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The effect of anthropogenic noise on songbird vocal communication

by

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Abstract

Anthropogenic noise is increasingly widespread as human development continues. Noise can negatively affect humans and wildlife, but the most deleterious effects are incurred by species that rely on vocal communication for mating, territory defence, and other vital functions. Songbirds are particularly susceptible, often experiencing declines in richness and abundance in noise-affected areas. Yet, some species remain abundant in noisy environments. High frequency vocalizations, or the ability to shift to higher frequencies, is one adaptation that may allow birds to communicate above low frequency anthropogenic noise. However, the mechanisms underlying frequency shifting, and the relationship between vocal frequency and abundance, are still not fully understood. I examined whether black-capped chickadees produce songs at higher frequencies in noisy areas, and whether these differences could be due to altered vegetative structure rather than noise. I also examined whether chickadees could plastically change song frequencies as noise increased. Finally, I surveyed abundance and recorded vocalizations from several songbird species to evaluate whether plasticity in song frequency, or mean song frequency, could predict how abundance and urban prevalence would be affected by anthropogenic noise. I found that black-capped chickadees shifted to higher song frequencies in noise-affected areas, and that vegetative differences did not account for these changes. Further, chickadees at roadside locations plastically increased their song frequencies as noise levels increased. Vocal plasticity, however, was not related to abundance in my multi-species comparison. Instead, noise-related changes in abundance were predicted by a species minimum song frequency. Nevertheless, minimum song frequency did not necessarily predict whether a species would be widespread in urban areas. In addition to frequency parameters, urban species may avoid overlap with noise through spatial and temporal mechanisms, but those that lack any mechanisms to communicate within anthropogenic noise may experience declines. Thus, reducing anthropogenic noise may increase the quality of urban habitats for birds.

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Chapter 1

General introduction

Anthropogenic – human induced – noise is increasing across the globe as industrial areas and the roads that connect them continue to expand (Forman 2000; Forman 2004; McDonald, Forman and Kareiva 2010). While the percentage of the landscape affected by anthropogenic noise is steadily increasing, an equally important issue is the increasing intensity of anthropogenic noise within already developed networks (Forman 2003). Higher volumes of vehicular and air traffic, combined with denser industrial development, are increasing the amplitude of anthropogenic noise, and reducing the length of quiet gaps between noise events in even the most remote landscapes (Barber, Crooks and Fristrup 2010). Anthropogenic noise in urban areas has reached levels that affect human behaviour (Stansfeld et al. 2009) and speech (Kujala and Brattico 2009), as well as our ability to learn (Shield and Dockrell 2008), and sleep (Stosic, Belojevic and Milutinovic 2009). Yet, the effects of anthropogenic noise on wildlife may be more severe.

Early investigations into the affect of noise on wildlife focused on whales and other aquatic mammals (Myrberg 1990; Richardson 1995). Low frequency sounds (<1 kHz) from boats and drilling procedures appear to alter vocal communication in several marine species (Fristrup, Hatch and Clark 2003; Foote, Osborne and Hoelzel 2004), and have in some cases been linked with avoidance behaviour and individual mortality (Gordon et al. 2003; Weilgart 2007). More recently, anthropogenic noise has also been shown to alter population structure and distribution of many terrestrial organisms; including mammals, birds, and amphibians (Laiolo 2010). Many wildlife species are averse to noise, and thus, linear sources of anthropogenic noise such as highways may subdivide populations, potentially contributing to a decline in abundance (Jaeger et al. 2005; Jones 2008; Schaub, Ostwald and Siemers 2008; Rabanal et al. 2010). Wildlife populations exposed to high levels of anthropogenic noise also exhibit more agonistic behaviour (Goudie and Jones 2004), increased stress levels, and potentially suffer hearing loss (Bowles and McBride 1998; Blumstein 2010). Interruption of vocal communication, however, may be the primary factor by which anthropogenic noise affects wildlife (Reijnen and Foppen 2006).

Animals communicate via vocal, visual, or chemical signals (Maynard-Smith and Harper 2005). Studies on animals that employ multiple modes for signal transmission, or rely heavily on visual or chemical signals, have found mixed or no effect of noise on these species. For example, the effect of noise on fishes is variable (Popper 2003), small mammals do not avoid noisier roads (McGregor, Bender and Fahrig 2008), and elk do not avoid crossing highway underpasses during the highest traffic periods (Gagnon et al. 2007). In contrast, species that rely primarily on vocal communication generally respond to noise through avoidance or modification to both communication and behaviour. Many species of whales modify their communication in noisy environments (Nowacek et al. 2007); bats avoid foraging in areas with high noise (Schaub, Ostwald and Siemers 2008); insects alter courtship (Polajnar and Cokl 2008; Samarra et al. 2009); frogs produce more advertisement calls (Kaiser and Hammers 2009), but elicit less female response (Bee and Swanson 2007); and birds either avoid noise or alter their communication (Reijnen, Foppen and Veenbaas 1997; Slabbekoorn and den Boer-Visser 2006).

Vocal communication in songbirds

Anthropogenic noise is of particular concern for songbirds because mating and territorial defence are facilitated by vocal communication (Kroodsma and Byers 1991). For successful communication to occur the sender - the individual producing the signal - must generate a signal with a unique and discernable message. In turn, the receiver must be able to detect and discriminate this message from other competing sounds (Wiley 2006). As long as the signal is much louder than ambient noise (i.e., good signal-to-noise ratio; Andersson and McGregor 1999), discrimination by the receiver is relatively straightforward. However, signal-to-noise ratio decreases with increasing distance from the source, obstructing objects, and ambient noise (Wiley and Richards 1982). Thus, at some distance the receiver will no longer be able to detect or discriminate the message in the signal. The range in which a signal can be heard is known as the ‘active space’ for that signal (Brenowitz 1982). As anthropogenic noise increases, the active space of a signal is reduced, because its signal-to-noise ratio is lower. This was demonstrated empirically in three passerine species by Lohr, Wright and Dooling (2003). Captive birds were conditioned to respond to playback of a stimulus for a food reward. Vocal stimuli were then played back in conjunction with different amplitudes of white noise and road noise. At higher noise amplitudes the correct detection of vocal stimuli decreased significantly. These empirical results, combined with the known properties of sound, suggest that high levels of anthropogenic noise do reduce the range of communication between individuals, which may decrease a songbirds' ability to attract potential mates and repel rivals.

Birds also use vocal and non-vocal acoustic signals for functions other than mate attraction and territorial defence. For example, the begging calls of nestlings elicit food provisioning by adult birds. If these calls are masked by anthropogenic noise, parents may reduce their provisioning rates, potentially resulting in altered vocal and physical development of the nestlings (Leonard and Horn 2005; Leonard and Horn 2008). Other vocal signals are used to communicate within a flock, or to one particular individual (McGregor and Peake 2000). To avoid deleterious eavesdropping by predators and conspecifics some of these vocal signals are structured for short transmission distances. For example the high frequency 'variable see' of the black-capped chickadee is uttered between mates prior to copulation and may signal female responsiveness (Ficken, Ficken and Witkin 1978). Other vocalizations are produced at low amplitudes; such as the *tseet* call of the black-capped chickadee, which functions as a contact call among flock mates (Guillette et al. 2010). Some species also use 'soft songs' as indicators of dominance status in close range territorial bouts (Anderson et al. 2008). Since these vocalizations are produced at low signal-to-noise ratios, they may be particularly susceptible to masking by anthropogenic noise. Other non-vocal acoustic signals, such as a wing whirs, may play an important role in the detection of prey and avoidance of predators (Barber, Crooks and Fristrup 2010).

Masking of these signals may alter community level interactions. In sum, much critical behaviour in songbirds is facilitated by vocal communication. By hampering vocal communication, anthropogenic noise may alter the associated behaviours.

The effects of anthropogenic noise on songbirds

If anthropogenic noise inhibits communication by masking the vocal signals used to maintain reproductive and territorial functions, this may explain its deleterious effects on many songbirds. This hypotheses was tested explicitly in a controlled laboratory experiment where female zebra finches (*Taeniopygia guttata*) preferred their mated male when presented with two males under quiet conditions (Swaddle and Page 2007), but randomly chose either male when white noise was used to mask vocal signals. In addition to weakened pair bonds, anthropogenic noise has been linked to reduced songbird abundance and richness, altered age structure, weakened reproductive success, and altered community level interactions (Table 1).

In the Netherlands, songbird density in many species was reduced up to 1 km from a particularly ubiquitous source of anthropogenic noise – busy highways (Reijnen and Foppen 1995; Reijnen et al. 1995; Reijnen, Foppen and Meeuwsen 1996; Reijnen and Foppen 2006). Highways also increase vegetative edges, introduce exotic plant species, deposit sediment, increase visual stimulus, and add air pollutants; but, noise was implicated in these declines because it was the only road effect that permeated wooded habitats at greater than 400 m from a road

(Reijnen and Foppen 2006). Similarly, Stone (2000) documented a decrease in species richness across multiple habitat types as anthropogenic noise increased. More recently, Bayne, Habib and Boutin (2008) found that songbird density at quiet well pads was 1.5 times the density at noisy compressor stations in Northern Alberta, Canada. By using locations with similar habitat characteristics, this study circumvented many of the confounding habitat changes that accompany roadside and urban habitats. In a similar study, species richness was higher at quiet, non-operational well sites in New Mexico, USA, in comparison to noisy, operational well stations (Francis, Ortega and Cruz 2009). Finally, Dube et al. (unpublished data) found that songbird abundance was higher near (< 400 m) a low use transportation corridor than near the high use TransCanada Highway in Banff National Park.

In addition to altering abundance and species richness, anthropogenic noise alters the age structure of the species that remain in the affected areas. Less experienced (first year) breeders are more likely to inhabit noisy locations than more experienced individuals. For example, the lower number of willow warblers (*Phylloscopus trochilus*) observed near (< 200 m) Dutch highways was primarily due to the absence of experienced breeders (Reijnen and Foppen 1994). Habib, Bayne and Boutin (2007) found that 48% of ovenbirds (*Seiurus aurocapilla*) breeding near noisy compressor stations in the Boreal forests were first year breeders, while only 30% were first year breeders at quiet well pads. Dube et al. (unpublished data) found that inexperienced red-breasted nuthatches (*Sitta canadensis*) were more likely to be found near the TransCanada Highway. In these studies, lower dominance status may relegate these first year breeders to 'lower quality' roadside territories (Fretwell and Lucas 1970). A similar situation was noted in two North American warbler species, where first year breeders were more likely to breed at higher elevations, where environmental conditions are harsher (Rohwer 2004).

Since noisy habitats appear to represent lower quality territories for songbirds, it is not surprising that anthropogenic noise has also been associated with lower pairing success and reproductive output. Ovenbirds near noisy compressor stations in Northern Alberta were less likely to be paired when compared to quiet sites (Habib, Bayne and Boutin 2007), and willow warbler reproductive output was reduced by 40% in roadside habitats in the Netherlands (Reijnen and Foppen 1994). Interestingly, Reijnen and Foppen (1994) failed to detect a decrease in willow warbler nest success near roads once eggs were laid, and Francis, Ortega and Cruz (2009) actually documented an increase in nest success for songbird species at noisy, operational well sites. Francis, Ortega and Cruz (2009) suggest that anthropogenic noise interfered with a local predator's ability to detect prey, resulting in reduced abundance of predatory species at noisy sites; the western scrub-jay (*Aphelocoma californica*) in this case.

Community level interactions are complex, and while many species are affected negatively by noise, others may benefit (Francis, Ortega and Cruz 2009; Slabbekoorn and Halfwerk 2009). As demonstrated by the increase in nesting success at noisy well sites, ecological communities are dynamic. Just as some species have adapted to counter parasitic nest predation by cowbirds and cuckoos

(Davies and Brooke 1989; Briskie, Sealy and Hobson 1992), some songbirds have favourable adaptations for communication in high levels of anthropogenic noise.

Modification to songbird vocalizations in response to anthropogenic noise

Patricelli and Blickley (2006) summarize the salient features of animal vocal signals in four categories: 1) the timing of vocal delivery, 2) temporal structure of the vocalization, 3) amplitude, and 4) frequency structure. Each of these can be modified to increase the efficacy of vocal communication in anthropogenic noise. I briefly review the first three categories in order below and then more thoroughly address the role of frequency structure as it most directly relates to my research objectives.

1) *Timing of vocal delivery*

Most songbirds concentrate their vocal output into a short burst of singing in the morning – known as the dawn chorus – which occurs when environmental conditions such as temperature and humidity are ideal for song transmission (Henwood and Fabrick 1979). Unfortunately, the hours of the dawn chorus occur over the most intense period of anthropogenic noise – rush hour traffic (Patricelli and Blickley 2006; Warren et al. 2006). At least one species, the European robin (*Turdus migratorius*), sings nocturnally in areas with higher levels of anthropogenic noise, presumably to avoid the overlap with peak traffic intensity (Fuller, Warren and Gaston 2007). Nocturnal singing has been observed in other urban songbirds, but has often been attributed to higher levels of light (Molenaar

J.G.de, Sanders M.E and Jonkers D.A 2006). The role of anthropogenic noise in nocturnal singing warrants further examination.

Anthropogenic noise is also highly variable on a short time scale. For example, noise near roads can rise and fall with the passing of each vehicle. Some birds may produce songs at high repetition or during noise gaps to take advantage of fluctuating noise levels (Warren et al. 2006). Chaffinches increased repetition with high noise levels in laboratory studies (Brumm and Slater 2006), and several songbird species produce songs during gaps in conspecific singing (Cody and Brown 1969; Ficken, Ficken and Hailman 1974; Brumm 2006). Further research will reveal the prevalence and significance of temporal song shifts as a mechanism for communication in anthropogenic noise.

2) *Temporal structure of the vocalization*

The internal structure of a signal will also affect how it transmits in anthropogenic noise (Warren et al. 2006). Many songbirds modify vocal bandwidth and amplitude modulation (AM) to optimize transmission in habitats differing in vegetative structure, demonstrating that songbirds are able to modify the internal structure of their vocalizations to enhance transmission (Morton 1975; Boncoraglio and Saino 2007; Barker 2008; Ey and Fischer 2009). Lohr, Wright and Dooling (2003) found that songbirds in the laboratory were more likely to detect signals of narrow bandwidth (pure tones) and high AM when presented in conjunction with synthesized road noise. However, neither bandwidth reduction nor change to AM in response to anthropogenic noise has been examined in the field.

3) *Amplitude*

In addition to amplitude modulation, an overall increase in amplitude improves the signal-to-noise ratio of a vocalization, and thus, increases the distance it will transmit (Brumm and Slabbekoorn 2005). This phenomenon – known as the Lombard effect (Lombard 1911) – has been documented in humans (Junqua 1993), and more recently in birds. In both laboratory (Cynx et al. 1998; Manabe, Sadr and Dooling 1998) and field experiments (Brumm 2004a; Brumm 2004b), songbirds increased the amplitude of their signals with increasing noise. Amplitude modulation may provide a short-term mechanism for adaptation to anthropogenic noise in songbirds.

4) *Frequency structure*

When presented simultaneously, two vocal signals will be more detectable if they are produced at different frequencies (Klump 1996). If both signals are produced at the same frequency, the louder signal will partially or completely mask the other. Anthropogenic noise is primarily contained within low frequencies (< 4K; (Skiba 2000)), and it decreases in intensity as frequency increases. Thus, by singing at higher frequencies, songbirds may experience spectral release from anthropogenic noise. Specifically, their vocalizations will be more detectable to con- and heterospecifics (Wiley 2006). Therefore, songbirds that sing at higher frequencies could remain more abundant in noisy environments. This idea was tested by surveying songbirds along two parallel transects near (100 m) and far (950 m) from a busy roadway (Rheindt 2003). While overall abundance was reduced near the roadway, species with the highest song frequencies did not experience this decline. Unreplicated sampling and weak statistical power limit the generalizability of these results. However, in a recent survey of song frequencies used by urban birds – a group more likely to experience anthropogenic noise – and rural birds, minimum song frequency of urban species was higher than their rural counterparts (Hu and Cardoso 2009).

Some songbirds that sing at frequencies that are overlapped by anthropogenic noise are shifting their vocalizations to higher frequencies when exposed to long-term anthropogenic noise. For examples, great tits (*Paris major*) inhabiting noisy sites sang at higher frequencies than their counterparts at non-noisy sites (Slabbekoorn and Peet 2003). A follow-up study found that the overall frequencies of urban great tit populations were also higher than those in rural areas (Slabbekoorn and den Boer-Visser 2006). Shifting song frequencies in anthropogenic noise has now been documented in several bird species (Fernandez-Juricic et al. 2005; Wood and Yezerinac 2006; Brumm, Schmidt and Schrader 2009; Nemeth and Brumm 2009; Parris and Schneider 2009; Hu and Cardoso 2010; Luther and Baptista 2010). While the observed frequency shifts are not always dramatic in scale, it is notable that all studies to this point have found the same pattern – higher frequency vocalizations in higher levels of anthropogenic noise.

Dissertation Objectives

Anthropogenic noise is increasing thought to cause some songbird species to alter the frequency structure of their vocalizations. However, at least one potential confound still needs to be addressed. Vegetative structure in urban areas and roadside habitats is often dramatically different from that found in rural and protected areas (Bowles and McBride 1998; Chace and Walsh 2006; McEwan and McCarthy 2008; Flory and Clay 2009). Because birds alter their vocalizations in response to the vegetative composition of their associated habitats, a consistent vegetative difference between high and low noise habitats could account for observed shifts in song frequencies (Morton 1975). Specifically, if sites with anthropogenic noise are less densely treed than low noise sites, the acoustic adaptation hypothesis (Rothstein and Fleischer 1987) would predict that birds would use higher song frequencies based solely on habitat structure (Wiley and Richards 1982). Recent studies at well sites have established that songbird density can be affected by noise alone (Habib, Bayne and Boutin 2007; Francis, Ortega and Cruz 2009), but no study has explicitly contrasted the role of vegetation and noise in frequency shifting behaviour.

The timescale at which birds alter song frequency in response to their environment is also poorly understood. Frequency modification may result froms individual behavioural plasticity (Patricelli and Blickley 2006; Slabbekoorn and Ripmeester 2008). If this is the case, species with the ability to produce vocalizations across a broad range of frequencies may be able to shift to higher frequencies as noise increases, and thus, may be pre-adapted for communication in noisy areas. However, the higher frequencies observed in birds living in noisy environments could also develop over several generations through the processes of learning and selection (Sung and Park 2005). In this case, frequency shifts may represent directional adaptation with the potential to create population divergence and speciation (Slabbekoorn and Smith 2002; Podos and Warren 2007). The first step to addressing this issue is to test whether species known to shift song frequencies can do so in a relatively short time period.

In addition to frequency shifting, absolute frequency may also be an important indicator of whether a species can communicate in noisy environments, and thus, remain abundant (Hu and Cardoso 2010). Frequency, and frequency plasticity, may be particularly important for birds inhabiting urban areas. The exclusion of species without vocal adaptations for communication in noise may partially explain lower avian diversity in urban environments (Rabin and Greene 2002; Slabbekoorn and Ripmeester 2008; Hu and Cardoso 2009). However, this prediction has not been directly tested. Further, the relative importance of absolute song frequency and frequency plasticity has not been examined.

