Effects of Urban Noise on Vocalisations of Tūī *(Prosthemadera novaeseelandiae)*

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Miriam Robin Ludbrook

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Abstract

The two most important functions of avian acoustic communication are territory defence and mate attraction. As such the effective communication of these signals is critical for individual reproductive success. However if these vocal signals are masked by anthropogenic noise, their signal efficiency is reduced and this may result in direct negative fitness consequences. Therefore knowledge on how urban habitat features including anthropogenic noise affect avian vocal communication is important in understanding the evolution of animal communications in urban ecosystems. Such knowledge is also important for the management of endangered and declining species in urban areas.

Little is known about how birds respond to the highly variable levels of urban noise in urban habitats. In this study I investigated spectral and temporal differences in songs between populations of tūī (*Prosthemadera novaeseelandiae*) in urban habitats with both high noise levels (near motorway) and lower noise levels (distant from motorway). Male long-range tūī songs were collected during the breeding season (October 2012 to February 2013) at three paired sites, with one of each pair situated within 100m of a motorway and the matching site within 2-3 kilometres from the first site and the motorway. Urban noise levels (dB) were measured at all sites. I compared motorway and non-motorway urban songs to determine whether tūī shift the frequency, duration, trill components and output of songs in response to anthropogenic noise. Songs were also recorded at two paired non-urban sites over 50 kilometres from the urban sites (Mahurangi Regional Park and Wenderholm Regional Park) and spectral characteristics were also compared between these non-urban and the urban sites. I compared song rate and singing rate to investigate whether song output varied with noise levels and between urban and non-urban habitats. Through comparison of the degree of syllable sharing and proportion of unique syllables and phrases at these sites, I explored the presence of song dialects at urban and non-urban sites.

From 63.5 hours of field sampling, I collected a total of 1017 long-range broadcast songs (627 songs from motorway sites and 390 songs from non-motorway sites). A significantly higher minimum frequency was found in songs from the noisier, motorway sites compared with those from non-motorway sites. Motorway songs had shorter song durations and decreased syllable diversity than non-motorway songs. There were also a significantly lower proportion of trills in the songs at sites near to motorway. As predicted a smaller syllable repertoire size was found in the sites near the motorway compared to repertoires at non-motorway sites.

The presence of site-specific syllables and phrases and site-specific clusters in a Ward cluster analysis, as well as a reduced degree of syllable sharing between urban sites indicated the formation of local dialects in these fragmented urban sites.

This study has provided data of bird song variation within urban ecosystems of varying noise levels. These findings aid our understanding of modifications to tūī songs to avoid the masking effects of low frequency traffic noise. Song duration, trill proportion and repertoire size have all been demonstrated as being subject to sexual selection. Changes in these aspects at noisy urban sites are considered adaptations to urban effects. Such changes may have further implications for other important behavioural aspects such as mate choice and can have profound effects on tūī population dynamics between urban fragments. Understanding these urban effects on bird songs and other important behavioural aspects are important not only for advances in ecological theory in urban ecology, but also for conservation management of urban habitats. For example, dialects between urban fragments may create a reproductive barrier for dispersing birds, therefore reducing gene flow between sites. Habitat corridors should be considered in urban designs, not only to increase gene flow of species with poor dispersal ability, but may also help to connect populations of highly mobile species such as tūī.

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CHAPTER 1

General Introduction

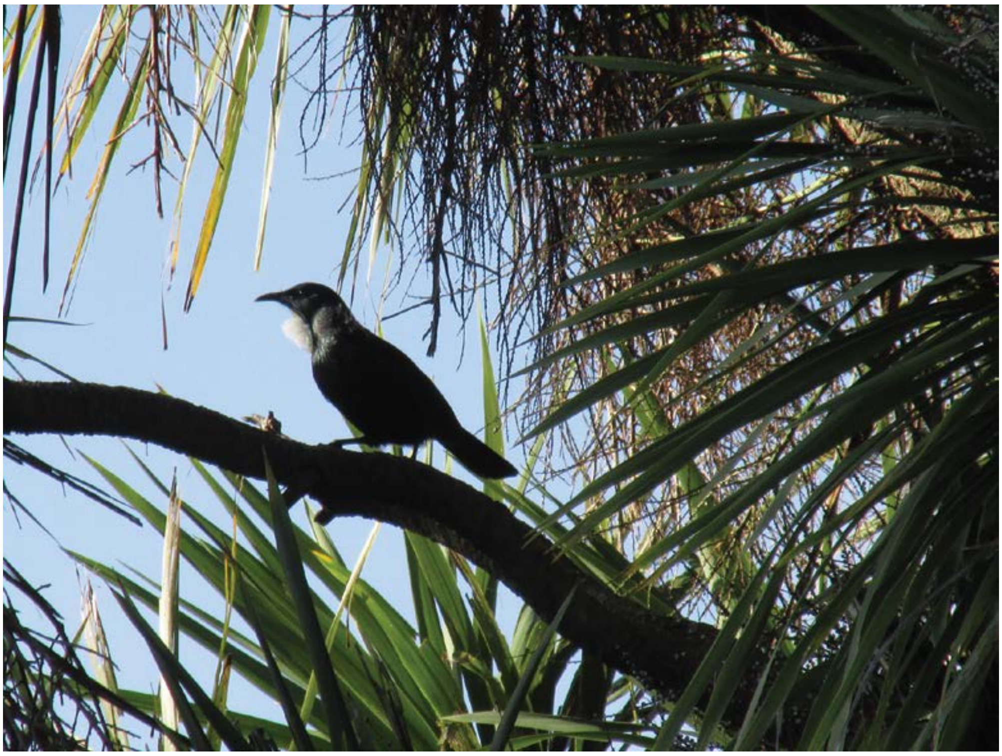


Plate 1: Tūī in Cabbage Tree (photograph by author)

1.1 Introduction

New Zealand's unique terrestrial biota has evolved in geographical isolation for 80 million years prior to the arrival of humans (Cooper and Millener, 1993). Much of the fauna has high levels of endemism and has evolved in absence of mammalian predators making them particularly vulnerable to environmental disturbances (Daugherty et al., 1993; Wilson, 2004). New Zealand was the last landmass to be colonised by humans, with Polynesian peoples arriving some 700-1000 years ago (Craig et al., 2000). The early Polynesians introduced the Pacific rat or kiore (*Rattus exulans*) that became major predators of several native species (Holdaway, 1989). European arrival in the 1700s led to the introduction of at least ten mammalian species, many of which are known to prey on native avifauna (Clout and Russell, 2006). These mammals are considered to be the greatest cause of recent bird extinctions and declines (Holdaway, 1989). Over the past 1000 years New Zealand is thought to have lost 40-50% of its avifauna due to habitat loss, hunting and predation (Holdaway, 1989).

Cities are rapidly expanding into adjacent rural landscapes, altering ecosystem structure and processes (Grimm et al., 2008) and threatening biodiversity (McKinney, 2002). The division of continuous habitat into smaller fragments separated by roads and houses, can result in the loss of species due to increased edge habitat, reduction in remnant size and decreased habitat connectivity (Gibb and Hochuli, 2002; Marzluff and Ewing, 2001). This fragmentation can also isolate populations and restrict dispersal and functional connectivity (Magle et al., 2012).

Native birds continue to decline due to a combination of predation and habitat loss, and secondary factors of fragmentation and competition with introduced species (Holdaway, 1989; Innes et al., 2010). However some native species including the native honeyeater, the tūī (*Prosthemadera novaeseelandiae*) have become common in human dominated landscapes including cities and the rapid scale of urbanisation in New Zealand provides a good opportunity to study the adaptations of native wildlife to such ecosystems. It is not known how such species are able to withstand the effects of urban noise and this study investigates whether tūī are able to modify their songs to effectively communicate in the presence of low-frequency motorway noise.

1.2 Bird Song Studies

Bird song is a communication signal of critical importance in the reproduction of Oscine species used for territory defence and mate attraction. These communication signals are critical for individual reproductive success and have important conservation implications in the management of endangered and declining species. A song contains large amounts of information, such as the identity, location and condition of the signaller (Catchpole and Slater, 2008). Bird song is a flexible trait, with some species able to respond to changes in noise conditions by altering songs over a short time period (McCarthy et al., 2013). Because of these important biological functions of song, it is crucial that signal efficacy is maintained in a variety of habitat types (McCarthy et al., 2013).

The term ‘vocalisations’ encompasses songs and calls, both having many communicative functions (Catchpole and Slater, 2008). Songs can be described as longer, more complex vocalisations most commonly produced by males during the breeding season, whereas calls tend to be shorter, simpler and produced throughout the year by both sexes (Catchpole and Slater, 2008). Calls generally occur in particular contexts related to threat and alarm and are often directed towards conspecifics at a close range. Songs are acquired through the process of learning from parents or local conspecifics, whereas calls are innate (Catchpole and Slater, 2008).

1.2.1 Territory Defence

Bird song is used to advertise the presence of a territorial male and to repel potential intruders to his territory (Slabbekoorn and Ripmeester, 2008). Male territory holders typically respond to playbacks of conspecific song with aggressive behaviour; either rapidly approaching the speaker, or increasing singing rate when territory boundaries are crossed (Nowicki and Searcy, 2004). Males will also react to conspecific songs during the breeding season in song matching contests (Nowicki and Searcy, 2004). These contests enable birds to interact with specific individuals, rapidly switching between different song types. This combination of territoriality and vocal aggression indicates the importance of vocalisations as indicators of a male's ability to hold a territory (Nowicki and Searcy, 2004). The ability of birds to differentiate between songs from neighbours or intruders is also important as it reduces the necessity to engage in high risk confrontations (Catchpole and Slater, 2008; Molles and Vehrencamp, 1999).

1.2.2 Female Mate Choice

Nowicki and Searcy (2004) outlined four song features that appear to be important in female choice of birdsong reflecting male quality; 1) song output, 2) complex song repertoires, 3) local song structure or dialect and 4) vocal performance. Direct benefits to females from choosing males with preferred song characteristics include access to a better quality mate and increased parental care. Indirect benefits include genetic quality that increases the survival and future reproductive success of her offspring (Nowicki and Searcy, 2005). The effect of song on female reproductive behavior has been proven in studies showing an increase in a female's nest building activity and courtship displays when exposed to song (Ballentine et al., 2004; Kroodsma, 1976; Searcy and Marler, 1981).

1.3 Parameters for Bird Song Study

The main song characteristics that have been used in bird song studies include spectral and temporal variables, trill proportion, song repertoire size, syllable diversity and dialect.

1.3.1 Spectral and Temporal Variables

Spectral variables are contained within the frequency spectrum of the sound and include measurements such as minimum frequency (F_{min}), maximum frequency (F_{max}), peak frequency (the frequency with the greatest energy level), and bandwidth, the difference between the maximum and minimum frequency measures.

Temporal (time-based) variables include song duration and song rate, which are examples of costly signals of male quality. Because singing is time and energy costly, males in better condition can afford to devote more time and effort to singing than those in poorer condition (Nowicki and Searcy, 2004). Previous research found that male blue tits (*Parus caeruleus*) that produced longer songs were more successful in gaining extra-pair fertilisations (Kempenaers et al., 1997).

Song rate is defined as the amount of singing activity in a defined time period and is an important cue used in male competition and female choice (Garamszegi and Møller, 2004; Marler and Slabbekoorn, 2004). Song rate is thought to reflect the amount of energy an individual can devote to song and is linked to their neuromuscular capacities, performance abilities, body condition and ability to garner resources (Hamilton and Zuk, 1982; van Hout et al., 2012). Village indigobirds *(Vidua chalybeata*) with higher song rates were found to have increased reproductive success (Payne et al., 2000). Female pied flycatchers (*Ficedula hypoleuca*) selected males that had the highest song rates and had acquired superior territories (Gottlander, 1987). The song rate of male pied flycatchers was also correlated with food availability and temperature suggesting that males with more time and energy sing more (Marler and Slabbekoorn, 2004).

Trill elements of song are selected by females as a predictor of male quality (Ballentine et al., 2004). Trills are rapidly repeated, frequency-modulated syllables that are costly to produce (Vehrencamp et al., 2013), and are considered honest signals of male quality. It has been suggested that males in better physical condition can afford the energetic costs of producing rapid trills more easily than those males in poorer condition (Nowicki and Searcy, 2004). An increase in the trill proportion in canary (*Serinus canaria*) song was correlated with increased testosterone levels in the breeding season, supporting the theory that trill syllables were selected by females (Bolhuis and Gahr, 2006).

1.3.2 Repertoire Size

Female songbirds are thought to assess male quality based on aspects of song, such as repertoire size, which is considered a measure of the complexity of male song (Ballentine et al., 2004; Nowicki and Searcy, 2004). Repertoire size is a measure of the number of different song types or syllable types in a male's song repertoire (Molles and Vehrencamp, 1999). The following hypotheses have been proposed to explain the evolution of song repertoires:

1) Song repertoires have evolved as products of sexual selection (Nottebohm, 1972). Female songbirds are thought to assess males based on aspects of song, such as repertoire size (Nowicki et al., 2000) that provides information about male quality (Ballentine et al., 2004). A larger repertoire size in great tits (*Parus major*) was found to correlate with higher measures of reproductive success, survival and territory habitat quality (McGregor et al., 1981). Male great reed warbler (*Acrocephalus arundinaceus*) repertoire was positively correlated with harem size and reproductive success (Hasselquist, 1998). Previous research found that the status of individual male red-winged blackbirds (*Agelaius phoeniceus*) was signalled by their repertoire size and was correlated with their reproductive experience (Yasukawa, 1981).

2) The ‘Beau Geste’ hypothesis states that males may use a larger repertoire to repel rival males from their territory by giving the impression that the territory holds several males (Catchpole and Slater, 2008; Krebs, 1977). The hypothesis assumes that non-territorial males are deterred from entering territories with large repertoires because they incorrectly assess population densities (Yasukawa, 1981). A previous study on the red-winged blackbird confirmed this hypothesis, however it is thought to mainly apply to species in which singing males are difficult to see (Yasukawa, 1981).

3) Males with larger repertoires are predicted to obtain larger or better quality territories through song matching with rival males (Krebs, 1977). Song matching often occurs between territorial neighbours who will share elements of their repertoires and try to ‘match’ a neighbour’s songs with identical song types (Price and Yuan, 2011). Those individuals possessing a larger pool of songs can increase the number of rivals that can be matched (Laiolo and Tella, 2005). The function of this behaviour may be to signal the aggressive state of the singing male indicating its ability to hold a territory (Byers and Kroodsma, 2009; Nowicki and Searcy, 2004). Species with large repertoire sizes such as tropical mockingbirds (*Mimus gilvus*) shared more song types with territorial neighbours than non-neighbours (Price and Yuan, 2011). Song matching with neighbours was correlated with

territory acquisition in song sparrows (*Melospiza melodia*) (Beecher et al., 2000) and with breeding success in the great reed warbler (Catchpole, 1986).

4) The ‘anti exhaustion’ hypothesis proposes that the singing behaviour of birds can be ranked according to repertoire size and the way the repertoire is performed (Lambrechts and Dhondt, 1988). This hypothesis argues that males with a larger repertoire size can avoid neuro-muscular exhaustion by regularly switching to another song type after several song type repetitions (Lambrechts and Dhondt, 1988). This switching behaviour would allow for a higher singing rate and lead to the development of a larger song repertoire (Brumm and Slater, 2006). A previous study found that great tits regularly switched song types to prevent muscular fatigue and developed larger song repertoires (Lambrechts and Dhondt, 1988).

1.3.3 Syllabic Diversity

Syllable diversity is defined as the number of different syllables that are produced per song and is seen as a reliable predictor of song complexity. It is also a sexually selected trait (Nowicki et al., 1998). Syllable repertoire size can be measured either as syllables per song or as the number of different syllables within an entire repertoire, comparing between songs. There can be a large within-song repertoire and small between-song syllable repertoire or vice-versa between different species (Read and Weary, 1992). There may be a basis for sexual selection for this variation in song and syllable diversity, with the production of particular syllables more attractive to females (Gil and Gahr, 2002). The larger the male repertoire, the higher the likelihood of these syllables appearing in the song (Gil and Gahr, 2002).

1.3.4 Dialect

Song dialects can form through geographical distance or other barriers between populations and can also occur over shorter distances with distinct boundaries occurring between dialect regions (Kroodsma, 2004; Marler and Tamura, 1964). Dialect describes variation in song whereby populations in adjacent areas sing similar songs and separated populations sing different songs (Nowicki and Searcy, 2004). Culturally acquired signals, such as vocal learning in songbirds, can be transmitted within and among generations between unrelated and related individuals (Wilkins et al., 2013). During the song learning process, copying errors or novel variants can occur, leading to the formation of local variation or dialects (Podos and Warren, 2007; Wilkins et al., 2013). Such dialects are thought to arise when neighbouring populations exhibit different song types, and when the variation in songs between populations is greater than the within-population variation (Luther and Baptista, 2010).

Hypotheses formulated to explain the evolution of dialects include the ***local adaptation hypothesis***, whereby females gain fitness advantages by mating with males from their natal territory because their offspring will express adaptations to local ecological conditions (Marler and Tamura, 1962). This hypothesis also predicts that birds dispersing from their natal territories will tend to settle in locations where natal rather than foreign dialects are sung, however results in mark and recapture studies have so far been inconclusive (Podos and Warren, 2007). A previous study found that female yellowhammers (*Emberiza citrinella*) responded more often and more vigorously to local than to foreign songs (Baker et al., 1987).

The social adaptation hypothesis proposes that males will gain fitness advantages by learning similar songs to those of dominant males in their area, and that males who sing different songs may not achieve breeding success (Podos and Warren, 2007). This hypothesis predicts that accurate mimics should elicit less aggressive responses from dominant males, and that males are more aggressive towards songs from neighbouring dialects than to their own local dialects (Podos and Warren, 2007). Juvenile male indigobirds were found to mimic songs of neighbouring dominant male neighbours to attract females (Payne et al., 2000).

The vocal convergence hypothesis states that dialects are long term features maintained by preferential learning of local call types by immigrants into a territory and purifying selection against foreign songs (Wright et al., 2008). Such vocal convergence was detected in yellow-naped amazon (*Amazona auropalliata*) dialects over a ten-year time period (Wright et al., 2008).

The male exclusion hypothesis proposes that males will try to repel outsiders from adjacent foreign dialect areas from their territory thus maintaining local dialects and prevent dialect mixing (Baker and Cunningham, 1985). Studies found that aggressive responses were strongest to an adjacent foreign dialect, weaker to the local dialect, and the weakest response was given to distant foreign dialects (Baker and Cunningham, 1985).

1.4 Urban Ecology

Over 50% of the global human population now live in cities and the rate of urbanisation is accelerating (Dearborn and Kark, 2010). Cities are rapidly expanding into adjacent rural landscapes, altering ecosystem structure and processes and threatening biodiversity (Grimm et al., 2008; McKinney, 2002). The division of continuous habitat into smaller fragments, separated by roads and built environments, can result in the decline and loss of species (Marzluff and Ewing, 2001). Effects of urbanisation include homogenisation of species whereby a small number of urban-adapted (often introduced) avian species become increasingly widespread and abundant, often displacing native species (McKinney, 2006; Slabbekoorn and den Boer-Visser, 2006). Bird abundance in urban areas is reflected by a species-specific adaptability to urban resources and levels of nest predation and parasitism (Chace and Walsh, 2006).

Multiple factors are involved in determining which native bird species survive in the urban habitat, including: 1) predation risk, 2) size and structure of remnant native vegetation patches, 3) competition with introduced avian and mammalian species (Chace and Walsh, 2006; Marzluff, 2005), and 4) food availability. These are explained in detail below. Additionally, many indirect effects can contribute to native bird biodiversity in urban environments such as climate change, physiological stress, disease transmission, pollution and disturbance (Chace and Walsh, 2006).

1) Exotic mammalian predators are the single most important factor limiting populations of New Zealand songbirds (Innes et al., 2010). Human-associated predators including cats (*Felis catus*), rats (*Rattus rattus*) and brushtail possums (*Trichosurus vulpecula*) can reach high densities in urban environments (Møller, 2008; Remes et al., 2012). Comparisons of three urban bird species found that

abundance in urban areas was related to nest survival and juvenile mortality caused by predation (van Heezik et al., 2008a).

2) The clearance of native vegetation and fragmentation of remaining habitats due to urbanisation is thought to threaten biodiversity due to increased edge habitat, reduction in remnant size, and decreased habitat connectivity (Chan and Blumstein, 2011). Habitat fragmentation can also isolate populations and restrict their dispersal and functional connectivity (Magle et al., 2012). Fragmentation can also lead to increased invasion from weedy plant species that can threaten native vegetation and fauna (Esler, 1988). Previous research has found that urban bird assemblages were more affected by patch size than by isolation between patches, and responded more positively to increased structural complexity of habitat and species richness of woody vegetation (Evans et al., 2009).

3) In the New Zealand environment, introduced avian species such as starlings (*Sturnus vulgaris*), mynas (*Acridotheres tristis*) and magpies (*Cracticus tibicen*) can depredate eggs, destroy nests and compete for food and nest resources. Other species such as the introduced Eastern rosella (*Platycercus eximius*) and native silvereyes (*Zosterops lateralis*) may also compete with native species for nectar resources.

4) A meta-analysis on the effects of urban landscapes on avian biodiversity found that food availability is a key driver of differences in passerine biodiversity, and that lack of natural foods may lead to lower productivity per nesting attempt (Chamberlain et al., 2009).

Urban vegetation comprises a mosaic of small forest remnants, parks and reserves, and suburban gardens, (McKinney, 2002) and exerts a strong influence on native avian diversity (French et al., 2005). Mature suburban gardens may provide food sources and habitat for nesting, and can serve as extensions of natural remnants and contribute to wildlife corridors (Doody et al., 2010; Marzluff, 2005). Conversely, gardens provide a seed source for weed species where garden escapees rapidly colonise disturbed areas and establish under the forest canopy (Esler, 1988; Sullivan et al., 2009), threatening native forest biodiversity.

1.4.1 Habitat Effects on Bird Song

Some species alter the frequency of their songs in response to different habitats (Boncoraglio and Saino, 2007). Lower frequency songs with narrow frequency ranges should occur more often in densely vegetated habitats, whereas high frequency songs including trills transmit more effectively in open habitats (Morton, 1975; Nemeth et al., 2006).

Habitat fragmentation has been shown to have an influence on song features. A previous study found that repertoire size and song diversity correlated with population size and forest remnant size in kōkako (*Callaeas wilsoni*) (Valderrama, 2012). Habitat fragmentation and decreases in population size are also thought to have an effect on the maintenance of dialects through reduction in cultural transmission of song (Valderrama, 2012). Previous research found increased song-type sharing among neighbours in fragmented populations of Dupont's larks (*Chersophilus duponti*), thought to be related to increased competition for resources in remaining habitat patches (Laiolo and Tella, 2005). However the significance of song variation as a consequence of habitat fragmentation, population structure and isolation is still poorly understood (Valderrama, 2012).

1.4.2 Effects of Urban Noise on Bird Song

Traffic noise may reduce the ability of bird species to effectively communicate important vocal signals (Cartwright et al., 2014). In comparison with the effects of ambient sources of noise in a bird's natural environment such as wind in trees, waves, arthropods and other avian species (Slabbekoorn and Peet, 2003), anthropogenic noise is generally louder and more persistent (Patricelli and Blickley, 2006). Urban noise in cities is becoming a more prominent feature as human population growth increases and cities expand outwards (Slabbekoorn and Ripmeester, 2008). Low frequency traffic noise has been linked to the decline of bird species in cities, even when other habitat requirements are available (Slabbekoorn and Ripmeester, 2008). Increased noise levels in urban environments can mask predator arrival and associated alarm calls, and can interfere with acoustic signalling important in territory defence and mate selection (Slabbekoorn and Ripmeester, 2008).

While overall bird population density and species diversity tend to decrease with increased proximity to traffic noise (Potvin et al., 2011), those species able to coexist in urban areas in the presence of urban noise have shown evidence of behavioural flexibility (Katti and Warren, 2004). Habitat-dependent selection is an important driver in the evolution of acoustic signals (Slabbekoorn and Smith, 2002) and recent studies show that urban habitats also affect vocal behaviour (Luther and Derryberry, 2012). Cartwright et al. (2014) outlined five types of signal modification that alter the structural characteristics of song that birds use to avoid the effects of masking by low frequency noise; frequency, amplitude, type of signal, tonality and timing of the signal. Alterations to the frequency component of signals and the timing of singing have been found to coincide with off-peak traffic (Katti and Warren, 2004; Mendes et al., 2011), and song volume increases in noisy areas (Potvin et al., 2011). Traffic noise may also impact on other vocal behaviours such as begging calls, distress calls and alarm calls, with potential fitness consequences (Katti and Warren, 2004) It has been suggested that local adjustment of songs to the habitat through song learning could lead to song divergence between urban and non-urban populations of the same species (Katti and Warren, 2004).

Since most of the energy of traffic noise is emphasized at low frequencies, an increase in a song’s minimum frequency can reduce the degree of masking, thus increasing the signal-to noise ratio of the sound (Nemeth and Brumm, 2010). Many species have been observed to use a higher minimum frequency in the presence of urban noise, such as urban great tits (Katti and Warren, 2004; Slabbekoorn and Peet, 2003), orange-tufted sunbirds (*Nectarinia osea*) (Leader et al., 2005), blackbirds (*Turdus merula*) (Mendes et al., 2011), and silvereyes (Potvin et al., 2011). Some species are physically restricted to producing low frequency songs that fall within the range of masking traffic noise (Rabin and Greene, 2002), and these species are predicted to have reduced communication success in noisy areas. Other species have responded to increased noise levels by altering the bandwidth of their songs (Katti and Warren, 2004; Mendes et al., 2011). The Lombard effect has been described in several studies as a response to elevated noise levels, described as an increase in amplitude in order to maintain a high signal to noise ratio (Katti and Warren, 2004). Studies found that zebra finches (*Taeniopygia guttata*) (Cynx et al., 1998), nightingales (*Luscinia megarhynchos*) (Brumm, 2004) and European robins (*Erithacus rubecula*) (Potvin et al., 2011) all produced higher song amplitudes in response to higher levels of anthropogenic noise. Red-winged blackbirds reduced song production at noisy times of the day (rush hour) (Cartwright et al., 2014). These are thought to be behavioural adaptations that decrease the masking effects of low frequency traffic noise.

Previous research on the effects of urban noise has emphasised the perceived benefits to signallers of behavioural modifications in vocalisations. However the potential fitness costs of these modifications, such as increased risk of predation and increased energy budgets, could have implications for population viability in noisy environments (Read et al., 2014). Luther and Magnotti (2014) recently found that songs with a raised minimum frequency gained weaker responses than average-frequency songs. This suggests that there is a potential tradeoff for signallers: through producing higher frequency songs to avoid noise, the low frequency components of the signal containing potentially important information are lost (Slabbekoorn and Ripmeester, 2008).

1.5 New Zealand Avifauna and Urban Landscapes

Kelly and Sullivan (2010) outlined two different community types in New Zealand: disturbed habitats (both urban and rural) dominated by naturalised or domesticated flora and fauna compared with less disturbed habitats (dominated by native species) such as predator-free islands and predator-controlled regenerating forests and parks. Deforestation, intensification of agricultural land use and urban development have reduced New Zealand’s once continuous forest cover to small, disconnected forest fragments (Meurk and Swaffield, 2000). Both urban and non-urban landscapes have been greatly modified and may provide different sets of food and territorial resources for native birds (Innes et al., 2010). Urban environments in New Zealand are dominated by non-native plant species, including imported amenity and production species with native plant species in decline (Sullivan et al., 2009). Auckland’s benign temperate climate has made it susceptible to invasion by weeds and it has twice as many naturalised non-native than native plant species (Esler, 1988; Sullivan et al., 2009).

However, both exotic and native nectar and fruit producing trees in urban areas can provide important energy supplies, and the density of nectarivores (nectar-feeding birds) correlates with suburbs containing prolific nectar-producing plants (McGoldrick and Mac Nally, 1998). The abundance of such trees can provide important energy supplies during the breeding season, a year round source of nectar and may compensate for losses of habitat in some areas (Heather and Robertson, 2000; McGoldrick and Mac Nally, 1998). Indeed, some native birds have been found to breed in urban habitats. For example, tūī (*Prosthemadera novaeseelandiae*), a native honeyeater and songbird harvests nectar from a wide variety of exotic and native plants in cities (French et al., 2005) and will travel large distances daily to exploit these nectar sources (McGoldrick and Mac Nally, 1998).

1.6 Ecology of the Tūī

The tūī is a protected endemic honeyeater (males, 120 g, females 85 g, average mass) (Higgins et al., 1990). The IUCN Red List category for tūī is ‘Least concern’ as it does not approach the threshold for ‘Vulnerable’ within the range size or population trend criterions (BirdLife International, 2012). Tūī are common throughout mainland New Zealand, but are sparse in large deforested regions, especially east of the central Southern Alps in the South Island, and Manawatu, south Taranaki and central Waikato in the North Island (Robertson, 2007).

Although tūī are commonly found in urban areas, they have suffered serious declines in some areas, including cities. Tūī abundance in Christchurch declined rapidly in the 1990s (Day, 1995), and tūī were recorded as absent from Hamilton in 1993 (Innes et al., 2005). Cities or towns with large adjoining forest patches are considered capable of supporting tūī year round, whereas cities lacking forest remnants were only utilized by tūī during winter and spring, and breeding occurred in outlying forest patches (Innes et al., 2004). A recent study found that urban tūī abundance and distribution increased significantly in Hamilton city after mammalian pest control was implemented in at tūī breeding sites in surrounding forests (Innes et al., 2015). These results suggest that recolonisation of urban habitats by tūī is possible providing adequate food is available and effective pest control is implemented (Innes et al., 2015). Tūī became locally extinct from Banks Peninsula in the mid 1990s due to habitat loss and predation (Schmechel, 2002) and a translocation was conducted in 2009 along with revegetation and pest control programmes (Banks Peninsula Conservation Trust, 2014). Post-translocation monitoring has indicated that the project has been successful in the short-term (Banks Peninsula Conservation Trust, 2014). A subspecies of the tūī, the Chatham Island tūī (*Prosthemadera novaeseelandiae chathamensis*), is classified as Endangered by the IUCN Red List Category, and is in decline due to ongoing habitat destruction and the effects of introduced predators (Dilks, 2004).

The abundance of both of the two endemic New Zealand honeyeaters (family Meliphagidae), tūī and bellbirds (*Anthornis melanura*), has decreased rapidly since human colonisation, due mainly to a combination of mammalian predators, habitat loss, reduction in food sources and disease (Diamond and Veitch, 1981). Of the two honeyeaters, tūī are the larger and more dominant species (Bergquist, 1989) and are more abundant and widespread on the mainland (Gill et al., 2010). Tūī is an iconic New Zealand species with a distinctive song and it plays an important ecological role as one of the key pollinators (Anderson, 2003) and seed dispersers (Kelly et al., 2010) of many native plant species (Castro and Robertson, 1997).

