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The vocalisation of tui (*Prothemadera novaeseelandiae*)

A thesis presented in partial fulfilment of the requirements for the degree of

Master of Science in Conservation Biology

Massey University, Albany, New Zealand

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(2011)

Abstract

This study investigates the vocalisation of tui and its individual, gender and regional variations.

A population of tui at Tawharanui Regional Park was studied in order to investigate the characteristics, diversity, gender variation and seasonal variations of tui vocalisation. In 2.4 hours of recordings collected from 48.5 hours of field sampling between July and December, 2010, 303 distinctly different songs were recorded, which included four types of vocalisations. These were long-range broadcasting songs, short-range interactive songs, alarm calls and distress calls. In 30 randomly selected songs from different individuals, 264 distinctly different syllables were observed. The level of syllable repetition and syllable sharing between individuals were low. A significantly greater proportion of trill and a significantly lower minimum frequency were found in long-range songs than in short-range songs. A greater proportion of trill in the long-range songs is possibly due to: 1. Long trill components being more effective in long-range transmission than short bouts of trill, 2. High frequency trill is less likely to suffer from sound degradation in open habitats than lower frequency syllables and 3. Trill is costly to produce and may advertise the genetic quality of the singer, therefore are used more in long-range broadcast songs rather than in short-range interactive songs. Significantly lower minimum frequencies in long-range songs is likely to facilitate the transmission of sound further in distance and through vegetations. Minimum frequencies may also correlate with the size of the singer, which is likely important information to advertise in long-range songs for mate attraction and territory defence.

Male songs were not significantly longer in duration than female songs. Males however had a much larger repertoire of syllables and male songs contained a significantly larger proportion of rapid multiple note repetition syllables, both of which are likely sexually-selected traits linked to genetic diversity and the ability to defend high-quality territories. Tui songs in breeding season had a greater proportion of trill components compared to that in non-breeding season. Trill has been found to be another sexually-selected characteristic of males. Statistical analysis also suggested that at the population level, tui sing a greater number of songs during the non-breeding season than during the breeding season. However this observation is likely due to stronger territorial behaviour of tui in breeding season resulting in a reduction in the density of birds in one specific area.

Tui songs recorded from the Chatham Islands were compared to those from Tawharanui Regional Park in order to explore the regional variation in tui vocalisation. Long-range male songs recorded from Tawharanui had a significantly greater proportion of trill, inflection points in the terminal note and longer song duration than that from Chatham Island. These characteristics have all been demonstrated as being sexually-selected traits that are positively correlated with male genetic diversity, suggesting that the genetic diversity of individuals in the mainland population is higher than that of the island population. The acoustic adaptation hypothesis could also help to explain the significantly higher proportion of trill component in the long-range songs of the mainland population, as the mainland study site contained more open vegetation than the Chatham Islands sites and trill transmits more effectively in such habitats. The mainland population also had a larger song repertoire and syllabic diversity at the population level and the two populations exhibited 7.5% syllable similarity when comparing syllable repertoires. There was, surprisingly, no significant overall difference in the multivariate dispersion of spectral characteristics when comparing both short and long-range songs between populations, however this is likely due to the effect of sample size. Differences in habitat type, opportunities for immigration and emigration, levels of male-male competition and sexual selection pressures all likely drive the overall variation observed when comparing the structure of both long-range and short-range songs and would explain the difference observed in the song and syllable repertoire between the two populations.

This study has provided baseline data of song type, individual, gender, seasonal and regional differences in tui vocalisation, which will help develop our understanding of communication in tui. Knowledge of tui vocalisation can help in determining individuals' reproductive potential, past breeding success and the role of songs in tui breeding success. Such information is important for the conservation of tui, particularly in areas where tui population is declining and requires conservation efforts and management such as translocation.



Acknowledgements

I am extremely grateful to all those who have assisted me throughout my Masters project. First of all I would like to thank my supervisor Weihong Ji for her assistance, advice, support, time, effort and passion for this project. Thank you to Sarah Wells who shared her knowledge, skills and passion for tui with me and who gave me the opportunity to undertake tui fieldwork in the awe-inspiring Chatham Islands. I greatly appreciate the statistical advice given to me by Christophe Amiot and Kevin Parker.

Thank you very much to Ngāti Manuhiri and to all of the hard working staff at Tawharanui Regional Park for permitting me to carry out my research at Tawharanui and allowing me use of all the facilities. I am hugely grateful to the Department of Conservation staff on the Chatham Islands, especially Abigail Liddy, Jim Clarkson and Kenny Dix, for facilitating the field trip and assisting greatly with life on the Chatham Islands. I am very grateful to Jordi Segers for assisting me in the field. Thank you to Tanja and to all of my family for your phenomenal level of assistance, advice, understanding, support and encouragement, I love you all so much.

I would also like to thank all of those in the Massey University Ecology and Conservation research group for their assistance, passion, spirit and support; to Mike Westgate for helping to retrieve my Chatham Islands MiniDisc recordings and to Ben Smith for teaching me how to fish, on Rangatira Island!

This project was funded by Auckland Regional Council, Massey University Ecology and Conservation Group, The Selborne Trust and the Ministry of Social Development and permits were granted by Auckland Regional Council and the Department of Conservation.

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Chapter One – General Introduction



Tui at Tawharanui Regional Park (Photograph: S. Hill).

1.1 Bird Vocalisation

A highly specialised sound-producing organ, the syrinx, enables birds to produce complex vocalisations (Larsen & Goller, 1999; Beckers, 2006).

The term ‘bird vocalisation’ encompasses songs and calls, both of which have many communicative functions (Catchpole & Slater, 2008). Bird calls are described as short, structurally simple and contextual, often produced with reference to a particular function (Laiolo et al, 2004). They can act as distress signals, such as alarm calls, that warn other individuals of nearby predators or intruders, as well as to convey information to the predator about the bird’s strength, quality and escape capability (Laiolo et al, 2004). Calls can also be used in a mobbing or even sexual context (Marler, 2004). Bird songs are more complex, longer, and require the process of learning from conspecifics (Kumar & Bhatt, 2001; Catchpole & Slater, 2008). The main functions of bird vocalisation include territory defence (Nowicki & Searcy, 2004; de Kort et al, 2008), mate attraction (Eriksson & Wallin, 1986) and individual, sex and species recognition (Marler & Peters, 1977).

1.1.1 Territory Defence

Mate attraction and territorial defence are functions frequently studied due to their direct link to reproductive success through mate choice and male-male competition, thereby providing valuable insight into the adaptive significance of bird song (Harper et al., 2010).

In many territorial songbird species, experiments have shown that during the breeding season, if a male bird song is played on a loudspeaker within a male’s territory, that male will react aggressively, usually approaching rapidly and with intent to find the ‘intruder’ (Nowicki & Searcy, 2004). Males will also react vocally to the song of another male and will match each others’ songs, regularly switching between different song types. This combination of vocal aggression and territoriality strongly suggests that song acts as a signal to other males as a territorial defence signal (Nowicki & Searcy, 2004) towards other males either repelling or attracting rival males.

Experiments that rendered male red-winged blackbirds (*Agelaius phoeniceus*) mute showed that such individuals will lose territories more quickly than singing male birds, will defend their

territory with greater difficulty and will suffer a greater amount of territory intrusions and confrontations (Peek, 1972; Smith, 1979), highlighting the significance of song in territoriality. Furthermore, in experiments where males were removed from their territories and replaced by a loudspeaker regularly playing male broadcast song, territories took longer to be reoccupied than control territories where no songs were played (Yaskukawa, 1981; Nowicki et al., 1998a).