In Chapter 1, I evaluated whether shifts in the frequencies of the black-capped chickadee's (*Poecile atricapillus*) *fee-bee* song are more strongly related to differences in anthropogenic noise or vegetative structure. In Chapter 2, I determined whether black-capped chickadees can plastically alter their song frequency as noise levels change with traffic intensity over the morning rush hour on weekdays, and less intense weekends. I used the black-capped chickadee as a model organism for these two studies because they are successful adaptors to human-altered habitats (Smith 1991), and are closely related to the great tit, a species with documented song shifting capabilities (Slabbekoorn and Peet 2003). In Chapter 3, I conducted a census and recorded vocalizations from multiple songbird species to examine whether song frequency, or frequency plasticity, could predict a species' change in abundance with increasing anthropogenic noise; and more broadly, whether these frequency traits are related to a species ability to remain widespread in urban areas.

The objective of these three chapters is to increase our understanding of vocal communication in songbirds in response to anthropogenic noise. The rapid alteration of the environment over much of our planet due to human activity (Ehrlich 2009) presents us with an unprecedented opportunity to understand how dynamic vocal communication systems respond to novel and formidable stimuli, such as anthropogenic noise. However, rapid human-induced change to ecosystems may also negatively impact avian diversity. I aim to evaluate the effect of anthropogenic noise on the abundance of several avian species, and to provide urban planners and wildlife managers with an empirically tested metric for evaluating how anthropogenic noise will generally affect songbirds in relation to their vocal frequencies.

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Table 1-1. The effects of anthropogenic noise on avian communities and communication. (Reproduced from Kociolek et al. In review. Effects of the road transportation network on bird populations. Conservation Biology).

Category		Effect	References
Community			
	Species diversity	Reduced with increased noise	Stone 2000
	Total density / abundance	Reduced with increased noise	Reijnen et al. 1995; 1996; Kuitunen et al. 1998; Bayne et al. 2008
	Species densities / abundance	No overall reduction	Peris & Pescador 2004
		Reduced with increased noise	Reijnen & Foppen 1994; Reijnen et al. 1995, 1997
		Dependent on species	Kuitunen et al. 1998; Peris & Pescador 2004
		Higher abundance of birds with higher song pitch near roads	Rheindt 2003
	Age structure	Younger at noisy sites	Reijnen & Foppen 1994; Habib et al. 2007
	Physiological health	Increased stress at higher noise levels	Campo et al. 2005
		No stress difference at higher noise levels	Byers et al., unpublished data
Breeding cycle			
	Pairing and mate retention	Reduced courtship behaviour	Goudie & Jones 2004

		Reduced pair success	Habib et al. 2007
		Reduced pair preference	Swaddle & Page 2007
	Territory and nest site selection	Farther from noise sources	Francis et al. 2009
	Nest success	Increased with noise for some species	Francis et al. 2009
Foraging			
	Begging calls	Reduced parental discrimination in noise	Leonard & Horn 2005
	Prey location and predation risk	Predator reduction increases nest success in noisy locations	Francis et al. 2009
		Potential community level noise effects	Slabbekoorn & Halfwerk 2009
		Increased vigilance at higher noise levels	Quinn et al. 2006
Communication			
	Temporal adjustment	Sing more at night in noisy locations	Fuller et al. 2007
	Amplitude increase	Sing louder song with louder noise (Lombard effect)	Cynx et al. 1998; Brumm 2004a, 2004b; Brumm et al. 2009; Osmanski & Dooling 2009
		Louder begging calls in higher noise	Leonard & Horn 2005

	Pitch modification	Increased pitch in higher noise	Slabbekoorn & Peet 2003; Fernandez-Juricic et al. 2005; Slabbekoorn & den Boer-Visser 2006; Wood & Yezerinac 2006; Parris & Schneider 2009; Kirschel et al. 2009; Nemeth and Brumm 2009
		No pitch correlation with road noise	Skiba 2000
	Redundancy	More repetition in higher noise	Brumm & Slater 2006
	Detection of con- and heterospecific vocal signals	Reduced detectability of signals in noise	Lohr et al. 2003; Langemann et al. 1998
	Response to signals	Strongest response to played back signals when ambient noise levels are similar to local environment	Mockford & Marshall 2009
	Reviews	Effects of noise and implications	Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2008; Barber et al. 2009
Brain response			
	Gene activation	Does not differ when noise added to playback of song	Vignal et al. 2004

Chapter 2

Black-capped chickadees sing at higher pitch in elevated anthropogenic noise in both open and closed forests

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High levels of anthropogenic noise are related to changes in the diversity (Rheindt 2003; Francis, Ortega and Cruz 2009), density (Reijnen and Foppen 1995; Reijnen, Foppen and Meeuwsen 1996; Bayne, Habib and Boutin 2008; Foppen and Reijnen 1994), dispersal, and age structure (Habib, Bayne and Boutin 2007) of songbird communities. These changes presumably occur because anthropogenic noise interferes with acoustic communication (Slabbekoorn and Ripmeester 2008; Parris and Schneider 2009), on which birds depend for territorial defence, mate selection, nest provisioning, and predator detection (Catchpole and Slater 2008). Some bird species seem unaffected by high levels of anthropogenic noise and variation among species may be related to the song frequencies used by each species. Specifically, species whose song frequencies are overlapped by anthropogenic noise (generally between 0-4 KHz; Skiba 2000) are less likely to inhabit noisy areas, while the densities of species using non-overlapped frequencies appear to be less affected by anthropogenic noise (Rheindt 2003; Hu and Cardoso 2009).

Some species whose song frequencies overlap with anthropogenic noise may improve the efficacy of their vocal signalling by shifting to higher song frequencies (Rabin and Greene 2002). A pioneering study by Slabbekoorn and Peet (2003) found that urban great tits (*Parus major*) in noisy locations sang at higher frequencies than their counterparts in quiet locales. This initial observation has now been confirmed in a handful of other species (Fernandez-Juricic et al. 2005; Slabbekoorn and den Boer-Visser 2006; Wood and Yezerinac 2006; Mockford and Marshall 2009; Nemeth and Brumm 2009; Parris and Schneider

2009) leading to the noise-dependent frequency hypothesis (Halfwerk and Slabbekoorn 2009), which suggests that variation in anthropogenic noise is partially responsible for variation in the song frequencies of many songbird species (reviewed by Patricelli and Blickley 2006; Barber, Crooks and Fristrup 2010).

Despite its emerging prevalence, the association between anthropogenic noise and bird song frequencies has rarely been studied with concomitant attention to variation in habitat conditions. Areas with high levels of anthropogenic noise are typically closer to roads, human infrastructure, and areas of higher human habitation, all of which can dramatically alter vegetative structure (Bowles and McBride 1998; Chace and Walsh 2006; McEwan and McCarthy 2008; Flory and Clay 2009). Depending on the history of settlement and land use patterns in an area, forest patches in more developed areas can be more fragmented and open (Beissinger and Osborne 1982; Dorney et al. 1984), or older and denser (e.g., McBride and Jacobs 1986; Gallant et al. 2003; Raumann and Cablk 2008) than surrounding sub-urban and non-urban forests.

Vegetative structure is particularly relevant to the frequency of bird song because it appears to generate both inter- and intraspecific variation in bird song frequencies. In an extensive interspecific study of 177 tropical bird species, Morton (1975) discovered that bird species inhabiting different habitat types (e.g., forest, edge, grassland) exhibited different song characteristics. Subsequent work showed that in obstructed environments (such as forests) birds typically sing at relatively low frequencies (Marten and Marler 1977; Padgham 2004) whereas in more open environments (such as grasslands) birds sing higher frequency songs and use more trill-like vocalizations (Brown and Handford 1996; Naguib 2003). The reason for these differences may be that higher frequencies and broadband pulses are more susceptible to scattering and degradation by obstructing objects such as trees (Wiley and Richards 1978; Wiley and Richards 1982). Similar intraspecific differences in song structure have been demonstrated in populations that inhabit different forest types (Hunter and Krebs 1979; Nicholls and Goldizen 2006; Dingle, Halfwerk and Slabbekoorn 2008). These findings have given rise to the Acoustic Adaptation Hypothesis (AAH; Rothstein and Fleischer 1987), which posits that birds adapt their songs to local habitat conditions. The AAH has garnered extensive support in the literature (see reviews Boncoraglio and Saino 2007; Barker 2008), suggesting that it is a widespread phenomenon among songbirds.

Because habitat changes typically accompany anthropogenic noise, the increases in song frequency associated with noise may actually be caused by concurrent changes in vegetation structure. Previous studies of noise effects have typically either standardized or ignored variation in vegetation. Here, we explicitly test whether differences in vegetative structure can account for the higher frequencies observed in the songs of birds exposed to high levels of anthropogenic noise. We tested this hypothesis by recording black-capped chickadees (*Poecile atricapillus*; Linnaeus, 1766) inhabiting closed and open canopy forests in areas with high levels of anthropogenic noise, and open canopy forests in areas with low noise levels. Black-capped chickadees are closely related to great tits, but their ability to shift song frequency in response to elevated ambient noise has not yet been demonstrated. If vegetative structure is the primary factor driving changes in song frequency, we predicted that chickadees residing in the most open sites (noisy or quiet) would sing at higher frequencies. Conversely, if anthropogenic noise is the primary factor driving changes in song frequency, we predicted that only the chickadees residing in noisy sites would sing at higher frequencies.

Methods

Site selection

While urban centers often contain patchy, fairly open forests tracts, the City of Edmonton (53° 34' N 113° 31' W) has preserved several extensive forest patches along the North Saskatchewan River and its associated ravines. Fire has been suppressed in these forests for well over sixty years (J Helder, personal communication); a condition that often increases the density of trees, saplings and large shrubs in relation to the surrounding natural areas (Gilliam and Platt 1999; Penman et al. 2009). Fourteen sites with relatively high levels of anthropogenic noise were selected from forest patches within the City of Edmonton for recording black-capped chickadee songs (Figure 2-1). Sites were separated by no less than 300 m and up to 17 km, with a mean pairwise distance between sites of 6.71 ± 1.06 km (standard error of the mean; SEM). Based on measurements of canopy cover recorded by Mandryk and Wein (2006), seven of these sites were classified as relatively open canopy forests, and seven as relatively closed canopy forests. In addition, ten sites with relatively open canopy forests and minimal noise disturbance were identified in Elk Island National Park (53°35' N 112°59' W), approximately 30 km east of Edmonton. These sites were separated by no less than 300 m and up to 14 km, with a mean pairwise distance between sites of 5.82 ± 0.98 km (SEM). Despite the protected status of the park, forests there are generally less dense than nearby forests outside the park because of extremely high levels of herbivory (Hood and Bayley 2008; Didion, Kupferschmid and Bugmann 2009). All recordings were made in areas where there was at least 1 ha of forest with similar canopy cover.

We recorded chickadee songs in three forest categories: 1) high noise open-canopy sites (open noisy), 2) high noise closed-canopy sites (closed noisy), and 3) low noise open-canopy sites (open quiet). Deciduous tree cover was dominant in all sites and edge habitat was minimized by selecting continuous forest tracks with similar structural characteristics (i.e., stand age, species composition, density, and tree height; based on data from Mandryk and Wein (2006) and the Alberta Vegetative Inventory (AVI)). Each site was separated by > 300 m making it unlikely that a single black-capped chickadee was recorded at more than one site (territories ~175 m in diameter; (Stefanski 1967). To avoid confounding effects of anthropogenic disturbance, no site was closer than 400 m to a highly or moderately used paved road (> 5000 cars/day, 2007 Traffic Flow Map, City of Edmonton).

To confirm expected differences in canopy cover between our forest categories, overhead canopy cover was assessed in four locations at every point where a chickadee was recorded. To assess overhead canopy cover a photo was taken directly upward with a digital camera (Canon PowerShot S50; Canon Canada Inc.; Mississauga, Ontario, Canada) at 1.5 m above the ground within 20 m of the bird's location. A second photo was taken at 10 m and 90° to the right of the first location, a third at 10 m and 90° to the right of the second location, and a fourth at 10 m and 90° to the right of the third location. Using this method, habitat characteristics were quantified in the area where chickadees actually occurred.

Vocal Recording

Each site was visited twice between April 23 and May 11, 2007. Black-capped chickadees were recorded from 30 minutes before sunrise (~0500 hours) until 1300 hours. Multiple sites were recorded simultaneously so that birds were recorded at similar dates and times in all categories. All recordings were conducted using a Marantz PMD670 solid state recorder and a Sennheiser ME67 directional microphone (Saul Mineroff Electronics, Elmont, New York, USA). All chickadees were recorded within 25 meters of the microphone. Once a chickadee was located, recording continued until singing ceased or the recording time reached 5 minutes. We recorded up to six birds at each site. In some cases multiple birds were recorded simultaneously. We pooled these individuals for the analyses because it was not always possible to positively distinguish among individuals.

Analysis

Twenty black-capped chickadee songs, consisting of 2 tonal notes (*fee bee* song with *fee* and *bee* notes) were selected from each recording site for analysis. Song selections were spread evenly among all recording sessions made from each site and randomly selected within recording sessions. Once selected, each song was measured using SIGNAL 5.0 sound analysis software (Engineering Design 2008, Berkeley, California, USA). Peak frequency (i.e., frequency at maximum amplitude) of the *bee* note was measured using a power spectrum (i.e., fast Fourier transform; FFT) with a window size of 32,768 points for a frequency resolution of 1.3 Hz. The frequency of the *bee* note is highly conserved in chickadee songs, and is also highly correlated with the frequency of the *fee* note (Weisman et al. 1990; Horn et al. 1992). Thus, frequency of the *bee* note is a reliable predictor of the overall song frequency.

Overhead canopy cover was calculated by overlaying a standardized grid on each photo in Picasa 3.1 (Google Inc. 2003, Mountain View, California, USA), counting the number of cells with > 50% cover, and then dividing the total covered grids by the total number of grids (covered grids/108; method modified from aerial photography methods for estimation of canopy cover after (Jennings, Brown and Sheil 1999; Stewart et al. 2007)). Percent cover data were arcsine transformed to achieve normality (Zar 1999).

Ambient noise was measured directly from each audio track containing chickadee songs. To calculate ambient noise, each track was edited into six segments of equal length and the first 1,000 milliseconds in each section free from any bird vocalizations or unusual noise bursts was used for analysis. Similar to Slabbekoorn (2004), energy (in volts) was measured in eight 1,000 Hz bandwidths from 0 – 8,000 Hz. Each measurement was taken from a spectrograph with a spectral cutoff of -70 dB relative to the maximum amplitude and a window size of 1,024 points. Voltage measurements were converted to decibels (dB) via the formula $\text{dB} = -20 \log_{10} (\text{Volts})$. The six measurements were then averaged to create one measure of energy in each 1,000 Hz bandwidth for each recording track. All tracks within each site were then averaged to produce one mean measurement of ambient noise at each site within each frequency band. The lowest recorded dB level was set to zero, and all other dB measurements were relative to this point.

General linear mixed models were used to compare *bee* peak frequency and overhead canopy cover among the three forest types. Each model included site as a random factor to account for repeated recordings within sites (Cnaan, Laird and Slasor 1997). Post hoc pairwise comparisons were conducted to identify the source of significant main effects. For ambient noise, all eight frequency bandwidths were entered into a multivariate analysis of variance (MANOVA) to assess overall difference in noise between the aforementioned forest categories, with subsequent univariate F tests to evaluate significance of each bandwidth independently. Post hoc pairwise comparisons were conducted to determine significance between forest categories. All statistical tests were conducted in Systat V12 (Systat Software Inc. 2008, Chicago, Illinois, USA). Any p value ≤

0.05 was considered to be significant, and means are reported with standard error (SEM).

Results

Analysis of overhead canopy cover confirmed significant differences among the three categories used for forest type (Figure 2-2; $F_{2, 218} = 12.84$, $p < 0.001$). Pairwise comparisons revealed that overhead canopy cover was significantly different between each site type with open quiet sites (61.62 ± 2.66%) having less canopy cover than both open noisy sites (71.07 ± 2.43%; $t = -2.58$, $p < 0.027$) and closed noisy sites (81.81 ± 2.34%: $t = 5.07$, $p < 0.001$), while open noisy sites had less canopy cover than closed noisy sites ($t = 2.60$, $p < 0.026$).

As compared via MANOVA, ambient noise levels also differed between forest categories (Figure 2-3; Wilks' $\text{lambda}_{16, 26} = 0.09$, $p < 0.001$). These differences were consistent across all eight frequency bandwidths ($F_{2, 20} = 7.85$, $p < 0.005$). Posthoc pairwise comparisons revealed that ambient noise levels were significantly higher in both open noisy (40.47 ± 0.78 dB) and closed noisy sites (39.20 ± 0.74 dB) than in open quiet sites (22.19 ± 1.24 dB; Hotelling's $t^2 \geq 69.60$, $p < 0.022$), but did not differ between open noisy and closed noisy sites (Hotelling's $t^2 = 16.09$, $p < 0.673$).

Bee note peak frequency was significantly different between forest categories (Figure 2-4; $F_{2, 529} = 9.86$, $p < 0.001$). Pairwise comparisons revealed that *bee* note peak frequency was significantly higher in both open noisy (3295.09

± 26.35 Hz) and closed noisy sites (3305.05 ± 26.54 Hz) than in open quiet sites (3169.73 ± 22.68 Hz; $t \geq 3.61$, $p < 0.001$), but did not differ between open noisy and closed noisy sites ($t = 0.27$, $p < 0.962$).

Discussion

Black-capped chickadees sang at higher frequencies in high noise locations than in low noise locations. This pattern is congruent with other studies that compared song frequencies of birds in relation to noise levels (Fernandez-Juricic et al. 2005; Slabbekoorn and den Boer-Visser 2006; Wood and Yezerinac 2006; Nemeth and Brumm 2009; Parris and Schneider 2009), and is consistent with the noise-dependent frequency hypothesis (Halfwerk and Slabbekoorn 2009). In contrast, birds did not sing at higher frequencies in the more open habitats (high or low noise) as would be predicted if vegetative structure was causing frequency changes (Morton 1975). The lack of differences in song frequency between open and closed habitats suggests that vegetative structure may not be an important confound to the noise-dependent frequency hypothesis.

The non-significant effect of vegetative structure on song frequency in this study does not necessarily contradict previous findings of a relationship between habitat and song frequency (Boncoraglio and Saino 2007; Barker 2008; Ey and Fischer 2009). Rather, it may be that anthropogenic noise generally provides a greater obstruction to song transmission than vegetation, causing a greater reaction in vocalizing birds. To evaluate the ubiquity of this effect, it would be prudent to assess simultaneous differences between habitat and song frequencies for more species, and across more habitat types.

Frequency shifting in songbirds may be the result of obstruction, or masking, of vocal signals by anthropogenic noise (Slabbekoorn and Ripmeester 2008). However, it is important to thoroughly examine alternative explanations for frequency shifting. In this vein, our results suggest that one alternative explanation, differences in vegetative structure, cannot account for the observed effects of noise on song frequency. A second alternative explanation is that intra – specific variations in body size may account for higher song frequencies since high frequencies are easier to produce for small-bodied individuals (Fletcher 2004). Tarsus measures from black-capped chickadees studied in our lab (n = 127; 2002 – 2010) in the City of Edmonton and in rural Alberta (but not Elk Island) revealed that chickadees in Edmonton are significantly larger than rural birds (17.56 ± 0.35 mm, and 16.26 ± 0.38 mm respectively; $t = 2.44$, $p < 0.016$). Based on body size, birds from our high noise sites in Edmonton should have sung at lower frequencies. Thus, body size is unlikely to account for the higher frequencies observed in high noise sites. Other alternative explanations for frequency shifting that warrant further research include: alteration of acoustics by human structures (Slabbekoorn, Yeh and Hunt 2007); variation in territory sizes and resources distribution (Ripmeester et al. 2010); and vocal interference from different heterospecific species (Brumm and Naguib 2009).