Tūī are opportunistic foragers and feed on flower nectar, fruits, insects and honeydew in different proportions according to their availability but nectar being the most important food (Bergquist, 1989; Castro and Robertson, 1997). The uneven spatial and temporal distribution of nectar leads to competition between new individuals and residents in areas with high nectar resources (Craig, 1985) and aggressive behavior is used by males to displace conspecifics and other species when defending a nectar resource (Craig, 1984). Residents usually dominate non-residents, with their highly complex and diverse song acting as an indicator of residential status (Bergquist, 1985). Wing noise, larger size, wing flashes and loud warning calls are indicators of aggressiveness used by tūī to dominate both conspecifics and other species in defense of resources (Craig, 1984).

New Zealand native birds vary in their adaptability to urbanisation (Robertson, 2007) and less specialised, opportunistic species such as tūī regularly exploit native and exotic nectar resources provided in urban habitats (van Heezik et al., 2008b). Tūī were listed as the fifth most common New Zealand garden bird in surveys from 2007-2013, (Spurr, 2012) and are a common feature of urban parks and gardens. However, the percentage of gardens in which tūī occurred varied regionally, with tūī occurring in only 2% of gardens in Canterbury compared with 52% of gardens nationally (Spurr, 2012). Tūī are considered more pest-resistant compared with most natives (Innes et al., 2010) and are highly mobile, often travelling long distances to secure nectar (Schmechel, 2002). Outside the breeding season, tūī will travel up to 30 kilometres to gain access to winter food resources such as winter flowering Eucalyptus species, puriri (*Vitex lucens*), kowhai (*Sophora microphylla*) and kahikatea *(Dacrycarpus dacrydiodes*) fruit (Schmechel, 2002; Stevens, 2006).

During the breeding season, a pair of tūī will select a nest site near a patch of continuous vegetative cover and an adequate nectar supply, with the male using long-range songs to defend the nest (Bergquist, 1989). Tūī have a long breeding season (September through to the end of February) and a relatively short nesting period. Tūī can produce at least two broods in a year, and can therefore more easily withstand losses due to predation and disease than many other native birds (Bergquist, 1989).

The presence of private gardens and native bush fragments can potentially support a wider diversity and abundance of native birds in urban areas and tūī were found in greater numbers in residential areas with larger and more structurally complex gardens (van Heezik et al., 2008b). Urban forest fragments, such as scenic reserves, have the potential to act as a population source area for some bird species that then disperse into surrounding suburbs (Parsons et al., 2006; van Heezik et al., 2008b).

Tūī utilise many exotic nectar and fruit producing species in the urban landscape at different times of year, whereas non-urban, agricultural landscapes may offer less year-round supplies of native and exotic food resources such as flowering cherry (*Prunus campanulata*), flame tree (*Erythrina spp*), *Protea* species, bottlebrush (*Callistemon sp.*) and Moreton Bay fig (*Ficus macrophylla*). Urban environments may provide more food abundance than other areas. However how tūī adapt their songs and singing behaviour to successfully survive in the urban habitat has not been investigated.

1.7 Tūī Song

The loud, long-range broadcast song heard during the breeding season consists of a sequence of several phrases sung repeatedly with a pause between phrases, forming long but repetitive songs (Bergquist, 1989). Song matching is a common tūī behavior between males during the breeding season whereby a bird will try and match songs sung by other tūī in a male’s local environment in order to establish boundaries between the territories of tūī groups (Bergquist and Craig, 1988). Song matching occurs when a male replies to a rival’s song by singing the same song sequence, (Laiolo and Tella, 2005), and is considered to bring fitness advantages linked to mate attraction and territory defence thereby increasing mating success (Briefer et al., 2009). The use of song matching as a threat signal between males is thought to explain the evolution of complex song repertoires, whereby the possession of a large pool of songs can increase the number of rivals that can be matched (Laiolo and Tella, 2005). Tūī are known to mimic the songs of other bird species such as Eastern rosella, often with their own embellishments, (Higgins et al., 1990; Robertson, 1996). Recent studies focusing on tūī vocalisations found differences in song spectral variables between a New Zealand mainland population and those of a Chatham Island population (Hill et al., 2013). There was greater syllable diversity and a higher percentage of trills found in songs from the mainland population than those from the island population. These are seen as sexually selected traits, positively correlated with male genetic diversity. The higher degree of trill proportion on the mainland could be explained as an acoustic adaptation to greater areas of open vegetation where high frequency trills are transmitted more effectively than the more densely forested island habitat in the Chatham Islands (Hill et al., 2013).

1.8 Knowledge Gaps and Aims of this Study

How birds react to rapid urbanisation in New Zealand is unknown. Native bush birds such as tūī are valued highly by New Zealanders, however the reasons for their presence or decline in cities are not well understood (van Heezik et al., 2008b). Several native species seem able to exploit residential areas including tūī, fantails (*Rhipidura fuliginosa*), grey warblers (*Gerygone igata*) and bellbirds (van Heezik et al., 2008b). However, the effects of urban noise on avian birdsong have not previously been measured in New Zealand. This research aims to investigate whether there is an effect of urban traffic noise on structural and behavioural characteristics of tūī vocalisations. Geographic variation in tūī has been studied, finding structural differences in song structure and dialect between mainland and Chatham Island sites (Hill, 2011; Hill et al., 2013). However there have been no studies comparing geographic variation and song structure between urban and non-urban sites, and between motorway and non-motorway urban sites. In this study, I use tūī as a model to explore the effect of anthropogenic noise on bird vocalisations.

Research questions I aim to investigate include: 1) Does anthropogenic noise result in altered spectral characteristics of tūī songs? 2) Does anthropogenic noise have an impact on tūī singing behaviour such as song diversity and song rates? 3) Do urban tūī populations share syllables and form local dialects?

Song variation and local song diversity have recently been identified as critical factors in conservation biology (Laiolo, 2010). Song characteristics have been used to inform management decisions and increase the success rate of translocations in conservation programmes of endangered native species (Valderrama et al., 2013). Playback experiments on translocated populations of the endangered North Island kōkako found persistence of response to playbacks of nonlocal songs, despite vocal divergence between different source populations, thus aiding the establishment and persistence of these populations (Valderrama et al., 2013). The study of song dialects has also been used to identify the source population of a self-introduced population of bellbirds at Tawharanui Regional Park (Brunton et al., 2008). This study can also provide baseline information about the development of local dialects within urban areas and the effects of motorway noise on the selection of specific syllables that may be more easily transmitted in urban environments.

1.9 Thesis Structure

This thesis is organized into six chapters:

Chapter One is a general introduction to studies on bird vocalisations, urban ecology, and the effects of urban noise on tūī ecology and vocalisations. It identifies the knowledge gaps and states the aims of this study and outlines the structure of this thesis.

Chapter Two describes the general methods used for this study.

Chapter Three compares the effects of urban motorway noise on tūī vocalisations using song data collected from close to motorway and far from motorway sites.

Chapter Four is an investigation into syllable repertoire and song rate between motorway and non-motorway sites in urban areas.

Chapter Five is an investigation into differences in syllable repertoire, song rate, and local dialect between urban and non-urban sites.

Chapter Six is a conclusions and recommendations chapter, in which I summarise the main findings of this study, and its contribution to general knowledge on this subject, and furthermore, I make suggestions for future research in relation to my findings.

CHAPTER 2 Methods

Plate 2: Author Recording Tūī at Wenderholm (photograph by Sam Hill)

2.1 Study Sites

This study was conducted in Auckland city. Auckland encompasses significant areas of regenerating forest on its outskirts including predator-controlled regional parks such as Hunua Ranges, Waitakere Ranges and predator-free islands in the Hauraki Gulf and mainland islands (Tāwharanui and Shakespeare Regional Parks) where native bird assemblages are increasing and some native mobile bird species have recolonised.

Within the central Auckland area there are smaller areas of native regenerating forest in parks, reserves and suburban gardens, providing habitat for native birds. In Auckland there are extensive plantings of native and exotic street trees such as kowhai (*Sophora microphylla*), pōhutukawa (*Metrosideros excelsa*), puriri (*Vitex lucens*), flax (*Phormium tenax*), eucalyptus (*Eucalyptus spp*.), banksia (*Banksia spp*.), bottlebrush (*Callistemon spp*.) and flame trees (*Erythrina indica*) providing abundant supplies of nectar for honeyeaters such as tūī.

I sampled tūī songs in three urban areas, Central Auckland, North Shore and Manurewa within Auckland City and two non-urban forest fragments in Mahurangi Regional Park and Wenderholm Regional Park, 48 km north of Auckland City (Figure 2.1, Figure 2.2 and Figure 2.3).

In each urban study area, I selected two paired study sites, one near a motorway (motorway sites) and one in quieter urban area (non-motorway sites). The three motorway sites included Auckland Domain in Auckland central, Smiths Bush Reserve in North Shore and Auckland Botanic Gardens in South Auckland. The three non-motorway sites included Waitaramoa Reserve in Auckland Central, Le Roys Reserve in North Shore and Totara Park in Manurewa. The vegetation and pest control parameters for each site are listed in Table 2.1.

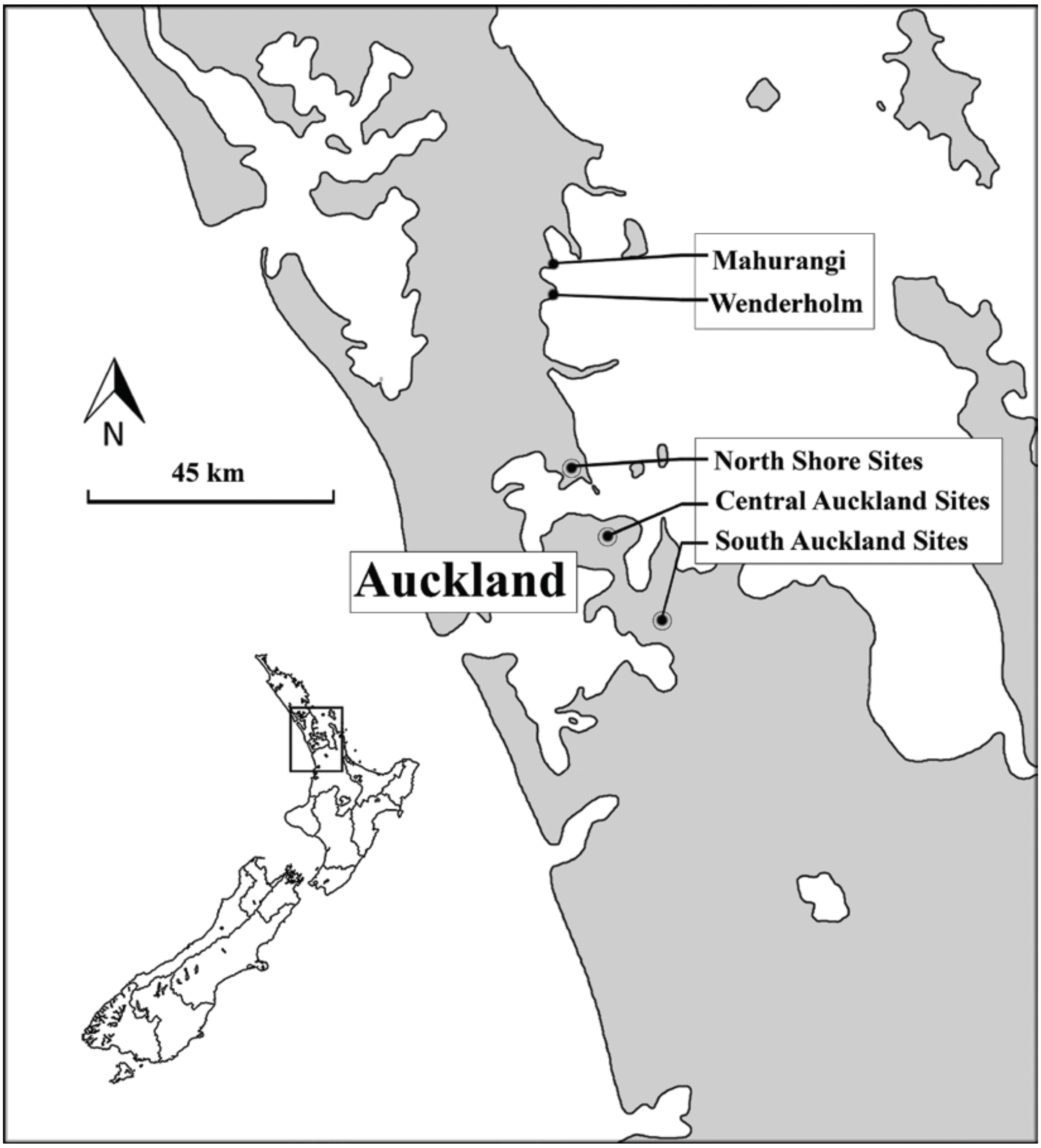


Figure 2.1: Map of New Zealand with an enlarged view of Auckland, showing locations of the three paired study sites within Auckland city and two non-urban sites.

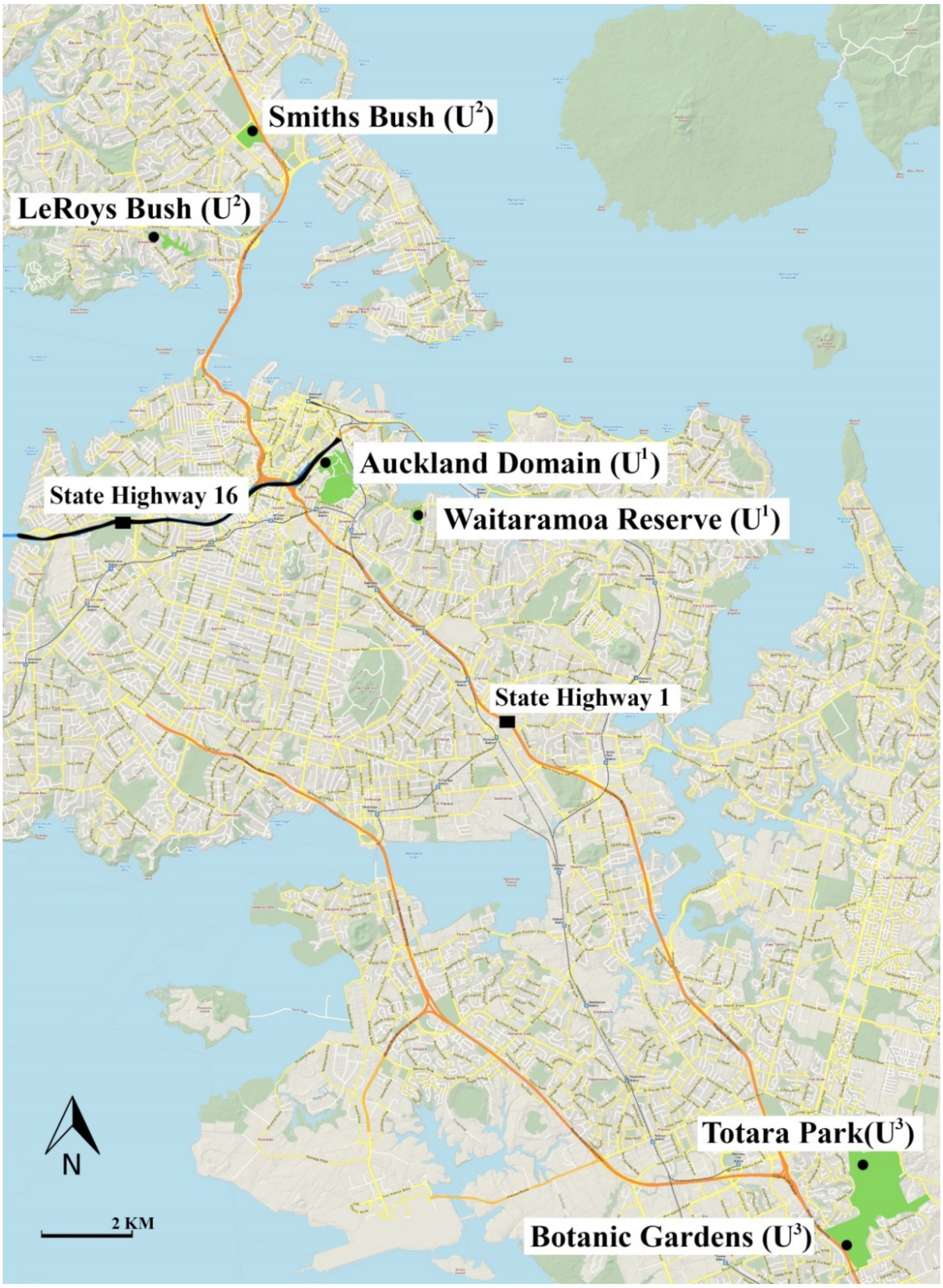


Figure 2.2: Study areas (circles) and adjacent motorways (squares) for tūī recording (Auckland Council GIS Viewer).

The six urban study locations: 1) U^1: Auckland Domain and Waitaramoa Reserve (Auckland City), 2) U^2: North Shore (Smiths Bush and Le Roys Bush) and 3) U^3: Southern (Auckland Botanic Gardens and Totara Park, Manurewa).

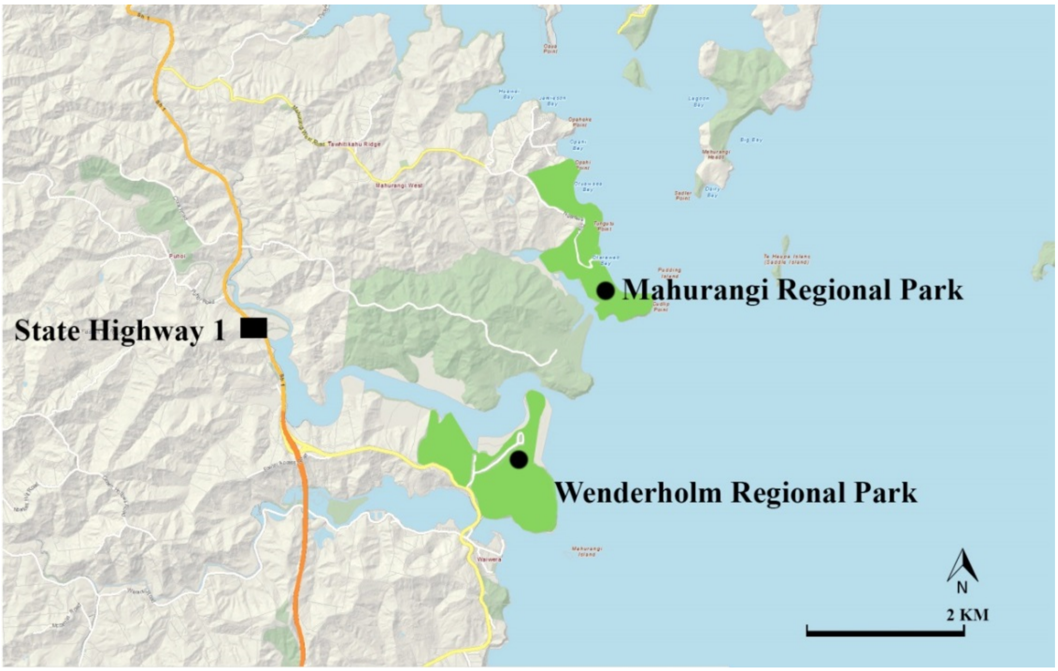


Figure 2.3: Non-urban paired study areas; Mahurangi Regional Park and Wenderholm Regional Park (Auckland Council GIS Viewer).

Table 2.1: Characteristics of tūī study sites including site size, forest patch size (ha), distance from motorway, pest control status (H = high, M= medium and L= low).

Paired sites	Sites	Size (ha)	Forest patch size (ha)	Motorway distance	Pest control status
U^1 Central Auckland	Auckland Domain	75	17.6	Adjoins motorway	M
	Waitaramoa Reserve	5	2.7	> 2 km	M
U^2 North Shore	Smiths Bush	8.9	8.9	Adjoins motorway	M
	Le Roys Bush	28.4	18.2	> 2 km	H
U^3 South	Botanic Gardens	64	20	Adjoins motorway	H
	Totara Park	200	20	> 2 km	M
Non-urban	Mahurangi Park	177	70	Non-urban	H
	Wenderholm Regional Park	134	80	Non-urban	H

2.1.1 Smiths Bush Reserve

Smiths Bush Reserve **(**36°47’30.08” S, 174°45’10.22” E) is an 8.9 ha mixed podocarp-broadleaf forest remnant at Onewa Domain, Northcote (Figure 2.4). Dominant tree species include large puriri, taraire (*Beilshmiedia tarairi*) and kahikatea (*Dacrycarpus dacrydiodes*). Other common tree species include tawa (*Beilshmiedia tawa),* karaka (*Corynocarpus laevigatus*), kowhai and totara (*Podocarpus totara*) (MacArthur, 1977). Smiths Bush was acquired as a reserve in 1943, and was subsequently partially destroyed and divided by the construction of the Northern motorway in 1959 (Cameron, 1988). Rodents and weeds are regularly controlled by local community and Forest and Bird (T.Lovegrove, pers comm).

Figure 2.4: Smiths Bush Reserve, Northcote, adjoining SH1, showing the location of recording sites for individuals SB01-SB06. (*Source*: ‘Smiths Bush’. 36°47’33.79” S 174°45’12.98 E. Google Earth. May 21, 2012. April 4, 2015).

2.1.2 Le Roys Bush

Le Roys Bush Reserve (36°48’46.24” S, 174°43’51.46” E, 28.4 ha) in Birkenhead contains 18.2 ha of regenerating kauri (*Agathis australis*)- tanekaha (*Phyllocladus trichomanoides*) forest, and a wetland area draining into Little Shoal Bay (Figure 2.5). The valley is filled with mature broadleaf forest with a high proportion of taraire, puriri and tawa. A rich understorey of tree ferns, kohekohe (*Dysoxylum spectabile*) and pate (*Schefflera digitata)* provides excellent riparian vegetation for the wetland. A pest animal control programme including rat (*Rattus rattus*), possum (*Trichosurus vulpecula*) and stoat (*Mustela ermina*) control has been operating in the reserve and surrounding gardens since 2009 and extensive weed control has been undertaken since 2008.

Figure 2.5: Le Roys Bush, Birkenhead showing the location of recording sites for individuals LB01-LB07 (*Source*: ‘Le Roys Bush’. 36°48’49.77” S 174°44’07.18 E. Google Earth. May 21, 2012. April 4, 2015).

2.1.3 Auckland Domain

Auckland Domain (36°51’32.15” S, 174°46’30.26” E, 76 ha) contains the crater and surrounding tuff ring of the Pukekawa volcano (Figure 2.6). This park contains a combination of native and exotic mature trees, planted from the 1850s. The park incorporates formally planted parkland areas with approximately 17.6 ha of regenerating forest fragments (Lovers Walk and Glade Walk). The glade walk features native conifers; kauri, rimu (*Dacrydium cupressinum*), totara and tanekaha, planted in 1865. The Centennial Walkway leading down to the city and SH16, is fringed with mature pōhutukawa, an important tūī nectar source (Wilcox et al., 2004). Pest control programme in operation (S.Peters, pers.comm).

Figure 2.6: Auckland Domain, adjoining SH16, showing the location of recording sites for individuals DO01-DO06. (*Source*: ‘Auckland Domain’. 36°51’26.30” S 174°46’29.18 E. Google Earth. May 21, 2012. April 4, 2015).

2.1.4 Waitaramoa Reserve

Waitaramoa Reserve **(**36°51’56.16” S**,** 174°47’40.48” E, 3 ha, (including adjoining Wharua Reserve), incorporates a narrow band of regenerating bush in parkland and adjoins a wetland area (Figure 2.7). Waitaramoa Reserve runs alongside Orakei Creek flowing out into Hobson Bay. This reserve has been ranked as high-medium priority for ecological restoration of a riparian area and there is a low level of pest control at the site (V. Wood, 2013).

Figure 2.7: Waitaramoa Reserve, Remuera showing the location of recording sites for individuals WR01-WR04 (*Source*: ‘Waitaramoa Reserve’. 36°51’59.06” S 174°47’42.17 E. Google Earth. May 21, 2012. April 4, 2015).

2.1.5 Auckland Botanic Gardens

Auckland Botanic Gardens (37°00’41.02” S, 174°54’25.28” E, 64 ha) is 25 km from Central Auckland and combines parkland with c.10 ha of lowland broadleaf conifer forest remnant (Figure 2.8). This remnant is contiguous with the adjacent Totara Park, the matching site in this survey. This forest remnant is the only remaining example of the flat alluvial forests of the Hunua Ecological District. Botanic Gardens provide ample nectar resources for tūī at different times of year; including flowering cherry (*Prunus campanulata*) trees which attract ecstasies of tūī in early spring and a New Zealand flax garden. The forest remnant follows the Puhinui stream, and includes totara, kahikatea, taraire, rimu, pukatea (*Laurelia novae-zelandiae)*, titoki (*Alectryon excelsus*), karaka and kowhai (Cameron, 1992). Continuous baiting for rats and annual possum and stoat control (*Mustela ermina*) were implemented from 2011 (E.Bodley, pers comm).

Figure 2.8: Auckland Botanic Gardens, Manurewa, adjoining SH1 showing the location of recording sites for individuals BG01-BG06 (*Source*: ‘Botanic Gardens’. 37°00’41.37” S 174°54’18.33 E. Google Earth. May 21, 2012. April 4, 2015).

2.1.6 Totara Park

Totara Park **(**37°00’4.84” S, 174°54”55.45” E, 200 ha) is a farm park comprising c.100 ha of farmland and c.20 ha of lowland broadleaf conifer forest (Council) (Figure 2.9). On the drier slopes are conifer forests including matai (*Prumnopitys taxifolia*), miro (*Prumnopitys ferruginea*), kahikatea, tanekaha, totara and occasional kauri. The second main forest type is broadleaved forest with a dense canopy, dominated by taraire, some large puriri with scattered rewarewa (*Knightia excelsa*) and pukatea, with a tawa, pigeonwood (*Hedycara arborea*), titoki, kohekohe and lancewood (*Pseudopanax ferox*) subcanopy in the damper gullies (Wilcox and Benham, 1997). There are good examples of totara, rimu, titoki, karaka, and kowhai by Puhinui Stream (Cameron, 1992). There is also pest control in some of the bush areas (E.Bodley, pers.comm).

Figure 2.9: Totara Park, Manurewa showing the location of recording sites for individuals TP01-TP04 (*Source*: ‘Totara Park’. 37°00’06.60” S 174°54’40.04 E. Google Earth. May 21, 2012. April 4, 2015).

2.1.7 Mahurangi Regional Park

Mahurangi Regional Park **(**36°30’37.96” S, 174°43’6.99” E, 157 ha) is 65 km north of Auckland and consists of grazed pasture interspersed with some areas of regenerating coastal forest remnants on two headlands, with some mature canopy tree species including pōhutukawa and puriri (Figure 2.10). The park contains some large forest fragments (approx. 70 ha) including the recently acquired forest at Te Muri Regional Park. Dominant species include nikau (*Rhopalostylis sapida)*, kanuka (*Kunzea ericoides*), totara, and karaka. There is a low level of pest control in the park including DOC200 traps along the northern boundary of the park, and rat, hedgehog and possum control along a small section of coastline during dotterel breeding season (Pattemore and Wilcove, 2011).

Figure 2.10: Mahurangi Regional Park showing the location of recording sites for individuals MP03-MP07 (*Source*: ‘Mahurangi Park’. 36°32’20.39” S 174°43’06.69 E. Google Earth. May 21, 2012. April 4, 2015).

2.1.8 Wenderholm Regional Park

Wenderholm Regional Park (36°32’14.7” S, 174°42’31.1” E, 134 ha) is a mainland managed peninsula 48 km north of Auckland, bounded by two tidal estuaries (Figure 2.11). Although the area was originally farmed, significant areas of coastal forest remain and Wenderholm became Auckland’s first regional park. Wenderholm consists of 80 ha of regenerating coastal forest and also open coastal pastureland and wetlands (Lovegrove et al., 2002). The dominant plant species include pōhutukawa, tarairi, manuka (*Leptospermum scoparium*), puriri, kowhai, cabbage tree (*Cordyline australis*), nikau and karaka. A programme of brushtail possum control was undertaken during the 1980s and 1990s, rodent control was implemented from 1992 and mustelid control from 1999 (Lovegrove et al., 2002).

Figure 2.11: Wenderholm Regional Park showing the location of recording sites for individuals WP01-WP05 (*Source*: ‘Wenderholm Park’. 36°30’54.34” S 174°43’24.14 E. Google Earth. May 21, 2012. April 4, 2015).

All six urban sites were used to test differences in song spectral and temporal variables between motorway and non-motorway sites (Chapter 3). For Chapter 4, syllable extraction and analysis was conducted to compare dialect between motorway and non-motorway sites for the U^1 (central Auckland sites) and U^2 (North Shore) urban sites. For Chapter 5, the same four urban sites; U^1 and U^2 and the two non-urban sites (Wenderholm Regional Park and Mahurangi Regional Park) were used to compare repertoire and dialect parameters between urban and non-urban areas.

2.2 Vegetation Surveys

The physical structure of vegetation can affect the species richness, abundance and distribution of bird communities and potentially the behaviour and microhabitat distribution of particular bird species (James and Wamer, 1982). Vegetation surveys were carried out at each study site using the point-centred quarter (PCQ) method (Bryant et al., 2005). A total of 14 sampling points were used along two parallel 140 m line transects. The distance between the two transects was 20 m and the distance between sampling points, 20 m. Where possible, the transects were positioned 10 m each side of a representative singing post where tūī were recorded, and 100 m distant from the edges of the site. At each sampling point, a north-south oriented cross was made on the forest floor to create four quarters each sampling point, the distance between the sampling point to the nearest shrub (<5 m height) and the nearest tree (>5 m height, with a DBH of more than 2.5 cm), to a maximum distance of 20 m, were recorded for each quarter. DBH (tree diameter at breast height 1.35 cm) and tree species were also recorded (Heck and Wetstone, 1977).

2.3 Bird Count Surveys

Bird count surveys were conducted to detect changes in avian communities in relation to motorway proximity. Each survey was conducted within 20 metres of an individual tūī song recording site. Detection probabilities of bird species were calculated for motorway versus non-motorway sites i.e. how many counts in which that species was detected divided by the total number of counts. To avoid confounding effects on song, overall bird density was measured at each site and noise and wind levels were recorded with the bird counts.

Ten minute bird counts were carried out at each recording station, 14 at motorway sites and ten at non-motorway sites (Dawson and Bull, 1975). Bird counts with high levels of wind noise or precipitation were discarded as this could reduce the detectability of some species. The observer stood still for ten minutes, with an initial period of two minutes silence, then recorded every bird seen or heard for the first five minutes, including the number of individuals, species and distance from observer. The counts were pooled for the two areas to assess the differences in detection probabilities (number of counts where a particular bird species made an appearance divided by the total number of bird counts per area).