1.1.2 Mate Attraction

Catchpole (1987) suggested that bird songs were an ‘acoustic equivalent of a peacock’s tail’. To demonstrate the importance of song in mate attraction, experiments using male decoys in nest boxes were set up using a mixed population of pied and collared flycatcher (*Ficedula hypoleuca* and *F. albicollis*). Half of these decoys were accompanied with male song playback. Most females were attracted to the nest boxes that emitted song (Eriksson & Wallin, 1986; Nowicki & Searcy, 2004). Similar experiments have been undertaken in the wren (*Troglodytes troglodytes*) and starling (*Sturnus vulgaris*) (Nowicki & Searcy, 2004), which again resulted in a larger number of female visitations to nest boxes emitting song.

Many studies show that male birds in temperate regions sing mostly during the breeding season, supporting the territory hypothesis, and that the timing of the most active singing periods coincides with the period where female birds are at their most fertile (Slagsvold, 1977). Males will also sing less and sometimes even stop singing following egg laying (Slagsvold, 1977). In the tropics, however, in most species, both sexes will sing all year round (Langmore, 1998).

Bird song stimulates female reproductive behaviour which has been demonstrated in solicitation assays, that showed that male song will stimulate females to exhibit a stereotypical precopulatory display (Searcy, 1992). These types of experiments are designed to gain insight into understanding the features of male songs preferred by females.

Females of many bird species, for example, will preferentially select males that sing long song bouts (Nowicki & Searcy, 2004). This has been seen in male starlings, where individuals that sing longer song bouts obtained more mates and kept mates for longer (Eens et al., 1991).

1.1.3 Individual, Species and Sex Recognition

In some species, song repertoires are used functionally for individual recognition within a population (Krebs, 1977; Brumm et al., 2009). Song repertoires have been found to be critical components in neighbour interactions in the song sparrow (*Melospiza melodia*), in which the repertoire of eight to nine song types is often enough to permit individual recognition by other males within a population (Nordby et al., 2007), although a distinctive voice will often be sufficient for individual recognition. Highly territorial birds such as the skylark (*Alauda arvensis*) have been shown to be able to distinguish intruding individuals from adjacent birds by recognising the syllable and syntactic arrangements of songs of neighbouring individuals (Briefer et al., 2009a). The ability for territorial bird species to distinguish neighbours' songs from songs of intruding individuals is important as it helps to avoid high cost and high risk confrontations (Molles & Vehrencamp, 2001).

Species-specific bird songs play a key role in mate choice and can act as an isolating mechanism among species, preventing hybridisation among species that are perfectly capable of interbreeding and producing fertile offspring (Slabbekoorn & Smith, 2002). The importance of song in species recognition was highlighted in a study on the development of songs in young male medium ground finches (*Geospiza fortis*) (Millington & Price, 1985; Ratcliffe & Grant, 1985). Female medium ground finches will mate only with males that sing the song of its own species (Millington & Price, 1985; Ratcliffe & Grant, 1985). Young birds learn their structurally simple songs from their fathers. However, it was observed that some male medium ground finches may mistakenly learn the song of the morphologically similar cactus finch (*Geospiza scandens*) and subsequently mate with female cactus finches instead of with females of the same species.

Bird song can also be advantageous in sexual differentiation and inbreeding avoidance. It has been shown to be advantageous for young finches to sing similar songs to their father so that their female siblings can avoid mating with them (Grant & Grant, 1996).

1.2 Why Study Bird Song?

Studying bird song advances behavioural and ecological knowledge of avian species (Bolhuis & Giraldeau, 2005). Studies have also advanced our understanding of how bird song is linked to acoustic adaptation, quality signalling, cultural evolution, neurobiology and conservation.

The evolution of particular song characteristics to maximise sound transmission may be influenced by different acoustic environments (Badyaev & Leaf, 1997). The acoustic adaptation hypothesis proposes that habitat type determines the acoustic properties of songs (Boncoraglio and Saino, 2007). Songs with lower frequency notes and longer pauses between sounds are more effectively transmitted in habitats containing dense, complex vegetation, because higher pitched notes would suffer degradation and decay in such habitats, consequently songs containing these note types are more effective in open habitats with greater herbaceous coverage (Nemeth et al., 2006). The amount of environmental variation on these song characteristics are, however, likely to be constrained by physical characteristics, such as body size (Badyaev & Leaf, 1997).

It is believed that the adaptation of different acoustic signals in different habitat types may provide females with acoustic cues to select males who are most suited to a particular habitat (Slabbekoorn & Smith, 2002). These males are likely to have high mate quality for that same habitat occupied by the female, highlighting the role song plays in the evolution of assortative mating (Slabbekoorn & Smith, 2002). Further to this, the ability of songbirds to switch habitats and subsequently learn songs acoustically suitable for that habitat type is an example of developmental plasticity. This adaptability to alter vocal characteristics to maximise survival and reproductive chances in different habitats can ultimately lead to speciation (West-Eberhard, 1989; Foster, 1999).

In many avian species, song is acquired through social learning, requiring complex social input (Fitch, 2009), therefore bird song is often considered to be an ideal subject to develop concepts of cultural evolution (Lynch, 1996). Cultural evolution is the non-genetic transmission of alterations in learned traits from one generation to the next (Cavalli-Sforza & Feldman, 1981; Luther & Baptista, 2010). Bird song can be transmitted either by vertical (direct from parents to offspring), horizontal (between members of the same generation) or oblique transmission (from members of one generation to members of another generation to individuals who are not direct descendants) (Cavalli-Sforza & Feldman, 1981). Song features, transmitted across generations, adapted to effectively communicate in urban environments is an example of cultural evolution in birds. An

example of an altered song feature in the white-crowned sparrow (*Zonotrichia leucophrys*), for instance, is an overall increase in minimum frequency, presumably to combat low frequency ambient urban noise (Luther & Baptista, 2010).

Studies further contributing to ecological theory have provided evidence that vocal performance in some species is a reliable predictor of male quality (Ballentine, 2009). Highly complex songs, defined as those with a large number of different syllables (Espmark, 1999; Hennin et al., 2009), sung by male swamp sparrows (*Melospiza georgiana*) are directly correlated with age and body mass. Producing and sustaining songs is very energy-costly, therefore when males produce complex songs, it is giving accurate information to the female about the quality of the male (Ballentine, 2009), moreover females of many bird species will preferentially select to mate with such individuals (Ballentine, 2009; Woodgate et al., 2010). Other factors such as the production of high frequency sounds have also been demonstrated to reflect male quality, in ocelated antbirds (*Phaenostictus mcleannani*), due to the high energy costs of producing and sustaining such vocalisations (Araya-Ajoy et al., 2009).

The neurobiological basis of bird song and bird song development is another important slant to which avian vocalisation has been researched (Nottebohm et al., 1976). Studying bird song helps scientists to understand the neurophysiological principles of how the brain organises itself during development. In many studies, parallels have been drawn between the development of song within the brain of the songbird and development of speech within the human brain (Bolhuis et al., 2010), hence the avian brain can be used as a model to help understand human speech impairments such as stammering and stuttering (Voss et al., 2007).

The role of bird vocal communication behaviour can, and has, often been applied to conservation projects in terms of counting and monitoring populations (Terry et al., 2005). However, knowledge of how individual birds communicate and the function and implications of their communication can be applied to gain important information on a species, not *only* for use in population counts or captive breeding programs but to generate knowledge of a whole spectrum of information from genetic fitness to measures of habitat and food source use (McGregor & Peake, 1998; McGregor et al., 2000). The advantage of using vocal individuality as a monitoring tool is that it is non-invasive thus far more favourable, ethically, than the highly invasive tagging and recapture techniques (Terry et al., 2005). Identifying individuals can allow scientists to make accurate predictions about survival and fertility of individual birds (Terry et al., 2005).