Although frequency shifting appears to moderate the effects of anthropogenic noise on bird song, it does not entirely compensate for it. The frequency shifts observed in chickadees (~130 Hz; Figure 2-5) result in songs that remain overlapped by traffic noise, and this also appears to be true in other bird species (e.g., 30, 42, 117, 130 and 488 Hz increase in minimum frequency in anthropogenic noise for five significantly affected species; (Hu and Cardoso 2010). Physiological and ecological factors may limit the ability or benefits of shifting to higher frequencies. For example, in black-capped chickadee calls, notes that are outside of a particular frequency range may be misclassified by conspecifics (Charrier and Sturdy 2005; Charrier et al. 2005; Guillette et al. 2010), effectively reducing successful communication. In addition, the acoustic space occupied by chickadees may be limited by the frequencies used by other heterospecifics (Nelson 1989; Kirschel et al. 2009). Unpublished recordings from our lab show that another common local resident, the white-throated sparrow (*Zonotrichia albicollis*), commonly sings between 3500-4500 Hz. While breeding cycles may not overlap entirely, white-throated sparrows are early migrants, and their vocalizations may limit the black-capped chickadees’ use of these frequencies during a portion of the breeding cycle. Thus, although the observed frequency shifts do not entirely avoid signal masking, they may reduce masking while avoiding other potential communication problems.

For species that exhibit vocal modification, more work is needed to understand the mechanisms by which songs are adjusted. Currently, it is not known whether song frequency in most bird species a) can be changed repeatedly in response to local conditions, b) is determined only once during song development (Podos and Warren 2007) or, c) is an evolved response (Slabbekoorn and Ripmeester 2008; Brumm and Naguib 2009; Luther and Baptista 2010). If frequency modification is due to individual vocal plasticity, translocation of birds from quiet to noisy environments should lead to changes in song frequency. Alternatively, if changes in song frequency are an outcome of directional evolution or occur only during song development, one might predict that changes in anthropogenic noise would not lead immediately to changes in song frequency production, but that changes would occur over multiple generations. Black-capped chickadees rapidly shift song frequency in response to playbacks of conspecific song (Shackleton and Ratcliffe 1994; Mennill and Ratcliffe 2004; Foote et al. 2008), and even during spontaneous song bouts amid the dawn chorus (Ratcliffe and Weisman 1985; Horn et al. 1992). In addition, individuals from a closely related species, the great tit, exhibit behavioural modifications of vocalizations to avoid overlap with anthropogenic noise (Halfwerk and Slabbekoorn 2009). These features make it likely that frequency adjustment to anthropogenic noise in chickadees results from rapid behavioural responses.

In addition to shifting song frequency, birds may adapt to anthropogenic noise by increasing song amplitude (Brumm 2004a; Brumm 2004b) or shifting song timing (Fuller, Warren and Gaston 2007). More work will be needed to know whether the net effect of these adaptations is positive or negative. For example, shifted songs may be more detectable by conspecifics (Slabbekoorn and Ripmeester 2008), but their higher frequencies may be less appealing to potential mates or less repelling to potential rivals (Mockford and Marshall 2009). In addition, the production of higher frequency songs may be energetically costly

(Oberweger and Goller 2001). Future work in this area should determine whether frequency shifts represent a successful and sustainable response to increased levels of anthropogenic noise for songbirds and other taxa.

In sum, we demonstrate that black-capped chickadees sing at higher frequencies when they are exposed to anthropogenic noise. We show that this shift in frequency is more strongly associated with increased levels of anthropogenic noise than with differences in vegetative structure. We suggest that further study is needed to understand the behavioural mechanisms underlying these observed frequency changes, and to identify the costs incurred by those animals that modify their vocalizations in response to anthropogenic noise. Answers to these questions could guide mitigation of anthropogenic noise for birds and many other species.

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Figure legends

Figure 2-1. Recording sites for black-capped chickadees. High noise sites were located in Edmonton, Alberta, Canada and divided into open and closed canopy forests. Low noise sites were located in Elk Island National Park, which is approximately 30 km from Edmonton. All sites were separated by at least 300 m, but were often several km apart.

Figure 2-2. Mean overhead canopy cover for high noise sites with open canopies (open noisy), high noise sites with closed canopies (closed noisy), and low noise sites with open canopies (open quiet). Error bars represent standard error of the mean.

Figure 2-3. Ambient noise in 1 kHz bandwidths for high noise sites with open canopies (open noisy), high noise sites with closed canopies (closed noisy), and low noise sites with open canopies (open quiet). Measurements have been converted from volts to decibels (dB) for clarity, but do not represent absolute sound pressure level (SPL). Error bars represent standard error of the mean.

Figure 2-4. Mean peak song frequency (PF) for the *bee* note of the chickadee song in high noise sites with open canopies (open noisy), high noise sites with closed canopies (closed noisy), and low noise sites with open canopies (open quiet). Error bars represent standard error of the mean.

Figure 2-5. Waveforms of a synthesized black-capped chickadee song recorded at 40 m and shifted to the mean peak *bee* note frequency observed in a) low and b) high noise sites. Similarity between the two waveforms shows that non-frequency song characteristics were not modified by synthesis. c) Spectrum of both songs mixed with one minute of anthropogenic highway noise at a level of 57dB (SPL). Low noise *bee* and *fee* note peaks are identified with gray arrows and labels and high noise peaks are identified with black arrows and labels. Slight differences in song amplitude are due to nonlinear additive relationships with ambient noise (see Dabelsteen, Larson and Pedersen 1993).

Figure 2-1


N
High noise sites
Closed Canopy
Open Canopy
0 750 1,500 3,000 4,500 6,000
Meters
30 km
N
Low noise sites
Open canopy
0 750 1,500 3,000 4,500 6,000
Meters

Figure 2-2

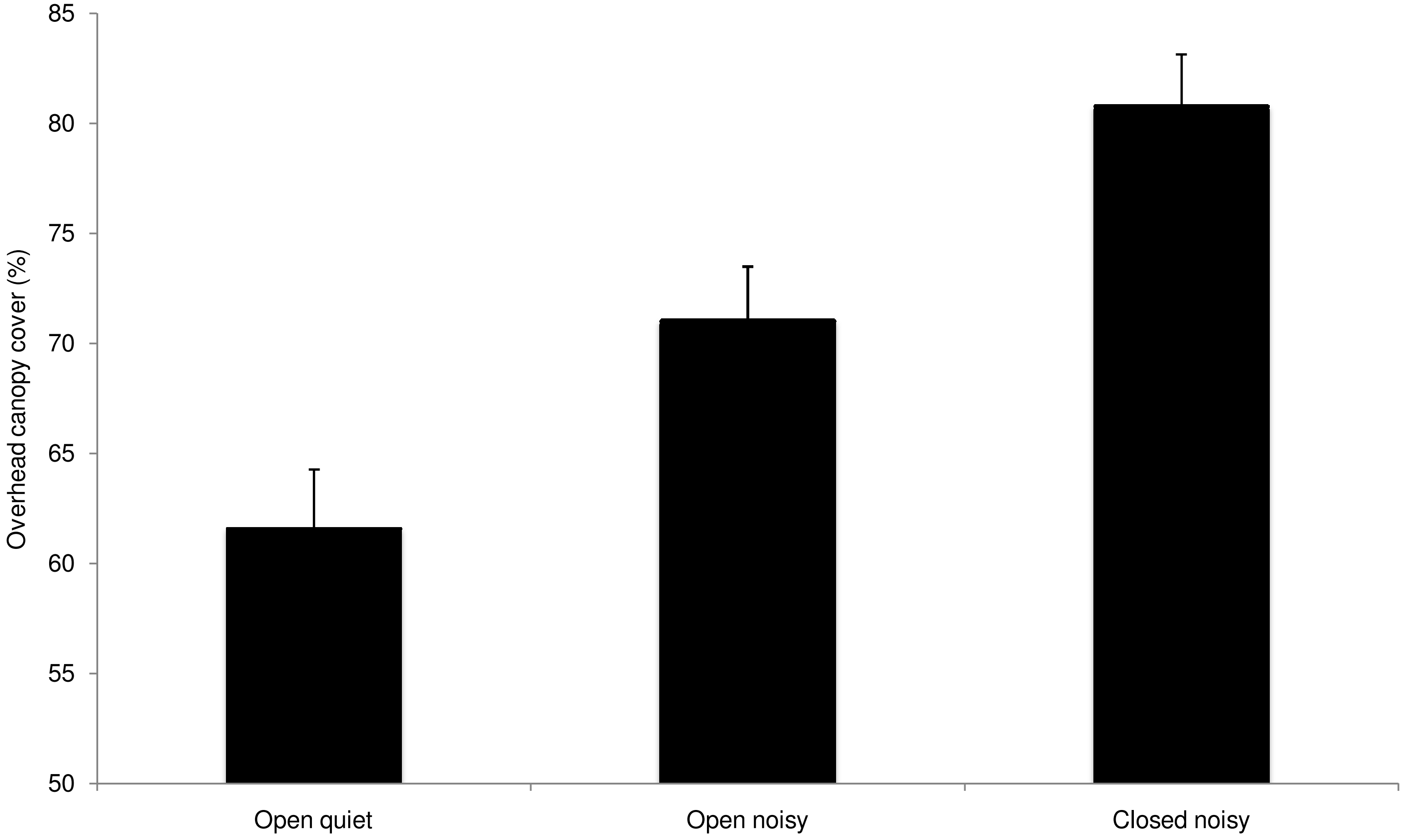

85
80
75
70
65
60
55
50
Overhead canopy cover (%)
Open quiet
Open noisy
Closed noisy

Figure 2-3

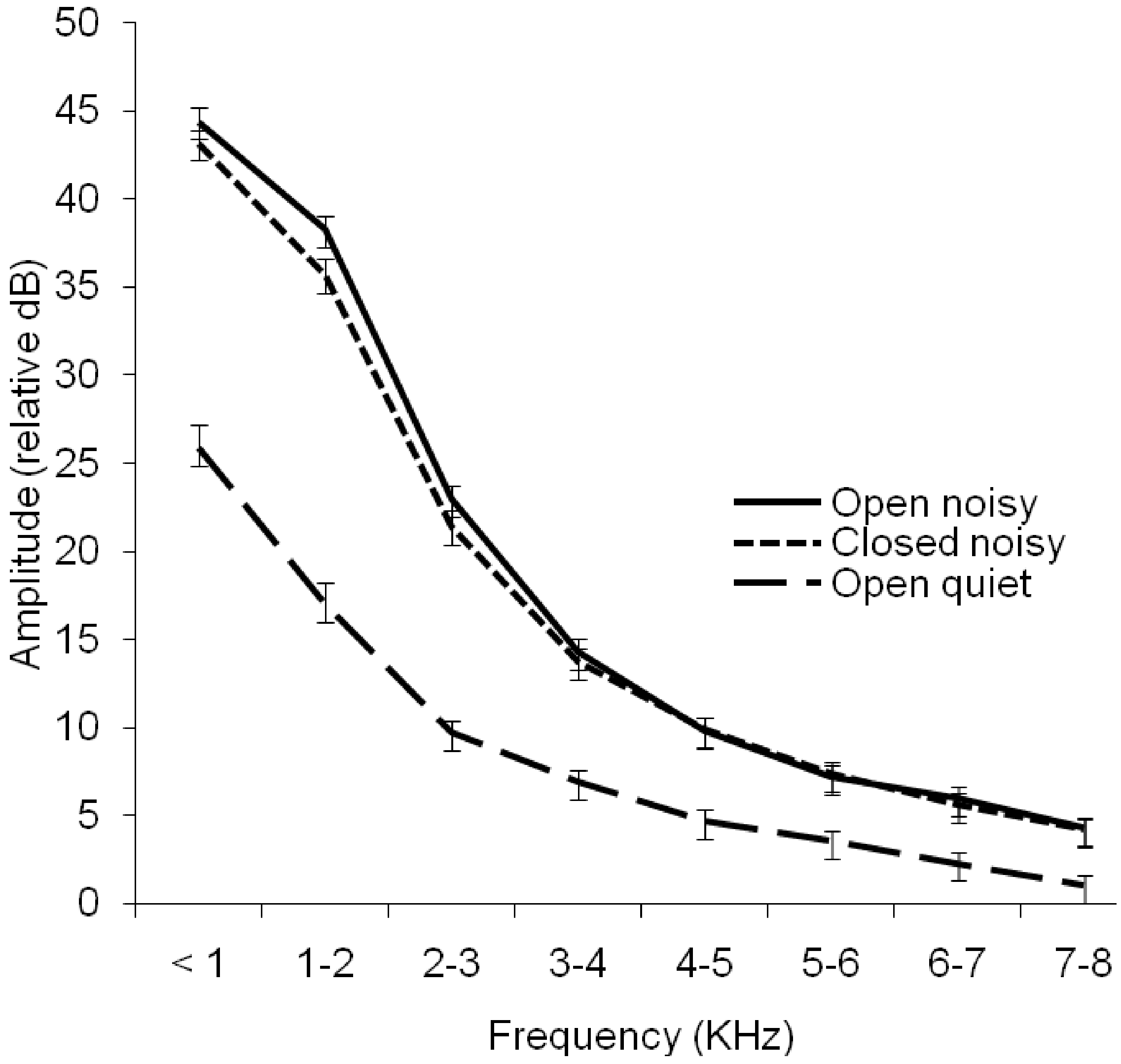

Amplitude (relative dB)
50
45
40
35
30
25
20
15
10
5
0
< 1
1-2
2-3
3-4
4-5
5-6
6-7
7-8
Frequency (KHz)
Open noisy
Closed noisy
Open quiet

Figure 2-4

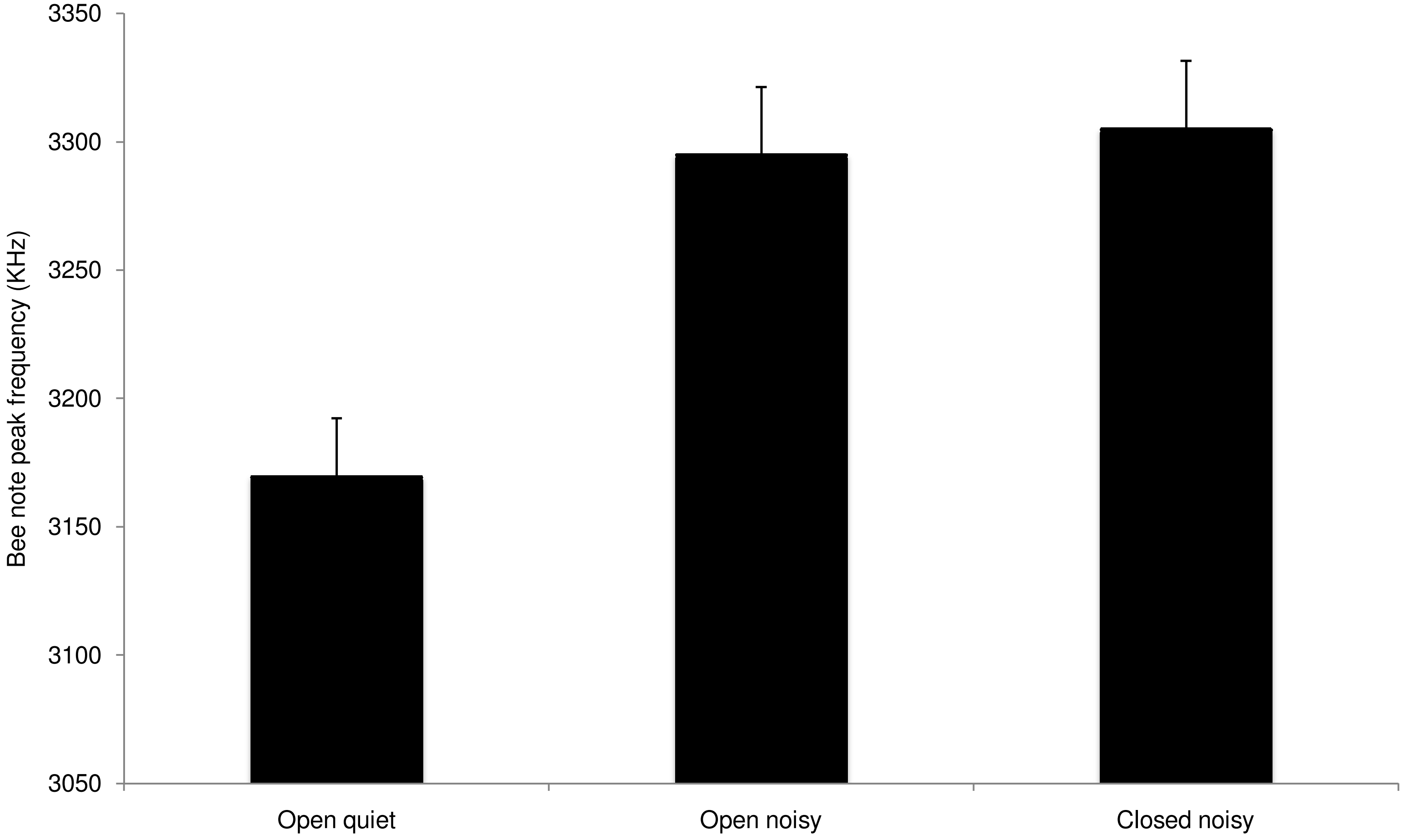
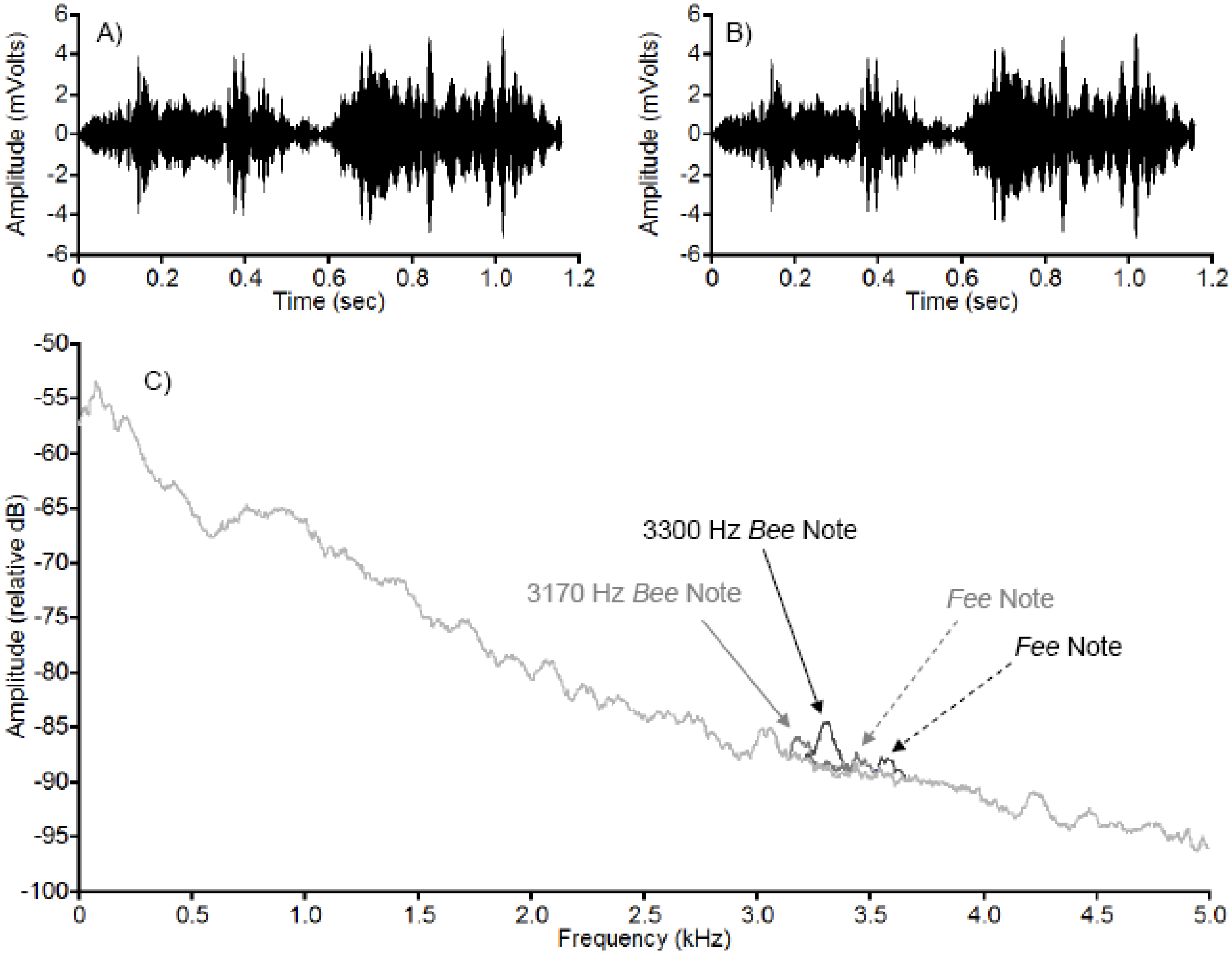