2.4 Song Recording Methods

Long-range songs were recorded during the tūī breeding season from mid-October 2012 to the end of January 2013 at each study site. At each site the researcher walked slowly through the bush to locate tūī breeding territories and singing tūī. When a singing bird was located, it was followed and over ten songs were recorded when possible for each individual. The minimum distance between tūī sampled was 50m, and the same territory was only recorded once in order to reduce the chance of sampling the same bird (pseudoreplication). Although I did not colour band birds for individual identification, only one bird was observed singing in each territory and each individual sang from only one or two perches throughout the study, so it is presumed I only recorded the songs of one male per territory. Recordings with a large amount of background noise (e.g. wind noise, rain, human voices, machinery) and/or low amplitude levels due to the long distance between microphone and tūī were discarded.

Tūī songs were recorded with a directional Sennheiser ME67 shotgun microphone (Sennheiser, Hanover, Germany) and a Marantz PMD661 Solid State recorder (Marantz, Kanagawa, Japan) or a M-Audio Microtrack II digital recorder. The recordings were taken at 44.1 kHz sample rate and 16-bit bit-depth and data was saved in wave format. Amplitude was standardized across recordings with the input gain set to 5 and individual tūī were recorded at a distance of 2-8 metres. The microphone and recorder were set to a flat frequency response (no filter).

2.5 Song Parameters

Temporal and spectral song parameters were used to explore differences in tūī song characteristics between motorway and non-motorway sites. Parameters were extracted from each song for analysis using Raven Pro 1.5 beta software (Cornell Laboratory of Ornithology, Ithaca, New York) (Parameters are defined in Table 2.2 and shown in Figure 2.12. These parameters have been utilised in previous studies examining changes in song spectral properties with urbanisation (Mennill and Rogers, 2006; Odom and Mennill, 2012). Aggregate entropy is a measure of the randomness or unpredictability of a sound (Kershenbaum, 2014): a pure tone has an entropy of zero, whereas white noise has a value nearer one (Hanna et al., 2011). Tūī syllables range from pure tone whistles and harmonic notes to harsh, broadband syllables (closer to white noise).

Table 2.2: Spectral and Temporal Song Parameters for Analysis.

Song Parameter	**Definition**
Song duration (seconds)	Time from the beginning of the first note to the end of the last note of a song
Minimum frequency (Fmin) (kHz)	The lowest pitch measured during a song
Maximum frequency (Fmax) (kHz)	The highest pitch measured during a song
Bandwidth (kHz)	Minimum frequency subtracted from maximum frequency
Peak frequency (FMA)	Frequency at which the highest energy level (dB) is emitted during a song selection
Aggregate entropy	The variability or randomness of sound*
Total syllables	Total number of syllables per song
Syllabic diversity	Number of different syllables per song

Song Parameter	**Definition**
Syllable rate	Total syllables over song duration
Trill duration	Cumulative duration of high frequency modulation sections within a song
Trill proportion	Percentage of each song containing trill

*Entropy is a measurement of the complexity of signals and represents the amount of randomness or variability in a system (Kershenbaum, 2014).

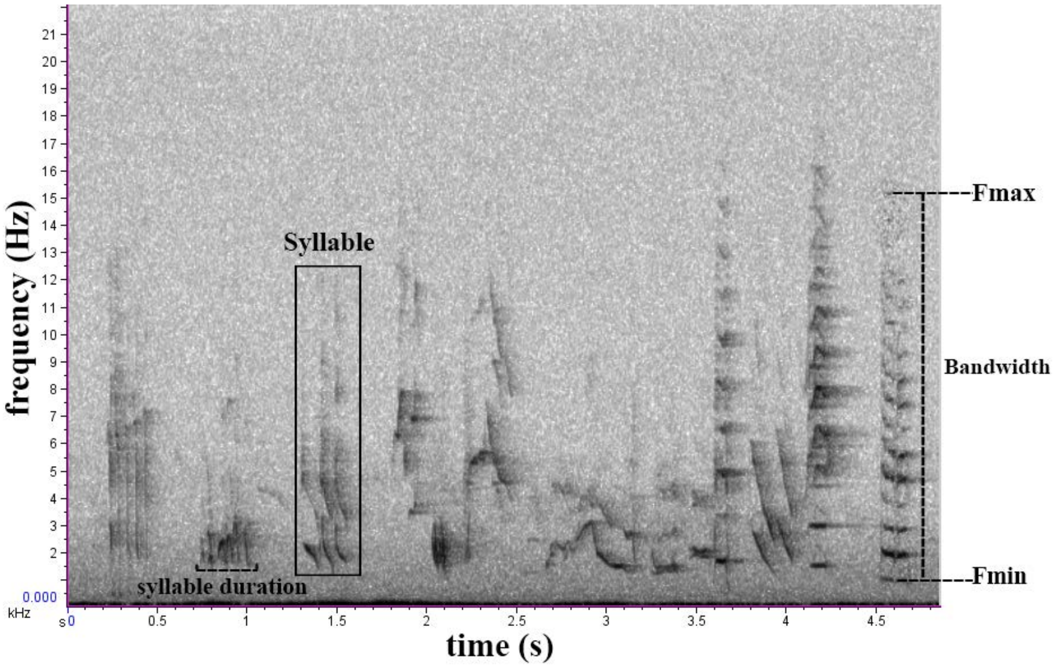


Figure 2.12: Spectrogram (Raven Pro beta 1.5) showing syllable parameters in a male long range tūī song; syllable duration, Fmin (the minimum frequency), Fmax (the maximum frequency), bandwidth and syllable duration.

2.6 Spectrogram Analysis

Calls were extracted from the recordings using Raven Pro 1.5 beta software (Cornell Laboratory of Ornithology, Ithaca, New York) using discrete Fourier transform, (DFT) = 256 samples, Hann Window, 3 dB filter bandwidth at 248 Hz, and 50% overlap in time grid. Temporal and frequency parameters were measured by manually drawing selection boxes around individual syllables with real time visualisation of the acoustic measurements (Charif et al., 2008). Song duration was measured using waveform and spectrogram views. Maximum and minimum frequency of songs and syllables were measured using Spectrogram view and Selection Spectrum view, which shows the average spectrum of a sound over the user-selected time interval. The power values shown at each frequency in a selection spectrum view displayed are expressed in decibels relative to an arbitrary power value of one (Charif et al., 2008).

Details of further data analyses and statistical analyses are given in each chapter accordingly.

CHAPTER 3 Urban Noise Effects on Tūī Song

Plate 3: Tūī singing (photograph by Kerri Walker)

3.1 Introduction

Urbanisation is an important component of global land transformation with nearly half the world's population now living in cities (Dearborn and Kark, 2010; Pickett et al., 2001). Cities are rapidly expanding and increasingly absorbing surrounding agricultural and forested landscapes (Pickett et al., 2001). Human-induced habitat modification is leading to a reduction in animal and plant populations and their habitats by around 1% annually, posing serious threats to biodiversity (Smith and Bernatchez, 2008). Habitat loss and degradation, higher pollution levels, invasive species, lack of nesting sites and predominance of alien plant species are some of the factors driving declines of wildlife diversity and abundance in urban areas (MacLeod et al., 2012).

3.1.1 Effects of Noise on Bird Song

Bird song is an important communication signal used to attract mates and deter rivals and is critical for survival and reproductive success for many birds (Nemeth et al., 2013; Slabbekoorn, 2013). Changes to the physical and acoustic environment in cities can generate new patterns of noise that may interfere with these communication signals (Leader et al., 2005). Tall buildings and other reflective surfaces can reflect and distort signals, causing song elements to be masked or blended (Leader et al., 2005). Low frequency urban noise can cause attenuation, degradation and masking of avian signals as they travel through the environment.

Research in acoustic communication in animals has shown ways in which organisms adapt their signals to the environment. The 'acoustic adaptation' hypothesis (AAH), proposes that song characteristics are driven by habitat type to maximise signal transmission (Morton, 1975; Patricelli and Blickley, 2006). Differences were found in the transmission properties of songs through forested and open grassland habitats, with less attenuation of high frequencies (such as trill components of song) found in open environments than in forests (Wiley and Richards, 1978). Narrower frequency ranges were also predicted to occur more frequently in densely vegetated habitats than in open grassy habitats (Boncoraglio and Saino, 2007).

Birds encounter considerable acoustic noise in natural environments from biotic sources such as cicadas and abiotic sources such as waves and wind noise (Lohr et al., 2003). However, anthropogenic noise has altered considerably in volume and acoustic structure as a consequence of rapid industrialisation and urbanisation (Wood and Yezerinac, 2006). In a previous study, traffic-generated noise levels in a city increased by over 5 dB, an almost doubling in volume, from 66 dB(A) to 71 dB(A), over a 35 year time period (Luther and Derryberry, 2012). The study also found that average traffic flows increased significantly over the same period (Luther and Derryberry, 2012).

Heightened noise levels can affect the ability of birds to communicate and could be a factor in the decline of bird species in cities (Cartwright et al., 2014; Slabbekoorn and Ripmeester, 2008). Urban noise can interfere with the ability of a signaller to defend a territory or attract a mate (Patricelli and Blickley, 2006; Warren et al., 2006). It can also reduce the efficiency of begging calls, and mask predator arrival and associated alarm calls leading to reduced reproductive success (Slabbekoorn and Ripmeester, 2008; Warren et al., 2006). Urban noise may affect breeding in species unable to tolerate noise or those unable to modify their signals to avoid acoustic interference (Hanna et al., 2011).

While overall avian population density and species diversity tend to decrease with increased proximity to traffic noise (Potvin et al., 2011), those species able to coexist in areas with urban noise have shown evidence of behavioural flexibility in characteristics of their song (Katti and Warren, 2004). Changes in signal design may occur as short-term or longer term (e.g. song learning) phenotypically plastic responses to anthropogenic noise (Warren et al., 2006). It has been suggested that local adjustment of songs to the habitat through song learning could lead to song divergence of populations between noisy and quiet locations within urban environments (Katti and Warren, 2004).

Cartwright et al. (2014) outlined five types of signal modification that alter the structural characteristics of song that birds use to avoid the effects of masking by low frequency noise: 1) frequency, 2) amplitude, 3) type of signal, 4) tonality and 5) timing of the signal. Alterations to the frequency component of signals and the timing of singing have been found to coincide with off-peak traffic flows (Katti and Warren, 2004; Mendes et al., 2011) and song volume increases have been reported in noisy areas (Potvin et al., 2011).

3.1.2 Impacts of Noise on Song Characteristics

3.1.2.1 Frequency Shifts

A large proportion of anthropogenic noise, predominantly traffic noise, occurs at relatively low frequencies (approx. 20 Hz to 3 kHz). Many avian songs overlap these frequencies, but also often extend into higher frequencies (Wood and Yezerinac, 2006). Some species were found to use a higher minimum frequency in the presence of urban noise, such as urban great tits (*Parus major*) (Katti and Warren, 2004; Mockford and Marshall, 2009), orange-tufted sunbirds (*Nectarinia osea*) (Leader et al., 2005), blackbirds *(Turdus merula*) (Mendes et al., 2011) and silvereyes (*Zosterops lateralis*) (Potvin et al., 2011). Previous studies found that urban great tits raised the minimum frequency and also reduced the frequency range or bandwidth of their songs in more noisy areas (Katti and Warren, 2004; Slabbekoorn and Peet, 2003). Grey vireos (*Vireo vicinior*) raised the maximum frequency of their song with increases in noise levels (Francis et al., 2011).

3.1.2.2 Temporal and Behavioural Parameters

The temporal structure of a song may also affect the ability of a receiver to detect a signal due to the masking effects of noise, and may be adjusted in noisy urban areas (Patricelli and Blickley, 2006). Signal transmission in noisy environments may improve with alterations in temporal parameters such as song duration and increases in the frequency of signalling such as song or syllable rate (Francis et al., 2011). Laboratory studies found that longer song duration increased the detectability of signals in the presence of white noise (Warren et al., 2006) and grey vireos sang shorter songs in response to increased noise levels (Francis et al., 2011).

3.1.2.3 Syllable Diversity

Syllable diversity or syllable repertoire is measured as the number of different syllables and the total number of syllables within a song and is a factor commonly used to measure song complexity (Garamszegi and Møller, 2004). Syllable diversity is a sexually selected trait that functions both to attract mates and deter rivals (Searcy and Nowicki, 2005). According to the 'Beau Geste' hypothesis, larger song repertoires have evolved to give the impression of a high density of conspecifics at a site to repel incoming males (Cartwright et al., 2014). If syllable diversity is reduced due to anthropogenic noise, it could result in more males competing for limited resources in noisy urban areas (Cartwright et al., 2014).

3.1.2.4 Trill Proportion

Trill (high frequency modulation) components of songs are considered to be costly to produce and play an important role in mate choice. Trill is intended for communication over longer distances and therefore an important aspect of long-range song. High frequency trill is less likely to suffer from signal degradation in open habitats than lower frequency elements, whereas the transmission of low frequencies is enhanced in closed forest habitats (Morton, 1975). Brumm and Slater (2006) recorded that chaffinches sang shorter bouts of song types with fast trills in noisier areas but the effects of urban noise on the trill components of song have not been fully studied.

3.1.3 Tūī Ecology and Song

Most studies on New Zealand's native avifauna have, until recently, concentrated on endangered species, whereas those more common species have received less attention. Although tūī are common and widespread throughout New Zealand, they are virtually absent in the west of the Southern Alps (Robertson, 2007) and like most New Zealand native forest birds, tūī are in decline in some areas (Elliott et al., 2010). Recent studies report microgeographic variation in song phrases of tūī (Hill and Ji, 2013), categorization of common syllable types (Hill and Ji, 2014), and seasonal variation in tūī song structure (Hill et al., 2015). Higher levels of syllable diversity and a higher percentage of trills in tūī songs were found in the mainland populations than those from isolated, island populations (Hill et al., 2013). Tūī abundance is variable in urban environments nationwide (Spurr, 2012), and population declines were reported in Christchurch and Hamilton since the mid-1990s, attributed to habitat loss and predation (Schmechel, 2002; Innes et al., 2005). Recent data confirms that if adequate food is available, mammalian pest control in nesting territories can rapidly increase tūī visits and nesting in managed forest remnants near cities and enable their recolonisation of urban habitats (Innes et al., 2015).

Although there have been many previous studies on the effects of urban noise on bird song, these have mostly compared urban and non-urban locations and there is very little knowledge about how urban noise affects song variables within the heterogeneous urban environment. The effect of anthropogenic noise on New Zealand native birds in urban environments is not known and it is vitally important to our understanding of the effects of cities on our native wildlife. It is unknown how birds react to rapid urbanisation in New Zealand. Native forest birds are valued highly by New Zealanders, however the causes of their presence or absence from cities is not well understood (van Heezik et al., 2008b). Several native species appear to be able to exploit residential areas e.g. tūī, fantails (*Rhipidura fuliginosa*), grey warblers (*Gerygone igata*) and bellbirds (*Anthornis melanura*) (van Heezik et al., 2008b). However, the effects of urban noise on avian wildlife have not previously been measured in New Zealand. The aim of this study is to investigate how traffic noise from motorways adjacent to urban sites affects tūī song characteristics and the potential implications of these results for wildlife conservation in noisy urban environments.

3.1.4 Research Aims and Predictions

The aims of this study were to 1) document the variation in song spectral characteristics across urban sites that vary in anthropogenic noise characteristics, and 2) to test the hypothesis that tūī can alter characteristics of their songs in the presence of anthropogenic noise.

My predictions are that there will be 1) a higher minimum frequency, increased bandwidth and peak frequency, and lower aggregate entropy at motorway sites compared with non-motorway urban sites, 2) shorter song duration in motorway sites than in non-motorway sites, 3) a lower syllable diversity and fewer syllables per song at motorway sites than at motorway sites and that tūī attempt to simplify their songs to reduce the effects of motorway noise, and 4) longer trill proportion of songs at non-motorway sites than at motorway sites.

3.2 Methods

For study site and recording methods, please refer to Chapter Two, p 23 and p 36.

3.2.1 Study Species

Tūī travel long distances to follow nectar resources year round often returning to nesting territories in the breeding season (Stewart and Craig, 1985). Nesting sites are restricted to areas with reliable sources of spring and summer nectar such as pōhutukawa (*Metrosideros excelsa*), flax (*Phormium tenax*) and kowhai (*Sophora microphylla*) (Stewart and Craig, 1985). This study was conducted during breeding season when male tūī defend their nests using long-range broadcast songs and are easier to identify by their breeding territory.

3.2.2 Data Collection

To explore the differences in song characteristics between motorway and non-motorway sites, 10 song variables were measured from a total of 1025 long-range songs from 35 individuals (627 songs from 18 individuals at motorway sites and 398 songs from 17 individuals at non-motorway sites). The following variables were compared; song duration, minimum frequency, maximum frequency, peak frequency, bandwidth, aggregate entropy, number of syllables per song, number of different syllables per song, trill duration and trill proportion. These parameters are defined in Table 2.2 of Chapter Two, p 37.

3.2.2.1 Ambient Noise Levels

Sound pressure level (SPL) measurements were recorded at varying distances from the motorway, using a Digitech QM-1589 compact digital SPL meter (Sound level: Low = 30-100 dB and High = 60-130 dB). Time weighting was set to slow response to measure the average ambient sound level, and set to dBA frequency weighting (used for general sound level measurements). The Max/Min hold mode was used, whereby the maximum noise levels were recorded for a one minute period. The microphone was positioned away from direct wind interference, and pointed towards the sound source (motorway).

Traffic flow is a good approximation of traffic-generated noise and is often used to estimate noise levels in cities (Luther and Derryberry, 2012). Motorway vehicle traffic data from New Zealand Transport Authority (NZTA) was taken from weekdays in the first three weeks of December 2012 for the three urban motorway sites. The volume of vehicles passing per hour, in both directions on the days sampled were averaged for each site with hourly traffic flow information on the motorway adjoining each of the three motorway sites during the sampling period. Time periods were separated into 04:00-07:00 (off peak), 7:00-10:00 (peak), and 10:00-13:00 (interpeak).

3.2.2.2 Vegetation Surveys

Refer to Chapter 2 General Methods for vegetation survey methods (p 35).

3.2.2.3 Bird Count Surveys

Refer to Chapter 2 General Methods for bird survey methods (p 35).

3.2.2.4 Sound Recordings

Refer to Chapter 2 General Methods for recording methods (p 36).

3.2.2.5 Song Analysis

Song extraction and analysis was conducted using Raven Pro 1.5 Beta interactive sound analysis software (Cornell Lab of Ornithology) to generate spectrograms of all songs. Recordings were analysed aurally as well as visually and vocalisations were identified by shape, energy and timbre. Recordings of songs with a low signal level or high levels of background noise were discarded. I measured the minimum frequency, peak frequency, maximum frequency, and syllable rate in each song. For this study a song was defined as a sequence of syllables preceded and followed by a period of silence of three seconds or more (Hill, 2011). Syllables were defined as one or more distinct notes that always occurred together.

3.3 Statistical Analysis

I tested whether there was a difference in spectral characteristics between motorway and non-motorway sites using a one-way permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). PERMANOVA is a non-parametric distance-based analysis of variance, which uses permutation procedures to obtain P values in data. In this case, Euclidean distance measure was used. In order to remove skewness, I used a $\ln(x) + 0.01$ transformation for spectral variables: song duration, number of notes, trill duration, minimum frequency, maximum frequency (FMA), bandwidth, peak frequency, and syllable diversity. These variables from motorway and non-motorway sites were examined using a one-way PERMANOVA in order to detect whether song structure between sites was significantly different. The conservative Bonferroni correction for multiple testing was used for all multivariate analyses. PERMANOVA was conducted using PAST software (version 2.17b) (Hammer et al., 2001). The song variables were then examined by a one-way analysis of similarity (ANOSIM) to detect significant differences between sites. ANOSIM is a non-parametric multivariate test using Euclidean distance measure in this case.

A Canonical analysis of principal co-ordinates (CAP) was performed on the multivariate data and averaged for individual birds, with each data point representing a different tūī. This analysis examines whether birds can be discriminated between different motorway distances, and then examines which variables are useful at finding those differences.

3.3.1 Song Parameters

Song parameters tested for differences between motorway and non-motorway sites include: frequency-related parameters- minimum frequency, maximum frequency, bandwidth and peak frequency; behavioural parameters- song duration, syllable rate, syllabic diversity, trill duration and aggregate entropy. Definition of these song parameters are presented in Chapter 2 (p 37).

I used non-parametric Mann-Whitney U tests, as the data were non-normally distributed to test my prediction that tūī would produce: 1) lower proportion of trills, 2) lower minimum frequency, 3) shorter trill length and 4) lower syllable rate at the motorway sites than at the non-motorway sites. All statistical tests were two-tailed and *P* values <0.05 were considered significant.

3.4 Results

A total of 102.9 hours of song recordings were collected during 31 days (63.5 hours) of field sampling at urban sites between November 2012 and February 2013. A total number of 1025 different long-range songs were recorded (627 from motorway and 398 from non-motorway sites) (Table 3.1). The frequency range of long range songs was from 556 Hz to 20 kHz at the motorway sites, and from 348 Hz to 20 kHz at the non-motorway sites. The range of song duration was 0.3 s to 60 s at motorway sites and 0.4 s to 68.8 s at non-motorway sites.

Table 3.1: Number of individual tūī recorded, mean number of songs per individual and songs per site.

Site	Number of songs	N	Mean±SE songs per individual	Range (min-max)
Smiths Bush^{M}	252	6	36.0±11.5	70 (6,76)
Domain^{M}	202	5	41.4±11.3	74 (8,82)
Botanic Gardens^{M}	173	7	24.7±7.5	59 (5,64)
Le Roys Bush	163	8	20.4±3.6	29 (10,39)
Waitaramoa Res	113	4	26.25±6.1	28 (16,44)
Totara Park	122	5	24.4±3.7	18 (16,34)
Total	**1025**	**35**		

^{M} = Motorway site

3.4.1 Urban Noise Levels

Motorway sites had a mean background noise level of 6dB higher than non-motorway sites (Table 3.2). Sound pressure level (SPL) averages were 58.59 dB for motorway sites and 52.47 dB for non-motorway sites (Table 3.2). There was very little difference in SPL's between peak and non-peak times at motorway sites

(Table 3.2). Traffic flow data showed that there was very little difference in traffic volume between peak (7-10am) and interpeak (10am-1pm) periods (Table 3.3). There was a reduction in traffic flow at the off-peak period (4-7am). However there was insufficient song data collected at these times to compare the effects of time of day and difference in peak traffic flows on tūī song characteristics.

Table 3.2: Average SPL measurements (dBA) ± standard error at recording sites at peak traffic flows (7am-10am) and non-peak traffic flows (4am-7am, and 10am-1pm).

Site	Peak (7-10am)	Non-peak	Total
Botanic Gardens	48.42±2.09	54.90±1.48	50.85±1.70
Domain	61.00±0.88	56.15±0.51	58.02±0.65
Smiths Bush	60.78±1.10	62.75±1.20	61.35±0.83
Motorway sites	58.85±1.09	58.30±0.80	58.59±0.68
Non-motorway sites			52.47±0.22

Averaged traffic volume data indicated high levels of traffic flow along State Highway 1, (100km speed limit) at Botanic Gardens and Smiths Bush and lower levels of flow along State Highway 16 (80km speed limit), adjoining Auckland Domain (Table 3.3) (Off peak = 4-7am, peak = 7-10am and inter-peak 10am-1pm).

Table 3.3: Weekday average motorway traffic flows (number of vehicles passing per hour) for December 2012 (NZTA, 2014).

Time of day **Recording site/motorway**	**04.00-07.00** **Off peak**	**07.00-10.00** **Peak**	**10.00-13.00** **Interpeak**
Botanic Gardens (Hill Rd Interchange, SH1)	1174.71±115.45	6255.93±69.32	5852.67±60.56
Auckland Domain (Grafton Rd Interchange, SH16)	271.711±27.57	2394.27±78.90	2506.13±24.53
Smiths Bush (Northcote Rd Interchange, SH1)	912±107.53	6222±142.14	6933±66.51

3.4.2 Vegetation Surveys

Comparisons between motorway and non-motorway sites were made using Mann-Whitney U tests as the data was non-normally distributed requiring non-parametric tests. There was no significant difference found between sites over distance (density) (Table 3.4). There was also no significant difference found between sites for DBH (maturity) (Table 3.4).

Table 3.4: Comparison of mean distance from Point Centred Quarter (PCQ) and mean diameter at breast height (DBH) of trees >5 m between motorway and non-motorway survey sites.

	Motorway	**Non-motorway**	**Mann-U sig**
Distance (m)	7.96	7.43	$p = 0.11$
DBH (cm)	19.41	11.56	$p = 0.09$

3.4.3 Bird Count Surveys

A total of 19 species were recorded in bird counts surveys with a total of 9 native and 10 non-native species (Table 3.5). A total of 16 species were recorded at motorway sites and 15 species at non-motorway sites. Tūī and silvereyes had the highest detection probabilities at both motorway and non-motorway sites (Table 3.5). There were also higher detection probabilities of species that may depredate tūī chicks such as myna (*Acridotheres tristis*), pukeko (*Porphyrio melanotus*) and magpie (*Gymnorhina tibicen*) at non-motorway sites (Table 3.5).

Table 3.5: Detection probabilities of bird species recorded at surveyed motorway and non-motorway sites in Auckland City.

Species	**Scientific name**	**Motorway (%)**	**Non-Motorway (%)**
Tūī	*Prosthemadera novaeseelandiae*	100	100
Silvereye	*Zosterops lateralis*	100	100
Blackbird	*Turdus merula*	83.3	66.67
Eastern rosella	*Platycercus eximius*	66.67	50
Chaffinch	*Fringilla coelebs*	66.67	0
Grey warbler	*Gerygone igata*	50	16.67
Sparrow	*Passer domesticus*	33.33	33.33
Myna	*Acridotheres tristis*	33.33	66.67
Song thrush	*Turdus philomelos*	33.33	0
Fantail	*Rhipidura fuliginosa*	33.33	66.67
Shining cuckoo	*Chrysococcyx lucidus*	16.67	16.67
Kingfisher	*Todiramphus sanctus*	16.67	50
Kereru	*Hemiphaga novaeseelandiae*	16.67	50
Black-backed gull	*Larus dominicanus*	16.67	0
Greenfinch	*Carduelis chloris*	16.67	0
Spotted dove	*Streptopelia chinensis*	16.67	16.67
Starling	*Sturnus vulgaris*	0	16.67
Pukeko	*Porphyrio melanotus*	0	16.67
Magpie	*Gymnorhina tibicen*	0	33.33

3.4.4 Variation in Tūī Song Structure between Motorway and Non-motorway Populations

A multidimensional scaling plot (Mann-Whitney U = 63751, z = -12.847, p ≤ 0.001, 2-tailed) shows separation of song characteristics between motorway and non-motorway sites (Figure 3.1). Variations were detectable for the minimum frequency, syllable rate and trill proportion variables. In the inner diagram, longer lines represent a greater level of similarity of individual cases of the dataset for visualisation of the data. The inner diagram shows separation between sites in variables such as minimum frequency, syllable rate and trill proportion.

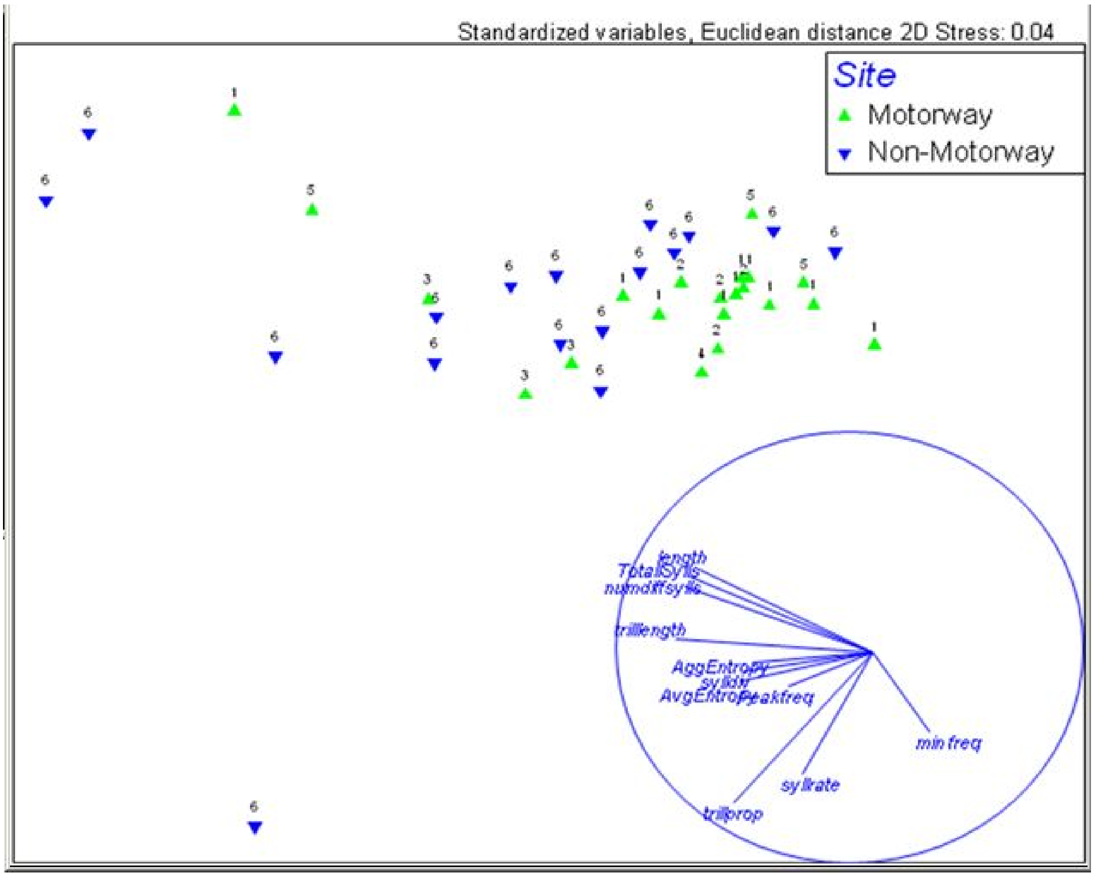


Figure 3.1: Multidimensional scaling (MDS) plot of separation of motorway (green triangle) and non-motorway (blue triangle) sites, Euclidean distance measure. Numbering denotes distance from motorway (1-5) at motorway sites and (6) non-motorway sites.

Results from a one-way Permanova test in PAST showed a significant difference in song structure between songs recorded at motorway sites and non-motorway sites**,** *n* = 38 individuals, (20 motorway, 18 non-motorway), Pseudo F= 4.913, $P \leq 0.001$ (Bonferroni), 9999 permutations, Euclidean distance measure. There was a significantly higher minimum frequency at motorway sites, and a significantly lower aggregate entropy, song duration, total and different number of syllables per song at the motorway sites compared with the non-motorway sites (Table 3.6). There was also a significantly lower trill proportion at the motorway sites (Table 3.6).

Results from a one-way ANOSIM (Euclidean) in PAST confirmed that there was a significant difference in song structure between songs recorded at motorway sites and non-motorway sites, n = 38 individuals (20 motorway, 18 non-motorway), R =0.1971, $P \leq 0.001$.