Knowledge of song types in the bellbird (*Anthornis melanura*) has been used as a non-invasive method to determine the source of self-introduced populations (Brunton et al., 2008). Songs at Tawharanui Regional Park were analysed and compared with songs from two offshore island populations and it was found that the songs on Little Barrier Island most closely matched the songs at Tawharanui, suggesting Little Barrier Island as the source of this self-introduced population. This method can also be employed for the detection of new individuals or groups of individuals within a population (Brunton et al., 2008).

New possibilities have opened up in this area, thanks to the advance in technologies. The sound spectrogram, originally used by Thorpe (1958) in his studies on song development of the chaffinch (*Fringilla coelebs*) was a major step in the research of bird song. Spectrograms give scientists the ability to measure, describe and analyse sounds. The recent advances in digital sound recording equipment and the development in the sound analysis computer programmes such as software “Raven” (Cornell Lab of Ornithology, Ithaca, NY, USA) has greatly advanced the studies of bird vocalisation.

1.3 The Study Subject - Tui

1.3.1 Tui Ecology

Tui (*Prosthemadera novaeseelandiae*) are honeyeaters in the Order Passeriformes, Suborder Oscine and the Family Meliphagidae. There are only two members of Meliphagidae endemic to New Zealand, the bellbird and the tui (Driskell et al., 2007), the tui being the larger and more territorial of the two species (Stewart & Craig, 1985; Bergquist, 1989).

Although relatively common and a familiar feature to even urban settings, the tui is not totally immune from habitat clearance and urbanisation and its overall abundance along with the bellbird has decreased since human colonisation of the New Zealand mainland (Castro & Robertson, 1997). The tui is facing a general decline in population trends (BirdLife International, 2010; Elliott et al. 2010). The conservation status of tui remains ‘Least Concern’, as the population is decreasing at a rate below 30% in a ten year period (BirdLife International, 2010). In the Chatham Islands, however, the number of endemic Chatham Island tui (*Prosthemadera novaeseelandiae*

chathamensis), a subspecies of the mainland tui (Oliver, 1955), has greatly declined on Pitt Island and Rangatira and became almost extinct from the main Chatham Island (Department of Conservation (DoC), 2001) and is currently classified as Endangered by the IUCN Red List Categories (IUCN, 1994).

In addition to being highly nectarivorous, tui will also eat fruits, seeds and arthropods (Craig et al., 1981; Bergquist, 1985). They inhabit mature mixed podocarp forests, coastal forests of pōhutukawa (*Metrosideros excelsa*), kowhai (*Sophora tetraptera*) and rewarewa (*Knightia excelsa*) and regenerating forests of puriri (*Vitex lucens*). Tui are also found in suburban gardens with introduced flowering plant species (Bergquist, 1989). Tui are important pollinators of native New Zealand plants mentioned above and other native plants such as New Zealand flax (*Phormium tenax*) (Wehi & Clarkson, 2007), kohekohe (*Dysoxylum spectabile*), haikaro (*Pittosporum umbellatum*) and fivefinger (*Pseudopanax arboreus*) (Anderson, 2003).

Effective dispersal of the small fruits of most plant species within the New Zealand forest relies heavily on tui (Kelly et al., 2010), which are also effective dispersers of seeds (Burns & Lake, 2009). Furthermore, the decline in tui numbers has seen a dramatic decline in endemic New Zealand mistletoe species *Peraxilla colensoi* and *P. tetrapatela* since 1840 (Robertson et al., 1999), which rely on tui and bellbird for successful pollination.

On the mainland, where bellbirds have become locally extinct, the tui is the only native bird which forages from the flowers of the widely celebrated native pōhutukawa (Schmidt-Adam et al., 2000), a tree species reported to have been reduced to just 10% of its original pre-human population levels in New Zealand by the late 1980s (Forest Research Institute, 1989) and calls have been made for a greater amount of effort to be directed toward the conservation of endemic pollinating bird species such as tui (Anderson et al., 2011) in terms of the management of regenerating native forest ecosystems.

1.3.2 Tui Song

A familiar and celebrated sound within the New Zealand forest is the song of the tui. Tui have very complex songs made up of complex syllables frequently comprised of multiple sounds, or notes. They have a range of bell and flute-like noises, cackles, barks, chimes, harsh clicks and wheezes

(Moon, 1996). The double syrinx allows Oscine birds such as tui to produce a wide array of vocalisations including multiple frequency components, superficially resembling harmonics (Nowicki & Capranica, 1986; DoC, 2006).

Tui song generally conveys information on locality, individual and group information and is designed to keep physical interaction with other individuals to a minimum (Bergquist, 1989).

Tui songs have been previously shown to exhibit sexual, seasonal and individual variation, furthermore they have been shown to match songs with other individuals within their local area, forming song similarity or dialects (Bergquist & Craig, 1988). Tui also tend to associate in large family groups, in winter moving large distances together in search of nectar. Tui will also nest close by to extended family individuals. The close association of family members and young individuals learning the songs of their family members may be factor that gives rise to local dialects (Bergquist & Craig, 1988).

Unlike results published for many species within the order Passeriformes, both sexes of tui sing throughout the year. Previous studies have also demonstrated that tui song exhibits sexual, regional, behavioural and individual variation (Bergquist, 1989). Tui will mimic other bird species such as parakeet (Robertson, 1996) and tui pairs will duet and match songs sung by mates and other tui within their region. This song-matching is believed to establish clear boundaries between territories of tui groups (Bergquist & Craig, 1988). Bergquist & Craig (1988) suggested that when the tui sang, it was more for avoidance than for aggressive territorial confrontation and that singing exhibited information about the individual's age, gender, area of origin and social status and this in turn affected access to food sources.

1.4 Knowledge Gaps and Aims of this Study

Although tui are well known for their diverse and complex vocalisations (Dawson, 1982), so far publications on tui song have been scarce and incomprehensive. A short report on tui mimicry of parakeet calls at Raoul Island was made by Robertson (1996), which was mainly anecdotal rather than an in-depth scientific study on tui vocalisation. No spectrographic images, for example, of parakeet and tui calls were presented and compared. However, this report did introduce the fact that tui do mimic other birds and that this mimicry becomes a regular component of tui dialect.

Bergquist & Craig (1988) verbally described tui songs briefly in the context of behavioural and social interactions. In a PhD thesis, Bergquist (1989) devoted a chapter to tui vocalisation describing male and female differences and seasonal and individual variation in song duration and syllable repetition. Although examples of spectrogram of some song types were given in this thesis, the parameters of song structure (such as proportion of song containing trill, song duration and minimum frequency), the diversity of syllables and the diversity of song repertoire of individual tui have not been reported. Furthermore, statistical analyses and comparisons of tui song variation within or between locations have yet to be carried out.

This study is the first research project to concentrate solely on the vocalisation of the tui. The aims of this study are to investigate structure and diversity of tui vocalisations, and to identify variations in song structure and diversity between individuals, sexes, seasons and populations. The research was undertaken in the Chatham Islands and Tawharanui Regional Park, a predator-controlled mainland island containing predominantly endemic flora, and several native birds that are not present outside the park in this area of the mainland. Therefore the data were collected from tui populations closer to their historically natural habitats, compared to the tui vocalisation study by Bergquist (1989), which was carried out at an urban site.