Bee note peak frequency (KHz)
3350
3300
3250
3200
3150
3100
3050
Open quiet
Open noisy
Closed noisy

Figure 2-5


A)
B)
Amplitude (mVolts)
Time (sec)
6
4
2
0
-2
-4
-6
0
0.2
0.4
0.6
0.8
1.0
1.2
C)
Amplitude (relative dB)
Frequency (kHz)
-50
-55
-60
-65
-70
-75
-80
-85
-90
-95
-100
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
3300 Hz Bee Note
3170 Hz Bee Note
Fee Note
Fee Note

Chapter 3

Chickadees adjust song frequency and duration in response to short-term changes in traffic volume

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Some songbirds that reside in areas with high levels of anthropogenic noise produce vocal signals that are different from those produced by the same species in quieter locations (Patricelli and Blickley 2006; Slabbekoorn and Ripmeester 2008). In general, noise-affected populations use vocal signals with higher frequencies (Slabbekoorn and Peet 2003), increased energy in high frequency elements (Wood and Yezerinac 2006; Ripmeester et al. 2010), reduced song length (Slabbekoorn and den Boer-Visser 2006), and increased amplitude (Brumm 2004a). Presumably, these modified vocal signals are more detectable in high levels of anthropogenic noise (Parris and Schneider 2009). Specifically, higher frequencies are less susceptible to auditory masking by overlapping anthropogenic noise which is concentrated in lower frequency ranges (< 4kHz; Skiba 2000), shorter vocal signals can be produced during gaps in anthropogenic noise, and louder vocal signals generate a better signal-to-noise ratio (Brumm and Slabbekoorn 2005). Several recent studies have confirmed the existence of noise-dependant vocal patterns in a number of songbird species (Brumm, Schmidt and Schrader 2009; Francis, Ortega and Cruz 2009; Kirschel et al. 2009; Nemeth and Brumm 2009).

Despite the prevalence of song differences in noisy areas, the mechanisms underlying these vocal modifications are not yet understood (Patricelli and Blickley 2006). It is plausible, but not yet demonstrated, that changes in vocal structure are due to individual vocal plasticity, with rapid changes occurring in response to concurrent environmental conditions (Patricelli and Blickley 2006).

Alternatively, changes in song frequency and duration could occur in response to selection, learning during song development, or a combination of the two (Slabbekoorn and Ripmeester 2008). Selection might occur rapidly if the naturally higher frequency vocalizations of some individuals are more easily discerned against anthropogenic noise; increasing the ability of these individuals to attract mates and, ultimately, achieve higher reproductive success. In turn, young individuals would be more likely to detect these high frequency vocalizations, and mimic them when developing their own adult repertoire (Beecher and Brenowitz 2005; Sung and Park 2005).

Two recent studies suggest that some degree of plasticity in song characteristics is possible through modification to song amplitude or song type. First, three individual nightingales (*Luscinia megarhynchos*) produced songs at higher amplitude (i.e., louder songs) on noisier weekday mornings than on quieter weekend mornings (Brumm 2004b). Second, when exposed to playback of low- or high frequency noise, individual great tits (*Parus major*) were more likely to switch to a song type that avoided the playback frequencies (Halfwerk and Slabbekoorn 2009). This kind of song switching would not be possible for the approximately thirty percent of songbird species that possess only one song type (MacDougall-Shackleton 1997; Beecher and Brenowitz 2005). For these species, a flexible response to anthropogenic noise would require the ability to modify the frequency or amplitude characteristics of their single song type.

The black-capped chickadee is a common North American songbird that possesses many vocalizations but only one song type (Ficken, Ficken and Witkin

1978). This chickadee species is an ideal candidate for the study of noise-dependent plasticity because it is found in both urban and non-urban areas (Smith 1991), it exhibits plasticity in song frequency in social contexts (Mennill and Ratcliffe 2004), and we have recently documented differences in song frequencies for birds in quiet and noisy locations. Here we modify the weekday / weekend comparison used by for nightingales (Brumm 2004b) to examine the hypothesis that black-capped chickadees near a roadway modify the frequency and duration of their *fee bee* songs in response to changing levels of anthropogenic noise. Specifically, we predict that song frequency will increase and song duration will decrease, as noise levels increase. Further, we expect these changes to occur in response to both diel cycles in traffic volume and to differences among days. Finally, because singing entails energetic expenditure (Oberweger and Goller 2001), we hypothesize that chickadees will sing at reduced rates when it is noisier (i.e., on weekdays relative to weekends).

Methods

Setup

Songs were recorded at 22 roadside locations (< 100 m from a high use road, >20,000 vehicles/day, 2007 City of Edmonton Traffic Flow Map) where a black-capped chickadee was heard singing on multiple visits and presumed to be a territorial resident. Each location was recorded on one weekday and one weekend morning between 0400 - 0800 hours in Edmonton, Alberta, Canada, (53° 34' N 113° 31' W) from April 23 – May 22, 2009. All vocalizations were passively recorded via an automated recording unit (Song Meter SM1; Wildlife Acoustics, Massachusetts, USA) attached to a tree 5m above the ground. Each unit had two omni-directional microphones (frequency range: 20-20000 Hz), which were positioned so that both microphones were parallel to the roadway. Both days were recorded consecutively from the same location, except in a few cases where inclement weather delayed recording for up to three days. Weekdays were recorded first at approximately half of the sites; weekends at the other half. Audio recordings were saved on 8 or 16 GB SDHC flash cards (SanDisk; California, USA) in 16-bit PCM formatting, with a sampling rate of 44,100 kHz.

Anthropogenic noise comparison between weekends and weekdays

To examine differences in anthropogenic noise between weekdays and weekends, we calculated mean ambient noise levels from all audio recordings (0400 – 0800 hours) in three minute blocks of time (80 bins). Similar to Slabbekoorn (2004), we measured root mean square (RMS) voltage in eight, 1 kHz bandwidths from 0-8 kHz on a power spectrum (fast Fourier transform; 65,536 points, frequency resolution of 0.7 Hz.) with SIGNAL 5.0 sound analysis software (Engineering Design 2008, Berkeley, California). All measurements were then converted to decibels (dB) via the formula $\mathrm{dB} = -20 \log_{10} (\mathrm{Volts})$. The frequency bands of interest were 2-3 kHz and 3-4 kHz since these encompass the frequencies used in the *fee bee* song. However, *fee bee* songs occurred during much of the recording period, affecting the measured noise levels in these bandwidths, and making them a poor representative of the level of ambient noise the bird experienced.

Because of the overlap with *fee bee* songs in the 2-4 kHz bands, we assessed the 1-2 kHz band as a proxy for ambient noise levels. We examined the correlation in these bands by comparing them in 852 samples; each 6 seconds in duration, from periods free from overlapping *fee bee* songs (see further description of these samples below). The 1-2 kHz band was highly correlated with both 2-3 (Pearson's $r = 0.929$) and 3-4 kHz (Pearson's $r = 0.900$) and, thus, was used subsequently as a proxy for estimating noise levels in the range of chickadee vocalizations. Measures from the 1-2 kHz band were standardized (i.e., lowest dB set to 0) and were categorized by hour to compare weekday noise levels to those on weekends for each hour via an ANOVA procedure.

Fee bee song frequency and duration measures

Twenty *fee bee* songs from weekday and weekend recordings at each site were selected for acoustic analysis. Songs were analyzed in pairs by randomly selecting a song for one day type (e.g., weekend) and then selecting the song that was closest in time from the other day type. We measured the peak frequency (frequency at the loudest amplitude; Proppe and Sturdy 2009) of the *fee* and the *bee* note from the power spectrum (32,768 points, frequency resolution of 1.3 Hz, high pass 2,200 Hz). *Fee* and *bee* note frequency measures were highly correlated (Pearson's $r = 0.925$) and thus we used only *bee* note frequency in our analysis (Horn et al. 1992). We also measured the duration of the entire song, the *bee* note, and the *fee* note, via a sound spectrograph (1,024 points, minimum cutoff = -50dB, visible frequency range 2,000 – 5,000 Hz). Duration was defined as time in milliseconds (ms) between note or song onset and offset. Due to the effects of degradation, *fee* and *bee* notes often have an associated "tail" of sound (Dabelsteen, Larsen and Pedersen 1993), but their tonal nature makes it possible to distinguish between the high energy note end (dark spectrographic trace) and the less energetic tail (light gray spectrographic trace). Both note type duration measures were highly correlated with song duration (Pearson's $r = 0.812$ and 0.766, respectively) so we used only song duration in our analysis.

Because birds may respond to changing ambient noise on different time scales, we measured ambient noise levels in the 1-2 kHz band from the minute prior to each analyzed song (instantaneous noise), and for the quarter hour in which the song occurred (average noise). Instantaneous noise was calculated by averaging the noise level in six randomly chosen one second samples free from *fee bee* vocalizations taken within the minute prior to each sampled song (also used to examine the correlation between 1-2 kHz and 2-4 kHz bands described previously). To calculate average noise, we determined the mean noise level for each fifteen minute time period from 0400-0800 hours. Measures of instantaneous and average noise were calculated and standardized using the same method described previously for three minute ambient noise measures. A paired t-test was used to assess whether the two noise measures differed statistically.

To test if *bee* note peak frequency and duration ($n = 425$ pairs) differed by day type, we conducted a paired t-test for each variable. To determine the relative effects of day type, time, and noise on *bee* note peak frequency and duration, we conducted a general linear mixed model, using site as a random effect to account for repeated measurements (in STATA 10.1: xtmixed; Rabe-Hesketh S and Skrondal A 2008). A noise × day type interaction term was added to the model to account for the potential that frequency or duration was correlated with noise for one day type but not the other. Because instantaneous and average noise were highly correlated (Pearson's $r = 0.876$), only the noise measure that produced the lowest Akaike's Information Criterion(AIC) value in a univariate mixed model regression was retained (Burnham and Anderson 2002).

To eliminate variables with little explanatory power, we reduced the full model via a forward stepwise procedure similar to that of Hosmer and Lemeshow (2000). We used a critical p value of 0.1 for variable inclusion in our final stepwise models. We then used effect size and the bootstrapped 95% confidence interval of the effect size (1,000 repetitions; Davison and Hinkley 1997; Efron and Tibshirani 1998) to evaluate the strength and validity of each relationship. Effect sizes are reported in the original measurement units for each variable.

Song rate

All visible *fee bee* songs from 0400 – 0800 hours were counted on a spectrogram (1,024 points, minimum cutoff = -96dB, visible frequency range 1,000 – 5,000 Hz) in Audacity 1.2.6 (distributed by Free Software Foundation, Inc.; Massachusetts, USA). To assure that a bird was present, we retained only recordings containing at least one chickadee song. Songs were tallied in three minute time periods, and then divided by three to calculate the rate per minute for each three minute period from 30 minutes before sunrise (calculated for each day) until 0800 hours (*n* = 3,174; 22 groups). Mean ambient noise was also calculated for each three minute period (see procedure for anthropogenic noise comparison above).

We evaluated whether song rate (*n* = 1,587 pairs) differed by day type with a paired t-test. To determine the relative effects of day type, time, and noise on song rate we used a general linear mixed model, using site as a random effect to account for repeated measurements. Because song rate data contained a large number of zeros, we used a Poisson mixed model regression (xtmepoisson; Rabe-Hesketh and Skrondal 2008). A noise × day type interaction term was added to the model to account for the possibility that song rate was correlated with noise for one day type but not the other. Because the dawn chorus of bird song typically increases and decreases over time (Burt and Vehrencamp 2005), and may exhibit a similar (but uncorrelated: Pearson's $r = 0.480$) relationship with noise, we used a quadratic term to describe time and noise whenever a likelihood-ratio test revealed that it significantly increased the explanatory power of the model. The model was reduced via a stepwise procedure and fit was assessed via bootstrapping as described previously. Statistics were conducted in Stata 10.1 (StataCorp LP, Texas, USA), and all results are reported as means ± standard error of the mean (s.e.m.).

Results

Anthropogenic noise comparison between weekends and weekdays

Ambient noise was an average of 4.70 ± 0.11 dB higher on weekday mornings than it was on weekends and was different for all hours (day type: $F_{1, 3167} = 455.41$, $P < 0.001$; time: $F_{4, 3167} = 106.80$, $P < 0.001$; Figure 3-1). A significant day type × time interaction ($F_{3, 3167} = 49.17$, $P < 0.001$) revealed that ambient noise increased more rapidly with each hour on weekdays than on weekends.

Fee bee song frequency and duration measures

Bee note frequency was an average of 32.29 ± 10.55 Hz higher on weekday than weekend mornings ($t_{424} = 3.05$, $P = 0.002$; Figure 3-2). Average noise was a better fit than instantaneous noise for *bee* note peak frequency (ΔAIC = 48.58), suggesting that peak frequency is modified in response to general, rather than instantaneous, noise conditions. The reduced mixed effects model retained only average noise ($z = 1.94$, $P = 0.052$) as an explanation for *bee* note frequency. The peak frequency of *bee* notes increased 8.66 Hz with each decibel increase in average noise (Figure 3-3). Upper and lower limits of the bootstrapped 95% CI (11.79 - 5.27 Hz) indicate a consistently positive effect, and the relatively small range suggests high repeatability of our results (Table 1).

Song duration was an average of 11.85 ± 5.95 milliseconds (ms) shorter on weekday than on weekday mornings ($t_{424} = -1.99$, $P = 0.047$; Figure 3-2). Instantaneous noise was a better fit than average noise for song duration (ΔAIC = 7.63), suggesting that song duration was modified quickly in response current noise conditions. The reduced mixed effects model retained only instantaneous noise ($z = -2.30$, $P = 0.021$) as a predictor of song duration. Song duration decreased 3.31 ms with each decibel increase in instantaneous noise (Figure 3-4). Upper and lower limits of the bootstrapped 95% CI (-0.95 - -4.23 ms) indicate a consistently negative effect, and the relatively small range suggests our results are unlikely to differ in repeated experiments (Table 3-1).

The mean amplitude of instantaneous noise was 3.35 ± 0.09 dB lower than average noise ($t_{850} = -38.31$, $P < 0.001$).

Song rate

On average, 46% fewer *fee bee* songs were recorded per minute on weekday mornings than on weekend mornings ($t_{1586} = -8.31$, $P = <0.001$; Figure 3-2). Quadratic terms for time (time^2) and noise (noise^2) were retained in the initial mixed effects model because they significantly increased model fit (likelihood ratio $\chi^2 = 161.94$, $P < 0.001$; likelihood ratio $\chi^2 = 161.94$, $P < 0.001$, respectively). The reduced mixed effects model retained all the original variables including day type, time, noise, and day × ambient noise (Table 3-1). Song rate increased and then decreased with increasing ambient noise (noise $\beta = 9.96 \pm 0.27$; noise^2 $\beta = -0.85 \pm 0.02$), but this pattern was different on weekend and weekday mornings, revealing decreased song rates at both low and high ambient noise levels on weekday mornings (day × ambient noise $\beta = -0.54 \pm 0.06$; day × ambient noise^2 $\beta = -0.01 \pm 0.01$; Figure 3-5). Song rate followed a quadratic increase and decrease with time (time $\beta = 9.96 \pm 0.27$; time^2 $\beta = -0.85 \pm 0.02$) and was lower on weekday than weekend mornings (β = -10.38 ± 1.20; Figure 3-6). Low sample sizes likely contributed to high variability in the lower amplitudes. However, truncation of the decibel range to include only those with 10 or more replicates produced similar statistical results. Bootstrapped 95% CIs suggest the modeled effects are highly repeatable (Table 3-1).

Discussion

Black-capped chickadees plastically altered their *fee bee* songs in response to changes in anthropogenic noise that occurred both within mornings as ambient noise increased and among days of the week. Chickadees both increased the frequency, and decreased the duration of their songs in concert with increasing levels of ambient noise. Moreover, we detected fewer *fee bee* songs on weekdays than weekends, presumably due to a lower rate of song production on weekdays when ambient noise was higher. These data provide evidence that the structure and use of a single vocal signal can be modified plastically and adaptively over a period of minutes in response to changing levels of anthropogenic noise.

Additional evidence that chickadees respond rapidly to changes in anthropogenic noise is provided by the fact that song duration was better explained by noise levels immediately prior to song initiation than it was by the ambient noise level averaged over a 15 minute period. This relationship did not hold for *bee* note peak frequency, which was better explained by average noise. The difference in these responses may result from song characteristics. Because the frequency ratio of the *fee* and the *bee* note are highly stereotyped, chickadees are unlikely to alter song frequency once a song is initiated (Ratcliffe and Weisman 1985; Shackleton, Ratcliffe and Weary 1992). However, the amplitude of ambient noise near a roadway is highly stochastic and may change quickly with passing traffic (da Paz and Trombetta Zannin 2010). Thus, noise levels are likely to vary even over the duration of a single *fee bee* song. Generating *fee bee* song frequencies in relation to average ambient noise level may reduce the likelihood that a noise event after song initiation will mask the signal. By contrast, song duration may be more easily adjusted after song initiation.

Because ambient noise immediately prior to each song was significantly lower than average noise, we suggest that chickadees target their singing for gaps between noise events. They may further regulate their song duration to increase the likelihood that each song will be contained entirely within these noise gaps. Black-capped chickadees also shorten their songs in response to conspecific overlap, another situation where vocalizing in gaps may reduce signal masking (Mennill and Ratcliffe 2004). Nightingales and great tits also time song production to avoid overlap with interfering sounds (Langemann et al. 2000; Brumm 2006), and great tits decrease their song length as the length of played back sound increases. Urban great tits sing shorter songs than their rural counterparts, although this result was attributed to habitat differences (Slabbekoorn and den Boer-Visser 2006). Conversely, some whales increase signal duration in the presence of anthropogenic noise, presumably to increase transmission efficacy (Fristrup, Hatch and Clark 2003; Foote, Osborne and Hoelzel 2004).