3.4.4.1 Frequency spectral variables

The median minimum frequency of songs was significantly higher at the motorway sites (1098 Hz) compared with the non-motorway recording sites (760 Hz) (Table 3.6 and Figure 3.2). There was no significant effect of noise on the maximum frequency, bandwidth or peak frequency song variables (Table 3.6). However there was a slight trend showing a lower peak frequency at the non-motorway sites.

3.4.4.2 Song duration, syllable diversity and syllable rate

The median song duration was significantly longer at mon-motorway recording sites than at the motorway recording sites (Table 3.6 and Figure 3.2).

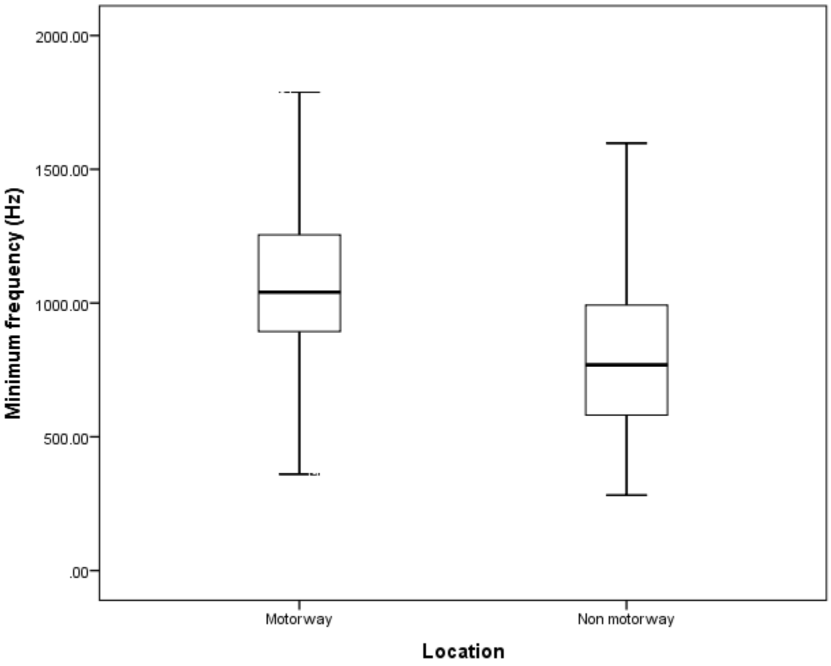
The total number of syllables per song and number of different syllables per song (syllable diversity) were both significantly higher at the non-motorway sites than at the motorway sites. Trill proportion was significantly higher at non motorway sites than at motorway sites (Table 3.6 and Figure 3.2). There was no significant difference in the syllable rate between motorway and non-motorway sites.

Aggregate entropy was also higher at the non-motorway sites than at the motorway sites (Table 3.6 and Figure 3.2).

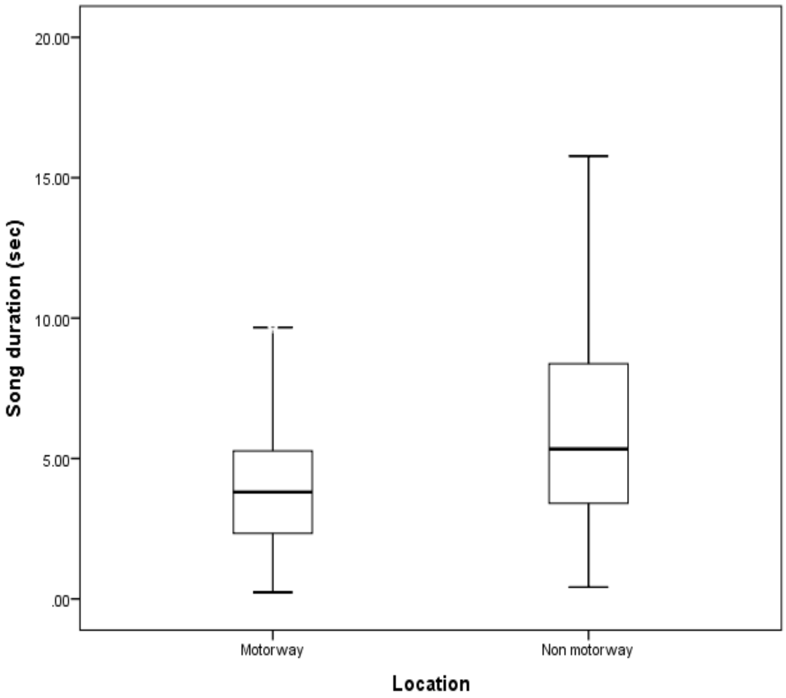
Table 3.6: Median value (range) of the song variables of tūī songs of motorway and non-motorway populations, Mann-Whitney U significance (2-tailed). Statistically significant results (p ≤0.05) are highlighted in bold.

Variable	**Motorway** Median (range)		**Non-motorway** Median (range)		**(2-tailed MU)**
n	20		18		
Minimum frequency (Hz)	1,098	(633)	760	(884)	**0.00**
Maximum frequency (Hz)	16,388	(7378)	16,036	(5289)	0.75
Bandwidth (Hz)	15,330	(7664)	15,150	(4460)	0.94
Peak frequency (Hz)	2,215	(3357)	2178	(1,667)	0.89
Aggregate entropy	4.43	(1.56)	4.97	(3.06)	**0.00**
Song duration (seconds)	4.78	(12.3)	8.24	(15.13)	**0.00**
Total syllables/song	15.27	(47.96)	20.26	(50.07)	**0.02**
Different syllables/song	9.43	(38.62)	14.67	(43.62)	**0.05**
Syllable rate	3.49	(2.09)	3.36	(3.42)	0.37
Trill proportion (%)	0.21	(0.48)	0.41	(0.64)	**0.00**

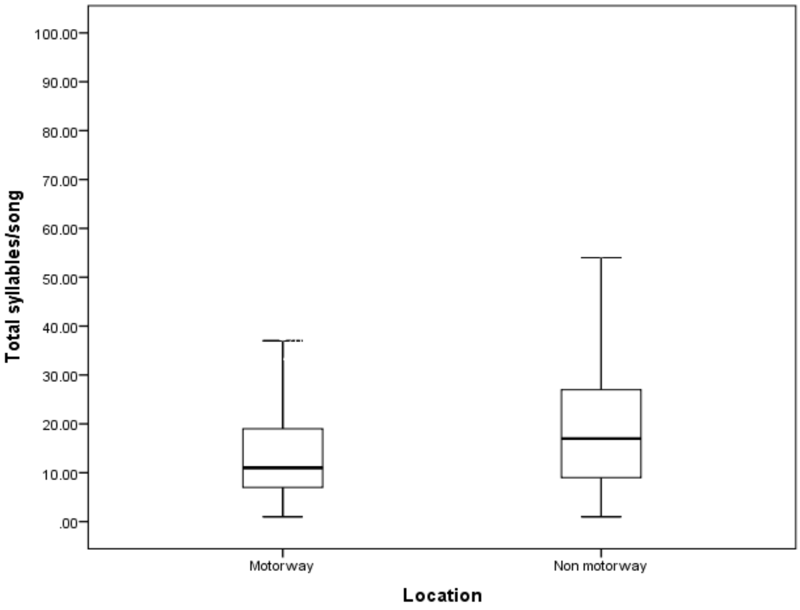
a) Minimum Frequency (Hz)



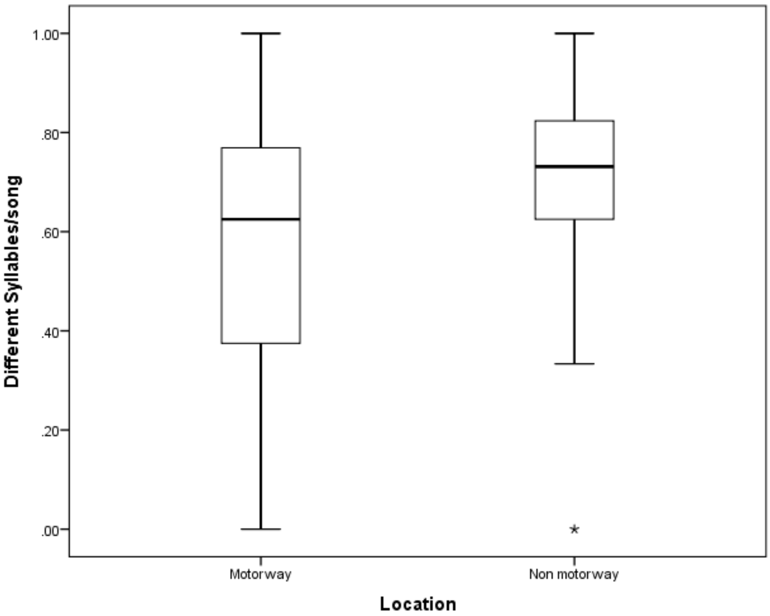
b) Song Duration (sec)



c) Total Syllables Per Song



d) Different Syllables Per Song



e) Trill Proportion

f) Aggregate Entropy

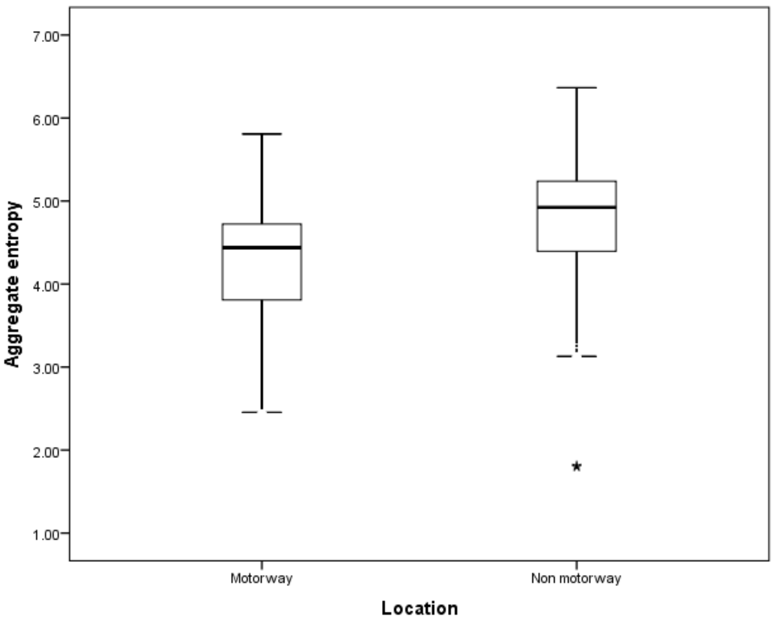


Figure 3.2: Boxplots showing differences in song parameters between motorway (n = 20) and non-motorway sites (n = 18); a) minimum frequency, b) song duration, c) number of syllables/song, d) different syllables per song e) trill proportion and f) aggregate entropy.

3.4.5 Distance from Motorway

Most of the tūī songs recorded at non-motorway sites were clustered together in the CAP analysis (Figure 3.3). Those variables in the circle (inset diagram, Figure 3.3) correlated with specific vectors on the CAP analysis, so distances of 6 (non-motorway) tend to be on the bottom right of the CAP graphic, this correlates with larger values of average and aggregate entropy, and the proportion of unique syllables. There were only a small sample of tūī at a distance of 5 from the motorway, but they tended to cluster towards the upper right of the graphic and correlated with maximum frequency and bandwidth.

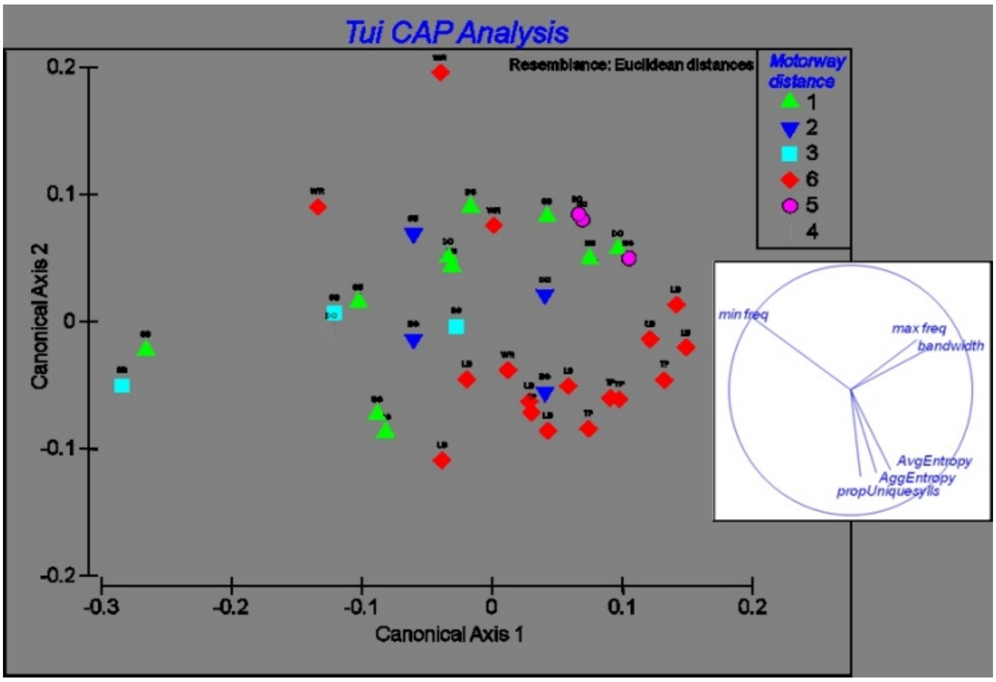


Figure 3.3: Canonical analysis of principal coordinates (CAP) of tūī song parameters at varying distances from motorway (Motorway distance: 1= 1-100 m, 2 = 100-200 m, 3= 200=300 m, 4= 300-400 m, 5 = 400-500 m, 6 = non-motorway sites).

3.5 Discussion

3.5.1 Habitat Surveys

The average noise levels at the motorway sites were 6.12 dB higher than at non-motorway sites, which represents a doubling in volume (Luther and Derryberry, 2012). This confirms a direct link between proximity to motorway and ambient noise levels between sites. Traffic flow data for all motorway sites showed that there was a much lower flow rate at the off peak period (4-7 am) compared with both the peak time (7-10 am) and the following time period measured (11 am-1 pm). This data showed that the traffic flow and ambient noise levels were fairly consistent during the main recording period for this survey (7 am-1 pm).

Vegetation surveys revealed that there was no significant difference in density or maturity of trees at motorway and non-motorway sites, indicating that vegetation structure is similar at the six sites. However there was a trend showing a larger tree size at the motorway sites, which reflects the mature planted trees in parkland at the Domain and Botanic Gardens sites, but these differences were not expected to have an impact on song characteristics.

There were minimal differences in species diversity and the detection probability of tūī and other species among the motorway and non-motorway sites. Noise levels could be sufficiently high as to mask bird calls from the observer, particularly distant birds, or those species with relatively quiet calls (Mortimer and Clark, 2013). This could have the effect of reducing detection probabilities for some species at the noisier sites such as Smiths Bush. Tūī had the highest detection probabilities at both the motorway and the non-motorway sites, but there were more species known to depredate tūī chicks (e.g. myna and pukeko) at the non-motorway sites.

3.5.2 Song Variables

A consistent detectable difference was found between long-range male tūī songs in territories at motorway and non-motorway sites in Auckland city. Song elements were of a higher minimum frequency, lower peak frequency and shorter song duration at motorway sites. Furthermore, songs had a shorter trill duration and lower syllable diversity at motorway sites.

3.5.3 Alterations in Frequency-related Song Variables

Tūī populations close to motorways were singing songs at a higher minimum frequency than those at non-motorway sites. An elevation in average noise level of 6.dB at motorway sites compared to non-motorway sites may have contributed to this difference. My finding is consistent with previous studies of urban avian species which recorded a raised minimum frequency of bird songs under noisy urban conditions (Katti and Warren, 2004; Leader et al., 2005; Mendes et al., 2011; Potvin et al., 2011; Slabbekoorn and Peet, 2003). Local song adjustment within acoustically different urban habitats could drive divergent selection between populations at noisy and quiet locations (Slabbekoorn and Peet, 2003). Thus noisy urban habitats could select for different songs than those in quieter urban habitats (Slabbekoorn and den Boer-Visser, 2006). Other factors that could influence differences in tūī song characteristics between the two locations include habitat differences. A recent study recorded variation in the structural characteristics of tūī song between remote island and mainland sites with variation attributable to habitat differences between open and dense forested types (Hill et al., 2013). However, the vegetation density and maturity in this study were not significantly different between motorway and non-motorway sites and this factor is therefore not thought to influence this variation in minimum frequency.

The observed shift in minimum frequency is potentially a form of behavioural plasticity whereby individuals modify their songs between or during song bouts, according to the prevailing noise levels (Wood and Yezerinac, 2006). Another form of plasticity is selective attrition, whereby individuals learn selectively from a restricted range of their repertoire (Slabbekoorn and Peet, 2003). Another hypothesis is that individuals go through a process of ontogenetic change resulting in a repertoire that matches the noise levels of their territory (Wood and Yezerinac, 2006). Song matching in tūī could also be used to selectively filter out songs or portions of songs that are lower frequency and more easily masked by traffic noise. Other ontogenetic influences of noise on song could occur during the critical learning stage of tūī (Nowicki et al., 1999) whereby juvenile tūī don’t learn to sing the masked low-frequency notes from other males in the noisier urban populations compared with the quieter urban populations. However very little is known about how juvenile tūī learn their songs and how much they adjust their song during interactions with neighbours. If these observed frequency shifts in tūī song are in response to the selection pressure of low frequency noise, and result in an increase in signal communication distance, and influence breeding success, they may be adaptive. However there are currently very little data on differences in breeding success of birds with high or low frequency songs in noisy urban environments (Potvin et al., 2011).

The effects of signal alteration by raising minimum frequency could have a negative effect on the transmission efficacy of songs and affect a male's ability to defend its territory or attract mates (Mockford and Marshall, 2009). Females may be less attracted to males that produce modified songs and these same songs may also be perceived by other males as less threatening, thus reducing a male's ability to defend his territory (Hanna et al., 2011). Higher minimum frequency songs elicited a reduced response from receivers than average minimum frequency songs in male northern cardinals (*Cardinalis cardinalis*) (Luther and Magnotti, 2014). Although singing at higher frequencies may improve signalling efficiency in tūī songs at motorway sites, females may be less responsive to these higher frequency songs. However, in the Australian magpie, frequency differences in song across noisy and quiet habitats did not affect receiver responses (McCarthy et al., 2013).

Maximum frequency and bandwidth parameters were not significantly different between sites. Tūī songs can typically extend at least to the upper limit of the recording medium and the upper range of human hearing (20 kHz). These findings are confirmed by studies that found no or little variability in maximum frequency or bandwidth measurements between noisy and quieter sites. Motorway noise has the greatest energy in the 1 kHz- 4 kHz frequency range and therefore is not likely to have an effect on these parameters.

As predicted, there was no significant difference between sites in peak frequency. This result is in accordance with other studies (Slabbekoorn and den Boer-Visser, 2006), and peak frequency has been reported to be particularly sensitive to recording distance and therefore difficult to measure accurately (Ey and Fischer, 2009).

Aggregate entropy was significantly greater at the non-motorway sites, reflecting the increased complexity of song at these sites.

3.5.4 Temporal Variables

Songs at the motorway sites were significantly shorter than those at non-motorway sites. In accordance with my findings, other studies found that song duration was negatively correlated with increasing background noise (McCarthy et al., 2013; Slabbekoorn and den Boer-Visser, 2006). The temporal shift in song duration observed in tūī could be associated with noisier habitats and indicate an unwillingness to communicate and expend energy in noisy areas where extra effort may be futile.

3.5.5 Syllable Diversity

There was significantly lower syllable diversity at the motorway sites compared to the non-motorway sites. This result was confirmed in a previous study that found fewer syllables per song amongst urban silvereyes than in rural populations (Potvin and Parris, 2012). In many species the number of different syllables produced is a measure of song complexity and may be sexually selected by females (Buchanan and Catchpole, 2000). The total number of syllables per song, which is connected to syllable diversity measures, was also significantly lower at the motorway sites. Cartwright et al. (2014) suggested that if the number of syllables in a song is reduced due to anthropogenic noise, then this could limit the formation of larger repertoires. Based on the 'Beau Geste' hypothesis that suggests that larger repertoires evolved in birds to mimic sites with high density in order to repel strangers, this reduction in repertoire size could lead to increased competition for territories, and more males with smaller territories in urban areas (Cartwright et al., 2014).

3.5.6 Trill Proportion

A significantly greater proportion of trill was found in songs at the non-motorway sites compared with those at motorway sites. However this finding was not supported by previous studies. Trills are an example of a song element that is difficult to produce and is thus subject to strong sexual selection because performance levels are related to the sender’s condition or genetic quality (Vehrencamp et al., 2013). High frequency trills are more easily transmitted in open habitats than closed, forest habitats due to the sound transmission properties (Boncoraglio and Saino, 2007). The trill component of tūī song may be quieter and less easily transmitted in noisy environments than the more broadband harsh tones used in urban areas. The reduced proportion of trills in the motorway sites could be related to the energetic costs associated with producing trill sequences at a level that would transmit over the background noise level (Hanna et al., 2011).

3.5.7 Syllable Rate

There was no significant difference in syllable rate (number of syllables over song duration) between motorway and non-motorway sites. This was in contrast to previous studies that found a decreased syllable rate in noisy motorway habitats (Potvin et al., 2011).

Another strategy used by birds to increase signal detectability in noisy environments is to increase signal amplitude. However, this aspect was not investigated in this study due to difficulties in measuring amplitude at varying distances in noisy environments. Future studies using an amplitude calibrated recording system could quantitatively measure whether tūī alter the amplitude of their song in response to noise.

CHAPTER 4

The Effects of Urban Noise on Repertoire and Song Output

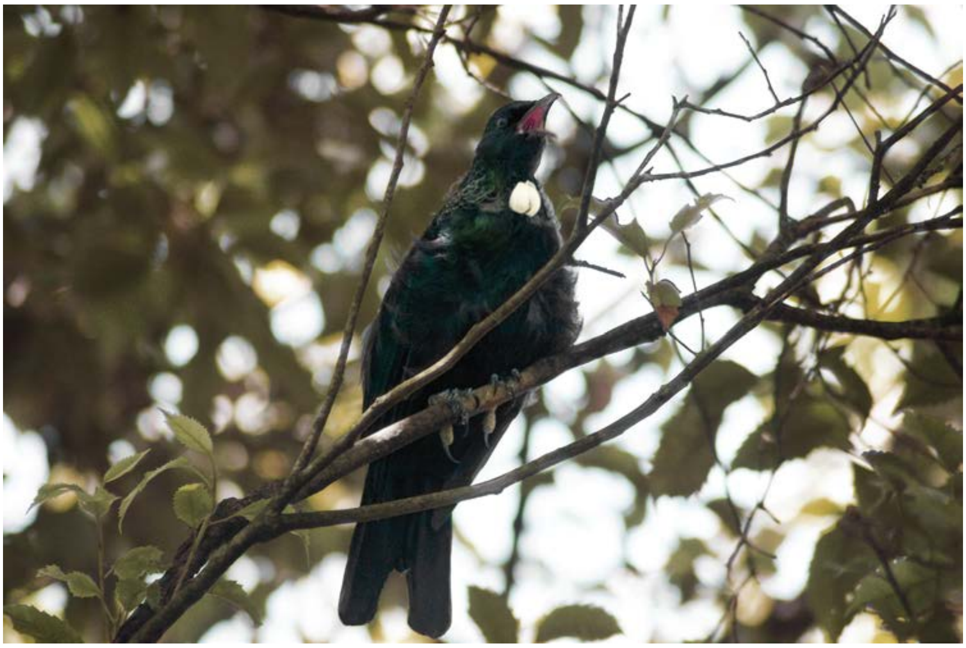


Plate 4: Tūī in Urban Garden (photograph by author)

4.1 Introduction

The considerable impact of urbanisation on ecosystems and biodiversity has prompted a great variety of research into urban ecology. Effects of urbanisation include native habitat fragmentation and loss, alteration of ecosystem structure and processes, and a reduction in biodiversity (Grimm et al., 2008; McKinney, 2002). Small native forest remnants are open to colonisation by invasive plants and common urban predators such as rats (*Rattus rattus*), brushtail possums (*Trichosurus vulpecula*) and cats (*Felis catus*) (McKinney, 2002). These isolated remnants are also subject to increased artificial light levels (Longcore and Rich, 2004), accelerated phenology (Neil and Wu, 2006), and increased levels of anthropogenic noise (Chace and Walsh, 2006). Changes to urban habitats can selectively filter for species that are able to adapt to these ecological pressures (Chace and Walsh, 2006; Marzluff, 2005). Urbanisation has been shown to have an impact on behavioural traits of animals, and the study of avian vocalisations provides a good model to investigate such effects. Numerous studies have focussed on the effects of urban noise on structural features of avian vocalisations. There has been a clear effect in many species of a raised minimum frequency of songs in response to the masking effects of traffic noise (Warren et al., 2006). Other song characteristics such as song and syllable repertoire and temporal song features such as song rate, are important elements of birdsong that are sexually selected, but few studies have investigated the effects of urban noise on these aspects of song. Understanding the factors that enable certain native species to sustain populations in urban habitats while excluding others is important in identifying the factors that promote and protect biodiversity in cities (Stracey and Robinson, 2012).

4.1.1 Song Characteristics

Traits such as repertoire size and song output are important factors used by females for mate selection in song birds (Ballentine et al., 2004; Nottebohm, 1972; Nowicki et al., 2000).

4.1.1.1 Repertoire Size and Syllable Diversity

Song repertoire size is defined as the number of different songs possessed by an individual. Syllable repertoire size is measured as the mean number of different syllables within a song (Garamszegi and Møller, 2004). A higher syllable diversity, or number of different syllables counted for each song or individual represents a larger and more complex repertoire. There is a vast variation in repertoire size between species from a single stereotyped song produced by the white crowned sparrow (*Zonotrichia lecuophrys*) (Soha and Marler, 2001) to repertoires containing hundreds of different songs produced with infinite variety such as the northern mockingbird (*Mimus polyglottos*) (Briefer et al., 2010; Gammon, 2014). For those species with complex songs, many studies focus on measurements of syllable repertoire (Petruskova et al., 2010). Male sedge warblers (*Acrocephalus schoenobaenus*) with larger syllable repertoires were found to obtain mates earlier in the breeding season (Buchanan and Catchpole, 2000). A larger repertoire size was found to correlate with higher measures of reproductive success, survival and territory quality for many species (McGregor et al., 1981; Nowicki and Searcy, 2004). Female great reed warblers (*Acrocephalus arundinaceus*) chose males with a larger repertoire size, which tended to correlate with better quality territories and higher rates of offspring survival (Dennis Hasselquist et al., 1996). Male red-winged blackbirds (*Agelaius phoeniceus*) with larger repertoires had greater pairing success (Yasukawa et al., 1980). A larger repertoire size in marsh wrens (*Cistothorus palustris*) was associated with year round residency, higher densities, and stronger competition for territories and females (Molles and Vehrencamp, 1999).

A larger repertoire size in song birds can also evolve through competitive song matching contests among males that can determine territory acquisition (Molles and Vehrencamp, 1999). Song matching between rival males is thought to contribute to the evolution of complex repertoires, such that a larger number of songs in an individual’s repertoire can increase the number of rivals that can be matched (Laiolo and Tella, 2005). Territorial tropical mockingbirds (*Mimus gilvus*) with a large repertoire size shared a greater portion of their repertoire with neighbours than with non-neighbours and it is thought that increased repertoire size would allow for more successful song matching (Price and Yuan, 2011).

4.1.1.2 Song Rate

Song rate is a performance-related trait defined as the number of songs per unit time and singing rate measured as the amount of time spent singing in a defined time period. These temporal variables are both examples of costly signals that express male quality and these are subject to sexual selection. Males in better condition can afford to devote more time and effort to singing than those in poorer condition (Nowicki and Searcy, 2004). Higher song rates of male blackcaps (*Sylvia atricapilla*) were correlated with higher quality territories and greater nesting success (Hoi-Leitner et al., 1995). Higher song rates in indigobirds (*Vidua chalybeata*) were found to correlate with increased reproductive success (Marler and Slabbekoorn, 2004).

4.1.1.3 Individual-Specific Syllables

Individual-specific syllables are sung by one individual only and may be important cues used for individual recognition of mates or neighbours. There is evidence that birds can recognise the songs of individual males in both neighbour-stranger and intersexual interactions (Petruskova et al., 2010). The presence and number of individual-specific syllables in a population may signify the amount of individual variation there is within that population and this could vary from population to population. Such syllables may also be selected by individuals for effective transmission in noisy urban environments. The effect of urban noise on this aspect of song has not been studied.

4.1.2 Effects of Urban Noise on Aspects of Song

Urban noise can occur in both homogeneous forms, such as chronic traffic noise or as infrequent forms such as construction work or plane noise (Díaz et al., 2011). The nature and degree of noise can vary greatly within the urban environment and traffic noise can form a gradient from motorways and roads to quieter, less disturbed areas (Díaz et al., 2011). Such noise can interfere with the effective transmission of avian singing, having a negative effect on the ability of the signaller to defend a territory or attract a mate (Patricelli and Blickley, 2006; Warren et al., 2006). The masking effect of chronic noise on ovenbird (*Seiurus aurocapilla*) songs was shown to reduce pairing success irrespective of territory quality or individual male quality (Habib et al., 2007).

The ability of a species to adapt to anthropogenic noise may be crucial to its reproductive success (Hanna et al., 2011). Avian communities have been shown to use different strategies to cope with low frequency traffic noise, such as raising minimum frequency of their songs (Katti and Warren, 2004), increasing signal amplitude or timing signals to avoid overlap (Brumm and Slabbekoorn, 2005). However there have been few studies focussing on the effect of urban noise on song features such as repertoire and temporal parameters such as song rate (Halfwerk and Slabbekoorn, 2009).

4.1.2.1 Repertoire

Some avian species can modify attributes of their song to avoid masking from noise through short or long term processes (Patricelli and Blickley, 2006; Ríos-Chelén et al., 2012). Short-term responses include an immediate reaction to current noise levels such as increased signal tonality (Hanna et al, 2011) or choosing songs with higher minimum frequency elements within a repertoire (Halfwerk and Slabbekoorn, 2009). Song sparrows (*Melospiza melodia*) in urban areas selected higher frequency songs from their repertoire that were less masked by prevailing noise (Wood and Yezerinac, 2006). Long-term changes include cultural selection whereby individuals learn those songs from their repertoire that are easily detected in noisy conditions, as in the great tit (*Parus major*) (Slabbekoorn and Peet, 2003). The selective attrition hypothesis predicts that from a large pool of songs learnt during vocal development, only a part of this repertoire is retained in adulthood (Patricelli and Blickley, 2006). Song sparrows were shown to tailor song selection to the acoustic environment of their new breeding territory after they had dispersed from their natal territory (Nordby et al., 2001). Birds may also incorporate more syllables or song types with a narrow frequency band in their repertoire that may be transmitted more effectively in the presence of noise (Halfwerk and Slabbekoorn, 2009). Great tits were found to respond more easily to narrow frequency range songs in noisy conditions (Pohl et al., 2009) and red-winged blackbird songs showed increased signal tonality when exposed to low-frequency noise (Hanna et al., 2011).