1.5 Thesis Structure

This thesis is organised into six chapters. **Chapter One** gives a general introduction of studies on bird vocalisation and existing knowledge on tui ecology and vocalisation. It identifies the knowledge gaps and gives the aims of this study and the structure of this thesis.

To reduce repetition, information about the study sites and methods that applies to most chapters are given in **Chapter Two**.

Chapter Three examines the song and syllable repertoire of a tui population at Tawharanui Regional Park, highlighting the size of repertoire for both syllables and songs.

Chapter Four is an investigation into individual, gender and seasonal variations of songs, syllables and song structure.

Chapter Five researches the geographical variation in tui song, concentrating on the differences between songs recorded from a population of Chatham Island tui and a population of mainland tui at Tawharanui Regional Park.

Chapter Six is a short chapter summarising the main findings of this study, its contribution towards general knowledge and the implications to conservation management. Future research direction in tui vocalisation were also suggested in the light of findings from this study.

To reduce repetition the references cited in all chapters are given at the end of the thesis.

Chapter Two: General Methods



Tui at Ecology Bush, Tawharanui Regional Park (Photograph: W. Ji).

2.1 Study Sites

Tawharanui Regional Park

The main study site of this research was Tawharanui Regional Park (36°22.143' S Longitude: 174°50.247' E), 90 kilometres north of Auckland. Tawharanui Regional Park is a 588 hectare (ha) 'mainland island' surrounded by a predator-proof perimeter fence. The coastal park became predator-free in 2004 following a successful poisoning and trapping programme (Brunton et al., 2008) and continues to be predator controlled.

Tawharanui Regional Park consists of predominantly grazed pasture (Bercusson & Walsby, 2008) with patches of regenerating manuka (*Leptospermum scoparium*) bush and some areas of mature coastal forest remnants (i.e. Ecology Bush and Possum Gully) in the central eastern part of Tawharanui. The canopy tree species in these forest remnants include pōhutukawa (*Metrosideros excelsa*), kauri (*Agathis australis*); rimu (*Dacrydium cupressinum*), puriri (*Vitex lucens*) and nikau (*Rhopalostylis sapida*) (Auckland Regional Council, n. d).

Bellbird (*Anthornis melanura*), the only endemic New Zealand honeyeater other than tui, were self-introduced to Tawharanui Regional Park from Little Barrier Island (Brunton et al, 2008) in 2006 and are now widespread throughout the park. Other endemic avian species present at Tawharanui aside from the tui include kereru (*Hemiphaga novaeseelandiae*) and kaka (*Nestor meridionalis*). Translocation projects at Tawharanui have also resulted in the introduction of North Island brown kiwi (*Apteryx montelli*), kakariki (*Cyanoramphus novaezelandiae*), robin (*Petroica longipes*), whitehead (*Mohoua albicilla*) and brown teal or pāteke (*Anas chlorotis*) (Auckland Regional Council, n. d).

Tui are abundant in the park. A proportion of the tui population are banded for this project and another study investigating their genetics and mating systems. Data collection of tui songs at Tawharanui was carried out between July 2010 and February 2011. Recordings were made in eight locations within the park: Jones Bay (partly situated outside of the predator fence), the Lagoon area, Home Bush, Possum Gully, Anchor Bay, Ecology Bush, Maori Bay and North Coast Trail where tui are abundant (Figure 2.1).



Figure 2.1: The main study site – Tawharanui Regional Park. The letters (A-J) on the map denote the areas of Tawharanui Regional Park where the majority of tui songs were recorded. A. Jones Bay Bush, B. Bunkhouse/Lagoon Area, C. Home Bush (Lower, Middle and Upper Levels), D. Possum Gully, E. Anchor Bay Car Park Area, F. Anchor Bay, G. and H. Ecology Bush, I. Maori Bay, J. North Coast Track. Adapted from the Auckland Council website, retrieved on August 17, 2010 from: <http://www.arc.govt.nz/parks/our-parks/parks-in-the-region/tawharanui/>. Adapted with permission from Auckland Council.

Chatham Islands

A trip (October 20th to November 18th 2010) was made to the Chatham Islands to record songs from Chatham Island tui (Chapter Five). The Chatham Islands are situated 800km east of Christchurch, New Zealand. The two study areas on the Chatham Islands were Rangatira (Figures 2.4 & 2.5), or South East Island, and the predator-fenced Ellen Elizabeth Preece Conservation Covenant (Caravan Bush) on the east coast of Pitt Island (Figures 2.2 & 2.3). Pitt Island is located 25km south east of the main Chatham Island and Rangatira is situated 2.5km south east of Pitt Island. On both Rangatira and Pitt Island, the flax (*Phormium chathamis*), on which the tui primarily feed during late spring and early summer, was flowering during the period of data collection. This ensured a relative abundance of tui.

The uninhabited and mammalian predator-free Rangatira Island has been described as one of the world's premier bird islands (Department of Conservation (DoC), n.d.). It is 219 ha in area and is managed by the Department of Conservation. Rangatira Island is the main breeding site of the Chatham Island tui (DoC, 2001) and is the last main stronghold of the Chatham Island robin (*Petroica traversi*) and the Chatham petrel (*Pterodroma axillaris*).

Rangatira has a year-round average temperature of 11°C. Frosts are uncommon although hail showers are common in winter months. Rangatira's annual rainfall is between 715-1050mm, skies are often overcast however in the summer it can be sunny and dry for up to a month and have up to 80% humidity. The wind on Rangatira is almost continuous and at times very strong (Roberts et al, 2007). The highest point on Rangatira is 224m and the clears in the south east of the island gently slopes up towards the peak. Whalers, along with farm animals such as goats (*Capra hircus*), cattle and sheep (*Ovis aries*), arrived on Rangatira around 1839 and much of Rangatira's native forest was cleared for pasture (Ritchie, 1970; Holmes, 1984). Rangatira became a reserve in 1954 and the last remaining agricultural stock cleared from the island by 1961 (Ritchie, 1970). Since grazing has ceased, forest regeneration has occurred in the lower part of the island in Woolshed Bush and in the top part of the island, around Top Bush (Roberts et al, 2007) (Figure 2.5). *Muehlenbeckia australis* and bracken (*Pteridium esculentum*) cover much of the forest margins (Roberts et al, 2007) and the main forest trees are ribbonwood (*Plagianthus betulinus var. chathamica*), ngaio (*Myoporum laetum*), akeake (*Olearia traversii*), matipo (*Myrsine chathamica*), karamu (*Coprosmachathamica*), mahoe (*Melicytus chathamicus*) and hoho (*Pseudopanax chathamicus*),

with kawakawa (*Macropiper excelsum*) and supplejack (*Ripogonumscandens*) common in the understorey (Dilks, 2004). An estimated 45% of Rangatira, approximately 98 ha, is covered by forest (Nilsson et al, 1994).

On Rangatira Island, other Chatham Island endemic avian species present include the tomtit (*Petroica macrocephala chathamensis*), Chatham Island warbler (*Gerygone albofrontata*), red-crowned parakeet (*Cyanoramphus novaeseelandiae chathamensis*), snipe (*Coenocorypha pusilla*) and fantail (*Rhipidura fuliginosa penitus*) (Nilsson et al, 1994).

Chatham Island tui will winter on Pitt Island (DoC, 2001) and many will fly across to Rangatira in the spring (September and October) to re-establish breeding territories (Walls et al., 2000). Flax nectar is the most important food source during the breeding season and there is an abundance of flowering flax on Rangatira in spring and in certain areas of Pitt Island. On Rangatira, the fruit of the ngaio is also an important food source. On Pitt Island, the fruit of the hoho provides much of the tui's energy requirements, supplementing flax nectar (Walls et al., 2000).