We observed higher rates of song production on weekends relative to weekdays. Higher weekend song rates were found throughout the dawn chorus (Figure 3-6) even when the two days types experienced similar noise levels (Figure 3-5). We suggest this difference is due to a generalized decrease in song output on noisier weekday mornings, but it could also occur because our automatic recorders were less likely to detect songs on the noisier weekdays. This alternative explanation is plausible because noise is known to decrease detectability generally (Pacifici, Simons and Pollock 2008) and ambient noise level was also a significant predictor of song rate in our model. Yet, if differences in detection were responsible for this result, we would expect to have detected song fragments in our recordings; we did not. Thus, we suggest that chickadees adaptively increase song output on the weekends because it is a generally quieter then. Because song production incurs some energetic costs (Oberweger and Goller 2001), chickadees should reduce song rate when the potential for successful signal transmission or communication is also reduced. Reduced receiver discrimination of vocal signals when it is noisy has been demonstrated in songbirds (Lohr, Wright and Dooling 2003) as well as humans (Muller-Gass et al. 2001). Combining this finding with our earlier results suggests that chickadees respond to ambient noise at two temporal scales; at the time of song production and as an average of daily experience.

Noise levels are increasing across the globe (Barber, Crooks and Fristrup 2010) as more and more of the planet is altered by human development (Ehrlich 2009). For species that rely on auditory communication, adaptive vocal plasticity may be increasingly associated with and required for population persistence. The potential for this behaviour is certainly not limited to songbirds and may also occur in the many anurans (Bee and Swanson 2007; Lengagne 2008), insects (Polajnar and Cokl 2008; Samarra et al. 2009), cetaceans (Nowacek et al. 2007; Weilgart 2007), pinnipeds (Kastak et al. 2005), and other mammals (Gordon et al. 2003; Brumm and Slabbekoorn 2005), that rely on acoustic communication. Identifying the species which do and do not exhibit environment-induced plasticity in acoustic signals may help to determine causes for population declines and also suggest avenues for mitigation (Slabbekoorn and Ripmeester 2008).

In sum, we show that black-capped chickadees modify the frequency and duration of their *fee bee* songs in conjunction with anthropogenic noise levels, and appear to reduce their vocal output in response to high noise levels. We also show that chickadees exhibit this flexibility in vocal behaviour at the scale of minutes and days. More research is needed to understand the full temporal scale of plastic responses to anthropogenic noise and to identify both the mechanistic basic and the ecological consequences of these changes in auditory signals. We suggest that vocal plasticity may be an underappreciated correlate of population persistence in areas with high levels of anthropogenic sound and it be may be particularly relevant to the changing patterns of abundance and distribution in songbirds (Butcher G.S. 2007).

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Figure legends

Figure 3-1. Mean ambient noise levels (± s.e.m.) recorded from 0400-0800 hours on twenty two weekend and weekday mornings. Noise levels were higher on weekday mornings and increased with time.

Figure 3-2. Mean observed a) *bee* note peak frequency, b) song duration, and c) song rate on weekend and weekday mornings (± s.e.m.). * = significant at $P \leq 0.10$.

Figure 3-3. Predicted *bee* note peak frequency from mixed model regression and scatter plots of observed mean *bee* note peak frequency for each decibel and each day type plotted by average noise level (15 min average). *Bee* note peak frequency increased significantly with average noise. Error bars are s.e.m. Points without error bars were unreplicated, and had little effect on statistical results.

Figure 3-4. Predicted song duration from mixed model regression and scatter plots of observed mean song duration for each decibel and each day type plotted by instantaneous noise (1 min prior to song production). Song duration decreased significantly with instantaneous noise. Error bars are s.e.m. Points without error bars were unreplicated, and had little effect on statistical results.

Figure 3-5. Predicted song rates from mixed model regression and scatter plots of observed mean song rates for each decibel and each day type plotted by ambient noise (3 min average) and grouped by day type. Song rate changed in response to ambient noise, but the pattern differed by day type. Error bars are s.e.m. Points without error bars were unreplicated, and had little effect on statistical results.

Figure 3-6. Scatter plot of observed mean song rates plotted by time and grouped by day type. Time (with quadratic term) and day type were both significant at $P \leq 0.10$.

Table 3-1. Statistical results from general linear mixed models reduced via a stepwise procedure for each dependent variable. Confidence intervals were derived via bootstrapping (1000 iterations).

Peak frequency	**β**	**s.e.m.**	**z**	**P>|z|**	**Bootstrap 95% CI**	
average noise	8.66	4.46	1.94	0.052	5.52	11.79
Song duration						
instantaneous noise	-2.59	1.21	-2.14	0.032	-4.23	-0.96
Song rate						
day type	-10.38	1.20	-8.67	< 0.001	-15.83	-4.93
time	9.96	0.27	36.21	< 0.001	8.40	11.52
time^2	-0.85	0.02	-39.46	< 0.001	-0.987	-0.72
noise	-0.44	0.07	-6.30	< 0.001	-0.78	-0.10
noise^2	-0.01	<0.01	-5.99	< 0.001	-0.01	<-0.01
day*ambient noise	-0.54	0.06	-8.53	< 0.001	-0.82	-0.25
day*ambient noise^2	-0.01	<0.01	-8.29	< 0.001	-0.01	<-0.01

Figure 3-1

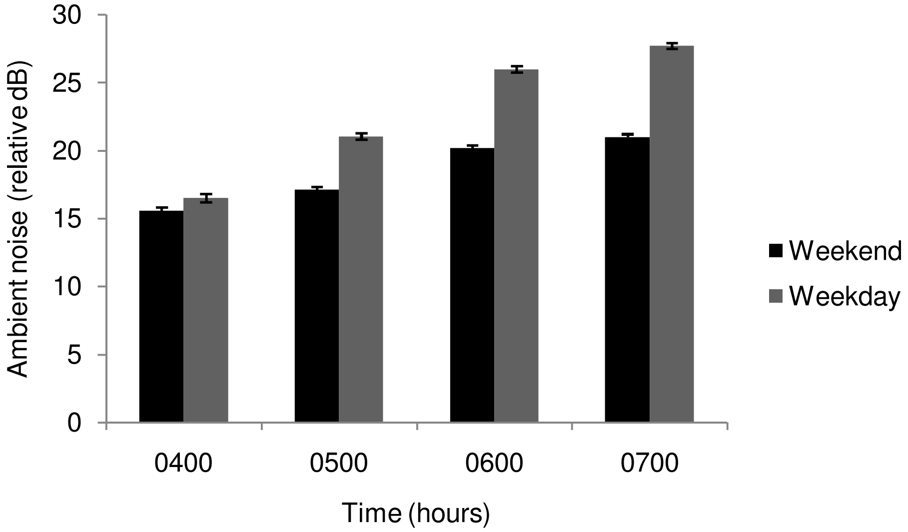

30
25
20
15
10
5
0
Ambient noise (relative dB)
0400
0500
0600
0700
Time (hours)
■ Weekend
■ Weekday

Figure 3.2

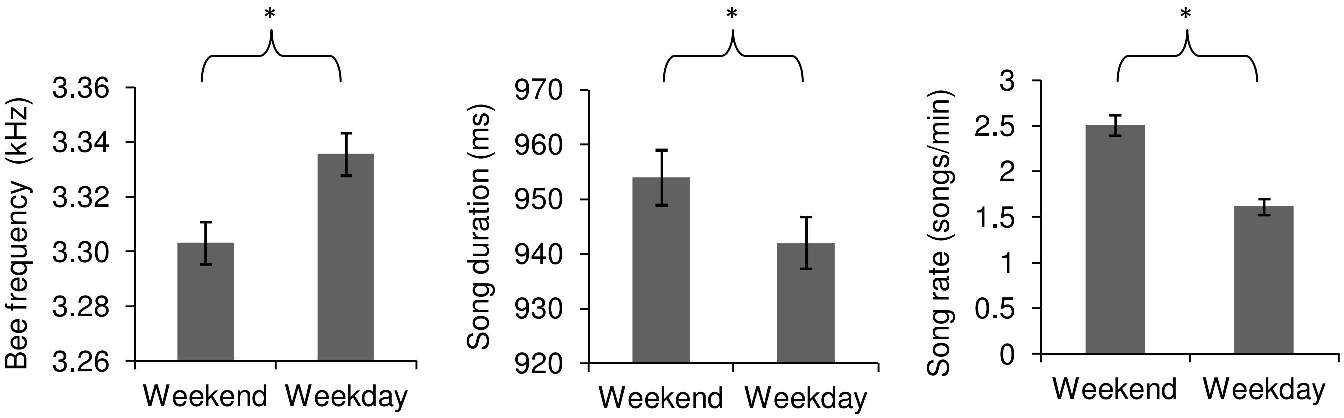

*
Bee frequency (kHz)
3.36
3.34
3.32
3.30
3.28
3.26
Weekend
Weekday
*
Song duration (ms)
970
960
950
940
930
920
Weekend
Weekday
*
Song rate (songs/min)
3
2.5
2
1.5
1
0.5
0
Weekend
Weekday

Figure 3-3

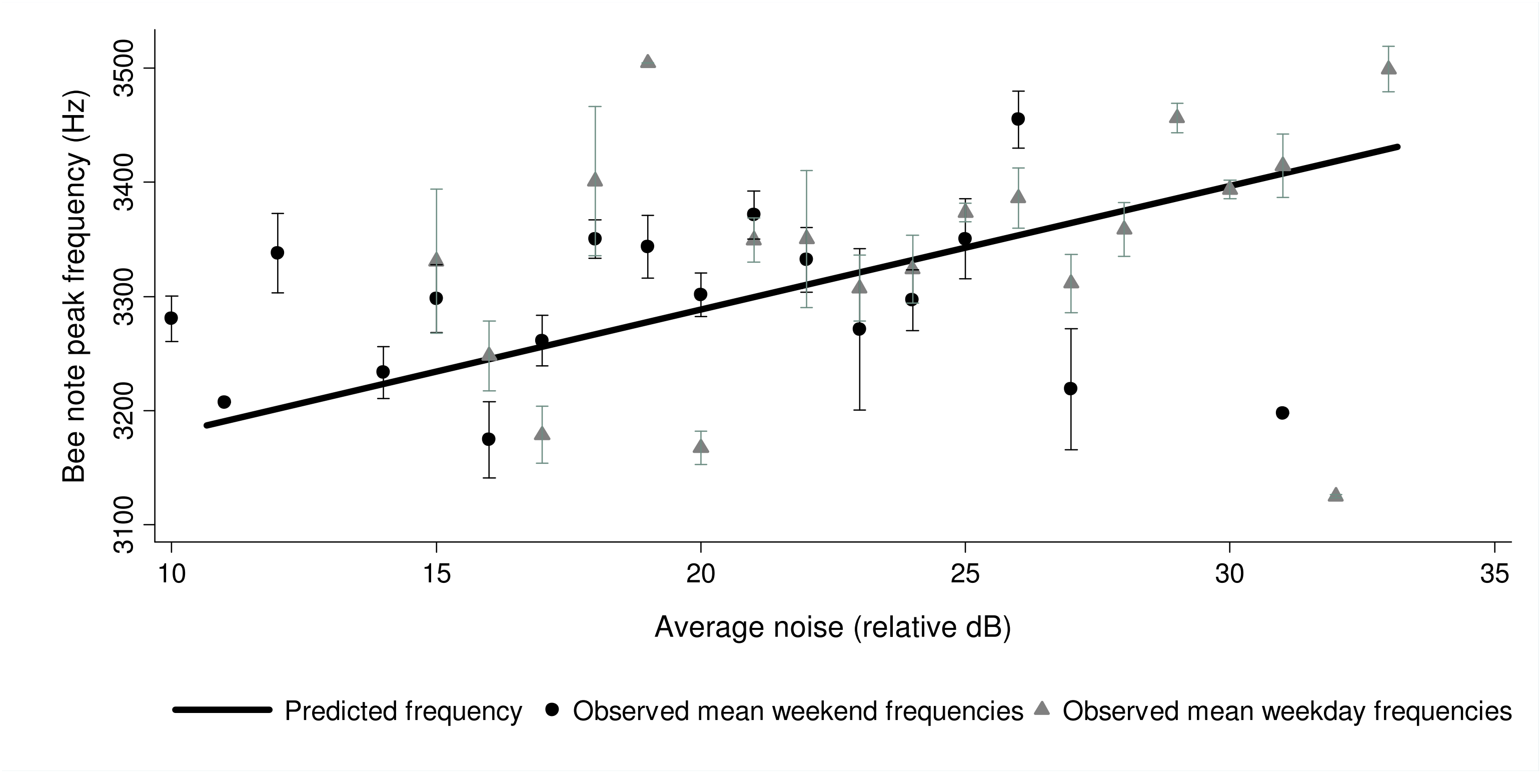

Bee note peak frequency (Hz)
3100
3200
3300
3400
3500
10
15
20
25
30
35
Average noise (relative dB)
Predicted frequency
Observed mean weekend frequencies
Observed mean weekday frequencies

Figure 3-4

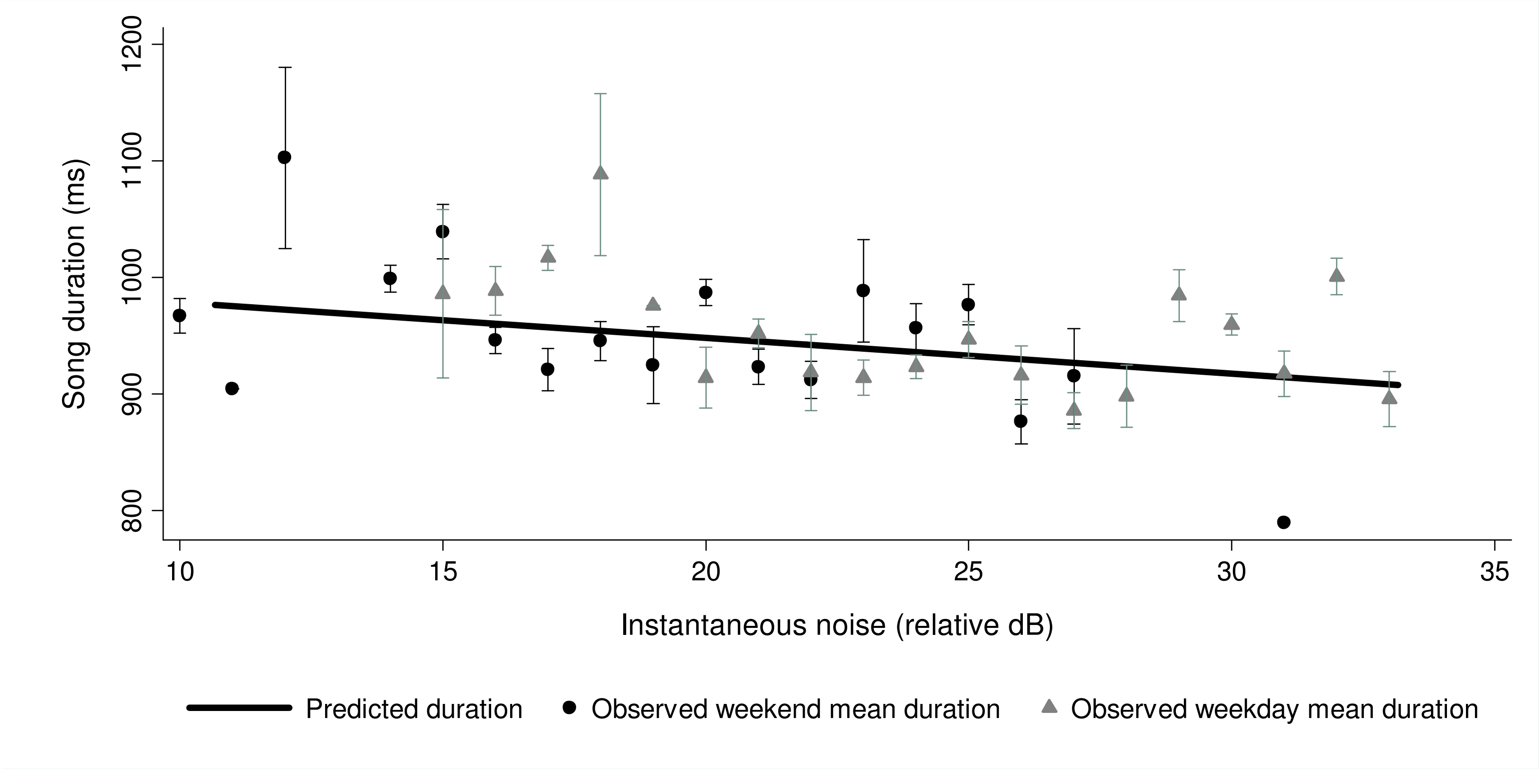

Song duration (ms)
1200
1100
1000
900
800
10
15
20
25
30
35
Instantaneous noise (relative dB)
Predicted duration
Observed weekend mean duration
Observed weekday mean duration