4.1.2.2 Song Rate

There are few studies about how birds alter the timing of their vocal signals such as song duration, song rate and syllable rate, and the number of syllables in a song, in response to the masking effects of urban noise (Parris and McCarthy, 2013). Silvereyes (*Zosterops lateralis*) in noisy urban populations were found to sing slower songs (fewer syllables per second) and fewer syllables per song than in rural populations (Potvin et al., 2011). Urban Australian magpies (*Gymnorhina tibicen*) sang shorter songs than those in rural populations, but did not show a difference in song rate (McCarthy et al., 2013). Grey shrike-thrushes (*Colluricincla harmonica*) and great tits were found to decrease their syllable rate in response to urban noise (Parris and Schneider, 2009; Slabbekoorn and den Boer-Visser, 2006). Urban blackbirds (*Turdus merula*) sang significantly shorter songs with fewer elements and shorter between song intervals than rural birds (Nemeth and Brumm, 2009). The song rates of great tits decreased after experimental exposure to white noise treatments (Halfwerk and Slabbekoorn, 2009). Chaffinches (*Fringilla coelebs*) near noisy waterfalls were found to sing longer bouts of the same song type before switching in order to successfully convey their signal (Brumm and Slater, 2006).

Other urban aspects that could affect repertoire size and song rate within urban areas include differences in the size and isolation of forest remnants. Smaller forest patches could lead to lowered density of avian populations, and a reduction in repertoire sharing between individuals. Differences in structural and acoustic features of habitats, such as the presence of buildings and other reflective surfaces may also affect song characteristics such as repertoire and song output. Modified habitats were shown to alter the acoustic transmission of higher frequency trills in the songs of orange-tufted sunbirds (*Necatarinia osea*) (Leader et al., 2005).

4.1.2.3 Tūī Song Repertoire

The tūī (*Prosthemadera novaeseelandiae*) is an endemic New Zealand honeyeater that produces a large number of highly variable and complex songs (Hill et al., 2013). Tūī are common in both urban and rural forest fragments and exhibit high site fidelity during the breeding season. Tūī are therefore a good model for investigating the effect of anthropogenic noise on song repertoire and song rate. Earlier studies have demonstrated a complex song repertoire with a high degree of individual variation for this species (Bergquist, 1989; Hill, 2011). Tūī song repertoire was found to vary between two geographically distant sites, with the larger mainland population showing a larger song repertoire and syllable diversity then the smaller geographically isolated island population (Hill et al., 2013). Repertoire size is a product of male competition for resources and tūī social systems favour large repertoires and song matching ability (Bergquist, 1989). Tūī song performance and repertoire play an important role in the acquisition of mates and territory during the breeding season when breeding pairs are restricted to a small foraging area and to defending resources close to their nest (Bergquist, 1989). Song matching with neighbours can result in clear boundaries of territories of tūī groups with different dialect areas (Bergquist and Craig, 1988).

Tūī have breeding populations in both rural and urban areas and are considered to have successfully adapted to urban habitats, although studies have found that tūī require reasonably sized forest patches and predator control of breeding areas in order successfully reproduce in cities year round (Innes et al., 2005). Tūī show similarities to other successful urban species such as blackbirds that have high densities in cities and have been shown to adapt song frequency and inter-song intervals in the presence of urban noise (Nemeth and Brumm, 2009).

4.1.3 Research Aims and Predictions

Understanding the factors that enable certain native species to sustain populations in urban habitats while excluding others is important in identifying the factors that promote and protect biodiversity in cities (Stracey and Robinson, 2012). There are few studies investigating the differences in levels of urban noise within the heterogeneous urban environment and how these affect certain aspects of birdsong. Further studies are required to understand how anthropogenic noise affects song aspects such as repertoire and singing rate of song birds. The aims of this study are to 1) document the variation in repertoire size and temporal song parameters across urban sites that vary in anthropogenic noise characteristics, and 2) to test the hypothesis that tūī can alter these characteristics of their song in response to different levels of anthropogenic noise.

I predict that there will be:

1) a higher syllable diversity (number of syllables per individual) and a higher total number of syllables per individual at the two non-motorway sites (n = 6) compared to the two motorway sites (n = 6), due to the masking effect of motorway noise.

2) a greater amount of individual variation in syllable repertoire at non-motorway sites than at motorway sites.

3) less individual-specific syllables at the motorway sites compared to the non-motorway sites, due to differences in acoustic environments. The presence of these syllables are also an indicator of repertoire size and individual variation within sites.

The information obtained from this study will advance our knowledge on behavioural responses of birds to urbanisation and help in the conservation of wildlife habitats.

4.2 Methods

4.2.1 Study Sites

I used two urban areas for this study, Central Auckland (U^1) and North Shore (U^2) Auckland. Each study area included two paired sites; a noisy urban habitat (near motorway) and a less noisy habitat (distant from motorway), separated by approximately 2.5 km. This study compared song characteristics between two groups; 1) noisy sites (Auckland Domain of U^1 and Smiths Bush of U^2) and 2) two less noisy sites (distant from the motorway) (Waitaramoa Reserve of U^1 and Le Roys Bush of U^2). For site details, refer to Chapter 2, p 2323 and for recording methods, refer to Chapter 2, p 36.

4.2.2 Data Collection

Syllables were extracted from the six longest songs of three randomly chosen individuals from each site. Saturation curves were plotted to analyse the rate of syllable acquisition for individuals. The number of syllables used by individuals was used for comparison of syllable repertoire (syllable diversity and total syllables measurements) between individuals and sites. Only long range broadcast songs were used (Hill et al., 2013).

Details of vegetation survey methods are given in Chapter 2, p 35. Details of bird survey methods are given in Chapter 2, p 35.

4.2.3 Syllable Extraction

A syllable was defined as a continuous trace on the sound spectrogram or a group of continuous traces separated from other sounds by more than 50 ms of silence (Briefer et al., 2008). Syllables were extracted from long-range tūī songs in Raven Pro 1.5 using the drawing tool to select the syllable, and extract parameters for analyses (Figure 4.1). The waveform view (showing amplitude of the signal) was used to determine the start and end points of a syllable. The selection spectrum view shows the average spectrum of a selected portion of the signal and was used to determine the minimum and maximum frequency of the syllable. For each spectrogram, the spectrogram window size was set to 733 units and brightness and contrast settings were adjusted to get the highest resolution image of each song or syllable. The following song spectral variables were extracted; minimum frequency, maximum frequency, bandwidth, aggregate entropy and syllable duration. Each new different syllable identified was given a unique ID code. Images of all extracted individual-specific syllables were linked to wav audio files to create a syllable key in Powerpoint (Appendix A). This key was used for comparison of existing syllables with each new syllable extracted from further songs. Any new (unique) syllables identified were added to the key. The Raven correlation tool was used to check the consistency of the methods of syllable identification. The correlations were performed by calculating a correlation value between the two spectrograms being compared at different time offsets to provide a measure of similarity between the two images (Charif et al., 2008).

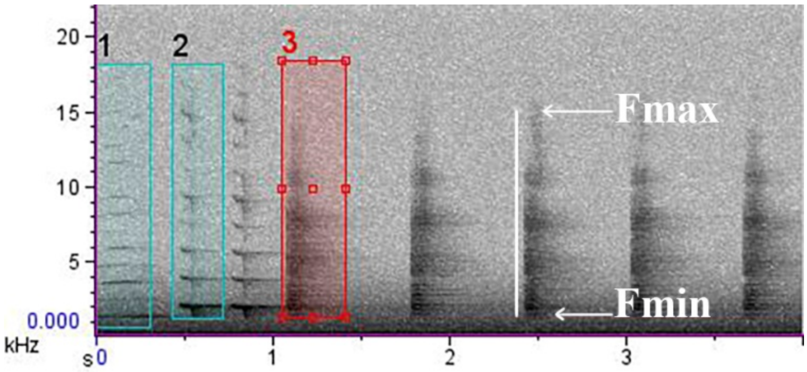


Figure 4.1: Spectrogram showing three individual-specific syllables, with the syllable number labelled at the top of each selection box. The drawing tool is used to capture the parameters such as maximum and minimum frequency (F_{min} and F_{max}).

For pitched syllables, the peak frequency of the fundamental was extracted to give the frequency (Hz) of the syllable. Syllables with a similar visual harmonic structure, but dissimilar sound were considered different syllables, and those syllables with a similar sound but dissimilar visual structure were also regarded as different syllables.

4.3 Parameters

4.3.1 Repertoire Size and Syllable Diversity

Syllable repertoire size for each individual was estimated as the total number of different syllables found within the sample (Buchanan and Catchpole, 1997). Saturation curves were plotted measuring the number of new syllables against the total number of syllables analysed to estimate the syllable repertoire for each individual. Syllable diversity was measured as the number of different syllables per song. Due to the large number of syllables encountered in each song and time constraints, the number of syllables could only be obtained from the six longest songs from three individuals at each site. Saturation curves were plotted in order to estimate the syllable repertoire of individuals and populations.

4.3.2 Individual-Specific Syllables

The number of individual-specific syllables, defined as syllables sung by one individual only, was measured for each individual and compared between motorway and non-motorway sites.

4.3.3 Song Output

For this study a song was defined as a sequence of syllables preceded and followed by a period of three seconds or more (Hill, 2011). A new song was defined as a sequence of syllables unseen in any previous songs recorded. Two aspects of song output were measured; song rate defined as the number of songs produced over unit time (15 minutes) and singing rate defined as the proportion of time spent singing over unit time of 15 minutes.

4.4 Statistical Analysis

Mann-Whitney U tests were used to compare song variables between the two groups; motorway and non-motorway sites as the data were non-normally distributed due to the small sample size. All statistical tests were two-tailed and P values <0.05 were considered significant.

4.5 Results

From 72 songs (six songs from three individuals at four sites), a total of 1255 syllables were recorded: 534 from motorway sites and 721 from non-motorway urban sites. Of this total number of syllables, 264 of these were different tūī syllables which were entered into the syllable key (Appendix A).

4.5.1.1 Urban Noise Levels

Motorway sites had a mean background noise level of 58.59±0.68 dB compared with 52.47±0.22 dB at non-motorway sites. Motorway sites had a mean background noise level of 6.12 dB higher than the non-motorway sites. (Refer to Chapter 3, p52)

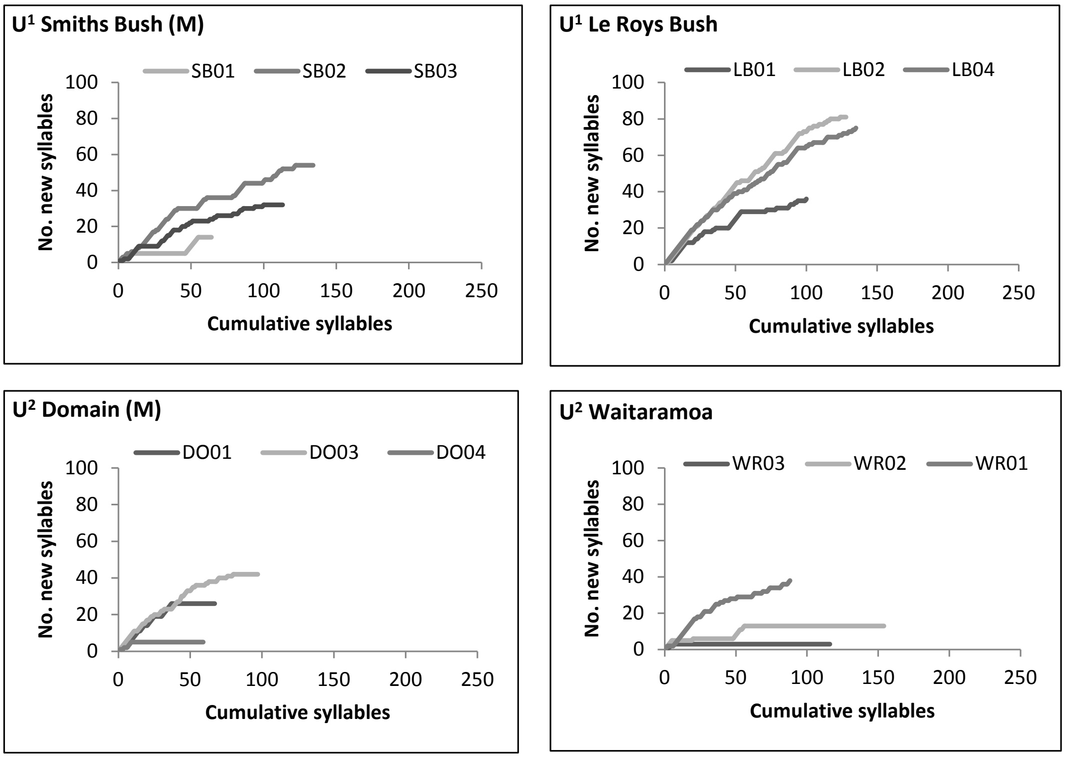
4.5.1.2 Habitat Surveys

There was no significant difference found in vegetation density and maturity between the motorway and non-motorway sites. (Refer to chapter 3, p54)

There was also little difference in bird detection probabilities and species diversity between the motorway and non-motorway sites (Refer to chapter 3, p54).

4.5.1.3 Syllable Accumulation Curves

From the six songs from three individuals at each site, there was a range of cumulative syllables from 97 to 134 of which 5 to 54 were new syllables that were not repeated syllables at the motorway sites (Figure 4.2). At the non-motorway sites, the number of cumulative syllables ranged from 135 to 154 from which 3 to 75 were new, non-repeated syllables (Figure 4.2). For some individuals, new syllables were encountered at a progressively slower rate as the total number of syllables extracted increased (Figure 4.2) whereas for other individuals, there was a levelling off, suggesting the use of repeated syllables, before the rate of accumulation would rise again. However new syllables and thus repertoire size were still increasing even after analysing over 150 syllables for many individuals. The number of accumulative new syllables started to reach a plateau with a smaller number of total syllables in the Central Auckland (U^1) sites than in the North Shore (U^2) sites when plotted against both accumulative total syllables (Figure 4.2) and six songs (Figure 4.3).



M = Motorway site

Figure 4.2: Saturation curves of cumulative new syllables from the total number of syllables from individuals at motorway (Smiths Bush and Domain) and non-motorway (Le Roys Bush and Waitaramoa Reserve) sites.

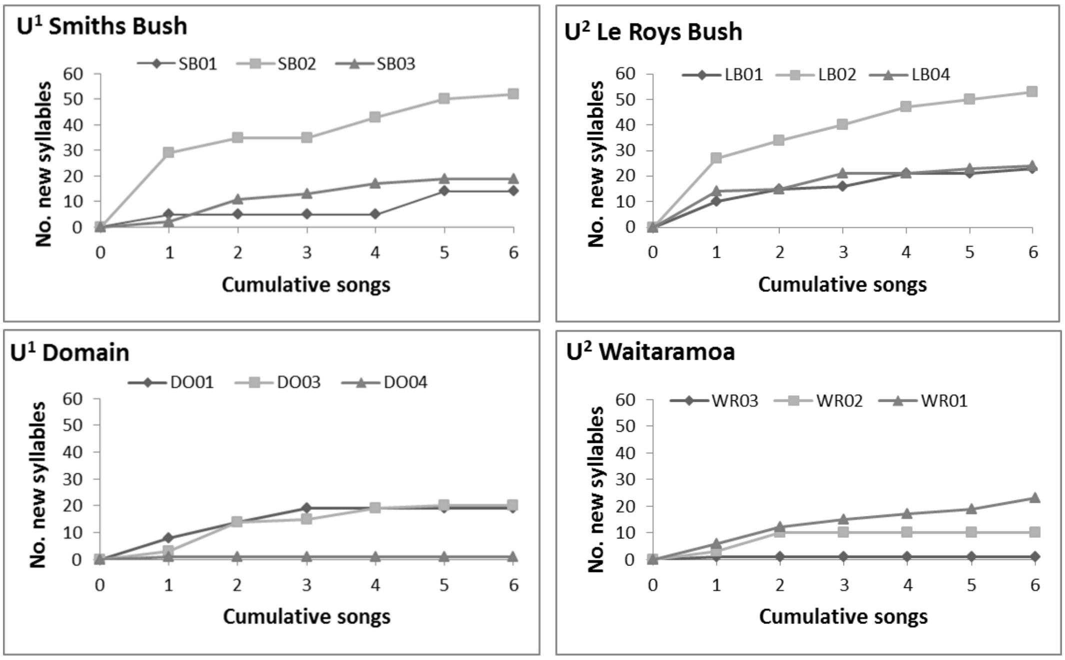


Figure 4.3: Saturation curves of cumulative syllables found within six songs from individuals at motorway and non-motorway sites.

4.5.2 Repertoire Size and Syllable Diversity

There was a significantly greater number of total syllables per song at non-motorway sites U = 320, p = 0.00 (Table 4.1, Table 4.2, Figure 4.4). The same trend was also found of a higher number of total syllables per individual at non- motorway sites than at motorway sites, although it did not reach statistical significance (n = 6, n = 6, U = 7, p = 0.09) (Table 4.1, Table 4.2).

There was also a trend of a higher number of different syllables per song in the non-motorway sites, although it did not reach statistical significance (U = 480, p = 0.06) (Table 4.1, Table 4.2, Figure 4.4). No difference in the number of different syllables per individual was detected between motorway and non-motorway sites (U = 15, p = 0.63) (Table 4.1).

Individual variation was found in syllable diversity per individual with the standard deviation at urban sites of 18 and at non-motorway sites of 31.7, indicating that variation in syllable diversity between individuals is greater at non-motorway sites than at motorway sites.

Table 4.1: Summary of statistical analysis on syllable diversity and total number of syllables for songs and for individuals between motorway and non-motorway sites (significant values in bold)

Parameter	**n**	**Median (Range)**		**Mann-Whitney U Test**	
		Motorway	**Non-motorway**	**U**	**p**
Different syllables per song	36	5.5 (2-30)	12.5 (3-39)	480	0.06
Total syllables per song	36	11 (8-54)	18 (11-45)	320	**0.00**
Different syllables per individual	6	29 (5-54)	37.5 (3-79)	15	0.63
Total syllables per individual	6	82 (59-134)	122 (88-154)	7	0.08

Table 4.2: Total number of syllables and number of different syllables of tūī songs at Central Auckland (U^1) and North Shore (U^2) sites.

Study Area	**Site**	**Tūī ID**	**Different syllables /individual**	**Total # syllables /individual**	**Median(range) different syllables/song**	**Median (range) total syllables/song**
North Shore	Smiths Bush *	SB01	14	64	5 (4-11)	10.5 (9-13)
		SB02	54	134	10.5 (3-30)	15 (12-54)
		SB03	32	113	13 (2-17)	19.5 (8-25)
		Total	85	311	9 (2-30)	14 (8-54)
	Le Roys Bush	LB01	36	100	13 (10-17)	17.5 (12-20)
		LB02	81	128	15 (13-39)	17 (14-45)
		LB04	75	135	18.5 (11-36)	19.5 (12-45)
		Total	130	223	15 (10-39)	18 (12-45)
Central city	Domain *	DO01	26	67	5.5 (3-14)	9 (9-18)
		DO03	42	97	11 (4-25)	13.5 (10-28)
		DO04	5	59	5 (4-5)	10 (9-10)
		Total	54	363	5 (3-25)	10 (9-28)
	Waitaramoa Reserve	WR01	38	88	11.5 (10-16)	14.5 (11-20)
		WR02	13	154	5.5 (5-13)	22.5 (12-42)
		WR03	3	116	3 (3-3)	19.5 (16-24)
		Total	47	358	5.5 (3-16)	18.5 (11-42)

*** = near motorway sites**

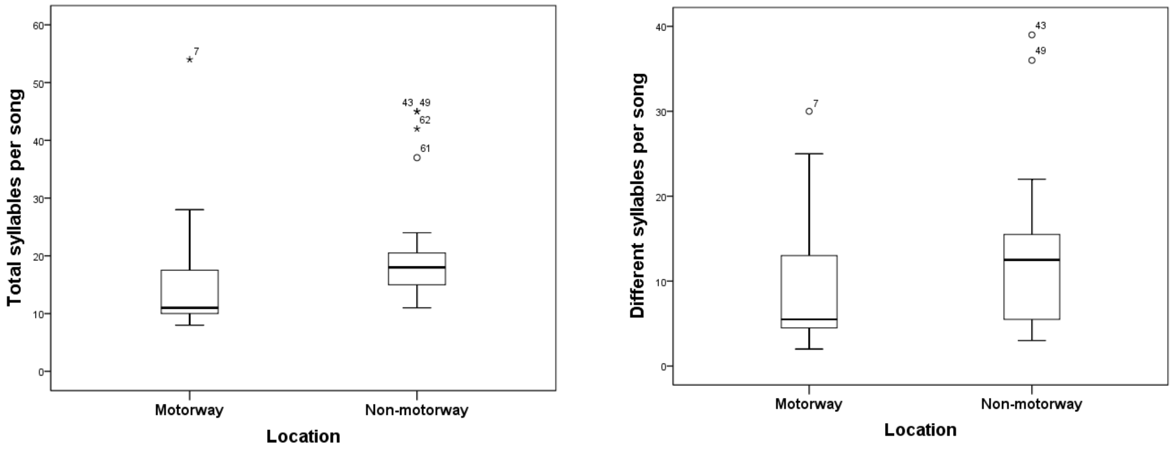


Figure 4.4: Number of total syllables per song, and different syllables per song at motorway and non-motorway sites.

4.5.3 Individual-specific Syllables

There were a total of 55 individual-specific syllables found in the motorway populations and 77 in the non-motorway populations. There was no significant difference found in the number of individual-specific syllables per individual between motorway and non-motorway sites (U = 13.5, p = 0.47) (Table 4.3).

Table 4.3: Median number of individual-specific syllables per individual at motorway and non-motorway sites.

Individual-specific syllables per individual	Median (range:min-max)
Motorway	5.5 (1-23)
Non-motorway	13 (0-21)

4.5.4 Song Output

There was no significant difference in song rate between the motorway and non-motorway sites (n = 9, n = 9, U = 31, p = 0.40). However there was a trend showing a higher song rate at motorway sites than at non-motorway sites (Figure 4.5). There was also no significant difference in singing rate between the motorway sites and non-motorway sites (n = 9, n = 9, U = 34, p = 0.61) (Figure 4.5).

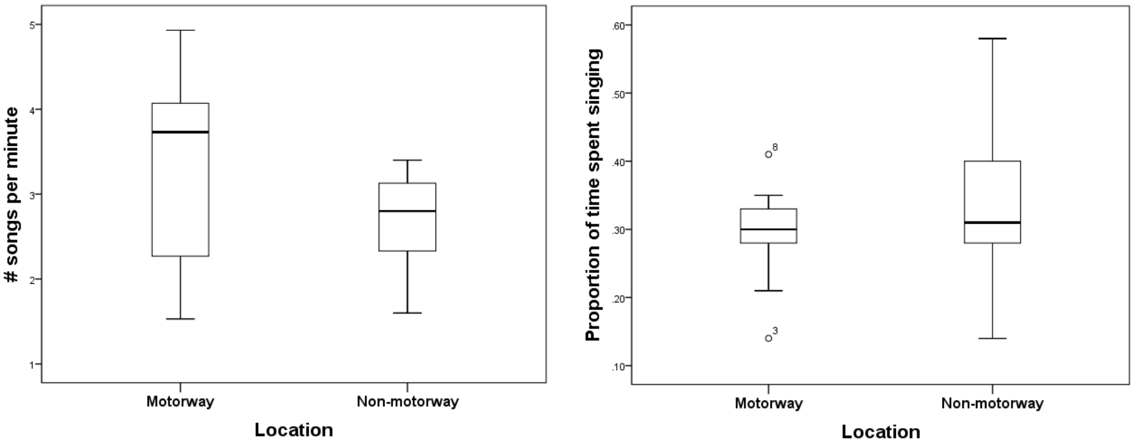


Figure 4.5: Boxplots showing song rate (number of songs per minute) and singing rate (amount of time spent singing) at motorway and non-motorway sites.

4.6 Discussion

4.6.1 Repertoire

There was a significantly higher number of total syllables at the non-motorway sites compared to the motorway sites. There was also a trend of a higher number of different syllables at the non-motorway sites although these results were not significant. These differences could be as a result of tūī at motorway sites using a reduced pool of syllables that transmit more effectively in noisy acoustic environments. A previous study found that male great tits switched to song types with a higher minimum frequency when exposed to low-frequency noise (Halfwerk and Slabbekoorn, 2009). Another study found that red-winged blackbirds used syllable types with a narrow frequency range when exposed to noise (Pohl et al., 2009) and great tits responded more easily to these narrow bandwidth signals in the presence of noise (Hanna et al., 2011). The reduction in syllable diversity and total syllables at motorway sites could also reflect a reduction in the use of rapid, high frequency trill syllables. My data taken from a larger dataset found a significantly lower proportion of trill in tūī songs from the motorway sites compared with non-motorway sites (Chapter 3, Table 3.6).

The degree of syllable diversity showed a difference between locations, with a higher diversity in the North Shore sites than at the Central Auckland sites. No significant difference in syllable diversity was found between the motorway and non-motorway sites. The paired central Auckland sites both contained smaller sized forest fragments with more open habitat, and were surrounded by busy roads. In contrast, the suburban North Shore paired sites contained more enclosed and larger forest areas, surrounded by suburban gardens. This heterogeneity of habitats and noise levels within the urban environment could also account for a smaller population of tūī breeding pairs at the central sites, and have potential effects on repertoire size (Valderrama, 2012).

4.6.2 Individual Variation in Syllable Repertoire Size

Plotting of the accumulative new syllables for the songs analysed showed great variation between individuals in the number of syllables used to reach saturation. For some individuals, the number of accumulative new syllables did not reach a plateau, indicating that the full repertoire had not been reached, and therefore I could not discuss the total syllable diversity at each site. A previous study found that an asymptote was not obtained from 30 accumulative new songs for tūī males and thus song repertoire size could not be determined (Hill, 2011). There was also a greater similarity in patterns of syllable acquisition between geographically paired sites than between motorway and non-motorway sites. This pattern could reflect the broad ecological differences in habitat and forest remnant size, conspecific density, and degree of urbanisation and isolation from resources between the central (U^1) sites and the North Shore (U^2) urban sites. These results suggest that a variety of factors, including anthropogenic noise, could influence changes in urban bird populations.

Some individuals at the noisier motorway sites had a simple repertoire of as few as five different syllables and had limited variation in the sequence of these syllables. This could be due to the effects of motorway noise inhibiting the transmission of more diverse songs. Alternative explanations for differences in repertoire size between populations include a positive correlation found between population size, repertoire size and song diversity (Valderrama, 2012). A previous study found that in larger populations of kōkako (*Callaeas wilsoni*), increased song sharing and other vocal interactions were necessary to maintain territories and pair bonds, resulting in increased song similarity and larger repertoire size (Valderrama, 2012).

4.6.3 Individual-Specific Syllables

There was a trend that tūī at motorway sites sang less individual-specific syllables than those at non-motorway sites, which combined with the syllable diversity trends suggest a larger repertoire size at the quieter non-motorway sites. Individuals at motorway sites may select a small number of simple, more easily transmittable syllables from their repertoire to avoid masking from traffic noise.

4.6.4 Song Rate and Singing Rate

There was a trend showing a higher song rate at the motorway sites compared with non-motorway sites, although this result was not significant. This result is consistent with a previous study that found that song rates of urban great tits were faster than those in rural forests, however these findings were attributed to more open city habitats (Slabbekoorn and den Boer-Visser, 2006). Another study found that northern cardinals (*Cardinalis cardinalis*) sang longer songs at faster rates in urban areas, however these differences were attributed to conspecific densities to a greater degree than from the effects of urban noise (Narango, 2012). There was no significant difference found in the singing rate, measured as the amount of singing over unit time, between motorway and non-motorway sites. However this result may have been the effect of the small sample size. Results from Chapter 3 (Table 3.8) using a larger dataset found that tūī songs showed significantly longer song duration at non-motorway sites compared with motorway sites. This result confirms findings from a previous study showing shorter song durations in areas with high levels of noise in great tits (Halfwerk and Slabbekoorn, 2009). Blackbirds sang shorter simpler songs in urban areas although differences were attributed to a higher bird density in the urban areas and associated increased territorial interactions between conspecifics (Nemeth and Brumm, 2009). A previous study on tūī song also found that song duration was linked to a larger population size where there could be more intraspecific competition leading to longer songs (Hill, 2011). Further study with a larger sample size and comparing sites with different noise levels but the same tūī population size is needed to separate out the influence of these factors on song duration.

As predicted, trends showed higher syllable diversity, more individual-specific syllables and a higher number of total syllables per song at non-motorway sites. However due to the small sample size in this study, the effects of noise on these differences cannot be fully separated out from other factors such as habitat size and fragmentation and population size. The great versatility in tūī song repertoire, the ability to mimic other species and song match within populations has likely assisted tūī in adapting their songs in the presence of urban noise and may contribute to their ability to breed successfully in urban environments. Further studies using a larger sample size are recommended to provide more compelling evidence of the effects of motorway noise on song in urban areas.

CHAPTER 5

Urban Effects on Tūī Syllable Repertoire and Dialect

Plate 5: Tūī in Urban Garden (photograph by Felicity Moore)

5.1 Introduction

Urbanisation has significantly modified natural habitat and biodiversity globally. Habitat loss and degradation, increases in invasive plants and predators, reduction of food and nesting resources and increased anthropogenic noise are some of the factors driving avian biodiversity declines in urban areas (MacLeod et al., 2012). Habitat fragmentation and decreased habitat connectivity can lead to restricted avian dispersal from natal areas and increased isolation of populations (Chan and Blumstein, 2011; Magle et al., 2012). These effects have not only resulted in the decline of wildlife populations but may also have an impact on animal behaviour such as vocal communication. Many aspects of songs in songbirds, such as repertoire and song output are known to be sexually selected traits which are important indicators for their fitness. These aspects may be affected by anthropogenic effects in urban ecosystems. Urban fragmentation and fluctuating levels of urban noise may also have an effect on the local variations (dialects) in songs and singing behaviour of song birds. Studies on these aspects will advance our knowledge on urban effects on animal behaviour and behavioural adaptations of song birds to urban ecosystems.

