select among males of differing quality, resulting in potential fitness costs to both sexes.

While there is no evidence that female mountain or black-capped chickadees prefer low-frequency songs, there are other metrics they use that may be affected by vocal adjustment. For example, while it is not clear why mountain chickadees use both songs and calls during the dawn chorus, there is some indication that calls may be directed towards females whereas songs are directed towards males (McCallum *et al.*, 1999). Therefore, in noisy conditions, males that switch to songs from calls may be reducing communication with females in favour of males. This may have consequences on extra-pair mating behaviour or even pairing longevity. Similarly, although black-capped chickadees use a different mechanism of vocal adjustment, this mechanism may also affect signal content. Pitch-shifting in black-capped chickadees functions as a signal to neighbouring males and also contains information on dominance which may be used by females to assess male quality (Otter *et al.*, 2002; Christie *et al.*, 2004). If male black-capped chickadees are constrained to avoid their lower bandwidths due to masking from anthropogenic noise, they are also constrained to pitch-shift within a smaller range, perhaps making it more difficult to demonstrate their abilities. Further, there is evidence that lower-frequency songs are actually better at indicating male dominance than higher-frequency songs (Christie *et al.*, 2004). Therefore, as a result of vocal adjustment, female black-capped chickadees may be less able to assess male quality.

7.4 Other chickadee species

Two other chickadee species common to British Columbia are the chestnut-backed (*Poecile rufuscens*) and boreal (*Parus hudsonicus*) chickadees. These two species form the brown-headed chickadee clade, and, with the grey-headed chickadee (*Poecile cinctus*), form the sister group to the black-headed clade (mountain and black-capped chickadees; Gill *et al.*, 2005). Of particular interest is the fact that none of these species use songs during the dawn chorus; they only use calls (Hailman *et al.*, 1994). I hypothesized that mountain chickadees maybe less able to adjust to anthropogenic noise, due, at least in part, to the fact that they use calls during their dawn chorus, which do not transmit as well as songs (Chapter 2). It is therefore possible that chestnut-backed and boreal chickadees would be even more negatively affected by anthropogenic noise. Chestnut-backed chickadees are quite common in sub-urban areas in Vancouver and in Victoria (personal observation), but whether they selectively avoid noisy areas is not clear. An informal scan of E-Bird (http://ebird.org) reveals that while boreal chickadees are not common in urban areas, they have been observed numerous times in the Greater Toronto Area, Montreal, Quebec, and Halifax (to name a few cities). Therefore, future studies addressing whether or how these two species deal with noise would yield further insight into the mechanisms of vocal adjustment and the consequences of anthropogenic noise on different chickadee species.

7.5 Overall Conclusions

Through this dissertation I provide evidence that anthropogenic noise can interfere with chickadee vocalizations more than structural changes to urban habitats. I also found evidence that two closely related species adjust to noise in different ways and that even immediate responses to noise may vary according to local ambient noise levels. Finally I provide some evidence that adjusted vocalizations do improve audibility in noise, but further studies and clarification are required. Beside specific implications for this field of study, these findings have broader implications for conservation issues as well as for society in general.

In British Columbia, Canada, most areas outside of Vancouver are not highly urbanized, yet I still found evidence that chickadees are being affected by anthropogenic noise. From the literature, it is evident that noise affects birds in many different places and situations, and noise exposure is likely to grow as populations grow. The findings of this dissertation suggest we can predict how well a species can adjust to anthropogenic noise by considering its ability to learn, vocal variability, and natural singing styles. Better assessment of a species' vulnerability to urbanization will help conservationists foresee problems before they arise, and hopefully help mitigate them, thus preventing species homogenization and preserving species richness and diversity (Proppe *et al.*, 2013). However, an important finding of this dissertation is that even immediate responses to noise may be the product of a longer-term exposure to ambient noise. Thus immediate plasticity may not be as immediate as previously thought, and even species which demonstrate immediate plasticity may take longer than expected to adjust their vocalizations to noisy conditions. Additional research into the time frame required to develop these responses would be beneficial.

These conclusions also assume that vocal adjustment is a benefit to species living in urban, noisy habitats. But whether vocal adjustment actually improves fitness is not well understood. Research into exactly how avian communication is being disrupted and how such disruptions can be mitigated is helpful, but research into the potential consequences of vocal adjustment are still needed (Read *et al.*, 2013). In addition, noise interferes with more than simply communication. Noise can result in increased stress, with consequences on foraging, health and reproductive output, and can mask cues associated with either predating or avoiding being predated (Barber *et al.*, 2010; Ortega, 2012; Francis, 2015).

While it is useful to assess which species will be most challenged by urban noise, ultimately noise pollution should be reduced. Humans are generally more affected by the "annoyance" factor of noise (Goines & Hagler, 2007) than by communication disruption. However, the problem of noise to humans has become such a serious issue that the World Health Organization (2011) has released a report on the issues surrounding noise pollution. Although avian communication is the focus of this dissertation, it should be recognized that any changes made to alleviate the effects of noise on birds would likely benefit humans as well (Slabbekoorn & Ripmeester, 2008). It is my hope that the results from this dissertation offer yet more evidence in support of noise mitigation measures.

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