Pitt Island's Caravan Bush is a diverse and fertile habitat (Walls et al, 2000) consisting of regenerating forest tree species similar to those found on Rangatira but with more hoho and kopi (*Corynocarpus laevigatus*), and additionally, hokotaka (*Corokia macrocarpa*), and prevalent tarahinau (*Dracophyllum arboreum*) (Dilks, 2004), as well as shrubland and rank pasture (Miskelly & Emberson, 2008). Caravan Bush is 40 ha in area and is surrounded by a predator-proof fence. All introduced mammals have been eradicated from the covenant apart from mice (*Mus musculus*).

The climate on Pitt Island is very similar to that of Rangatira and is usually cool and cloudy, with strong, often south-westerly, winds (Shepherd et al, 2009).

Chatham Island endemic avian species present at Caravan Bush, besides tui, include Chatham Island warbler, fantail, red-crowned parakeet and tomtit (Walls et al, 2000).

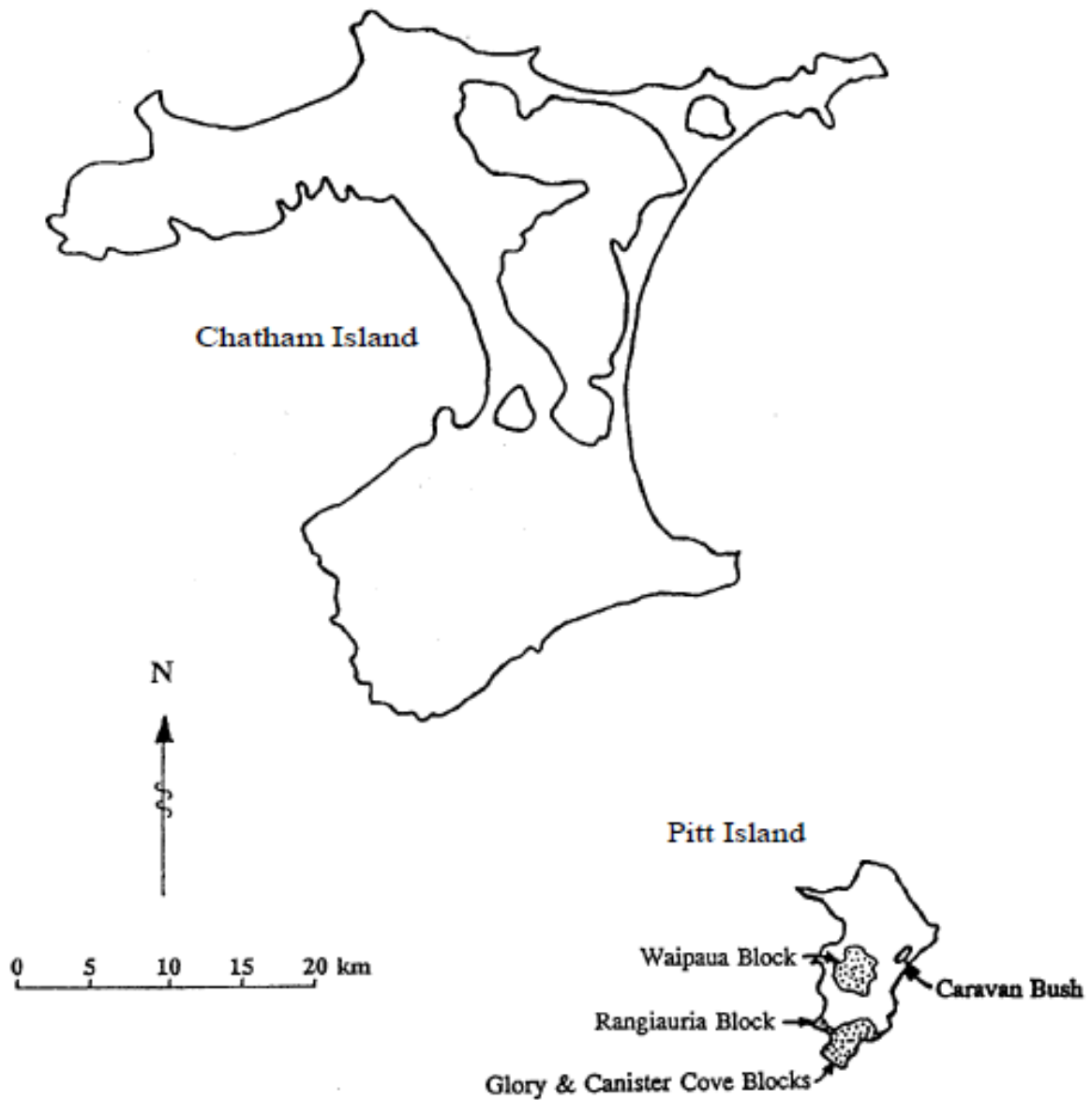


Figure 2.2: Map showing the location of Caravan Bush on Pitt Island. Adapted from Walls et al. (2000), with permission from DoC.



Figure 2.3: Ellen Elizabeth Preece Conservation Covenant (Caravan Bush), Pitt Island.



Figure 2.4: West Landing, Rangatira Island.



Figure 2.5: Map of Rangatira Island (South East Island). The letters (A-I) denote the areas where the majority of Chatham Island tui songs were recorded. A. West Landing, B. Hut Track, C. Woolshed Bush/West Woolshed Bush, D. Merlin's Bush near Thinornis Bay, E. Thinornis Bay, F. Lower Summit Bush/Track, G. Flax Island, Lower Summit Bush, H and I. Upper Summit Bush/Track. Map provided by: Department of Conservation, Chatham Islands Unit (courtesy of Abigail Liddy, Ranger, Biodiversity Assets, Chatham Islands Unit). Adapted with permission from DoC.

2.2 Recording Methods

Four devices have been used to record tui songs, Sony Portable High-Definition Minidisc Recorder, Marantz PMD671 Professional Solid State Portable Recorder, M-Audio Microtrack II and a Marantz PMD 620 Professional Handheld Solid State Recorder. These recorders were used along with a Sennheiser ME67 shotgun directional microphone. The Minidisc sound files were converted to wave (.wav) files using software ‘Sonic Stage’. On the other three recording devices, the files were saved directly as .wav files. On all devices, the songs were recorded at a sampling frequency of 44.1 Kilohertz (KHz) and with a linear pulse-code modulation (PCM), a digital storage method of analogue recordings (Gibbert et al, 2006), at a resolution of 16-bits.

The song spectrograms were produced and parameters were measured using software “Raven Pro” 1.4 Beta Version (Cornell Lab of Ornithology, Ithaca, NY, USA).

2.2.1 Field Data Collection

A transect was set up at each sampling area. During sampling sessions, the transects were walked slowly to locate tui. When a tui was located, the recording was initiated and was ended when either the tui ceased singing or flew away. During each recording, the location, time, the band combination of the tui (if applicable), behaviour and song type were also recorded.

All songs included in the analysis were recorded at a distance of 5m to 10m from the bird. Care was taken as much as possible not to disturb the birds during the recording.

2.3 Song Parameters Extracted from the Recorded Songs and Definitions

To investigate characteristics of tui vocalisations, variation of songs between song types (Chapter Three), sexes (Chapter Four), between the breeding and non-breeding season (also Chapter Four) and between regions (Chapter Five), twelve parameters were extracted from each tui song for analysis. The definition of these parameters are given in Table 2.1 and Figure 2.4. These parameters have been employed in previous studies for characterising bird songs (Mennill and Rogers, 2006; Hennin et al, 2009; Odom and Mennill, 2010).