5.1.1 Song Parameters

5.1.1.1 Song and Syllable Repertoire

Repertoire size can be assessed as the number of different vocal elements that a bird can produce and is a sexually selected trait used by females to assess the quality of males (Briefer et al., 2010). Repertoire can be measured at two levels, song repertoire (the number of different songs produced) or syllable repertoire (the number of different syllables produced) (Catchpole and Slater, 2008). A larger repertoire size in great tits (*Parus major*) was found to correlate with higher reproductive success, survival and territory habitat quality (McGregor et al., 1981). A larger repertoire size in the male great reed warbler (*Acrocephalus arundinaceus*) was positively correlated with harem size and reproductive success (Hasselquist, 1998). The repertoire size of male red-winged blackbirds (*Agelaius phoeniceus*) was found to correlate with reproductive success, and males with larger repertoires gained an advantage in competition for territories (Yasukawa, 1981). Although song repertoire is a typical measure of song variation for many species, it cannot be easily measured for birds with complex songs (Petruskova et al., 2010). Therefore many studies focus on the variation at the syllable level (Tracy and Baker, 1999). Male sedge warblers (*Acrocephalus schoenobaenus*) with larger syllable repertoires were found to obtain mates at an earlier date in the breeding season (Buchanan and Catchpole, 1997).

5.1.1.2 Song Rate and Singing Rate

Song rate is the number of songs produced in a defined time period and has been shown to be an important cue in male competition and female choice (Garamszegi and Møller, 2004; Marler and Slabbekoorn, 2004). Song rate is thought to reflect the amount of energy an individual can devote to singing, and indicates the health of the individual (Hamilton and Zuk, 1982). These energy reserves are a reflection of an individual’s neuromuscular capacities, performance abilities, body condition and ability to gain resources (van Hout et al., 2012). Village indigobirds (*Vidua chalybeata*) with higher song rates were found to have increased reproductive success. Female pied flycatchers (*Ficedula hypoleuca*) selected males that had the highest song rates and had acquired superior territories (Gottlander, 1987). The song rate of male pied flycatchers was also correlated with food availability and temperature, suggesting that males with more time and energy were able to sing at a higher rate (Marler and Slabbekoorn, 2004). Individual song rate is correlated with the date of pairing in pied flycatchers (Alatalo et al., 1990). To increase song rate, an individual can reduce the length of single songs or reduce pauses between songs (Kunc et al., 2005). Therefore singing rate, the time spent singing during a defined time period is another temporal variable that was used to measure the amount of energy a bird invests in singing.

5.1.1.3 Individual-Specific Syllables

Individual-specific syllables and phrases are sung by one individual only and may be important cues used for individual recognition of mates or neighbours. There is evidence that birds can recognise the songs of individuals in both neighbour-stranger and intersexual interactions (Petruskova et al., 2010). A small number of individual specific syllables and phrases were found to permit individual recognition in a population of song sparrows (*Melospiza melodia*) (Nordby et al., 2007). These distinctive elements were thought to arise from copy errors during the song learning process (Nordby et al., 2007). The presence and number of individual-specific syllables in a population could signify the amount of individual variation there is within that population and this could vary from population to population.

5.1.1.4 Song Variation and Dialect

Dialects of bird song, significant variations in songs, are found in populations separated by geographical distance or other barriers (Kroodsma, 2004; Marler and Tamura, 1964; Mundinger, 1982). A recent study found a higher level of song diversity in a mainland population of tūī compared with a remote Chatham Island population (Hill, 2011). Geographical isolation of the island population was suggested as an explanation for these differences (Hill, 2011). However, dialects also occur in populations across smaller spatial scales and a dialect shared by a small group of neighbours is an example of microgeographic variation (Briefer et al., 2008; Mundinger, 1982). Dialects have been reported in skylarks (*Alauda arvensis*) across a heterogeneous habitat where territories are contained in patches spaced a few kilometres apart (Briefer et al., 2011). Within a given patch, all neighbouring males shared particular syllable sequences whereas males occupying different patches had very few sequences in common (Briefer et al., 2011). Such microgeographic song dialect has also been described in tūī populations approximately 500 m apart (Hill and Ji, 2013). Cultural transmission during song learning can both favour and constrain song divergence resulting in the complex variation that occurs within and between individuals, as well as between populations (Baker and Cunningham, 1985 ; Podos et al., 2004). Cultural transmission occurs when juvenile males learn songs or syllables from other individuals within a population and can lead to population-specific repertoires or dialects (Nelson et al., 2004; Potvin and Parris, 2012). Cultural mutations of song elements can be introduced through copy error or improvisation, leading to the introduction of new elements into a population (Podos and Warren, 2007). Transmission of song patterns across generations of male white-crowned sparrows (*Zonotrichia leucophrys*) was shown to facilitate dialect formation in laboratory studies (Marler and Tamura, 1964).

There are several hypotheses to explain the evolution of dialects. The local adaptation hypothesis predicts that females gain fitness advantages by mating with males from their natal territory because their offspring will express adaptations to local ecological conditions (Marler and Tamura, 1962). Female yellowhammers (*Emberiza citronella*) responded more often and vigorously to local than to foreign songs (Baker et al., 1987). The social adaptation hypothesis also proposes that males will gain fitness advantages by learning similar songs to those of males in their area, and that males who sing different songs may not achieve mating success (Podos and Warren, 2007). This hypothesis predicts that accurate mimics elicit less aggressive responses from dominant males, and that territorial males would be more aggressive towards males with different dialects than to those singing their local dialect (Podos and Warren, 2007). Male village indigobirds were found to mimic songs of more dominant male neighbours in order to attract female birds (Payne et al., 2000). This hypothesis ties in with the 'dear enemy' effect whereby territorial males use reduced aggression towards neighbours from their own dialect area than strangers from another dialect area (Briefer et al., 2011). It was found that when dispersing birds settle in new locations, birds sing the local dialects to attract mates rather than the songs from their natal areas, further supporting the local adaptation hypothesis.

In birds that acquire songs through imitations of conspecifics, song sharing is a consequence of this strategy (Beecher and Brenowitz, 2005). Song sharing has been shown to correlate with breeding success and territory tenure and may be used to discriminate between neighbours and strangers (Briefer et al., 2011) Studies of variation in bird song often focus on differences in songs or song types. However these are not easily differentiated in species with complex songs. Studies on differences in repertoires can also compare the distribution of the basic unit that songs are composed of, such as syllables (Petruskova et al., 2010). Only a small number of studies have focussed on syllable sharing within and between populations in order to reveal geographic variation in birds (Petruskova et al., 2010). Syllable sharing between individuals within populations provided evidence for geographical variation in the composition of repertoires of the serin (*Serinus serinus*) (Mota and Cardoso, 2001). A previous study found that some syllables and phrases (sequences of syllables) of skylarks were shared with all individuals within a population at a given location, and that these syllables were not shared by populations in other locations (Briefer et al., 2008; Briefer et al., 2009). These shared phrases formed a group signature that was used to discriminate between neighbours and strangers (Briefer et al., 2009).

5.1.2 Urban habitat effects on song characteristics

Variation in songs between urban and non-urban environments have been attributed to a combination of factors including 1) habitat structure and openness, 2) population density and 3) differences in the acoustic properties of habitats, including anthropogenic noise (Mockford and Marshall, 2009).

According to the acoustic adaptation hypothesis (AAH), birds adjust their acoustic signals according to their environment in order to increase signal transmission (Morton, 1975). Populations of the same species occupying a range of habitats are predicted to adapt their vocalisations to optimise signal transmission to each particular habitat type (Potvin et al., 2011), and birds occupying habitats with similar vegetation types or acoustic features will also share common song features (Date and Lemon, 1993). It is therefore predicted that birds occupying urban environments in different cities would share common urban-related song features. However, there is a great deal of heterogeneity within and between urban areas and there is evidence in some avian species that modifications in bird songs occur along an urban gradient from highly modified to rural habitats (Mendes et al., 2011). A previous study showed that blackbirds (*Turdus merula*) raised the maximum and minimum frequencies of songs along an urban gradient that correlated with changes in population parameters and ambient noise (Mendes et al., 2011).

Large song repertoire and song sharing are critical features in mate attraction and territory defence. These aspects can be strongly influenced by changes in the social environment caused by habitat fragmentation (Briefer et al., 2010). In both continuous and fragmented habitats, a stable spacing pattern between territories is necessary to reduce the energetic costs of territorial defence, and song sharing helps maintain this pattern by reducing the amount of aggressive interactions between neighbours (Briefer et al., 2010).

The effect of habitat fragmentation in urban environments could lead to altered densities of individuals competing for limited resources and altered syllable sharing among individuals in urban habitats. A recent study found increased syllable and sequence sharing patterns between skylarks in a fragmented habitat than between populations in a continuous habitat (Briefer et al., 2009). Another study found increased syllable sharing among tree pipit (*Anthus trivialis*) males in a small, isolated population (Petruskova et al., 2010). There are few studies comparing the degree of syllable sharing between urban and non-urban populations and further studies are required to understand the urban effects on these aspects of bird songs.

Signal interference from local ambient noise patterns may affect song variation between otherwise similar habitats (Slabbekoorn and Smith). Modification of song and syllable repertoire in response to urban habitats may include the use of particular syllables that transmit more effectively in urban environments, (Slabbekoorn and den Boer-Visser, 2006). A previous study found that certain song syllables were used more frequently in urban silvereye (*Zosterops lateralis*) populations and that this could reflect selection of these syllables from their repertoire in response to urban noise (Potvin and Parris, 2012). These modifications are thought to be linked to the formation of local dialects and this divergence between urban and non-urban songs could lead to reproductive isolation (Nemeth and Brumm, 2010). This selective use of syllables that transmit more effectively in urban environments could lead to only a portion of a large repertoire acquired during vocal development being retained in adulthood (Wood and Yezerinac, 2006). Song sparrows typically selected songs that matched those of their neighbours after dispersal to new territories, suggesting that habitat characteristics and the acoustic environment may have a role in repertoire selection (Nordby et al., 2001; Patricelli and Blickley, 2006). However the way in which urban noise can affect this song selection process is currently not fully understood.

A previous study found limited evidence for differences in syllable use between urban and rural dark-eyed juncos (*Junco hyemalis*), suggesting that urban populations modify syllables from their local repertoire in response to noise (Cardoso and Atwell, 2011; Potvin and Parris, 2012). A study comparing urban and rural populations of silvereyes found that urban songs were slower and contained fewer syllables per song (Potvin et al., 2011). Urban silvereyes also used a higher percentage of high frequency trills in their songs, contrary to predictions that they would use simpler syllables for increased clarity and transmission in urban areas. Song sparrows in urban areas selected higher frequency songs from their repertoire that were less masked by prevailing noise (Wood and Yezerinac, 2006). Urban blackbirds were found to sing significantly shorter songs with fewer elements and shorter inter-song intervals than rural birds (Nemeth and Brumm, 2009).

Urban areas are rapidly expanding worldwide. It is important to gain understanding of the effects of urbanisation on native bird repertoire and dialect. These are important factors that may influence the ability of a species to survive and reproduce in the urban environment. This study aims to investigate the effects of urbanisation (habitat fragmentation and urban noise) on song repertoire and dialect using tūī as a model.

5.1.3 Tūī Song

Tūī is a honeyeater native to New Zealand. Male tūī produce a large number of highly variable songs with a high degree of individual variation (Bergquist, 1989; Hill, 2011). A previous study found that tūī song repertoire varied between two geographically distant sites, with the larger mainland population showing a larger song repertoire and syllable diversity then the smaller geographically isolated island population (Hill et al., 2013).

Tūī are also known to match songs with neighbours and this can result in clear boundaries of tūī group territories with different dialect areas (Bergquist and Craig, 1988). Song matching between rival males is a crucial aspect of tūī vocalisation for maintaining territory during the breeding season. Tūī associate in large family groups after the breeding season, and this close association during song learning is thought to lead to the emergence of local dialects (Bergquist and Craig, 1988). In urban environments where fragmented habitats are separated by buildings and roads, dialects and song matching within these small fragments have been observed (Bergquist, 1989). Individuals moving from one area to the next may match the dialect of the population area it enters, even for brief foraging excursions (Bergquist, 1989). However, whether urban effects, such as increased degree of habitat fragmentation due to urban structures and elevated noise levels, have an impact on the song characteristics and singing behavior of tūī has not been investigated.

Using tūī as a model, this study aims to 1) investigate variation in tūī repertoire between urban and non-urban sites and 2) to compare the degree of syllable and phrase sharing between individuals and the number of individual-specific syllables and phrases at urban and non-urban sites, in order to detect and compare dialects.

I test the following predictions:

1) Due to higher degree of habitat fragmentation and the nature of the barriers (buildings and roads) between habitats, I expect urban fragments to have reduced numbers of breeding tūī as well as reduced individual movement between habitats during the breeding season. Therefore I predict the diversity of songs represented by syllable repertoire will be lower in urban sites compared to non-urban forest fragments.

2) To ensure the transmission of vocal signals in urban environments with higher levels of urban noise, I predict tūī in urban habitats have a higher song rate (number of songs per unit time) when singing but have longer intervals between singing bouts (singing rate) in compensation than in the non-urban habitats.

3) Due to the higher level of habitat heterogeneity in the urban environment, as well as a higher degree of habitat isolation between forest patches, I predict a higher degree of dissimilarity in tūī songs between sites (dialect) and reduced syllable sharing at the urban sites compared to non-urban sites.

5.2 Methods

5.2.1 Study Sites

To investigate the effects of fragmentation and urban noise on tūī songs within urban areas I selected two paired urban forest fragments, each containing a site close to the motorway and a corresponding quieter site approximately 2-3 km from the motorway site; 1) central Auckland sites (U^1) comprised of Auckland Domain (motorway site) and Waitaramoa Reserve, 2) North Shore sites (U^2) comprised of Smiths Bush (motorway site) and Le Roys Bush Reserve, and 3) a non-urban paired site 50 km north of Auckland; Mahurangi Regional Park and Wenderholm Park. Habitat details for these sites are given in Chapter 2 (p 23).

5.2.2 Habitat surveys

Details of habitat survey methods include vegetation surveys (Chapter 2, p 35), bird surveys (Chapter 2, p 35), and sound level quantification (Chapter 3, p 49).

5.2.3 Tūī Song Recording

Details of song recording methods are given in Chapter 2 (p 36).

5.2.4 Song Variables

Variables of songs include repertoire size, syllable diversity, individual-specific syllables, song rate and singing rate. Refer to Chapter 4 Methods (p 80).

5.2.4.1 Syllable and phrase extraction and categorisation

Syllables were extracted from the six longest songs from three individuals from each site. The syllable dataset and syllable key have been used to identify syllables. Refer to Chapter 4 Methods (p 78).

The following categories were used to distinguish tūī syllable types:

1) Harmonic syllables; 2) rapid multiple note repetition (RMNR); 3) harsh, broadband syllables; 4) rapid frequency modulation or trill syllables; 5) high frequency syllables (with a fundamental frequency of 5 kHz or above) and 6) low-frequency syllables (below 2 kHz) as defined by Hill and Ji (2014).

Phrases were defined as a combination of three or more syllables that followed a sequential pattern (Molles et al., 2006). Shared phrases were identified from each site and the number of individuals singing that phrase was recorded.

5.2.5 Statistical Analysis

Mann-Whitney U tests were used to compare song variables between paired sites within the urban environment (n = 6, n = 6). If there was no significant difference, these urban data were pooled for testing against the non-urban control sites.

Mann-Whitney U tests were used to compare song variables between individuals from the two groups; urban (n = 12) and non-urban (n = 6) paired sites as the data were non-normally distributed. All statistical tests were two-tailed and p values <0.05 were considered significant.

A Hierarchical Cluster Analysis (Ward, 1963) using syllable sequences of songs was conducted to visualise similarity of songs among populations in urban and non-urban sites. For this analysis, 72 songs were recorded from three individuals at each site from six sites with a total of 279 individual-specific syllables. Ward's minimum-variance method adds up the distance between two clusters in the ANOVA sum of squares between the two clusters over all the variables. At each generation, the within-cluster sum of squares is minimized over all partitions obtainable by merging two clusters from the previous generation (Milligan, 1980). The sums of squares are divided by the total sum of squares to give proportions of variance (squared semi-partial correlations).

Due to the small sample size of phrases extracted from urban and non-urban sites, no further statistical analyses were conducted.

5.3 Results

5.3.1 Habitat Surveys

There was a significantly higher distance from the centre of the quarter to the nearest tree in non-urban areas than in the urban areas (U = 88891, p = 0.02). However there was no significant difference in DBH (forest maturity) between urban and non-urban sites (U = 18198, p = 0.61) (Table 5.1).

There was also a significant difference in tree density and in forest maturity between the two paired urban sites U^1 central and U^2 North Shore sites (Table 5.1b). The higher tree density at the North Shore sites reflects the closed canopy of regenerating native forest compared to the central sites that had larger areas of parkland. The higher maturity measure in the central Auckland sites is likely due to the presence of mature planted pōhutukawa (*Metrosideros excelsa*) trees in the recording area. There was no significant difference in tree density (U = 7252, p = 0.112), or in DBH (U = 1293.5, p = 0.248) between Wenderholm Park and Mahurangi Park non-urban sites.

Table 5.1: Comparison of mean distance from the sampling point to the nearest tree from the PCQ survey and mean DBH of trees >5m height and >2.5 DBH between a) urban and non-urban sites and b) within urban Central city (U^1) and North Shore (U^2) sites (significant values in bold).

a)

	Urban Median (min,max)	Non-urban Median (min,max)	p value of Mann-Whitney U test
Distance (m)	4.4 (0.2, 20)	5.0 (0.8,1.9)	p = **0.02**
DBH (cm)	20.1 (0, 324)	21 (4.1,148.1)	p = 0.61

b)

	Central city (U^1) Median (min,max)	NorthShore (U^1) Median (min,max)	p value of Mann-Whitney U test
Distance (m)	7.4 (0.6, 20)	2.6 (0.2,10)	p = **0.00**
DBH (cm)	25.9 (0,280)	11.5 (0,97.1)	p = **0.00**

The non-urban sites had higher detection probabilities for native species such as grey warbler (*Gerygone igata*), fantail (*Rhipidura fuliginosa*), kingfisher (*Todiramphus sanctus*), kereru (*Hemiphaga novaeseelandiae*) and pukeko (*Porphyrio melanotus*) whereas the urban sites had higher detection probabilities for introduced species such as chaffinch (*Fringilla coelebs*), eastern rosella (*Platycercus eximius*), and greenfinch (*Carduelis chloris*) (Table 5.2). Both urban and non-urban sites had equal detection probabilities for tūī and silvereyes.

There was a 1.83 dB higher average sound pressure level reading at the urban sites (55.53±0.22 dB) compared with the averaged non-urban sites (53.70±0.21 dB).

Table 5.2: Detection probabilities of bird species recorded at the four urban (U_1 and U^2) sites and two non-urban sites.

Species	Scientific name	Urban (U^1&U^2) (%)	Non-Urban (%)
Tūī	*Prosthemadera novaeseelandiae*	100	100
Silvereye	*Zosterops lateralis*	100	100
Blackbird	*Turdus merula*	75	50
Eastern rosella	*Platycercus eximius*	37.5	25
Chaffinch	*Fringilla coelebs*	37.5	25
Grey warbler	*Gerygone igata*	25	75
Sparrow	*Passer domesticus*	37.5	25
Myna	*Acridotheres tristis*	37.5	50
Song thrush	*Turdus philomelos*	12.5	0
Fantail	*Rhipidura fuliginosa*	37.5	50
Shining cuckoo	*Chrysococcyx lucidus*	25	0
Kingfisher	*Todiramphus sanctus*	37.5	50
Kereru	*Hemiphaga novaeseelandiae*	25	75
Black-backed gull	*Larus dominicanus*	12.5	25
Greenfinch	*Carduelis chloris*	12.5	0
Spotted dove	*Streptopelia chinensis*	12.5	0
Starling	*Sturnus vulgaris*	0	0
Pukeko	*Porphyrio melanotus*	12.5	25

There was no significant difference in song variables- syllable diversity, total number of syllables, song rate and singing rate or number of individual-specific syllables - between the paired urban sites, U^1 central and U^2 North Shore (Table 5.3). These data were then pooled for testing between urban and non-urban sites.

Table 5.3: Mann-Whitney U results for testing selected song parameters between urban paired sites; U^1 (urban central) and U^2 (urban North Shore).

Variable	U	(2 tailed)
Syllable diversity	15	0.63
Total number of syllables	7	0.08
Song rate	14	0.52
Singing rate	9.5	0.17
Individual-specific syllables	10	0.20

5.3.2 Repertoire and syllable diversity

There was a significantly higher degree of syllable diversity (number of different syllables per individual) at non-urban sites compared with urban sites (U = 14, p = 0.04) (Figure 5.1).

There was also a significantly higher number of total syllables per individual in the non-urban sites compared to the urban sites, n = 12 (urban), n = 6 (non-urban), (U = 2, $p \leq 0.001$) (Figure 5.1).

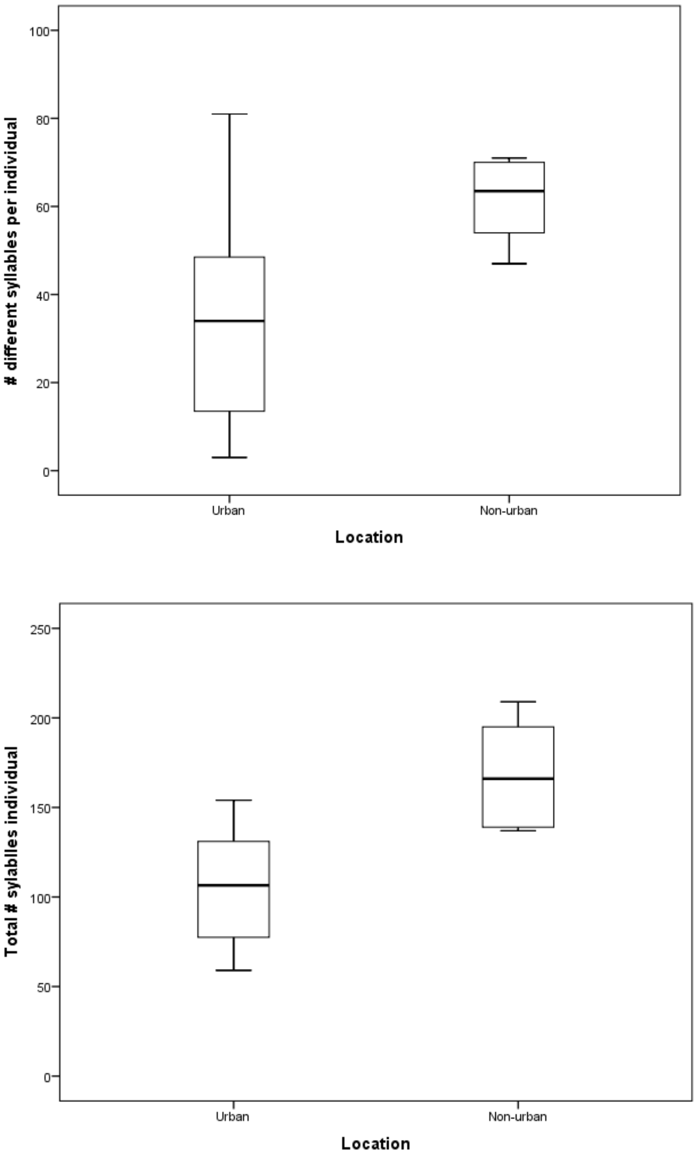


Figure 5.1: Number of different syllables per individual and total number of syllables per individual at urban and non-urban sites.

There was more individual variability in the accumulative new syllables over 6 songs at each of the urban paired sites compared with that of the non-urban sites (Table 5.4 and Figure 5.2). In the U^2 (North Shore sites) there was the largest difference in accumulation of new syllables between individuals (from 5 to 103), followed by the U^1 (central sites) (from 5 to 42) and the smallest difference were recorded at the non-urban sites (from 54 to 70) (Table 5.4 and Figure 5.2). This indicates that the song repertoire size is less variable between individuals at the non-urban sites.

Table 5.4: Cumulative number of new syllables and total different syllables

Site	Cumulative # total syllables (min-max)	Cumulative # new syllables (min-max)
U^1-Central	96-201	5-42
U^2-North	78-271	5-103
Non-urban	137-209	54-70

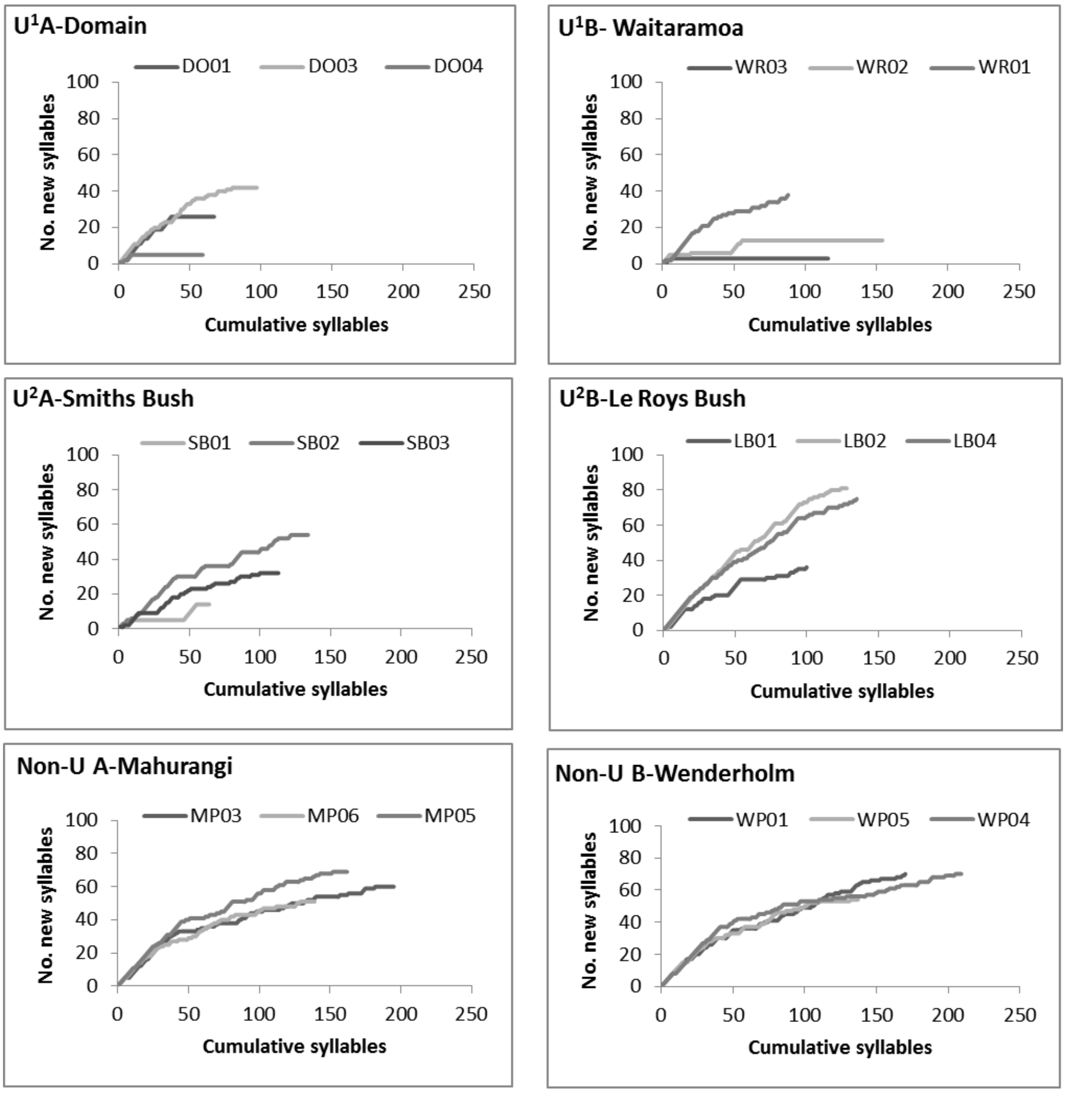


Figure 5.2: Saturation curves of cumulative new syllables versus the total number of syllables from three individuals at paired sites;

U^1; Central Auckland (U^{1}A Domain and U^{1}B Waitaramoa Reserve)
U^2; North Shore, (U^{2}A Smiths Bush and U^{2}B Le Roys Bush)
Non-urban; (Non-U A-Mahurangi Park and Non-U B-Wenderholm Park)

5.3.3 Song rate and singing rate

There was no significant difference in the song rate (number of songs per minute) ($U = 22.5$, $p = 0.21$) and the singing rate (proportion of time singing per minute) ($U = 23$, $p = 0.22$) between urban and non-urban locations (Figure 5.3). However, there was a trend showing more songs per minute in the urban populations. There was also a trend showing a greater amount of singing per unit time in the non-urban populations. This suggests that the non-urban tūī may sing fewer, longer songs than the urban tūī.

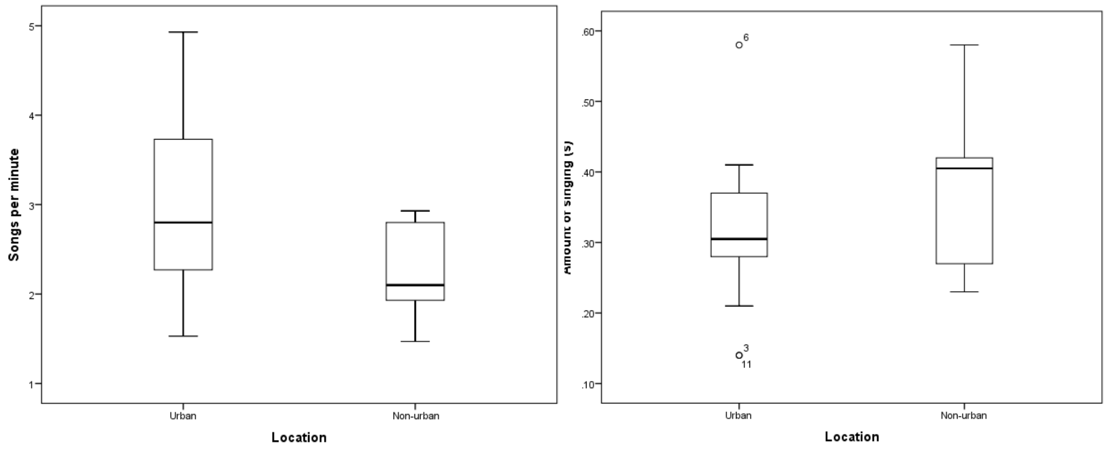


Figure 5.3: Boxplots showing difference in song rate (number of songs per minute and singing rate (amount of singing per minute) between urban and non-urban populations.

5.3.4 Individual-specific syllables

From 430 different syllables recorded from urban and non-urban populations, 246 syllables were unique to one individual (individual-specific syllables). There was a trend showing that individuals had more individual-specific syllables at the non-urban sites compared to urban sites (Figure 5.4, Figure 5.5). However this difference was not statistically significant (U = 16, p = 0.061). There was also a trend showing that the North Shore U^2 sites had a higher number of individual specific syllables than the Central Auckland U^1 sites (Figure 5.5). The number of individual-specific syllables at paired sites was U^1 (urban central) = 53, U^2 (urban north) = 78 and non-urban = 122. There was also a trend of a smaller number of individual-specific syllables at the two motorway sites compared with the two non-motorway sites (Figure 5.5).