Figure 3-5

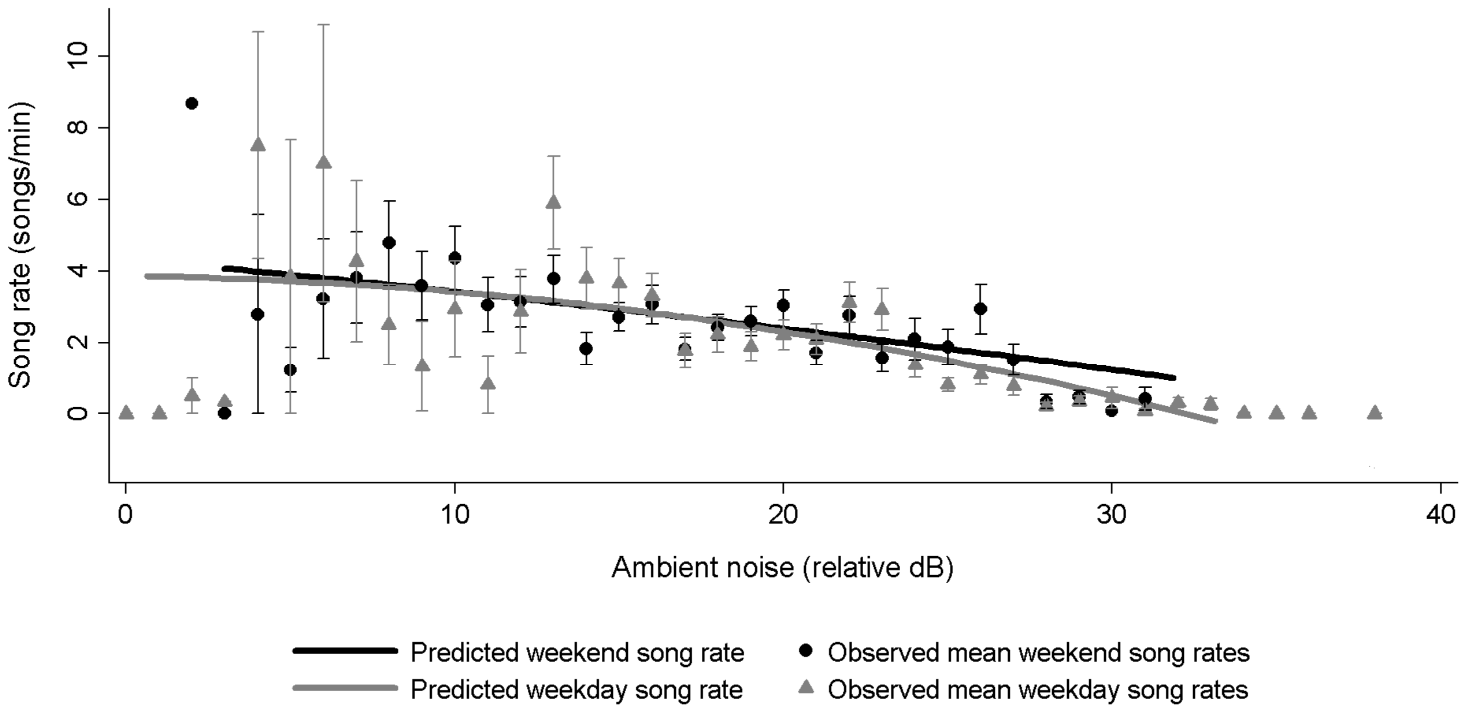
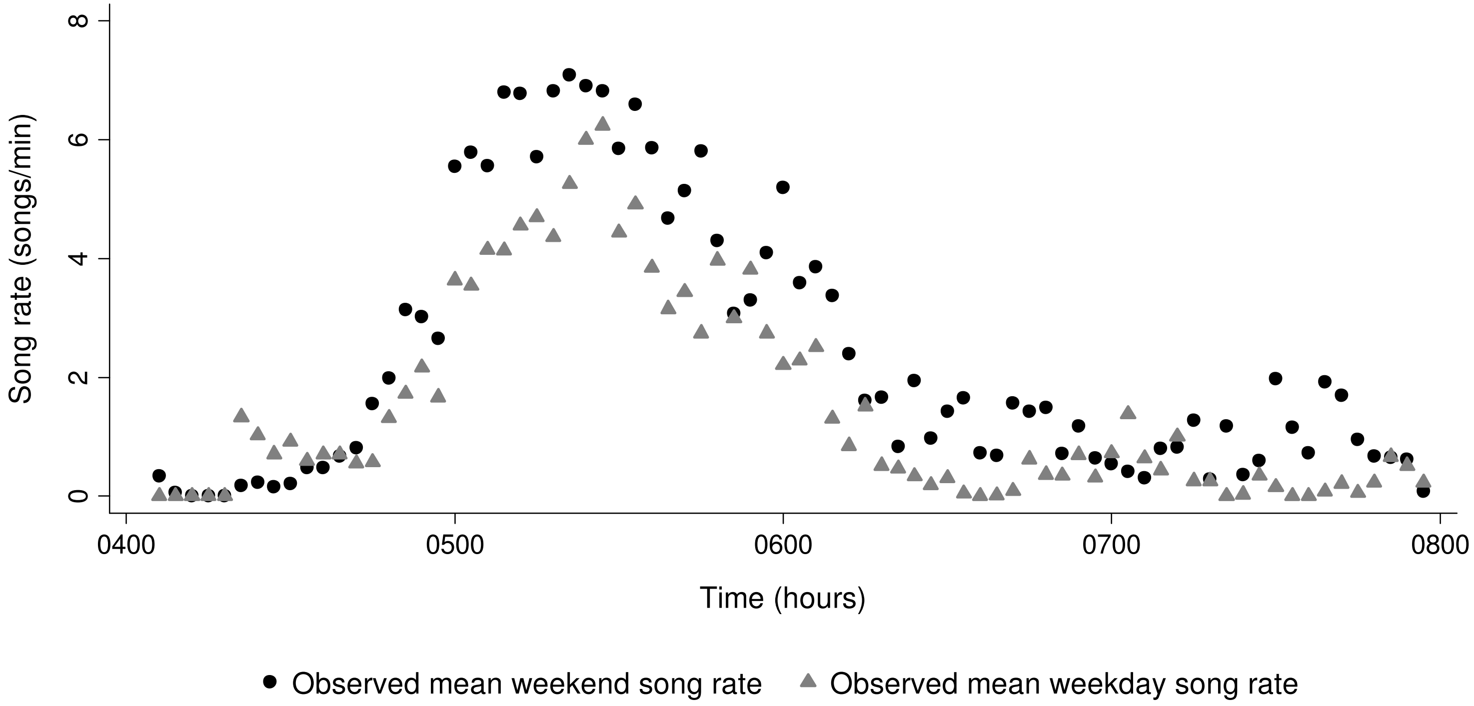

Song rate (songs/min)
0
2
4
6
8
10
0
10
20
30
40
Ambient noise (relative dB)
Predicted weekend song rate
Predicted weekday song rate
Observed mean weekend song rates
Observed mean weekday song rates

Figure 3-6


Song rate (songs/min)
0
2
4
6
8
0400
0500
0600
0700
0800
Time (hours)
● Observed mean weekend song rate
▲ Observed mean weekday song rate

Chapter 4

Minimum song frequency in passerine birds predicts sensitivity to anthropogenic noise, but not necessarily urban decline

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Human development is characterized by high levels of low frequency noise (Katti and Warren 2004). The consequences of anthropogenic noise may be substantial for wildlife; potentially reducing species richness and abundance, altering age structure, and decreasing reproductive success (Barber, Crooks and Fristrup 2010; Laiolo 2010). Songbirds are particularly susceptible to noise because they rely heavily on acoustic signals for communication (Catchpole and Slater 2008; Slabbekoorn and Ripmeester 2008). Increases in the intensity and area affected by anthropogenic noise may be contributing to declines in songbird abundance (Reijnen et al. 1995; Reijnen and Foppen 2006; Bayne, Habib and Boutin 2008; Francis, Ortega and Cruz 2009).

A likely mechanism by which anthropogenic noise affects songbirds is through masking of the frequencies used for vocal communication (Patricelli and Blickley 2006). The low frequencies of anthropogenic noise overlap the frequencies used by many, but not all, songbirds (<4 kHz; Skiba 2000). Species with high vocal frequencies that are not overlapped by anthropogenic noise may avoid these negative effects. Although poorly replicated, Rheindt (2003) documented this along a German highway, where the abundance of birds with high vocal frequencies did not decline closer to the highway, but species with lower song frequencies declined. Another recent study found that common urban bird species use higher frequency vocal signals than non-urban species (Hu and Cardoso 2009). These findings have led some to suggest that birds with higher song frequencies are pre-adapted to live in noisy environments (Slabbekoorn and Ripmeester 2008; Hu and Cardoso 2009).

Some songbirds in noisy environments also use higher frequency vocalizations than their rural counterparts. For example, great tits (*Parus major*) use higher frequency song types (Slabbekoorn and Peet 2003), song sparrows (*Melospiza melodia*) focus the intensity of their vocal signals in higher frequencies (Wood and Yezerinac 2006), and black-capped chickadees (*Poecile atricapillus*) shift their entire song to higher frequencies (Proppe, Sturdy and St. Clair in prep). Individual great tits plastically switch to alternate song types (Halfwerk and Slabbekoorn 2009) and black-capped chickadees rapidly alter the frequency of their single song type as noise conditions change (Proppe, Sturdy, St. Clair in prep). Vocal plasticity may allow these species to avoid frequencies masked by anthropogenic noise, while retaining the ability to sing at lower frequencies (which generally transmit farther; Wiley and Richards 1982) when noise levels are low. To accomplish this, however, a species must be able to produce vocalizations over a broad range of frequencies. Broadband vocal plasticity may be limited to particular species, and may also represent a pre-adaptation for life in noisy environments (Slabbekoorn and Ripmeester 2008).

Avian diversity is generally low in urban areas (Marzluff 2001; Huste and Boulinier 2007), but the mechanisms underlying reduced urban diversity are still not fully understood. Anthropogenic noise is particularly intense in urbanized landscapes (Warren 2006). We hypothesize that songbird species which remain widespread in cities are generally those that remain abundant in noisy environments. We further hypothesize these species remain abundant in noisy environments because their vocalizations 1) are sung at high frequencies that are not overlapped by anthropogenic noise, and/or 2) display sufficient variation in vocal frequencies to allow individuals to shift to higher frequencies as anthropogenic noise increases.

Methods

Study area

The City of Edmonton, Alberta, Canada (53°30'N, 113°30'W) has preserved one of the largest urban green spaces in North America, with over 7,400 hectares of park area (Hobson et al. 2008). Much of this parkland is comprised of mature forests similar to nearby rural locations (Mandryk and Wein 2006). Our work shows that some of these protected areas are sheltered from high levels of anthropogenic noise (30 - 40 dBA (SPL)), but other areas are exposed to high levels of noise from nearby highways (> 60 dBA (SPL)).

Species selection

Seven passerine species were selected for this study because their song frequencies partially overlap the dominant frequencies of anthropogenic noise (<4 kHz). Focal species included two common year round residents (black-capped chickadee, *Poecile atricapillus*; red-breasted nuthatch, *Sitta canadensis*), three common migrants (yellow warbler, *Dendroica petechia*; red-eyed vireo, *vireo olivaceus*; white-throated sparrow, *Zonotrichia albicollis*), and two locally declining migrants in Edmonton (Hobson et al. 2008) which are sensitive to urban development (western tanager, *Piranga ludoviciana*, Donnelly and Marzluff 2006); least flycatcher, *Epidomax minimus* Tremblay & St. Clair in prep).

Site selection and point counts

To evaluate whether the abundance of each species decreased as anthropogenic noise increased, point counts were conducted at 113 locations in natural areas throughout the North Saskatchewan River valley and adjoining drainages in the City of Edmonton. Sites were located along a gradient of exposure to anthropogenic noise, from adjacent to major highways to the interior of urban forests. To avoid double counting, point count locations were separated by > 300 meters. Upon reaching each point, a stationary observer recorded the mean ambient noise level for one minute via a sound level meter (dBA SPL; Brüel & Kjær 2239, Naerum, Denmark), and for the next ten minutes recorded all focal species located by sight or by sound as being in one of two distance bands; 0-50 or 50-100 meters (Hutto, Pletschet and Hendricks 1986; Bibby, Burgess and Hill 1992). Observations beyond 100 meters were disregarded due to potential non-independence from other points. Each point was visited four times from 30 minutes prior to sunrise to 1100 hours between May 2 and June 27, 2008. To increase the likelihood of detections at noisy locations, all points were visited at least once near sunrise and once later in the morning. Point counts were not conducted in precipitation or winds > 2 on the Beaufort scale (Bibby, Burgess and Hill 1992). For analysis, ambient noise was calculated as the highest and lowest reading from any one visit and the mean of all visits.

Vocal recording

From April 25 – June 26, 2008, observers collected audio recordings of song bouts from seven focal species. These recordings coincided with point counts, although observers stayed at least 500 meters from the active point count location. Once a focal individual was located, the observer moved as close to the bird as possible while minimizing disturbance. All audio recordings were made with a Marantz digital, solid state recorder (PMD 670) with a directional (Sennheiser ME67) and omni-directional (Sennheiser ME62) microphone recording simultaneously on independent channels (Saul Mineroff, Elmont, New York, USA). Directional recordings were used for analysis of song characteristics, and omni-directional recordings were used to assess ambient noise levels. Recording ceased when the focal individual was lost, or a sufficient number of songs (> 30) was recorded. Recording generally lasted < 5 min, and rarely exceeded 10 min. Digital files were recorded with a 44,100 Hz sampling rate, gain of 2.5/10, and stored in PCM, 16 bit format.

Vegetative Structure

To account for differences in bird abundance due to habitat, vegetative structure was assessed at each point count location in July and August, 2008 (methods modified from Hannon et al. 2002; Habib, Bayne and Boutin 2007). Using a random initial azimuth, four 100 meter transect lines radiated from the center of each point at 90° angles. All trees > 5 m tall within 1 meter of the transect line were counted, identified to species (aspen poplar (*Populus tremuloides*), white birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), and other species), and classified based on their diameter at breast height (DBH; 1 = < 8 cm, 2 = 8 - 15 cm, 3 = 16 - 23 cm, 4 = 24 - 28 cm, 5 = > 28 cm). The number of trees along each transect was used to calculate density and relative dominance for each species. In addition, we calculated the percentage of each transect characterized as forest (dominant canopy > 5 m in height), shrub (dominant canopy 2 - 5 m in height), open (dominant canopy < 2 m in height), and water. At 20, 40, 60, 80, and 100 meters along each transect we counted all snags (dead, but not downed trees > 8cm DBH) within 5 m, classified dominant canopy height (1 = 5 - 10 m, 2 = 10 – 15 m, 3 = 15 – 20 m, 4 = 20 – 25 m, 5 = > 25 m), and estimated canopy cover (tree canopies separated by: 1 = touching, 2 = 1 - 2 m, 3 = 3 – 5 m, 4 = 5 – 10 m, 5 = > 10 m). Visual estimation of distances were initially calibrated during training sessions with a range finder (Bushnell Yardage Pro X500; Ontario, Canada), and cross checked regularly throughout the season. To describe ground cover, a 1 m^2 quadrant was placed at each sampling point, and the percentage of cover belonging to lawn (manicured), grass (natural), bare ground, herbaceous plants, and leaf litter was assessed. The stems of large (> 2 m) and small (0.5 – 2 m) shrubs were also counted within each quadrant. Data were averaged for all four transect lines resulting in one measurement for each vegetative variable per site (Table 4-1).

Analysis

Abundance

The highest count at any one visit represents the maximum utilization for a species at each point count location. In contrast, incorporating all visits suggests that four abundance observations of 1,1,1,1 are equal to 2,0,2,0, despite the additional bird located in the latter site. We suggest highest counts best represents each site's potential for utilization (Forrest and Clair 2006; Blake and Karr 1987; Blondel, Ferry, and Frochot 1981). To account for detectability differences between quiet and noisier locations, we pooled all detections of all focal species, and divided them into four noise categories (quartiles) based on the average noise level at each site (35.8-40.3, 40.4-44.8, 45-49.5, and 49.6 - 62.1 dB). We then determined the detection probability (P_a) separately for each noise category using half-normal binomial distance methods (comparing the number of detections < 50 m and > 50 m, DISTANCE 6.0; Thomas et al. 2010). P_a for noise categories ranged from 0.32 - 0.25. Although the differences were not substantial we divided the raw abundance (*n*) for each species by the detection probability (P_a) derived for the corresponding noise category to minimize the confounding effects of noise on detectability (Buckland, Marsden and Green 2008). We used the formulas:

$$N = A * D \text{ and,}$$

$$D = n / a * P_a$$

Where N = corrected abundance, D = density, A = total area, a = survey area, and P_a = detection probability. Since abundance was calculated for each point count, A = a, and thus, these formulas simplify to

$$N = n / P_a$$

The result is a noise corrected measure of abundance for each species at each point count location.

We assessed the effects of noise and vegetation on detectability-corrected abundance with general linear models (GLM; Stata 10; Statacorp., Texas, USA). To account for the high numbers of zeros and potential over-dispersion in our abundance data, we used the negative binomial distribution (Hardin and Hilbe 2007). We obtained best fit models for each species through a hierarchical model building procedure (Tremblay and St Clair 2009). We established six categories that represented a grouping of similar variables and selected the most parsimonious model from each category via the lowest Akaike Information Criterion, corrected for small sample sizes (AICc; Burnham and Anderson 2002). Top models were developed for 1) ground cover 2) habitat type 3) forest stand qualities 4) shrubs, 5) tree species, and 6) ambient noise (Table 4-1). Correlated variables (> 0.6) were not included in the same model. In each category we retained the univariate model with the lowest AICc value, and then added additional variables from the same category until they no longer reduced the model AICc (i.e., forward stepwise). We then compared top models from each category and retained the most parsimonious category. Finally, we employed forward stepwise addition of categories with AICc selection to derive the most parsimonious final model. To examine the fit of the final model we compared its explanatory power to that of the null model. Each dependant variable in the final regression model was standardized ($\bar{x} = 0 \pm 1$ std.dev.) so coefficients could be used to compare the relative effects of modeled parameters.

Song frequency

Songs were randomly selected for analysis from 20 individuals of each species. To avoid recording the same individual twice, all recorded individuals were separated by > 300 meters (Bibby, Burgess and Hill 1992). Generally, we analyzed 10 songs per individual (Ripmeester et al. 2010). In a few cases < 10 songs were available from an individual and a suitable replacement could not be found. Thus, we analyzed between 4 - 9 songs for up to three individuals from each species. We selected individuals from a similar set of distance and noise ranges across species to minimize the inter-species variance in vocal frequencies due to these factors (Wiley and Richards 1982; Patricelli and Blickley 2006).

We measured three song frequency characteristics that potentially affect how easily a song can be detected and discriminated against background noise. Peak frequency (PF), or frequency at the maximum amplitude, signifies which frequencies were emphasized in each vocalization, and was measured on a frequency spectrum in SIGNAL 5.04.22 (FFT; ≥ 65,536 points, ≥ 0.7 Hz resolution; Berkeley CA, USA). Minimum frequency (F_{min}) shows to what extent the lower song elements overlap with anthropogenic noise, and maximum frequency (F_{max}) reveals how much spectral separation existed between the upper end of the signal and anthropogenic noise. F_{min} and F_{max} were calculated as the highest and lowest frequencies where the song amplitude was within 35 dB of the peak amplitude (Charrier, Bloomfield and Sturdy 2004; Proppe and Sturdy 2009). To increase the accuracy of our frequency measurements, we removed background noise from the audio files before measuring F_{min} and F_{max} (1,500 – 10,000 Hz band pass filter, and the noise reduction procedure in Goldwave 5.55; St John's, NL, Canada; (Baker and Logue 2007). For all frequency measures we calculated the mean and the variance for each species, because we hypothesized that both absolute frequency and plasticity could contribute to a species urban success. Because the perception of frequency change is relative to the absolute frequency (Weber's Law; Stevens 1955), we standardized the variance measures for each species (i.e., coefficient of variation; CV = $(\text{std.dev.}/\bar{x}) * 100$).

To test how each frequency measure related to a species willingness to inhabit noisy locations, we developed a dependant variable - called noise sensitivity - which represented each species change in abundance as anthropogenic noise increased. The noise sensitivity variable was calculated by calculating the residuals from the top abundance model for each species, with the noise variable removed (if included in the top model). The residuals were then standardized so that they could be compared across species ($\bar{x} = 0 \pm 1$ std.dev.). Next, we performed a linear regression with the standardized residuals and ambient noise. The beta coefficient for noise from this regression represented the noise sensitivity variable because it described the standardized change in abundance in response to increasing anthropogenic noise after accounting for abundance changes due to habitat structure. To determine whether any of the frequency measures correlated with noise sensitivity we performed separate linear regressions for each frequency measure. Because the final regression contained only one dependent variable, we used the p value (< 0.05) to determine significance.

Results

Abundance

Abundance declined significantly with increasing levels of ambient noise level for three of seven focal species (Table 4-2; Figure 4-1): western tanager ($\beta = -0.67 \pm 0.22$, $z = -2.43$, $p = 0.015$); least flycatcher ($\beta = -1.07 \pm 0.29$, $z = -3.72$, $p < 0.001$); and, red-breasted nuthatch ($\beta = -0.60 \pm 0.18$, $z = -3.27$, $p < 0.001$). Abundance for each of these species was also affected by vegetative characteristics (Table 4-3). In the final model for the western tanager, noise ranked below high shrubs ($\beta = -0.98 \pm 0.36$), but above six other predictive variables ($\beta \leq |0.65|$). For the least flycatcher, noise ranked below herbaceous cover ($\beta = 1.11 \pm 0.28$), but above seven other predictive variables ($\beta \leq |1.03|$). Noise was the strongest predictor of abundance in the red-breasted nuthatch, followed by seven other predictive variables ($\beta \leq |0.53|$).