Table 2.1: Song parameters used and their definitions.

Song Parameter	Definition
Syllabic Diversity	A syllable is a sound unit comprised of different notes, repeated notes or a single complex note. Total number of different syllables per song
Notes Per Song	Total number of notes per song A note is a single sound preceded by and followed by a silent interval
Song Duration (Seconds)	Temporal length of a song. A song is defined as a sequence of syllables preceded by and followed by a interval lasting for at least 3 seconds
Overall Mean Frequency (KHz)	Average frequency between maximum and minimum frequencies
Maximum Frequency (KHz) (F_{\max})	The highest level of frequency sung during a song
Minimum Frequency (KHz) (F_{\min})	The lowest level of frequency sung during a song
Frequency of Maximum Amplitude (FMA)	The frequency at which the highest energy level is emitted in a given song
Bandwidth (KHz)	The difference between F_{\max} and F_{\min}
FMA of Trill Component (KHz)	The frequency of the trill (modulation) component of a song at which the highest level of energy is emitted
Proportion of Song Containing Trill Component (%)	Percentage of each song (in terms of song length) containing the aforementioned trill component
Interval Between Notes (Sec)	Duration between notes
Inflection Points of the Terminal Note	The number of frequency modulation slopes in the final single sound of a song

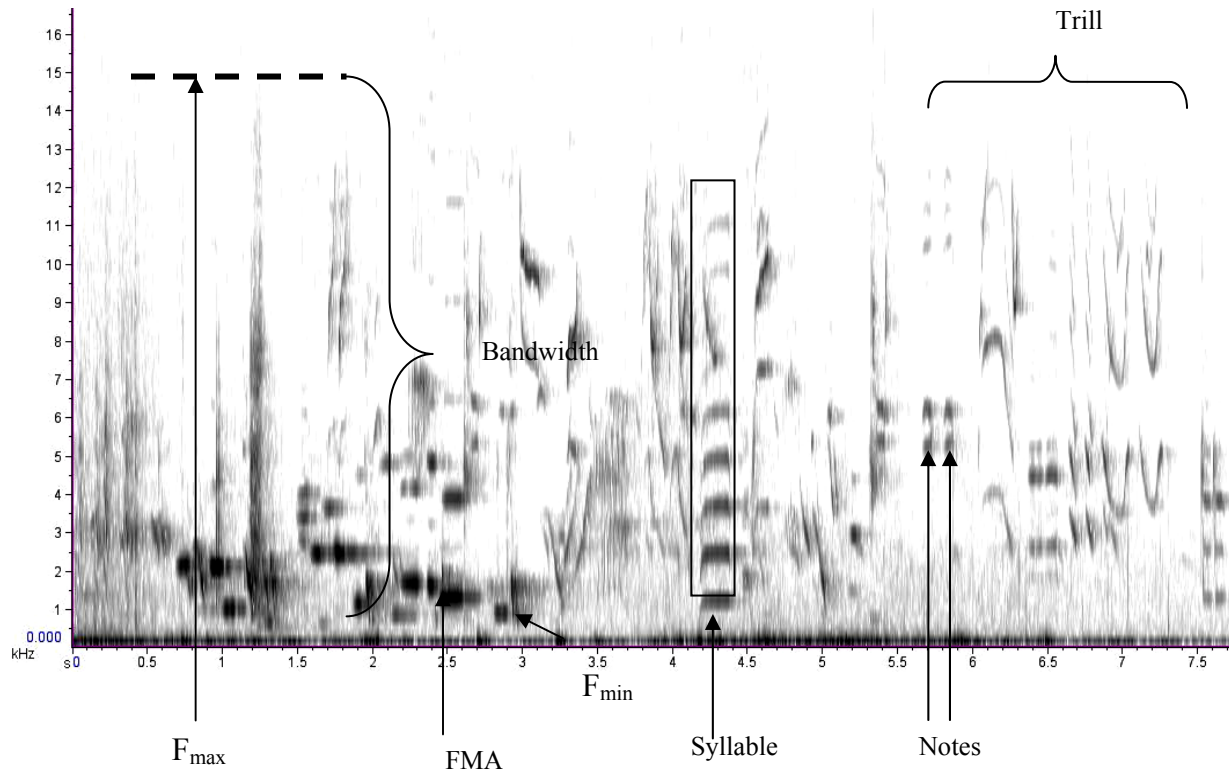


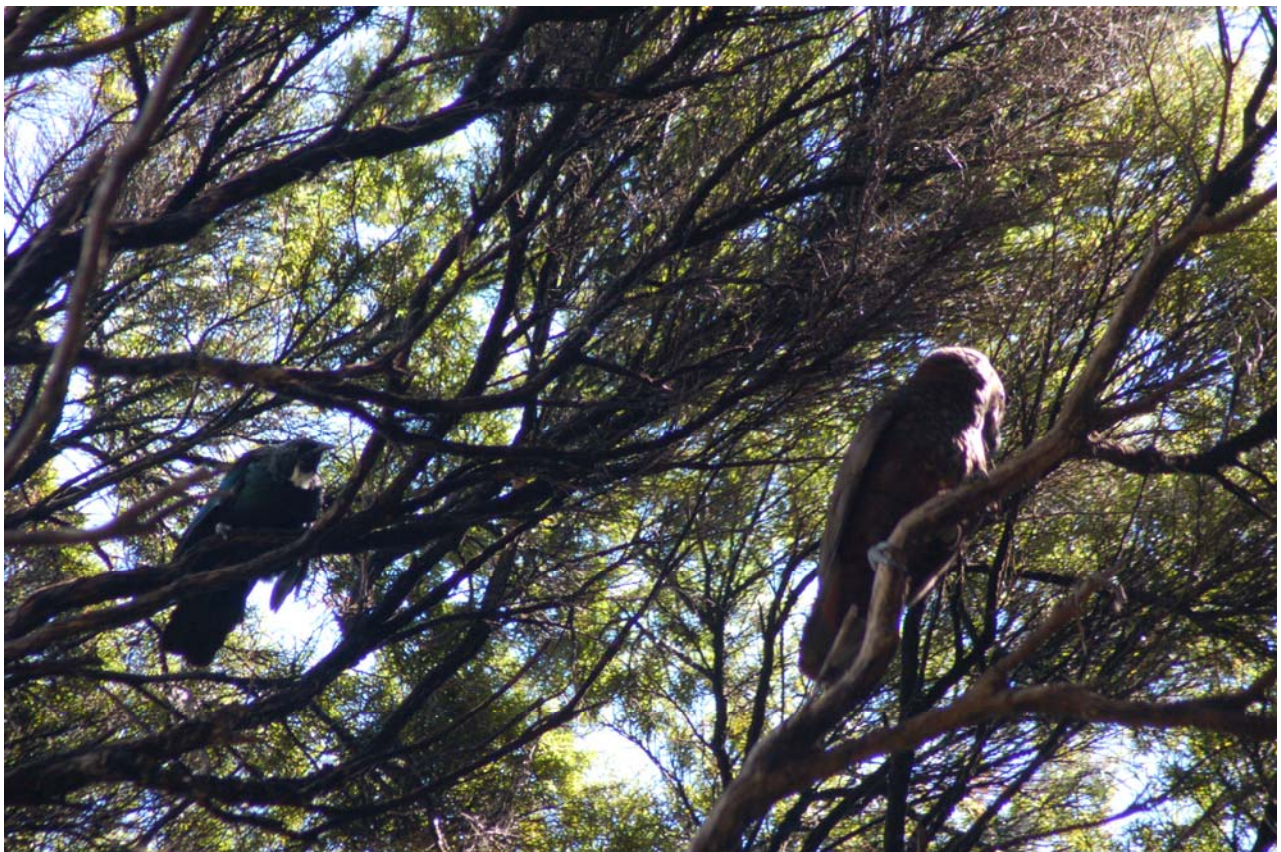
Figure 2.6: Diagrammatic representation of the main parameters employed in this study. The spectrogram used here is of a long-range tui song analysed in this study.