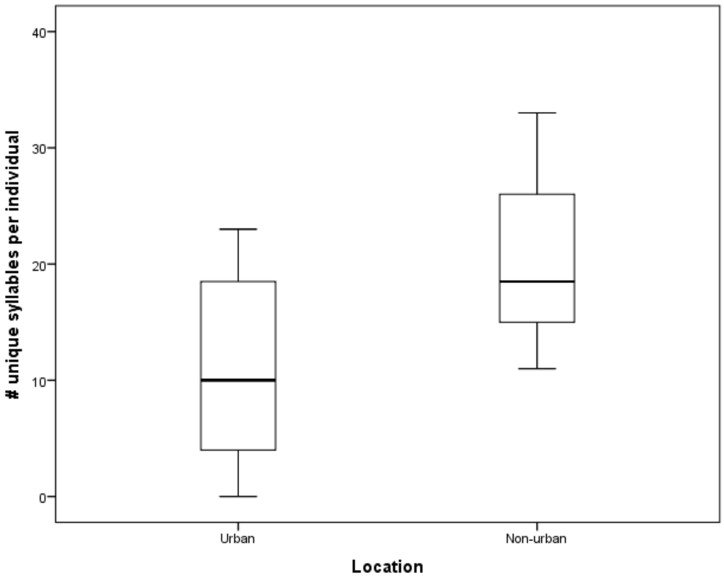


Figure 5.4: Percentage of individual-specific syllables per individual at urban and non-urban sites.

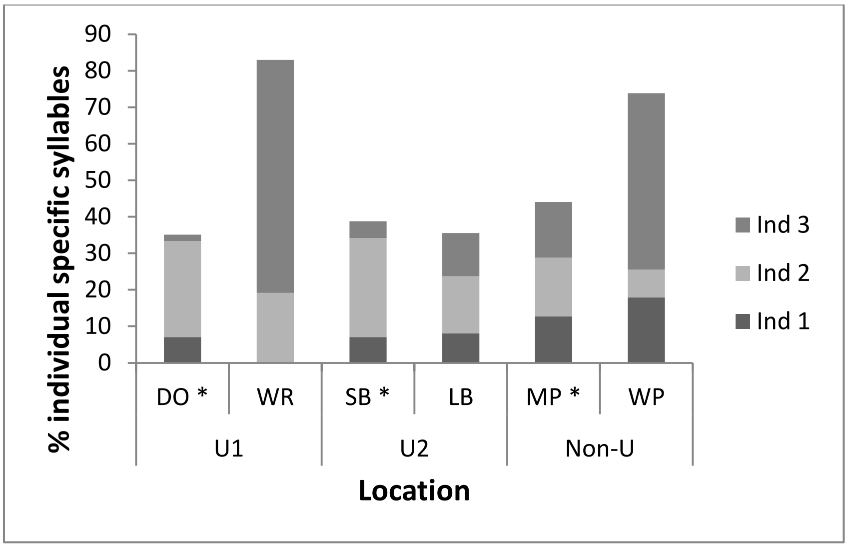


Figure 5.5: Percentage of individual-specific syllables at U^1: Domain (DO)* and Waitaramoa Reserve (WR), U^2; Smiths Bush (SB)* and Le Roys Bush (LB) and Non-Urban; Mahurangi Park (MP) and Wenderholm Park (WP) (*motorway sites).

5.3.5 Syllable sharing

Among 431 different syllables recorded at all six sites, only 25 syllables were produced by five or more individuals (Figure 5.6). The two most commonly shared syllables were (S0002) (harsh), and S0028 (squawk), both shared between

10 individuals (Figure 5.6). A total of 48 syllables were shared between urban and non-urban individuals.

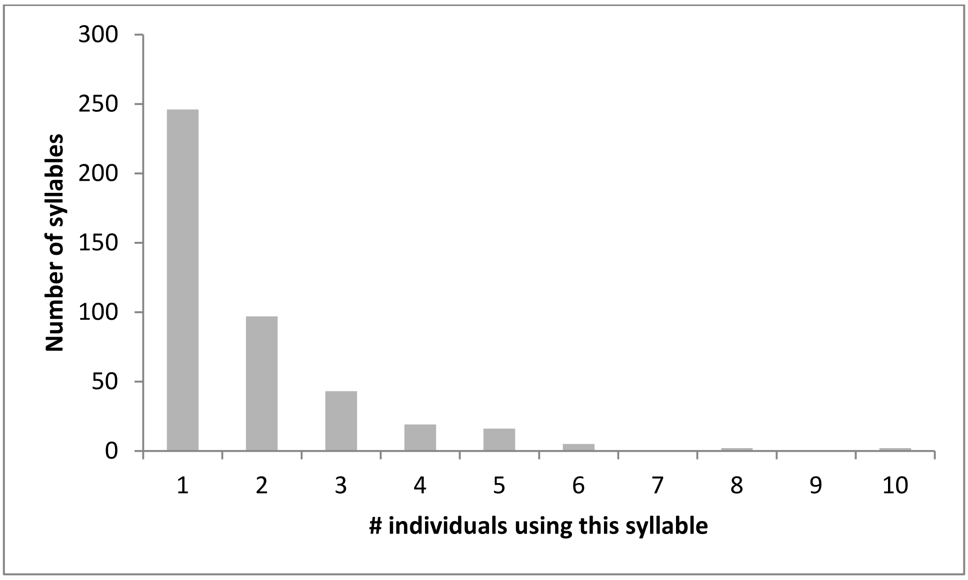


Figure 5.6: Syllable frequency distribution across all 6 sites (4 urban and 2 non-urban).

Within the urban populations a higher percentage of syllables were shared between individuals within sites at U^2 than at U^1 (Figure 5.7). Within the urban sites, Site 1 denotes a motorway site within each pair of sites. There was no correlation between the degree of syllable sharing and distance from motorway within the urban areas (Figure 5.7).

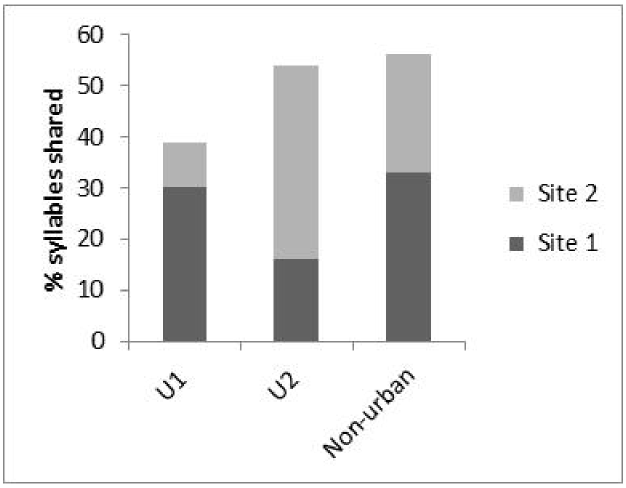


Figure 5.7: Percentage of syllables shared between three individuals within sites (U^1- Domain (Site 1*) and Waitaramoa Reserve (Site 2), U^2 (Smiths Bush (Site 1*) and Le Roys Bush (Site 2), and non-urban (Mahurangi Park (Site 1) and Wenderholm Park (Site 2). ***** indicates motorway site within the urban area.

The percentage of syllables shared between paired sites was variable between the urban and non-urban sites (Figure 5.8).

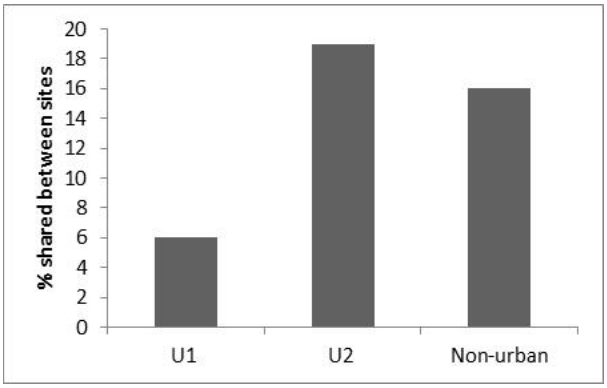
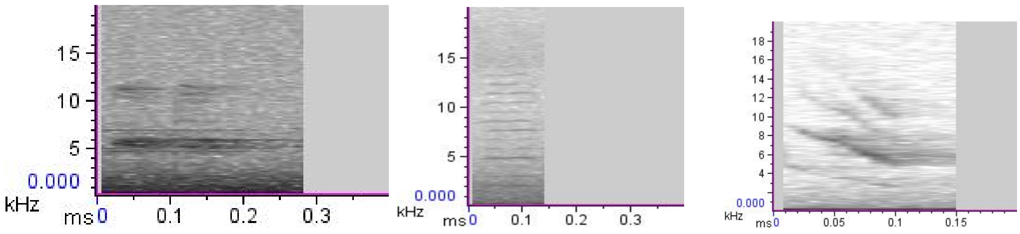


Figure 5.8: Percentage of syllables shared between paired sites at urban U^1, urban U^2 and non-urban areas.

5.3.6 Urban Syllables

A number of syllables were shared only between the urban sites. Three syllables were shared between all four urban sites (Figure 5.9). S0080 is a broadband harmonic syllable with peak frequency just above 5 kHz, above the frequency range for traffic noise (1-3 kHz). Syllable S0109 is another broadband harmonic syllable with maximum frequency around 12 kHz. Syllable S0159 is a harmonic slur down frequency modulated syllable, also quite broadband in nature.



S0080 S0109 S0159

Figure 5.9: Syllables shared between all four urban sites.

5.3.7 Urban phrase sharing

Ten phrases were shared within urban sites and five phrases were shared within non-urban sites (Table 5.5). Four phrases were shared by SB02 and SB03 at the Smiths Bush site (Table 5.5, Figure 5.10). Phrase PSB1 consists of a harmonic syllable (S0026) followed by a harsh syllable, (S0002) repeated. The second phrase (PSB2) consists of syllable S0002 repeated six times in rapid succession (Table 5.5, Figure 5.10). The loud, rapid delivery of short broadband harsh syllables is more commonly found at the urban sites than at the non-urban sites. However, syllable S0002 was sung by 10 individuals from both the urban and non-urban sites and is an iconic tūī syllable. There was no phrase (sequences of three or more syllables) sharing found between the urban and non-urban populations or between any two urban paired sites.

Table 5.5: Phrase sharing distribution in urban sites

Location	Site	Phrase ID	Syllable sequence	Shared between
Urban	Smiths Bush	PSB1	26, 2, 2	SB02,SB03
		PSB2	2,2,2,2,2,2	SB02,SB03
		PSB3	27,80,81	SB02,SB03
		PSB4	80, 81, 29	SB02,SB03
	LeRoys Bush	PLB1	125,125,125	LB01,LB02
	Domain	PDO1	241,241A,241B	DO01,DO03
		PDO2	225,225,226,226,225	DO01,DO04
	Waitara Res.	PWR1	3,3,3	WR01,WR02,WR03
		PWR2	267,267,267	WR01,WR02
		PWR3	267,3,3	WR01,WR02
Non-urban	Mahurangi Park	PMP1	311,311A,316A	MP03,MP05,MP06
		PMP2	87,330A,330A	MP05,MP06
		PMP3	300,300A,318	MP03,MP06
	Wenderholm Park	PWP1	384,385,383,382	WP01,WP04,WP05
		PWP2	383,382,2	WP01,WP04

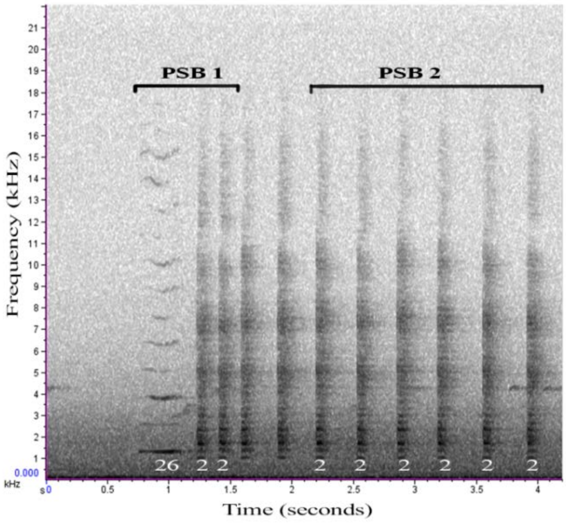


Figure 5.10: Two phrases (PSB1 and PSB2) shared by two individuals (DO01 and DO04) at Auckland Domain central site. Syllable ID's are denoted in white at the bottom of the figure.

5.3.8 Individual-specific phrases

There were more phrases unique to one individual repeated at the non-urban sites than at the urban sites (Table 5.6)

Table 5.6: Individual-specific phrases at different sites

Location	Site	# Individual-specific phrases
U^1	Domain	4
	Waitaramoa Res.	6
U^2	Smiths Bush	8
	Le Roys Bush	5
Non-urban	Mahurangi	11
	Wenderholm Park	7

Examples of two individual-specific phrases were commonly repeated and unique to individual DO01 at Auckland Domain (Auckland city central site close to SH16 motorway (Figure 5.11). The first phrase is composed of several short whistle syllables at different frequencies (pitches), followed by the broadband harsh syllable (S0002). The second phrase is comprised of a harmonic broadband syllable that is repeated in rapid rhythmical succession and is again followed by S0002. S0002 is one of the most commonly used syllables sung by ten individuals at both urban and non-urban sites.

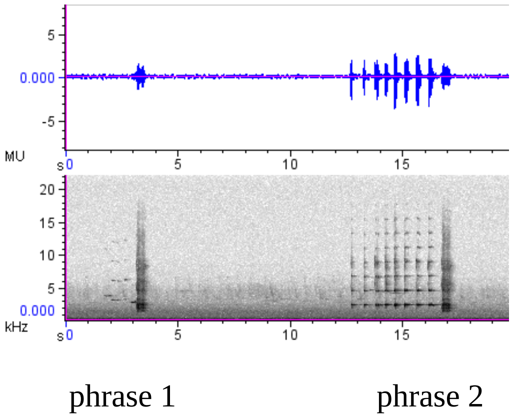


Figure 5.11: Sound waveform (amplitude) view and spectrogram (frequency) view showing two phrases regularly repeated by individual DO01 at Auckland Domain.

5.3.9 Site-specific syllables

The percentage of site-specific syllables, including both those shared within the site only and individual-specific syllables, was variable between sites with no clear difference between urban and non-urban sites (Figure 5.12).

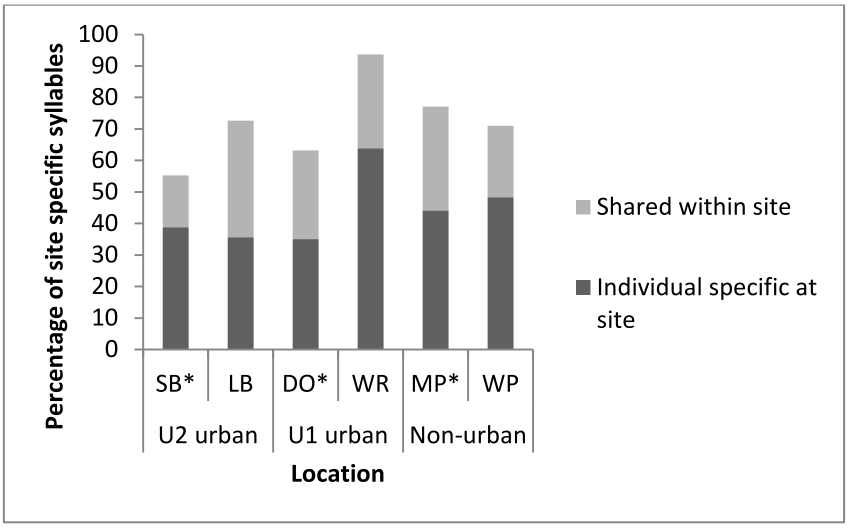


Figure 5.12: Syllables unique to each site (site-specific syllables).

A hierarchical cluster analysis (Ward, 1963) (Figure 5.13), using the syllable sequences of all songs analysed for this study showed two basal clades; one encompassing all songs from the non-urban sites and one including all songs from the urban sites. This indicates a significant difference between urban and non-urban tūī songs. Site-specific clusters formed in both urban and non-urban areas indicate the presence of local dialects.

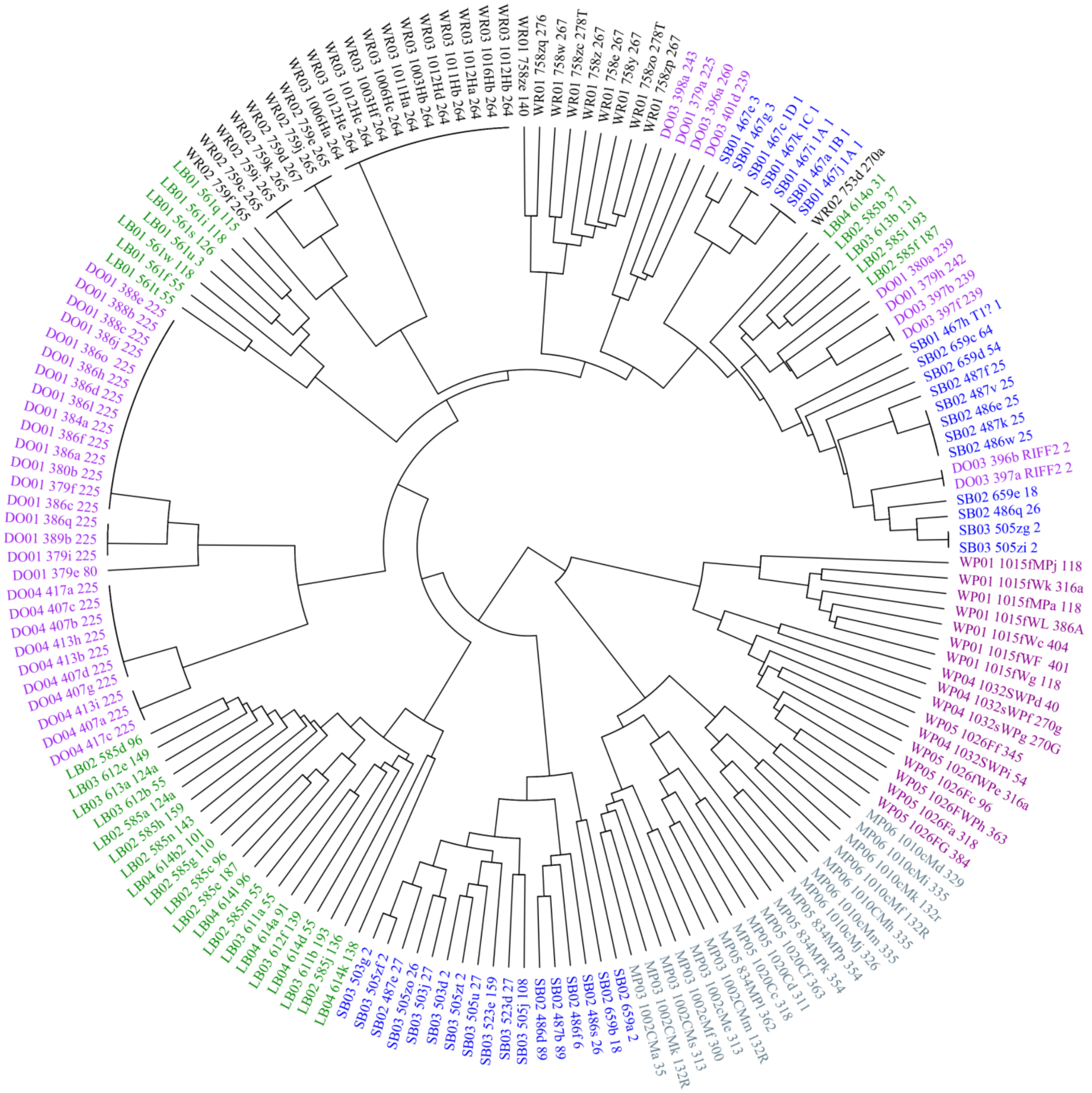


Figure 5.13: Hierarchical cluster analysis (Ward, 1963) minimising sum of squares distances using syllable sequences of all songs from urban and non-urban sites. Field sites are;

1) U^1 -Urban central: Domain; (DO01, DO03, DO04) and Waitaramoa Reserve (WR01, WR02, WR03), 2) U^2- Smiths Bush; (SB01, SB02, SB03) and Le Roys Bush (LB01, LB03, LB04), 3) Non-Urban- Mahurangi Park (MP03, MP05, MP06) and Wenderholm Park (WP01, WP04, WP05).

5.4 Discussion

5.4.1 Syllable repertoire

As predicted, there was a significantly lower syllable diversity and lower total number of syllables at the urban sites than at the non-urban sites, both at individual and population levels. This finding was supported by a previous study that found silvereye songs contained fewer syllables per song in urban environments (Potvin and Parris, 2012). Smaller syllable repertoire sizes of tūī in urban areas could result from individuals selectively using a range of syllables that transmit more effectively in the presence of urban noise. The higher degree of fragmentation in the urban habitats could also lead to smaller population sizes in small forest fragments and thus reduced song diversity. Previous research found that repertoire size and song diversity correlated with population size in kōkako (*Callaeas wilsoni*) (Valderrama, 2012).

There was a much higher degree of variation both between individuals and between paired sites in the rate of accumulation of new syllables over different songs in the non-urban sites than in the urban sites. Within the urban habitats, some individuals displayed very small repertoire sizes, and would continuously repeat a stereotyped phrase consisting of less than six syllables while other urban tūī would sing songs with a high degree of complexity. This variation may be due to the increased degree of habitat fragmentation and heterogeneity in urban environments.

5.4.2 Song rate and singing rate

As predicted, there was a trend that urban tūī sang a greater number of shorter songs whereas non-urban individuals sang less frequent but longer songs, although this result was non-significant. These findings were supported by previous research indicating that urban birds sing shorter songs with fewer elements than rural birds, as has been found in both blackbirds in Europe (Nemeth and Brumm, 2009) and Australian magpies (*Gymnorhina tibicen*) (McCarthy et al., 2013). It is thought that urban birds may sing shorter songs at a higher rate to increase signal redundancy in a noisy environment. Previous research has found that birds respond to a noisy environment by increasing signalling rate (Brumm, 2004). Urban great tits sang songs at a faster rate than those in rural forests, and this effect was attributed to adaptations to the more open city habitats (Slabbekoorn and den Boer-Visser, 2006). A previous study found that Northern cardinals (*Cardinalis cardinalis*) sang longer songs at faster rates in urbanised forests, however temporal attributes of their songs (syllable rate and length) were best explained by conspecific densities, not noise (Narango, 2012).

5.4.3 Individual-specific syllables and phrases

There were a higher percentage of individual-specific (unique to one individual) syllables found at non-urban sites compared with urban sites although this trend was not significant. The number of individual-specific syllables within sites followed a gradient from the most highly modified central urban sites to the non-urban sites, suggesting that individual variation in syllable use is restricted by urbanisation. Alternatively this finding could be a result of smaller population size in urban fragments thus containing fewer numbers of individual-specific syllables. Furthermore, within the urban sites, the prevalence of individual-specific syllables was even lower at the noisy motorway sites, giving further indication of the effects of urban noise on repertoire. Although these findings of differences in individual-specific syllables differ from one of the only previous studies to examine this aspect of song (Potvin and Parris, 2012), these results suggest urban associated habitat changes may have important effects on the number of individual-specific syllables at a site. The individual-specific phrases identified at the urban sites often consisted of very simple broadband syllables repeated in rapid succession. Further research is required to establish whether the simplicity and broadband nature of these phrases could indicate selective use of such syllable types to increase transmission in noisy, urban environments.

5.4.4 Syllable sharing

Individuals in the non-urban and more continuous urban habitats shared more syllables between sites than those in the more fragmented central urban habitats (Figure 5.8). These differences could be explained by a reduction in the use of syllables that are not so effectively transmitted in the presence of anthropogenic noise in fragmented urban areas. Alternatively this effect could be as a result of smaller tūī populations in smaller fragmented habitats, leading to reduced competition for resources and reduced syllable sharing in song matching contests. A previous study found a greater degree of syllable sequence sharing within sites, than between males occupying different patches (Briefer et al., 2010).

5.4.5 Urban-specific syllables

There was an indication of the use of urban-specific syllables found only at both central (U^1) sites and the North Shore (U^2) sites. Such syllables may be examples of selective syllable use for increased clarity and transmission in urban environments. These urban syllables were mostly wide frequency range, broadband syllables that may be more effectively transmitted in urban environments. A previous study supported the selective use of higher frequency songs from their repertoire that were less masked by prevailing noise (Wood and Yezerinac, 2006). The different syllable types used in urban habitats suggest possible convergence of song repertoire characteristics within the structure of these local dialects due to the influence of habitat features including background noise. Birds inhabiting urban areas could be affected by other selective pressures, such as lack of suitable breeding habitat or food resources that could intensify competition for quality nesting sites. In turn this could heighten male territorial competition and have an effect on characteristics of song (Potvin and Parris, 2012). However due to the small sample size used in this study, it is difficult to determine whether these are in fact urban-specific syllables.

5.4.6 Dialect

5.4.6.1 Site-Specific Syllables

Site-specific syllables included syllables that were shared only between individuals at a site and not shared with other sites, and also individual-specific syllables that were unique to individuals within those sites. The percentage of site-specific syllables in the urban areas ranged from 45-93%. The presence of these site-specific syllables indicates the presence of dialects in sites spaced 2-3 km apart. This finding is supported by a study that found increased syllable sharing among house finches (*Carpodacus mexicanus*) within a site than between individuals over greater distances (Tracy and Baker, 1999). This variation may be a product of the song acquisition process, due to a combination of cultural transmission during song learning and also song matching within small populations in habitat remnants (Bergquist, 1989; Petruskova et al., 2010). Only a small number of phrases were shared between individuals at all sites. There were no shared phrases between these paired sites. The presence of these phrases and of individual-specific phrases at these sites is further evidence of local dialects at sites only 2-3 km apart.

5.4.6.2 Cluster Analysis

The Ward cluster analysis clearly separated the urban and non-urban songs into different clades indicating the significant differences in urban and non-urban songs. There were also clades comprising songs from the same sites in both urban and non-urban sites indicating the higher degree of similarities of songs within a site than between sites. A higher number of syllables and phrases shared between individuals within a site are not shared between sites in both urban and non-urban areas. These results indicate the presence of dialect at both urban and non-urban sites. This presence of dialects was also supported by the percentage of site-specific syllables found at all sites. However due to the small number of non-urban sites included in this study, whether urban fragmentation results in more pronounced differences in songs from different locations (dialects) cannot be investigated. Further study on this aspect is required.

CHAPTER 6

Conclusion

Plate 6.1 Tūī in urban garden (photograph by Kerri Walker)

6.1 Effects of Urban Noise on Song Structural Parameters

The effect of motorway noise on male tūī song structural characteristics was measured by comparing three motorway sites and three distant from the motorway sites within the urban environment. Tūī songs at the motorway sites showed a raised minimum frequency, likely to be a strategy to avoid the masking effects of low-frequency traffic noise. Songs at the motorway sites were also significantly shorter, had reduced syllable diversity and a lower proportion of trill than songs from the non-motorway sites. These findings suggest that males adjust their songs in noisy areas in order to communicate more effectively. Although signal modifications in response to urban noise, such as raised minimum frequency may increase the detectability of signals, they could also impose significant costs to the signaller such as increased risk of predation and parasitism (Hanna et al., 2011). Females could also be less attracted to males producing modified songs (Patricelli and Blickley, 2006).

6.2 Song repertoire in the heterogeneous urban environment

As predicted, trends showed higher syllable diversity, more unique syllables and higher numbers of total syllables per song at non-motorway sites. However due to the small sample size in this study, the effects of noise on these differences cannot be fully separated out from other factors such as habitat size, fragmentation and population size. The great versatility in tūī song repertoire, the ability to mimic other species and song match within populations has likely assisted tūī in adapting their songs in the presence of urban noise and may contribute to their ability to breed successfully in urban environments. Further studies using a larger sample size are recommended to provide more compelling evidence of the effects of motorway noise on song in heterogeneous urban areas.

6.3 Variation in repertoire and dialect between urban and non-urban areas

Tūī in urban areas generally produced songs with lower syllable diversity, and less syllables per song as part of a smaller song repertoire than non-urban birds. Urban tūī also sang shorter songs at a higher rate than non-urban individuals. Evidence of local dialects in the central urban sites was reported.

These differences in repertoire and dialect between urban and non-urban areas could be as a result of the effects of urban noise, differences in tūī density and vegetation differences. There are also great differences in habitat types found between the disturbed urban habitats, mainly dominated by naturalised or domesticated flora and fauna, compared with the less disturbed sites at the non-urban parks dominated by native species in predator controlled regenerating forests.

The higher syllable diversity at non-urban locations could be correlated with larger habitat size and population size leading to greater levels of male competition for resources, food and mates. Confounding factors for differences in dialects may be that more individuals were sampled in non-urban areas and that differences may be due to higher tūī density. Sampling occurred in the breeding season when male tūī remained near nesting sites however tūī breeding is not entirely synchronous and therefore not all individuals were nesting at the same time during the sampling period. Due to time constraints, there was no replication of populations for each habitat type, and because my study compares three samples of individuals from different (four urban and two non-urban) tūī populations, I cannot assert with certainty that the observed differences in repertoire and syllable sharing between the three habitat types were not the result of population or location differences.

Syllable sharing characteristics and also individual-specific components of repertoires followed an urban gradient between the most intensely modified sites, through to the less modified habitats of suburban North Shore sites. An increase in both syllable diversity and the number of individual-specific syllables was found along this gradient ranging from highly urbanised to the non-urban habitats. This gradient in song characteristics could reflect the habitat effects on these parameters between the highly modified central sites with highly fragmented habitats and higher levels of noise, with the North Shore sites acting as an intermediary stage between central urban and non-urban sites.

6.4 Conclusion

This study has provided baseline data showing differences in frequency and temporal song characteristics between tūī populations at noisy motorway sites compared with quieter, non-motorway sites. Differences were also found in repertoire and dialect between urban and non-urban sites and these results suggest that tūī modify these elements of song in response to anthropogenic noise. This study has provided new information on song structure, syllable repertoire and dialects in urban and non-urban sites. I have shown differences in song structure consistent with a role of motorway noise such as a raised minimum frequency and reduced trill rate. These findings contribute towards understanding the effect of urban noise on songs and singing behavior of song birds and will provide useful baseline information for the conservation management of wildlife habitats in urban ecosystems.

6.5 Future research implications

The results from this study provide increased knowledge in the understanding of tūī vocal communication and may help in determining potential reproductive barriers between local populations in urban environments. These are important factors in the conservation of tūī and potentially other native species found in urban areas, and could be used to inform conservation efforts and translocations where tūī are scarce. Although tūī are commonly found in urban areas, they have suffered serious declines in some areas, including cities. Following a massive decline of tūī at Banks Peninsula in the 1990s, a translocation was conducted in 2009 along with revegetation and pest control programmes (Banks Peninsula Conservation Trust, 2014). Post-translocation monitoring has indicated that the project has been successful in the short-term (Banks Peninsula Conservation Trust, 2014).