Final models for three of our seven focal species did not include noise, but did retain vegetative predictors. Black-capped chickadee abundance increased with relative dominance of aspen ($\beta = 0.27 \pm 0.11$) and spruce ($\beta = 0.22 \pm 0.11$). Red-eyed vireo abundance increased with leaf litter ($\beta = .23 \pm 0.14$) and density of ‘other’ tree species ($\beta = 0.16 \pm 0.11$). White throated sparrow abundance increased with forest ($\beta = 0.54 \pm 0.14$) and shrub cover ($\beta = 0.23 \pm 0.14$).

The null model was a more parsimonious explanation for yellow warbler abundance than any combination of variables collected in this study (Table 4-2). However, AICc weight of the null model was only slightly higher (0.24) than the next best model which including high shrubs (0.16), suggesting that this variable may have some effect on yellow warbler abundance ($\beta = 0.11 \pm 0.10$).

Song frequency

The minimum song frequency (F_{min}) of a species' song was highly predictive ($r^2 = 0.82$) of a species noise sensitivity (i.e., change in abundance with increasing anthropogenic noise; $\beta = 1.54\text{E-}05 \pm 3.18\text{E-}06$, $t = 4.85$, $p < 0.005$; Figure 4-2). PF and F_{max}, however, had no effect on noise sensitivity ($p \geq 0.217$; Table 4-4). Contrary to our expectations, the plasticity of species-specific songs (CV) was not related to noise sensitivity for F_{min}, PF, or F_{max} ($p \geq 0.360$).

Discussion

Recent studies have suggested that anthropogenic noise may contribute to observed declines in songbird abundance, and may partially account for lower biodiversity in urban areas (Slabbekoorn and Ripmeester 2008; Laiolo 2010). Our results provide empirical evidence and support for this hypothesis. After accounting for differences in vegetative structure, the abundance of two locally declining species - the least flycatcher and western tanager - decreased with increasing anthropogenic noise, while the abundance of four common urban species was not affected by anthropogenic noise. Only the red-breasted nuthatch did not conform to our hypothesis, becoming less abundant as noise increased despite its common and stable population status in Edmonton, Alberta (Edmonton Christmas bird count summary 2008).

Minimum song frequency was highly predictive of whether the abundance of a species would be reduced with increasing anthropogenic noise, but was less predictive of whether a species was widespread in urban areas (Figure 4-3). Minimum song frequencies for the red-eyed vireo and red-breasted nuthatch are heavily overlapped by anthropogenic noise, yet both species are abundant in urban areas (nuthatch: Edmonton Christmas bird count summary 2008; vireo: Federation of Alberta Naturalists 2007). Finally, frequency plasticity did not predict noise sensitivity or urban distribution.

The negative effect of noise on the abundance of our two locally declining migrants suggests that noise potentially contributes to the decline of some species in urban areas. While acceptable habitat may already be sparse for many urban avoiders, anthropogenic noise may prevent settlement in the remaining parks and greenspaces. The observed relationship between reduced abundance and increasing noise in some species may be a result of an inherent aversion to noise, learned avoidance, or disruption to social processes such as mate attraction and recruitment (Reed and Dobson 1993). Experimental evaluation of individual and social avian behaviour in noise-affected environments will elucidate which mechanism(s) underlying noise-induced reduction in abundance.

The ability to predict which species’ are most susceptible to anthropogenic noise is important for the management of rare or declining species that inhabit urban areas, and while urban parks are inhospitable to many rare songbirds, other species may thrive in these areas (Sorace and Gustin 2010). It is noteworthy that minimum, peak, and maximum song frequencies were not correlated, and that only minimum frequency was predictive of a species' abundance. In some species minimum frequencies were almost entirely masked, but peak and maximum song frequencies were well above the frequencies of anthropogenic noise. For example, least flycatcher songs often exceeded 7 kHz. Songbirds relay information through specific elements of their songs (Charrier et al. 2005; Mahurin and Freeberg 2009), and low frequency elements are often particularly important for communication, as they indicate body size and dominance in many animals (Davies and Halliday 1978; ten Cate, Slabbekoorn and Ballintijn 2002; Soltis et al. 2009). For example, calls from male Tungara frogs (*Engystomops pustulosus*) without low frequency 'chucks' do not elicit normal female response (Ryan et al. 1990). Male fallow deer (*Dama dama*) and scops owls (*Otus scops*) with lower frequency vocalizations are more dominant individuals (Vannoni and McElligott 2008; Hardouin et al. 2009). Female songbirds that do not hear the low frequency elements of a vocal signal may perceive the singing male as an ill-suited mate. In addition, vocal signals perceived as altered or abnormal often elicit different behavioural responses, even if much of the signal remains intact (Nowicki et al. 2001; Derryberry 2007). Masked vocal signals may be less affective because they are perceived as abnormal.

Plasticity (CV) was not associated with noise sensitivity. We suggest that the ability to produce signals across a broad frequency range may only benefit species for which the upper limit of their range escapes overlap with anthropogenic noise. For example, the minimum song frequencies for the great tit (*Paris major*) and black-capped chickadee ranges from ~ 2 - 4 kHz, a range where the energy in anthropogenic noise quickly decreases with increasing frequency (Slabbekoorn and Peet 2003). Conversely, minimum song frequencies for the least flycatcher and western tanager in our study reached no higher than ~ 2.5 kHz, a frequency still heavily overlapped by anthropogenic noise. While the hypothesis that vocal plasticity pre-adapts some species for noisy environments was not supported, whether species differ in their ability to shift frequency in response to noise needs further testing. To incorporate species that did not occur in noisy locations we limited the noise range from which we drew our samples. In this limited range, none of the seven species demonstrated a relationship between minimum song frequency and noise level ($p \geq 0.12$). Yet, we know that black-capped chickadees do adjust song frequency across greater ranges of noise. In one comparative test of frequency shifting ability, Hu and Cardoso (Hu and Cardoso 2010) recorded 12 bird species in urban and non-urban environments and found that the largest frequency shifts were made by species whose vocal signals were near the limits of anthropogenic noise (1-5 kHz). They suggest that species whose songs were higher or lower in frequency would not experience spectral release by shifting frequencies. In sum, singing across a broad frequency range appears to be important for a limited number of species whose vocalizations naturally occur in the upper range of the frequencies that are overlapped by anthropogenic noise.

While minimum song frequency is predictive of noise sensitivity, it may be less useful for predicting general urban success. Two examples from our study suggest that noise intolerant species may use other mechanisms to avoid urban declines. First, the red-breasted nuthatch possessed the lowest minimum song frequency of all species in our study and was less common in noisy locations, as predicted. However, red-breasted nuthatches are common in Edmonton many urban areas (BirdLife International 2009). This may be related to the nuthatches propensity to inhabit suburban areas, and utilize backyard feeders (Blewett and Marzluff 2005). Suburban areas are generally quieter than urban parks (Nilsson and Berglund 2006), and may provide a noise refuge for some species. Species like the flycatcher and tanager require large, mature forest tracks, which may preclude their use of a suburban refuge (Dellasala and Rabe 1987; Stelfox et al. 1995). Suburbs may represent a valuable, but limited, escape from anthropogenic noise for species that can tolerate more isolated trees and a relative lack of understory.

Despite its low-frequency song, red-eyed vireos remained abundant in sites with high levels of anthropogenic noise, and are relatively unaffected by urbanization (Friesen, Eagles and MacKay 1995). We speculate that the persistence of red-eyed vireos at noisy sites may be related to their unusual tendency to sing throughout the day (Hartshorne 1956; Williams.P 1971). Most songbirds sing primarily near dawn, which overlaps with morning rush hour; the most ubiquitous and intense source of anthropogenic noise in the urban environment (Warren et al. 2006). This hypotheses is currently untested in vireos, but another species, the European robin (*Turdus migratorius*), sings before dawn in locations that are exposed to daytime anthropogenic noise (Fuller, Warren and Gaston 2007). This is especially interesting because robins are highly successful in Edmonton and most urban areas (Morneau et al. 1995), but their vocalizations are similar to that of the locally declining western tanager, which sings primarily during the dawn chorus. While other life history traits may also contribute to a species ability to use urban habitats, singing during predictably quiet time periods may increase the viability of bird species with low frequency songs.

In sum, we show that the relative abundance of seven bird species in urban areas can be predicted by the minimum frequency of their songs. Further work with more species and in more locations is required to demonstrate the generality of this relationship. In our study, species with lower song frequencies were less abundant at noisy sites, potentially because they suffered greater masking from traffic noise. Previously, we and others have shown that some species appear to minimize anthropogenic masking by increasing the frequency of their songs to (e.g., Slabbekoorn and Peet 2003; Wood and Yezerinac 2006), but other species may lack this ability. For those species, other means of adapting to noisy urban environments may be possible. We speculate that at least two other mechanisms could contribute to the persistence of some bird species in urban areas: the ability to sing through a larger portion of the day so as to avoid reliance on times when anthropogenic masking is greatest (e.g., red-eyed vireo) and the ability to use anthropogenically-modifed habitats that are buffered from anthropogenic noise (e.g., red-breasted nuthatches). Species that lack any of these abilities may be expected to decline in urban areas as appears to be the case for least flycatchers and western tanagers in our study area.

Our results have several implications for city planners and wildlife managers. First, minimum song frequency may be a useful metric for predicting how birds will react to anthropogenic, particularly road, noise in diverse locations. Second, if residential neighbourhoods provide a refuge for noise-sensitive species, their value might be increased for avian diversity by increasing habitat quality (e.g., understory plants, fruit and seed-bearing plants). Finally, mitigation aimed to conserve songbirds should identify methods for reducing the masking caused by anthropogenic noise, particularly road noise. New road surfaces and tire materials might be particularly helpful for birds as well as people (Benitez-Lopez, Alkemade and Verweij 2010).

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Figure legends

Figure 4-1. Maximum point count abundance adjusted for noise-based detectability differences, and plotted against ambient noise level for the three species whose abundance was affected by ambient noise levels. Solid black lines represent the predicted density values from negative binomial regression models after accounting for covariates. Grey circles represent observed abundance levels, after adjustment to account for detectability**.** Note that y axes are not on the same scale for different species. To improve visual acuity, one outlier (at 6.44) was removed from the observed Western tanager abundance.

Figure 4-2. Mean minimum song frequency for each bird species regressed against a coefficient representing each species change in abundance with increasing noise (termed noise sensitivity). A species whose abundance decreases with increasing noise levels with have a negative noise sensitivity coefficient, and vice versa.

Figure 4-3. Mean minimum song frequency and standard deviation for each species, overlaid on a frequency × time spectrograph of recorded of highway noise (57 dB SPLA). Background shading represents the relative level of energy produced by highway noise at each frequency with darker shading indicating more energy.

Table 4-1. Categories and variables for abundance models

1) ground cover
- Lawn
- Grass
- bare ground
- herbaceous
- leaf litter

2) habitat type
- Forest
- Shrub
- Open
- Water

3) forest stand qualities
- Snags
- tree density
- tree height
- tree diameter (DBH)
- canopy cover

4) shrubs
- high shrubs
- low shrubs

5) tree species
- *relative dominance*
  - aspen poplar
  - balsam poplar
  - white birch
  - white spruce
  - other species
- *species density*
  - aspen poplar
  - balsam poplar
  - white birch
  - white spruce
  - other species

6) ambient noise
- mean of all visits
- highest noise measure
- lowest noise measure

Table 4-2. Top three most parsimonious AICc selected general linear models for each focal species

Categories	Variables	Parameters	AICc	weight
Western tanager				
FOR, DB, SPEC, SH, GC	FOR, DB, SPEC, SH + lawn, leaf litter	9	193.93	0.43
Full	FOR, DB, SPEC, SH, GC + forest, shrub, water	11	194.31	0.36
FOR, DB, SPEC, SH	height, dbh + lowest noise measure + relative dominance: spruce + low shrubs, high shrubs	7	195.60	0.19
Least flycatcher				
GC, SPEC, DB, SH	GC, SPEC, DB + high shrubs, low shrubs	10	270.31	0.99
Full	GC, SPEC, DB, SH + forest, shrub, open, water + snag, tree height, dbh	17	281.78	0.00
GC, SPEC, DB	leaf litter, herbaceous + density: balsam, spruce, birch, aspen + highest noise measure	8	282.52	0.00
Red-breasted nuthatch				
DB, GC, FOR, HAB	DB, GC, FOR + forest, open, shrub	9	380.56	0.60
DB, GC, FOR	DB, GC + snag, canopy cover	7	382.67	0.21
DB, GC	lowest noise measure + bare ground, lawn, grass	5	383.23	0.16
Black-capped chickadee				
SPEC	relative dominance: white spruce, aspen	3	617.91	0.67
Null	no variables	1	621.76	0.10
HAB	Water	2	622.87	0.06
Red-eyed vireo				
GC, SPEC	GC, SPEC	3	584.73	0.34
GC	leaf litter	2	584.98	0.30
SPEC	density: other species	2	586.87	0.12
White-throated sparrow				
HAB	forest, shrub	3	486.03	0.66
FOR	canopy cover	2	488.36	0.21
GC	leaf litter, herbaceous	3	491.14	0.05
Yellow warbler				
Null	no variables	1	703.25	0.25
SH	high shrubs	2	704.09	0.16
SPEC	density: aspen	2	704.40	0.14

**FOR = forest stand qualities, DB = ambient noise, SPEC = tree species, GC = ground cover, SH = shrubs, HAB = habitat type

Table 4-3. Standardized effect sizes, significance level, and confidence intervals for variables in the top model for each species. *The null model was the top model for the yellow warbler but the second candidate model is shown because of the small difference in AIC weights (ΔAICw = 0.09).

Species	Variable	β	SEM	z	P>|z|	95% CI	
Western tanager	high shrub	-0.98	0.36	-2.76	0.006	-1.68	-0.29
	lowest noise	-0.67	0.22	-2.43	0.015	-1.21	-0.13
	dbh	0.65	0.21	3.15	0.002	0.25	1.06
	leaf litter	0.64	0.29	2.25	0.024	0.08	1.20
	rel. spruce	0.61	0.22	2.80	0.005	0.18	1.05
	low shrub	0.54	0.24	2.23	0.026	0.07	1.02
	tree height	0.23	0.25	0.92	0.356	-0.26	0.72
	lawn	-0.11	0.30	-0.37	0.715	-0.71	0.49
Least flycatcher	herbaceous	1.11	0.28	3.92	< 0.001	0.56	1.67
	highest noise	-1.07	0.29	-3.72	< 0.001	-1.63	-0.51
	den. spruce	-1.03	0.25	-4.08	< 0.001	-1.53	-0.54
	leaf litter	0.95	0.23	4.10	< 0.001	0.50	1.41
	high shrubs	-0.76	0.21	-3.67	< 0.001	-1.17	-0.35
	den. aspen	-0.71	0.20	-3.46	< 0.001	-1.11	-0.31
	low shrubs	-0.26	0.26	-0.98	0.327	-0.78	0.26
	den. poplar	-0.11	0.19	-0.59	0.558	-0.47	0.26
	den. birch	-0.11	0.17	-0.65	0.518	-0.43	0.22
Red-breasted nuthatch	lowest noise	-0.60	0.18	-3.27	< 0.001	-0.96	-0.25
	canopy cover	-0.53	0.22	-2.39	0.017	-0.96	-0.09
	open	0.52	0.21	2.49	0.013	0.11	0.93
	lawn	-0.30	0.23	-1.29	0.196	-0.74	0.15
	bare ground	-0.19	0.23	-0.82	0.414	-0.63	0.26
	snag	0.14	0.17	0.80	0.424	-0.20	0.47
	shrubs	0.06	0.18	0.35	0.725	-0.29	0.42
	grass	0.02	0.19	0.10	0.924	-0.36	0.39
Black-capped chickadee	rel. aspen	0.27	0.11	2.51	0.012	0.06	0.49
	rel. spruce	0.22	0.11	2.03	0.042	0.01	0.44
Red-eyed vireo	leaf litter	0.23	1.14	2.06	0.040	0.01	0.46
	den. other	0.16	0.11	1.43	0.152	-0.06	0.37
White-throated sparrow	forest	0.54	0.14	3.81	< 0.001	0.26	0.82
	shrub	0.23	0.14	1.63	0.103	-0.05	0.51
Yellow warbler*	high shrubs	0.11	0.10	1.09	0.276	-0.09	0.31

Table 4-4. Results from linear regression for A) absolute frequency, and B) coefficient of variation for minimum (F_{min}), peak (PF) and maximum (F_{max}) song frequencies. Frequency measures are the mean for each of seven focal species. Noise sensitivity is a standardized coefficient representing each species change in abundance in response to increasing noise levels. It is calculated by standardizing the residuals after linear regression with all variables from the top abundance model (except noise), and recording the beta coefficient for noise from a subsequent regression of the residuals and ambient noise. A species whose abundance decreases with increasing noise levels with have a negative noise sensitivity coefficient, and vice versa.