2.4 Data Analysis and Statistical Analysis

Parameters described in Section 2.3 were used to test the differences between song types (Chapter Three), gender and season (Chapter Four) and sites (Chapter Five).

The multivariate statistical procedure Principal Component Analysis (PCA) was used for data exploration and reduction for hypothesis testing in the relevant chapters. A Mann-Whitney U test (Mann & Whitney, 1947) was used for statistical analysis to check for significant differences between song types, gender and season and sites. Details of statistical methods are described in the relevant chapters.

Chapter Three – The Vocalisation of a Mainland Tui Population



Tui and kaka at Tawharanui Regional Park (Photograph: J. Segers).

3.1 Introduction

Song complexity varies greatly across different species. For example in the Meliphagidae, the repertoires of noisy miners (*Manorina melanocephala*) and New Holland honeyeaters (*Phylidonyris novaehollandiae*) consist of simple single note whistles (Jurisevic & Sanderson, 1994). Red wattlebird (*Anthochaera carunculata*) and the little wattlebird (*A. chrysoptera*) sing relatively simple songs, generally consisting of harsh syllables covering several frequencies (Jurisevic & Sanderson, 1994). Some honeyeater species such as the crescent (*Lichenostomus penicillatus*) and white-plumed honeyeaters (*Phylidonyris pyrrhoptera*) have varied and complex song repertoires that are generally musical in nature (Jurisevic & Sanderson, 1994).

Song complexity is thought to be the product of inter-sexual selection. In the common grackle (*Quiscalus quiscula*) (Searcy, 1992b) and in canaries (*Serinus canaria*) (Vallet et al, 1998), it has been demonstrated that female birds will preferentially select males which exhibit energy-expensive song features such as high levels of song complexity and large song repertoires. Males with more complex songs have been shown to arrive earlier into a breeding territory than the less experienced and lower-quality males (Alatalo et al, 1986; Lampe & Espmark, 1994), demonstrating that song complexity is an indicator of male fitness.

Song matching is when rival birds sing the same song or song type as another nearby individual, as observed in great tits (*Parus major*), for example (Krebs et al, 1979), and is considered to be of prime importance in mate attraction and territorial defence (Briefer et al, 2009). This coordinated singing will mainly occur between two or more rivalling territorial males (Catchpole & Slater, 2008).

Male indigo buntings (*Passerine cyanea*) that share songs with neighbouring rival males have a greater chance of mating, nesting and fledging young, suggesting that a male will have a competitive advantage over others if he is able to match the songs of other birds (Payne, 1982). In great tits, it has been shown that males with larger and more complex song repertoires will have larger territories than those with smaller repertoires (Barnard, 1983) and in red-winged blackbirds, it has been observed that the playback of the large repertoire of an individual male was more effective at decreasing the trespass rate by other birds, than playing single songs (Yasukawa, 1981). A dominant male would have a reproductive advantage over other males in being able to inhibit the matching of his songs by rival males and therefore have a greater chance of successfully defending

a territory (Payne, 1982). High levels of song complexity in male songbirds could be attributed to minimising the chances of song matching by rival territorial males.

Complexity of bird vocalisation can be investigated through studying the structure and measurable parameters of bird songs or calls. Important parameters used in previous studies researching song structure include bandwidth, which is defined as the difference between maximum and minimum frequency in any given song; song duration, defined literally as the length of each song; mean, maximum and minimum song frequency or pitch; syllabic diversity, which is the number of different syllables produced within a repertoire; and the frequency or proportion of trill component, or frequency modulation syllables.

Broad bandwidths are likely products of sexual selection. In male eastern whipbirds (*Psophodes olivaceus*), the signature ‘whip-crack’ syllable has a large bandwidth of approximately 8KHz, it is consistently and geographically the least variable sound unit within a male’s repertoire (Mennill & Rogers, 2006). It is therefore likely that a large bandwidth is a sexually-selected trait, presumably because the ability to produce such a sound reflects a male’s physiological and morphological capacity and therefore its overall quality (Potvin et al, 2011).

Another important parameter used in previous bird vocalisation studies is song duration. In zebra finches (*Taeniopygia guttata*), for example, it has been shown that length of male songs can accurately reflect an individual’s early developmental condition, thus is a measure of its overall fitness (Leadbeater et al, 2005). In male birds of several species, long songs are attractive to females (Catchpole, 1986) and have also been directly linked with age, experience, parental ability (Rehsteiner et al., 1998), body condition (Lampe & Espmark, 2003), immunocompetence (Duffy & Ball, 2002) and genetic quality (Lambrechts & Dhondt, 1988; Forstmeier & Leisler, 2004; Leadbeater et al., 2005).

Frequency of song is another parameter used in bird vocalisation studies. There is evidence supporting the hypothesis that songbirds will alter the pitch, or frequency, of their vocalisation in different habitats (Nemeth et al, 2006; Boncoraglio and Saino, 2007; Potvin et al, 2011). It has been shown that birds will sing at lower frequencies in areas with dense vegetation than in areas of open habitats (Nemeth et al, 2006). In urban habitats, it was shown that silvereyes (*Zosterops lateralis*) will sing at an overall higher frequency than rural birds (Potvin et al, 2011). This vocal alteration has also been observed in blackbirds (*Turdus merula*), where urban birds will sing higher

minimum and maximum frequencies than rural birds, adapted to counter low-frequency anthropogenic noise (Mendes et al, 2011), or as a result of more intense vocal interaction in densely populated urban areas (Nemeth & Brumm, 2009). In either case, the adaptability of bird vocalisation to urbanisation is a result of behavioural plasticity (Wood & Yezerinac, 2006).

Syllabic diversity, which is defined as the number of different syllables that are sung per song is a reliable predictor of song complexity. The complexity of a song is a sexually-selected trait linked to male genetic quality, due to the underlying neural mechanisms controlling bird song production and learning development during the early stages of life, when the bird is under the greatest levels of developmental and nutritional stress (Nowicki et al, 1998b; Espmark, 1999; Searcy and Nowicki, 2000 & 2005; Nowicki et al, 2003; Hennin et al, 2009).

Another parameter linked with song complexity is trill. Songbird trills are defined as rapid, high or low-frequency modulations (Nemeth et al, 2006). Female songbirds perceive rapid trill as a predictor of high male quality, such are the high energy demands of producing trill components (Ballentine et al, 2004; Hennin et al, 2009). Trills have also been shown to be aggressive signals in territorial male nightingales (*Luscinia megarhynchos*) (Schmidt et al, 2008) and swamp sparrows (*Melospiza georgiana*) (DuBois et al, 2009). Furthermore, it has been shown that in areas with dense vegetation, birds will sing less trill than in open habitats, to minimise sound decay (Nemeth et al, 2006).

Some aspects of song such as the production of complex syllables may be difficult to produce if for example they are dependent upon body size (Price et al, 2006) or require the fine coordination of special mechanisms within the respiratory system (Suthers et al, 1999). Experiments have shown that during territorial vocal contests in male Montezuma oropendolas (*Psarocolius montezuma*), the minimum frequency is negatively correlated with body size, based on average tarsus measurement (Price et al, 2006). This relationship suggests that the production of energy-expensive loud, low-frequency syllables exhibits honest signals of competitive ability during male-male conflict (Price et al, 2006). Other experimental work has shown that the production of complex syllables such as trill are under constraints of the vocal tract (Podos, 1997).