My findings could also inform conservation management practises for those species that are unable to modify their signals to avoid the masking effects of anthropogenic noise. Mitigations of the effects of traffic noise on wildlife include the installation of sound barriers alongside motorways and busy roads that adjoin native forest patches (Parris and Schneider, 2009). Other techniques include the use of porous road surfaces, speed limitations and restrictions on noise emissions for road traffic (Slabbekoorn and Ripmeester, 2008).

More research is necessary to investigate the effects of motorway noise on these important aspects of song. Only a small number of New Zealand native forest species such as tūī are evidently able to adapt and maintain their populations in urban areas such as Auckland city. Whether these populations diverge phenotypically from non-urban populations may be mediated by song characteristics and their effect on sexual selection. It is recommended that playback experiments be used to determine whether urban tūī can discriminate between songs from urban or non-urban populations. Further research is required to address the many more questions developed as a consequence of this study. Future studies using a larger sample size of songs from non-urban locations would allow for more rigorous testing between urban and non-urban sites. Including data from more urban sites could also increase our understanding of the presence of dialect between sites in the heterogeneous urban landscape. Further research on the effects of population dynamics and conspecific density on the studied song characteristics could assist in clearer separation of the importance of different factors affecting these aspects of song.

I found changes in song structure, proportion of trills and song rate consistent with increases in motorway noise. These song aspects are important in mate choice in song birds. Further studies are recommended that focus on whether these changes in song characteristics influence female preference in male songs.

This study also found presence of dialect in urban fragments. However the small sample size of my non-urban sites and differences in size between urban and non-urban habitats did not allow me to investigate whether urban habitat fragmentation resulted in more pronounced dialects between populations. Further studies using more fragments of similar conditions in both urban and non-urban areas should be carried out to address this question. Whether a high degree of differences in songs between fragments will affect the breeding success of dispersing individuals settling in sites of different dialect is also an aspect to investigate due to its implications for gene flow between patches.

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Appendix A: Syllable Key

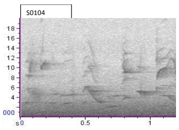
Syllable Key

- The syllable is longer than 1.2 seconds------- -- Slide 3
- The syllable is shorter than 1.2 seconds
  - The syllable is longer than 1 second-- Slide 4
  - The syllable is shorter than 1 second
    - The syllable is longer than 0.8 seconds ------------------------------------- Slide 5
    - The syllable is equal or shorter than 0.8 seconds
      - The syllable is longer than 0.6 seconds
        - » Contains flat and convex elements, no concave elements---------------------------- Slide 6
        - » Contains concave elements
          - Contains harmonic elements--------------------------------------- Slide 7
          - Does not contain harmonic elements---------------------------------- Slide 8
      - The Syllable is equal or shorter than 0.6 seconds
        - » The syllable is longer than 0.4 seconds
          - Contains flat and convex elements, no concave elements------------------- Slide 9
          - Contains concave elements---------------------------------
            - Starts with flat or descending elements------------------------- Slide 10
        - » The syllable is equal or shorter than 0.4 seconds
          - The syllable is longer than 0.3 seconds
            - Contains flat or convex elements, no concave elements
              - Contains narrow band flat harmonic elements (thin lines)--------------- Slide 11
              - Contains other form of elements
                - Does not contain harmonic elements
                - ✓ Continuous wide range of frequency (hush sound)------------ Slide 12
                - ✓ Others--------------------------------- Slide 13
                - Contains Harmonic elements-
                - ✓ Starts with flat or descending elements --------------------------Slide 14 +15
                - ✓ Starts with ascending element-------------------------------------- Slide 16
            - Contain concave elements
              - Starts with a flat element----------------------------------Slide 17
              - Starts with a ascending element--------------------------------Slide 17
              - Starts with a descending element-----------------------------Slide 18

- The syllable is equal or shorter than 0.3 seconds
  - The syllable is longer than 0.2 seconds
    - The syllable is broad frequency harsh element--Slide 19
    - The syllable contains harmonic elements
      - Contains narrow band flat harmonic elements (thin lines) -------------------------Slide 20+21
      - The syllable does not contain concave elements
      - ✓ Starts with flat elements --Slide 22
      - ✓ Starts with ascending elements---Slide 23
      - The syllable contains concave elements
      - ✓ Starts with flat or descending elements------------------------------------Slide 24
      - ✓ Starts with ascending elements---Slide 25
    - The syllable does not contain harmonic elements------------------------------------ Slide 26+27
  - The syllable is shorter than 0.2 second
    - The syllable is dominated by narrow band flat elements (thin lines)
      - Contains only continuous straight lines-------------------------------------Slide 28
      - Contains other types of elements, undulate or un-continuous lines -------------------Slide 29
    - The Syllable is not dominated by narrow band flat elements
      - The syllable is dominated by broad frequency harsh elements-----------------------
      - ✓ Starts with flat elements---Slide 30
      - ✓ Starts with descending or ascending elements--------------------------------Slide 31
      - The syllable is not dominated by broad frequency harsh elements
      - ❖ The syllable contains harmonic elements
      - ✓ The syllable contains mostly flat elements-----------------------------------Slide 32
      - ✓ The syllable contains mostly straight and convex element, no concave element-------------Slide 33+34
      - ✓ The syllable contains descending or concave elements--------------------------Slide 35
      - ❖ The syllable does not contain harmonic elements
      - ❖ Contains flat or ascending elements--------------------------------------Slide 36
      - ❖ Contains descending elements
      - ➢ Starts with flat or descending elements ------------------------------------Slide 37/38
      - Starts with ascending elements-- Slide 38
  - The syllable is shorter then 0.1 second-- Slide 39/40

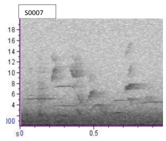
Longer than 1.2s

S0104



Longer than 1s

S0007



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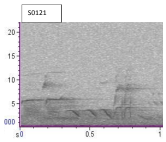
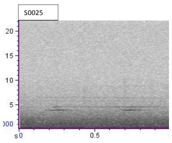


S0025



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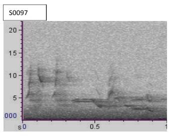
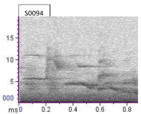


Longer than 0.8s

S0094



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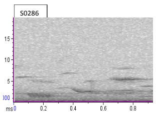

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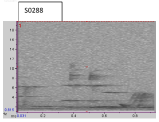
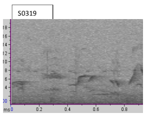
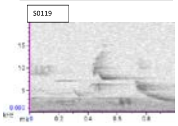


S0319

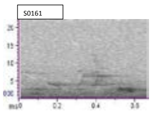


S0119



0.6-0.8s: contains flat & convex elements

S0161



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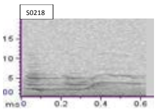

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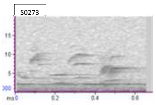

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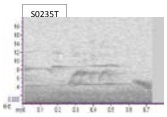

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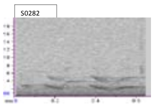
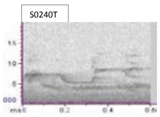


0.6-0.8s: convex elements, harmonic elements

S0240T



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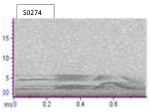

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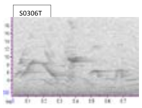

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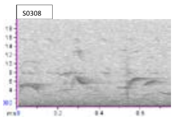

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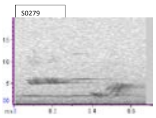

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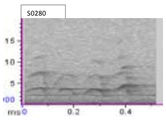
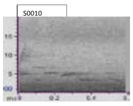


0.6-0.8s: concave elements, no harmonic elements

S0010



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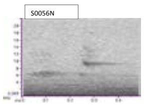

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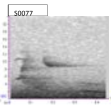

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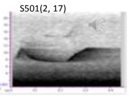

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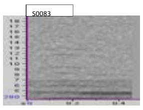

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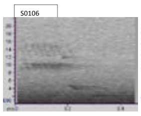

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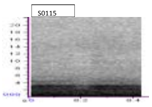

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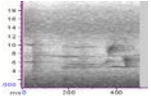

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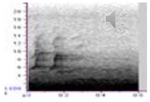
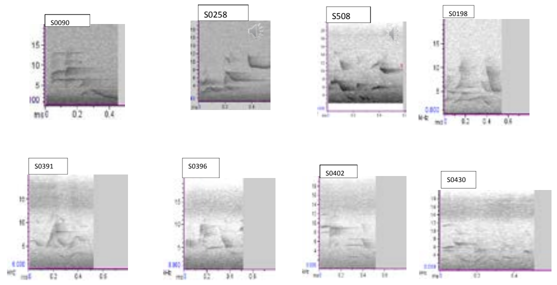
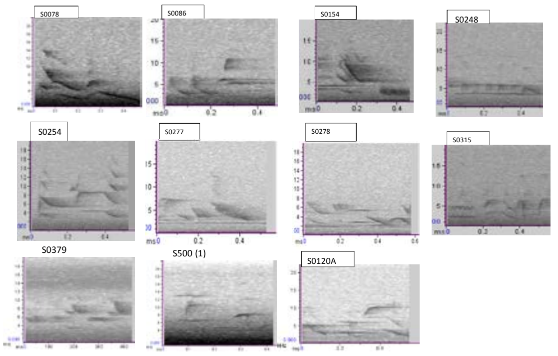


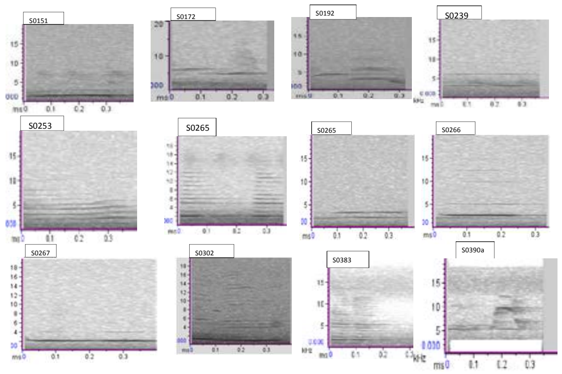
0.4-0.6s: flat and convex elements, no concave elements



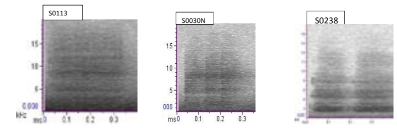
0.4-0.6s: contains concave: starts with flat or descending elements



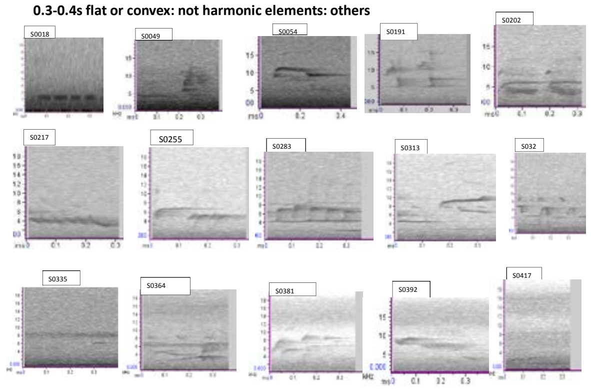
0.3-0.4s: flat or convex; narrow band flat harmonic elements, thin lines



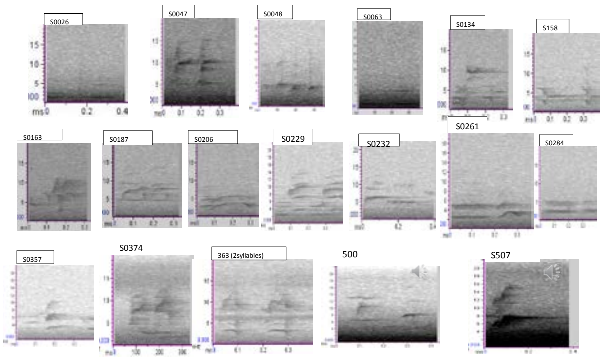
0.3-0.4s wide-frequency broadband elements



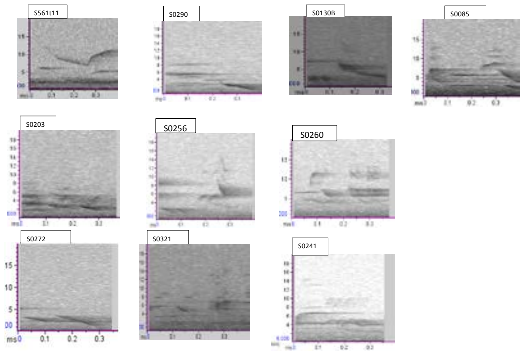
0.3-0.4s flat or convex: not harmonic elements: others



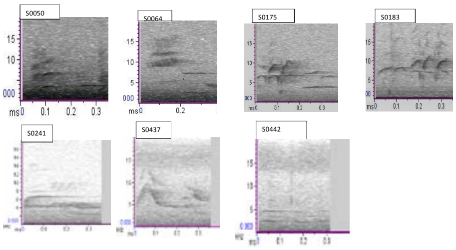
0.3-0.4s flat or convex; harmonic elements: starts flat/desc elements



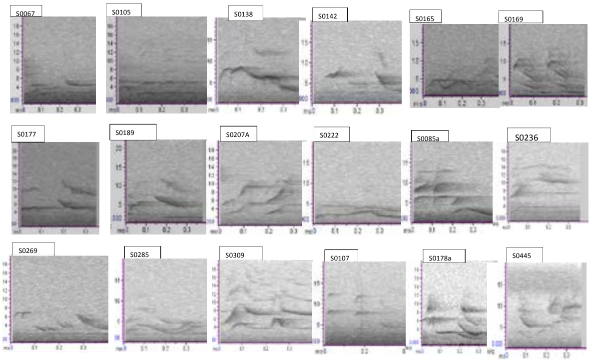
0.3-0.4s Flat or convex; Harmonic elements: starts flat/descending elements CTD



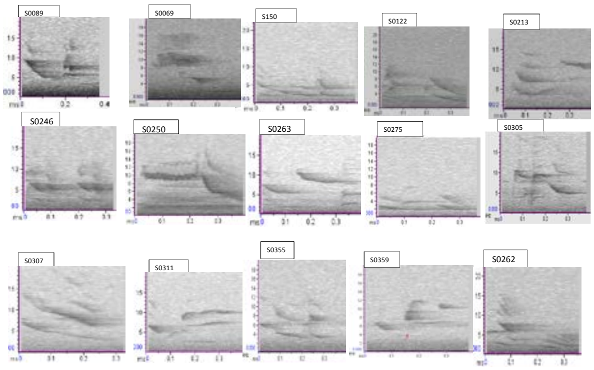
0.3-0.4s flat or convex; harmonic elements: starts flat/asc elements



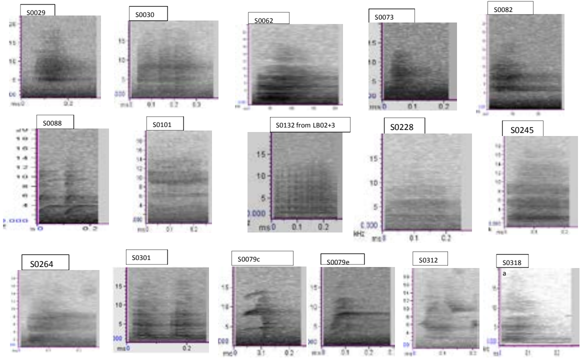
0.3-0.4s contains concave: starts flat or ascending elements



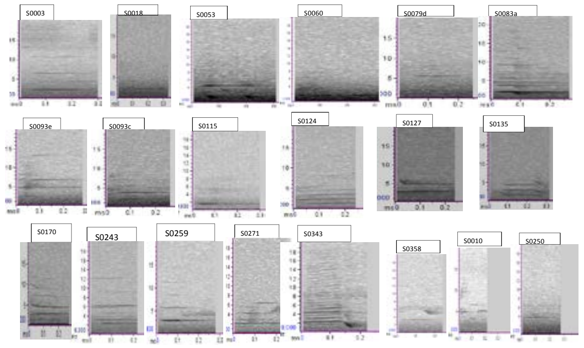
0.3-0.4s contains concave elements : starts descending elements



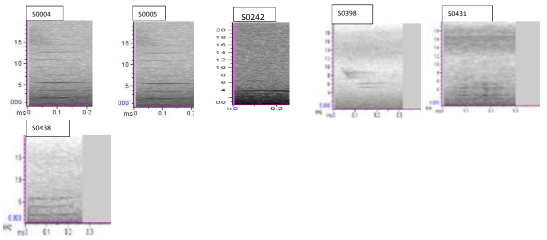
0.2-0.3s Broad frequency /harsh



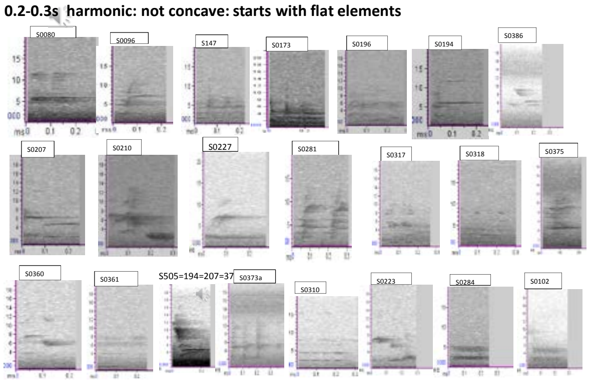
0.2-0.3s harmonic: narrow band flat elements



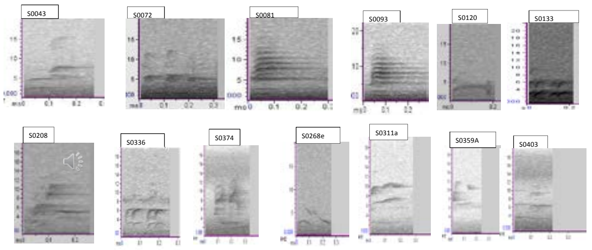
0.2-0.3s harmonic: narrow band flat elements CTD



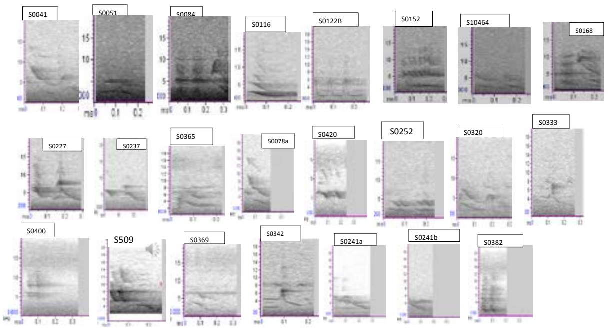
0.2-0.3s harmonic: not concave: starts with flat elements



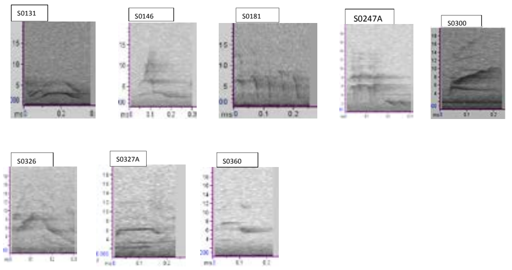
0.2-0.3s harmonic: not concave: start with ascending elements



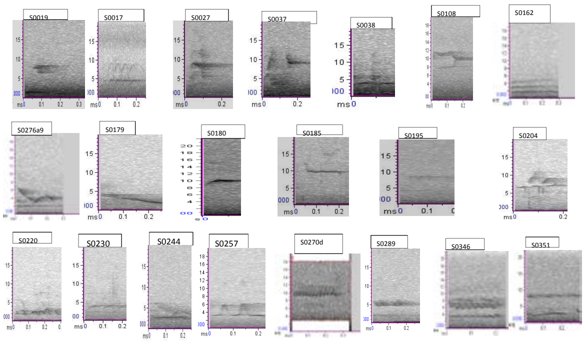
0.2-0.3s harmonic: concave: start with flat or descending elements



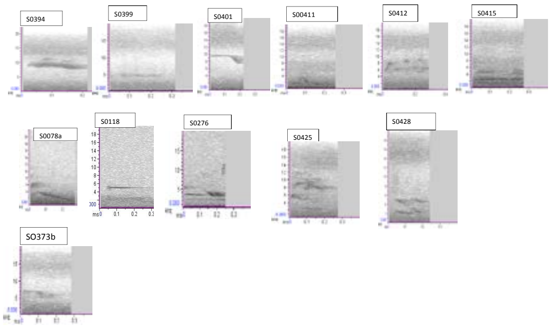
0.2-0.3s harmonic: contains concave: starts with ascending elements



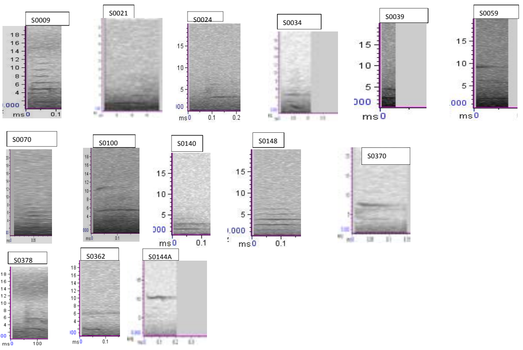
0.2-0.3s does not contain harmonic elements



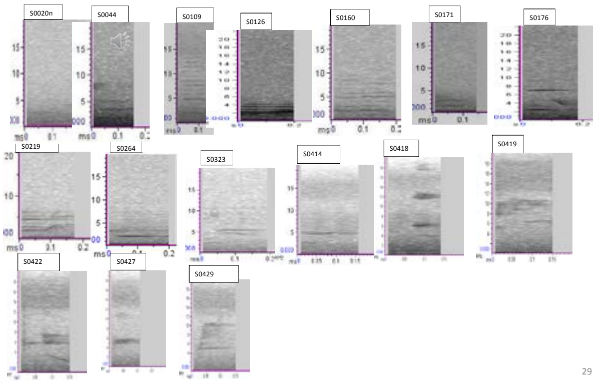
0.2-0.3s does not contain harmonic elements CTD



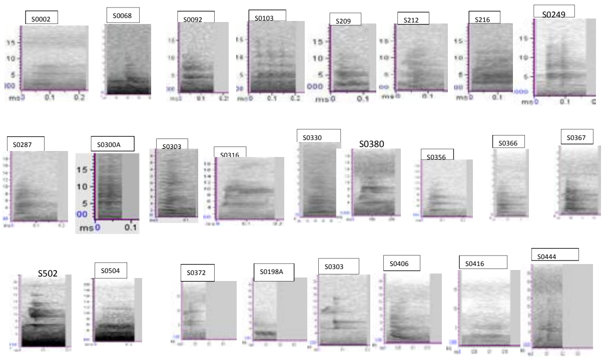
0.1-0.2s dominated by narrow flat-band elements-(only continuous lines)



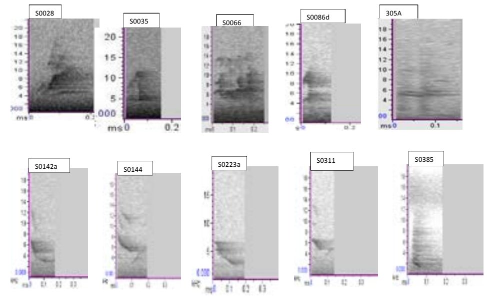
0.1-0.2s dominated by narrow-band flat elements; also undulate or non-continuous lines



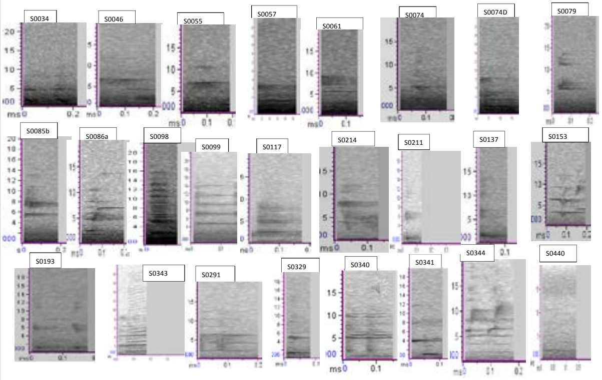
0.1-0.2s broad harsh elements: starts with flat elements

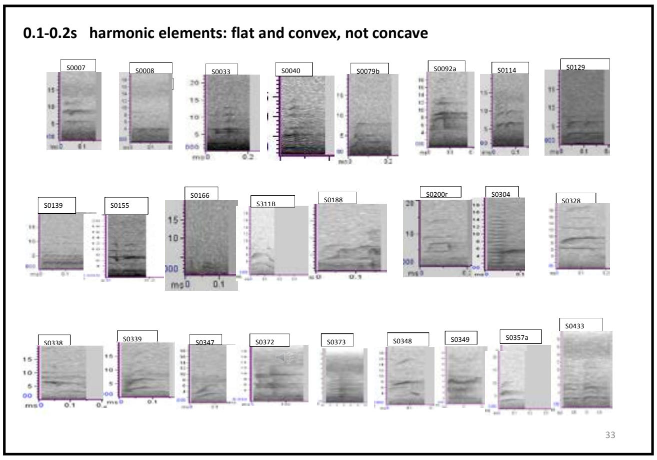


0.1-0.2s broad harsh elements: starts with desc/asc elements

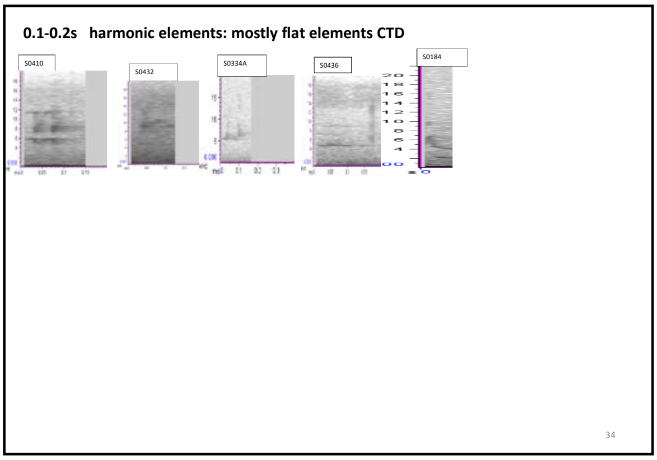


0.1-0.2s harmonic elements: mostly flat elements

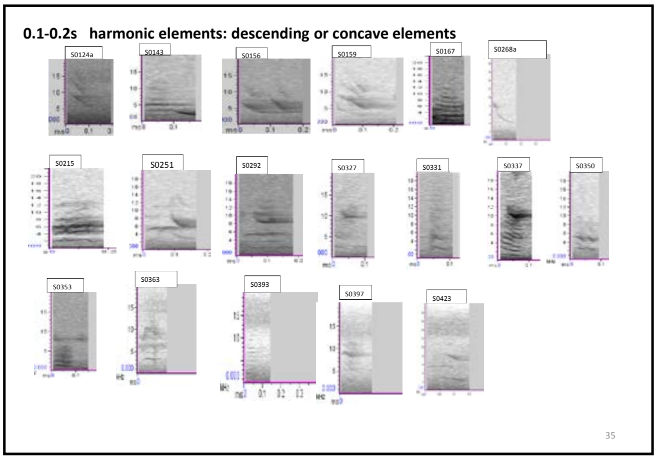




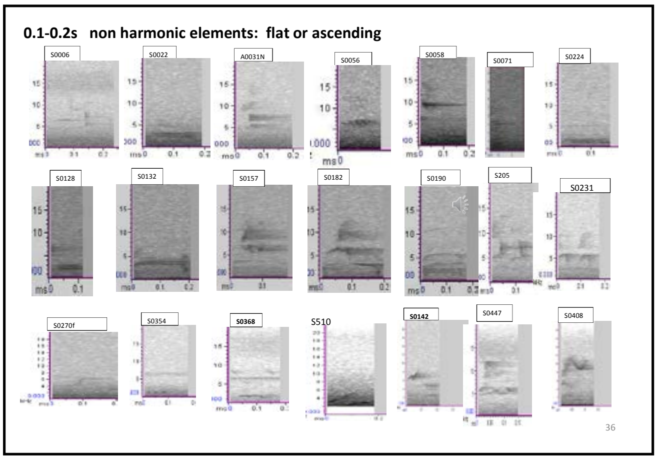
0.1-0.2s harmonic elements: flat and convex, not concave



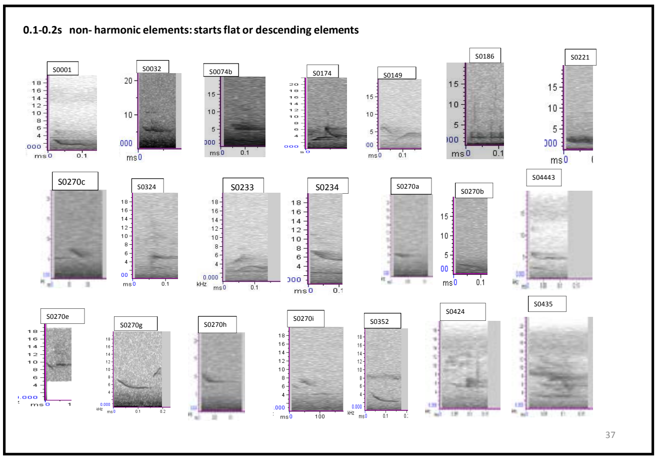
0.1-0.2s harmonic elements: mostly flat elements CTD



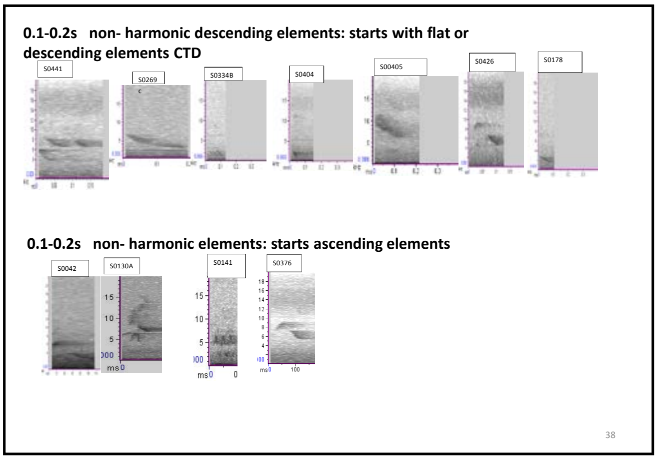
0.1-0.2s harmonic elements: descending or concave elements



0.1-0.2s non harmonic elements: flat or ascending



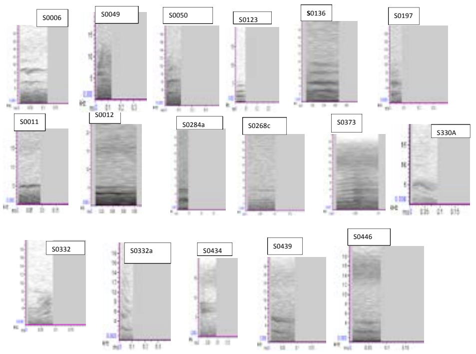
0.1-0.2s non- harmonic elements: starts flat or descending elements



0.1-0.2s non- harmonic descending elements: starts with flat or descending elements CTD

0.1-0.2s non- harmonic elements: starts ascending elements

Length is 0.1 or less: harmonic elements:



Length <0.1s : Non-harmonic elements