	Variable	**β**	**SEM**	***t***	***P*>|*t*|**	**95% CI**		***r*²**
A) Noise sensitivity	F_{min}	1.54E-05	3.18E-06	4.850	0.005	7.25E-06	2.36E-05	0.825
	PF	6.44E-06	4.56E-06	1.410	0.217	-5.28E-06	1.82E-06	0.285
	F_{max}	1.64E-06	2.74E-06	0.600	0.575	-5.41E-06	8.69E-06	0.067
B) Noise sensitivity	CV of F_{min}	-0.114	0.113	-1.010	0.360	-0.404	0.177	0.168
	CV of PF	-0.025	0.096	-0.260	0.803	-0.271	0.221	0.014
	CV of F_{max}	-0.057	0.100	-0.570	0.596	-0.315	0.201	0.060

Figure 4-1

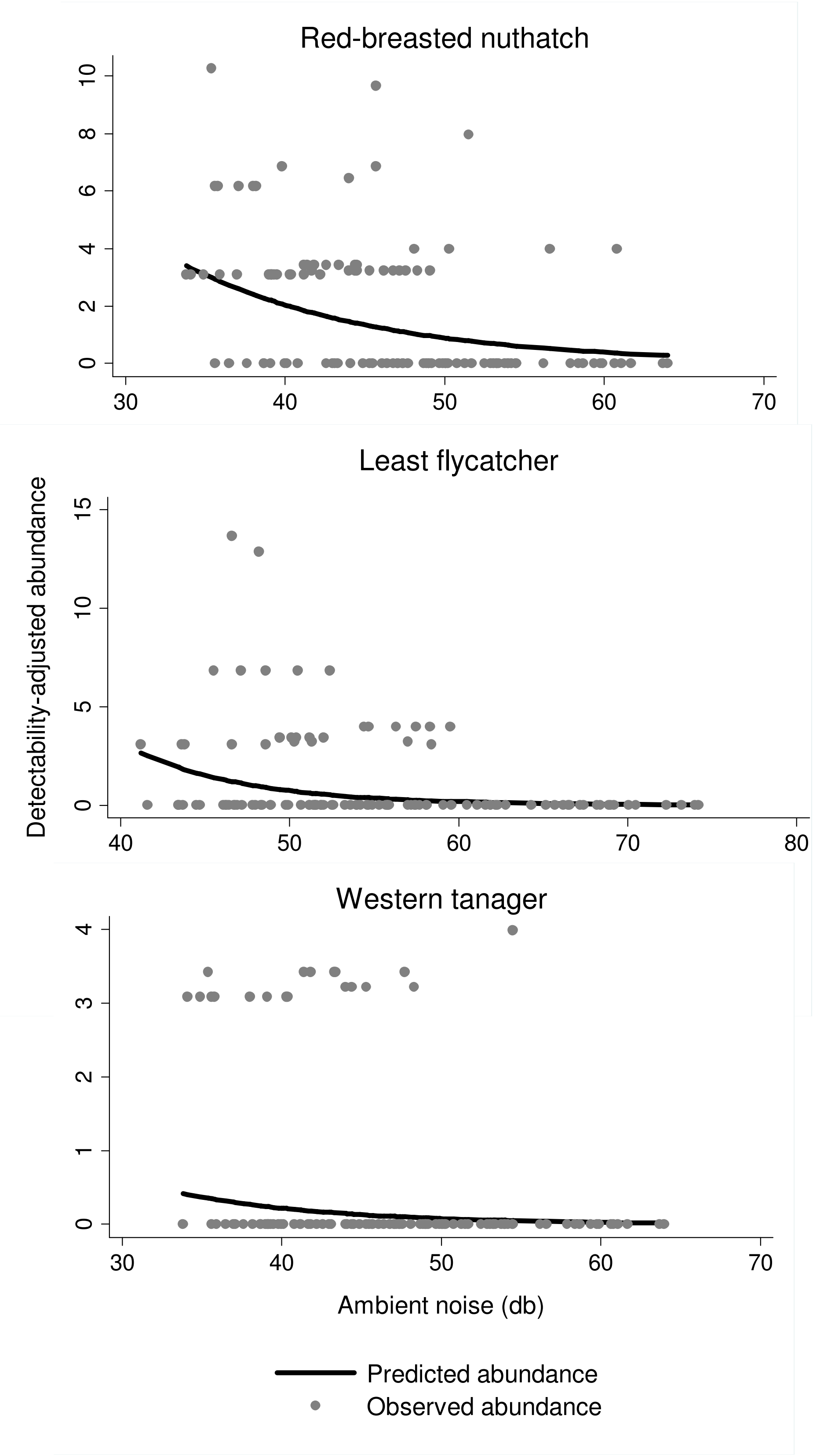

Red-breasted nuthatch
0
2
4
6
8
10
30
40
50
60
70
Least flycatcher
0
5
10
15
40
50
60
70
80
Detectability-adjusted abundance
Western tanager
0
1
2
3
4
30
40
50
60
70
Ambient noise (db)
Predicted abundance
Observed abundance

Figure 4-2

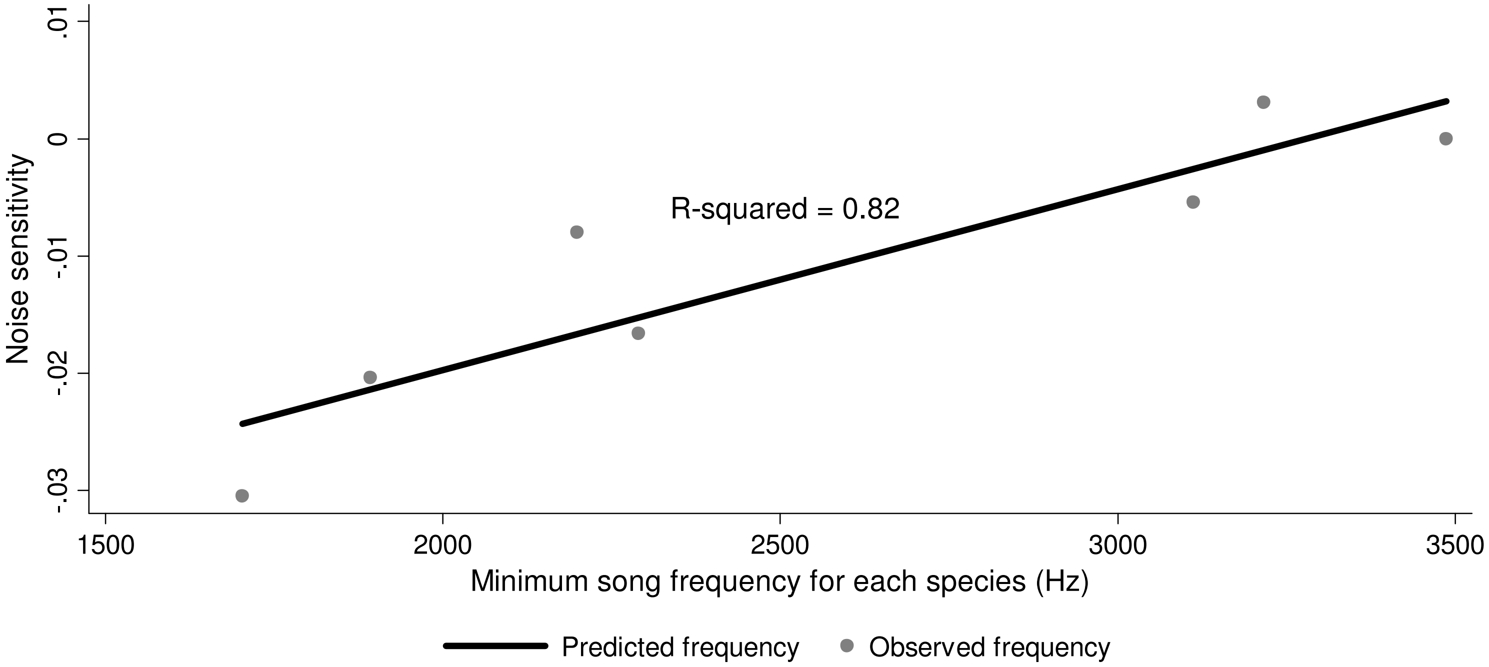
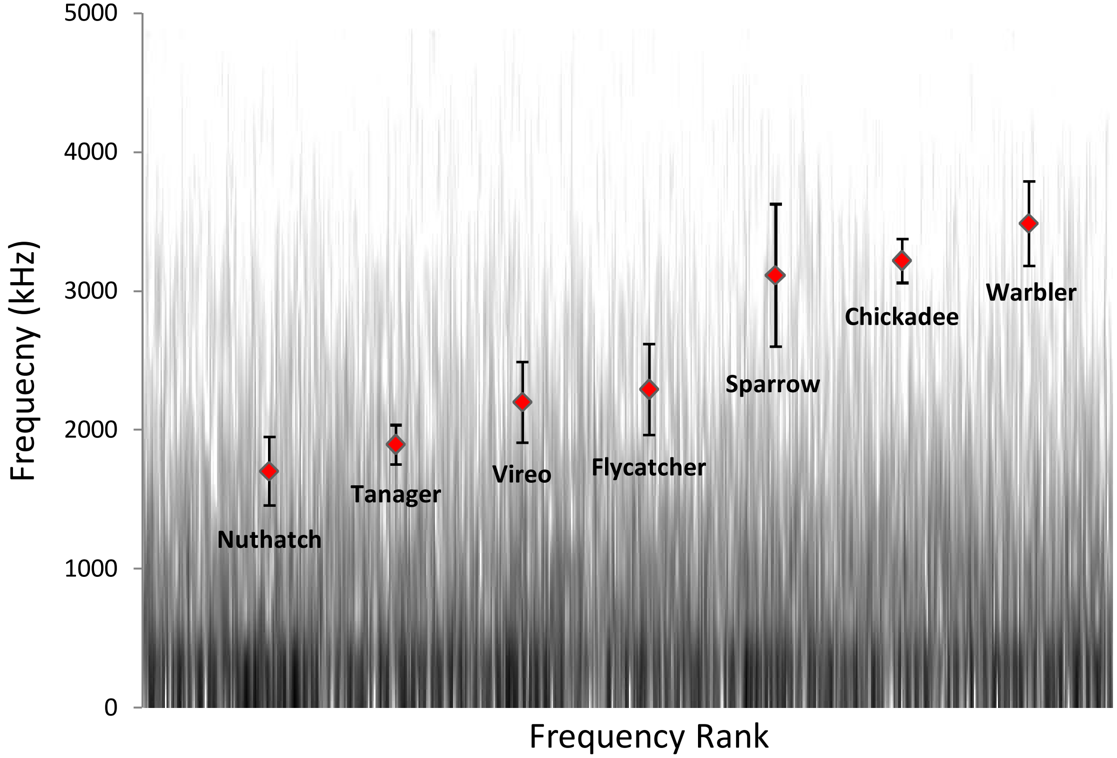

.01
0
-.01
-.02
-.03
Noise sensitivity
R-squared = 0.82
1500
2000
2500
3000
3500
Minimum song frequency for each species (Hz)
Predicted frequency
Observed frequency

Figure 4-3


5000
4000
3000
2000
1000
0
Frequecny (kHz)
Frequency Rank
Nuthatch
Tanager
Vireo
Flycatcher
Sparrow
Chickadee
Warbler

Chapter 5

General discussion

The objectives of my research were 1) to investigate the role of anthropogenic noise and vegetative structure in the observed shift to higher song frequencies for black-capped chickadees in noise-affected areas, 2) to examine whether behavioural plasticity underlies these frequency shifts, and 3) to evaluate whether frequency masking of vocal signals by anthropogenic noise predicts a whether a species' abundance will decline with increasing noise, and in urban environments. My first two objectives were designed to increase our understanding of avian vocal response to novel stimuli, and the behavioural mechanisms that facilitate these responses. Ultimately, these two studies provided additional information regarding the mechanisms by which vocal systems adapt to changing environmental conditions. My final objective addressed potential concerns regarding the negative impact of anthropogenic noise on some songbird populations and on avian diversity in urban areas. In the following sections I discuss my results in relation to songbird communication and conservation and management. For each topic, I address some of the important topics for future research.

Songbird communication

I found that black-capped chickadees altered the frequency of their songs with increasing anthropogenic noise. This is congruent with the acoustic adaptation hypothesis (AAH; Rothstein and Fleischer 1987), which posits that animal vocal signals are designed for optimal transmission distances within their respective environments (Morton 1975; Marten and Marler 1977). Many previous studies have shown that songbird vocalizations reflect the density and complexity of the vegetation in their local habitats (Hunter and Krebs 1979; Gish and Morton 1981; Kroon and Westcott 2006; Boncoraglio and Saino 2007; Barker 2008; Ey and Fischer 2009). More recent research has revealed that songbird vocalizations also reflect the types of noise present in the environment (Wasserman 1977; Mcgregor and Peake 2000; Slabbekoorn 2004; Poesel, Dabelsteen and Pedersen 2007; Kirschel et al. 2009). I examined how these two forces interact, by comparing black-capped chickadee songs in forests with different habitat characteristics and different levels of anthropogenic noise.

My work suggests that short-term acoustic adaptation of vocal signals may conform more strongly to noise conditions than to vegetative structure. Songs did not differ between sites with different habitat characteristics but equally high levels of anthropogenic noise. Conversely, songs in quiet sites were sung at lower frequencies despite having vegetative characteristics that favoured the use of higher frequencies. Some authors have suggested that local vegetative characteristics contributed to the evolution and divergence of vocal structure for many songbirds (Wiley and Richards 1978; Slabbekoorn 2004). Our results suggest that noise may also contribute to vocal divergence.

In my study, noise differed dramatically between categories of vegetative structure, but all birds were recorded in forests that differed only in the degree of canopy cover, representative of the extremes found within ‘typical’ chickadee habitat (Schroeder 1983). It would be interesting to test whether vegetative structure would more strongly affect vocal characteristics if songs recorded in dense forests and compared to those from entirely open habitats. In cases where vegetative differences are large and anthropogenic noise is modest, we may find that acoustic signals are designed for optimal communication in response to vegetation.

The degree to which vocalizations reflect noise or vegetative characteristics may also depend on how quickly vocal structure can be modified. Noise levels often fluctuate over short timescales (i.e., throughout the day (Thomas, Weijermars and van Berkum 2008), but changes to vegetative structure generally progress slowly (i.e., seasonally or over years; Chapman et al. 2010). If changes to vocal structure occur only over generations of learning and selection (Nelson, Khanna and Marler 2001; Beecher and Brenowitz 2005; Podos and Warren 2007; Mooney 2009), vocalizations probably conform only to vegetative characteristics or long-term noise conditions. Song variation is generally limited after a juvenile's first year (Nelson and Marler 1994; Marler 1997) and may be further constrained by the tendency for females to select males whose songs conform to the species norms (Harbison, Nelson and Hahn 1999; Nowicki et al. 2001; Hernandez et al. 2009). Yet, I found that breeding adult black-capped chickadees rapidly increased their song frequency as anthropogenic noise levels increased. Previous work has shown that adult house finches (*Carpodacus mexicanus*) and great tits (*Paris major*) also respond rapidly to increasing anthropogenic noise by switching to higher frequency song types (Bermudez-Cuamatzin et al. 2009; Halfwerk and Slabbekoorn 2009). These results align with previous behavioural (Proppe and Sturdy 2009) and neurobiological (Brenowitz

2004; Tumer and Brainard 2007) studies which have documented plasticity in the adult repertoire of some songbirds.

Vocal plasticity may allow some species to respond quickly to anthropogenic noise, but whether it provides any direct fitness benefit is relatively unknown. Increasing vocal frequency in the presence of low-frequency anthropogenic noise increases signal detectability by con- and heterospecifics (Wiley 2006; Slabbekoorn and Ripmeester 2008), but we do not know if these altered signal are as salient. One recent study tested the responsiveness of conspecific male great tits to playback of songs produced by males in high and low anthropogenic noise (Mockford and Marshall 2009). Songs differed predictably between noise categories, and interestingly, males responded more strongly to the song type produced in the noise conditions that were similar to those they inhabited. To my knowledge, this is the only study examining the salience of acoustically-adapted signals. Testing female response to acoustically-adapted signals would provide valuable insight into whether such signals directly alter reproductive fitness. Nonetheless, research to date has demonstrated a widespread pattern of acoustic adaptation of vocal signals in response to vegetative structure and ambient noise, and has not yet documented any negative fitness costs of these adaptations. While these vocal adaptations may not entirely overcome all acoustic obstacles, it is reasonable to suggest that they confer some communication benefits for the songbirds producing them.

Conservation and management implications

Since vocal communication in songbirds is necessary for successful mating and reproduction (Slater 2003; Catchpole and Slater 2008) anthropogenic noise may disrupt these functions, and negatively affect population viability (Slabbekoorn and Ripmeester 2008). My results, in conjunction with other studies (Stone 2000; Rheindt 2003; Hu and Cardoso 2009) show that anthropogenic noise from urban and highway development is associated with reduced abundance in some bird species. In my multi-species comparison, the abundance of species with higher song frequencies was less likely to be affected by anthropogenic noise than the abundance of species whose song frequencies overlapped with anthropogenic noise. The ability to sing across a broad range of frequencies, however, was unrelated to the effect of anthropogenic noise on a species' abundance. Several previous studies, including my own work with black-capped chickadees, have documented frequency plasticity in response to anthropogenic noise (Slabbekoorn and Peet 2003; Fernandez-Juricic et al. 2005; Wood and Yezerinac 2006), suggesting that this is a mechanism used by some species to avoid overlap with noise. Ultimately, the degree of separation between the frequencies of anthropogenic noise and the frequencies of a natural or altered vocal signal may determine a signal's detectability, and thus, its efficacy for communication in noisy environments.

Many of the widespread urban species in this, and other (Hu and Cardoso 2009), studies possessed high frequency vocalizations. Of the four species in my study whose song frequencies were overlapped by anthropogenic noise, three experienced significant declines in abundance as noise increased, and two are of local conservation concern (Hobson et al. 2008). However, two of the four species remain abundant in Edmonton and other urban areas (Butcher and Niven 2007). I suggest these species escape vocal masking from anthropogenic noise by singing before or after periods of rush hour traffic, or by inhabiting quiet suburban neighbourhoods. Possession of at least one adaptation to avoid vocal overlap with anthropogenic noise may partially explain the abundance of some songbird species in urban areas and the loss of others, resulting in reduced overall avian diversity (Chace and Walsh 2006; McKinney 2006).

Anthropogenic noise is only one aspect of urban development that is altering bird populations. Loss of habitat, especially mature native plant communities, affects the ability of many species to inhabit urban landscapes. For example, mature ashe juniper (*Juniperus ashei*) are often removed in Central Texas landscapes (Diamond, Rowell and Keddyhector 1995), but since the federally endangered golden-cheeked warbler constructs their nest from the bark of these trees, loss of mature juniper is related to declines in local warbler populations (Kroll 1980).

Habitat fragmentation also contributes to songbird declines by reducing the area available for forest interior species, and leaving patches that fall below minimum breeding requirements (Huste and Boulinier 2007; Hinam and Clair 2008; Butcher et al. 2010). Roads and human structures are movement barriers for some songbird species, exacerbating the effect of fragmentation (Tremblay and St Clair 2009). Finally, the increased presence of exotic species excludes some native bird species (Shochat et al. 2010), and some nest predators are more pervasive in urban habitats (Baker et al. 2005; Marzluff et al. 2007; Lopez-Flores, MacGregor-Fors and Schondube 2009).

There are many threats to the survival of urban songbird populations. Yet, as human development continues, urban parks and greenspaces are becoming more important for avian conservation initiates (Ricketts and Imhoff 2003; Mcdonald, Kareiva and Formana 2008). Urban parks also provide some advantages: some natural predators are absent in urban parks (Gering and Blair 1999; Ryder et al. 2010), feeding stations provide readily available food resources (Fuller et al. 2008; Robb et al. 2008), early succession habitats may be more commonplace (Gifford, Deppen and Bried 2010), and microclimates may be more favourable during winter (Atchison and Rodewald 2006). Fortunately, the preservation of larger urban parks that are less permeated by roads can simultaneously minimize the negative impacts of many of the aforementioned concerns. Many species may benefit from reduced fragmentation (Evans, Newson and Gaston 2009) and the maintenance of interior forest that are free of human structures (Suarez-Rubio and Thomlinson 2009; Benitez-Lopez, Alkemade and Verweij 2010). In addition, anthropogenic noise will permeate a smaller portion of the landscape. Placement of buildings and parking lots (Pandya 2001), landscaping (Erdogan and Yazgan 2009), installation of roadside barriers (Cheng et al. 2003), and development of noise-reducing tire and road surfaces (Bennert et al. 2005) may also contribute to an overall reduction in anthropogenic noise (Gilchrist, Allouche and Cowan 2003).

Summary

My research supports the notion that some songbirds possess vocal adaptations to avoid the masking effect of anthropogenic noise. Furthermore, my work demonstrates that one mechanism underlying these adaptations is short-term behavioural plasticity. My work strengthens the hypothesis that the ability to compensate for anthropogenic noise partially explains whether songbirds adapt to urban environments or avoid them (Slabbekoorn and Ripmeester 2008; Hu and Cardoso 2009). Further, I show that interference to vocal communication may underlie this effect. Future work is needed to understand the temporal and spatial scale at which birds adapt their vocalizations to the environment. I also suggest that the fitness benefits of vocal adaptation need to be more thoroughly examined. In sum, my research shows that some songbirds possess highly adaptable vocal systems, allowing them to alter vocal signals rapidly for communication within anthropogenic noise. For other species, anthropogenic noise appears to be an insurmountable acoustic obstacle. For these species, management of anthropogenic noise may be critical if worldwide industrialization continues at its current rate (Ehrlich 2009). Reduced levels of anthropogenic noise will also improve the quality of life for human beings (Ohrstrom et al. 2007), and thus, noise mitigation offers potential benefits for both human society and wildlife.

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