The production of trill has been shown in young swamp sparrows to be constrained by physical limits (Podos, 1995). Playback of conspecific song, containing trill syllables repeated at rates above normal levels, was presented to the young birds, resulting in the production of song that was

inaccurate and contained many pauses and broken syntax (Podos, 1995). The flawed songs of these young swamp sparrows demonstrates that the development of trill structure is limited by motor constraints on the production of song (Podos, 1995).

Another indicator of song complexity is the repertoire of songs of an individual or a species (Neubauer, 1999; Buchanan & Catchpole, 2000; Pfaff et al, 2007; Boogert et al, 2011). Large song repertoires have been shown to positively correlate with cognitive performance in male song sparrows (Boogert et al, 2011) and with learning ability in the zebra finch (Boogart et al, 2008). Male song sparrows with larger repertoires have been shown to contribute a greater number of independent offspring and grandoffspring to a population (Reid et al, 2005) and in common grackles, females will preferentially select those males with larger song repertoires, despite many male common grackles singing only one song type (Searcy, 1992b). Syllable repertoire, or syllabic diversity, is also a factor commonly used to measure song complexity in song bird studies (Garamszegi & Møller, 2003; Macdougall-Shackleton et al, 2009). The greater the syllable diversity, or number of different syllables counted either within a population or a song from an individual's entire repertoire, the more complex the song and the repertoire are considered to be.

Studying song structure and repertoire of a species is important for attaining knowledge of signaling functionality in sexual selection and in a social context (Boisseau, 2005). Song repertoire studies are also important for understanding the geographical variation, the acoustic adaptation of songs and speciation (Peshek & Blumstein, 2011).

3.1.1 Study Objectives

Knowledge of bird vocalisation can also be applied in conservation management. Data of a species' song repertoire collected using microphones in conjunction with advanced statistical analysis has been previously proven to be a good method for avian population surveying (Dawson & Efford, 2009). Such methodology is considered to be more ethical, accurate and less labour intensive than older methods and has been identified as a priority for research (Nichols et al, 2009).

The tui is one of the two New Zealand honeyeaters. While bellbirds (*Anthornis melanura*) have disappeared from the unprotected habitats in the north part of the North Island, tui are still abundant and have also adapted to colonise urban areas with high densities of introduced avian fauna and high levels of human disturbance. Tui are well known for their aggressive nature (Craig,

1984) and song complexity (Moon, 1996). They not only use songs but also the noise made by their wings, due to the presence of a notch in the eighth primary feather of the wing, in intra and inter-species interactions. These characteristics may have contributed to the success of this native honeyeater. So far, there have been no in-depth studies on tui vocalisation. Bergquist (1989) gave some information about tui songs in an urban population in a PhD thesis which showed that both male and female tui sang loud, complex songs all year round. It was shown that females will sing songs more complex than males. There are a lack of systematic studies of tui song structure, complexity and repertoire of songs and syllables.

In this study I aim to investigate the structure and diversity of tui vocalisations by investigating types of calls and songs, measuring spectral characteristics of their calls and songs and to explore the syllable and song repertoire in a population of tui in Tawharanui Regional Park. The research questions include:

1. How complex are tui vocalisations in terms of song and syllable repertoire? I predict a high song and syllable diversity both at the individual level and population level. I also predict a low level of syllable repetition within the population.
2. What are the differences between long range and short range songs in terms of spectral structure? Long-range broadcasting songs are usually for territorial defence and mate attraction. I predict that long range songs contain higher proportion of trills, which was shown to be more difficult to produce and may convey the genetic quality of the singer. Furthermore, I predict that long-range songs will contain a wider bandwidth than short-range songs due to sexual selection for songs that are costly to produce.

This study will provide baseline information for further investigations such as the individual, seasonal and regional variation of tui vocalisation.

3.2 Methods

This study has been carried out at Tawharanui Regional Park. Details of the study site and recording methods are given in Chapter Two.

Parameters Used and their Definitions

The following parameters were used in this study:

The spectrum parameters of calls and songs include syllabic diversity, number of notes per song, song duration, overall mean frequency, maximum frequency, minimum frequency, frequency of maximum amplitude (FMA), bandwidth, FMA of the trill component, the proportion of song containing trill, interval between notes and the number of inflection points in the terminal note. The definition of these parameters are given in Table 2.1 of Chapter Two.

1. Song Diversity: The number of different songs recorded. A song is defined as a sequence of syllables preceded, and followed, by, a period of three seconds or more. The number of different songs heard within the population was counted using spectrograms of the recordings. A new song was defined as a sequence of syllables unseen in any previous songs recorded. Songs were occasionally comprised of similar syllables but if the sequence of syllables was unique, it was considered a different song.

2. Syllable diversity: Number of different syllables recorded. A syllable is defined as an individual sound unit. Images of syllables were extracted from the spectrograms. Each individual syllable was compared to all other syllables using ear and spectrogram visual analysis (Ranjard & Ross, 2008) to identify new syllables and determine the number of times a particular syllable had been repeated. A sequence of syllables makes up a song. Due to the large number of syllables encountered in each song and time constraints, the number of syllables could only be obtained from 30 randomly selected tui songs from the study site. Of the 30 songs, 13 were from the non-breeding season and 17 were from the breeding season. Fifteen of the songs were long-range broadcast songs and 15 were short-range interactive songs.

Saturation curves were then plotted in order to estimate the syllable repertoire of this population. It involves the creation of a graph with the cumulative number of syllables recorded on the x axis and

the cumulative number of new syllables recorded on the y axis. When a plateau or an ‘asymptote’ is reached, the researcher can assume that most syllables within a repertoire have been recorded (Garamszegi et al, 2002; Molles et al, 2006).

3. *Song Types*: To investigate differences in the spectral characteristics between long-range and short-range songs, multivariate statistical procedure Principal Component Analysis (PCA), was used for data exploration and reduction for hypothesis testing. Mann-Whitney U test (Mann & Whitney, 1947) was used for testing the difference between song types by assessing whether or not the two independent samples of observations had equally large values, by comparing median values. Boxplots were then created to visualise the data (Figure 3.7). All statistical tests were performed using software R 2.12.2 (R Development Core Team, 2010) and Microsoft (Redmond, USA) Excel.

All PCA procedures were performed using package FactomineR; and all statistical tests were two-tailed. For the Mann-Whitney U test, only P values <0.05 were interpreted as significant for a 95% confidence interval.

3.3 Results

3.3.1 Population Song Repertoire

A total of 2.4 hours of song recording was obtained during 10 days (48.5 hours) of field sampling between July and December 2010. A total number of 303 distinctly different songs were recorded (Appendix 1). Within this 303 different songs, there were four main types of vocalisations recorded, alarm call (1), distress call (1), long-range broadcasting (168) and short-range interactive songs (133) (Figure 3.1). The range of frequency of short-range songs was 0.09 KHz to 18.97 KHz. The range of frequency of long-range songs was 0.25 KHz to 22.1 KHz. The alarm call ranged from 0.07 KHz to 22.1 KHz and distress call from 0.05 KHz to approximately 17 KHz. The range of song duration for short-range songs was 1.4 sec to 17.9 sec and the range of song duration for long-range songs was 1.3 sec to 40.4 sec. The length of the alarm call was 2.6 sec and the length of the distress call was 3 sec.

Because only one alarm call and one distress call were collected, further analysis was focused on investigating differences between long-range and short-range songs.

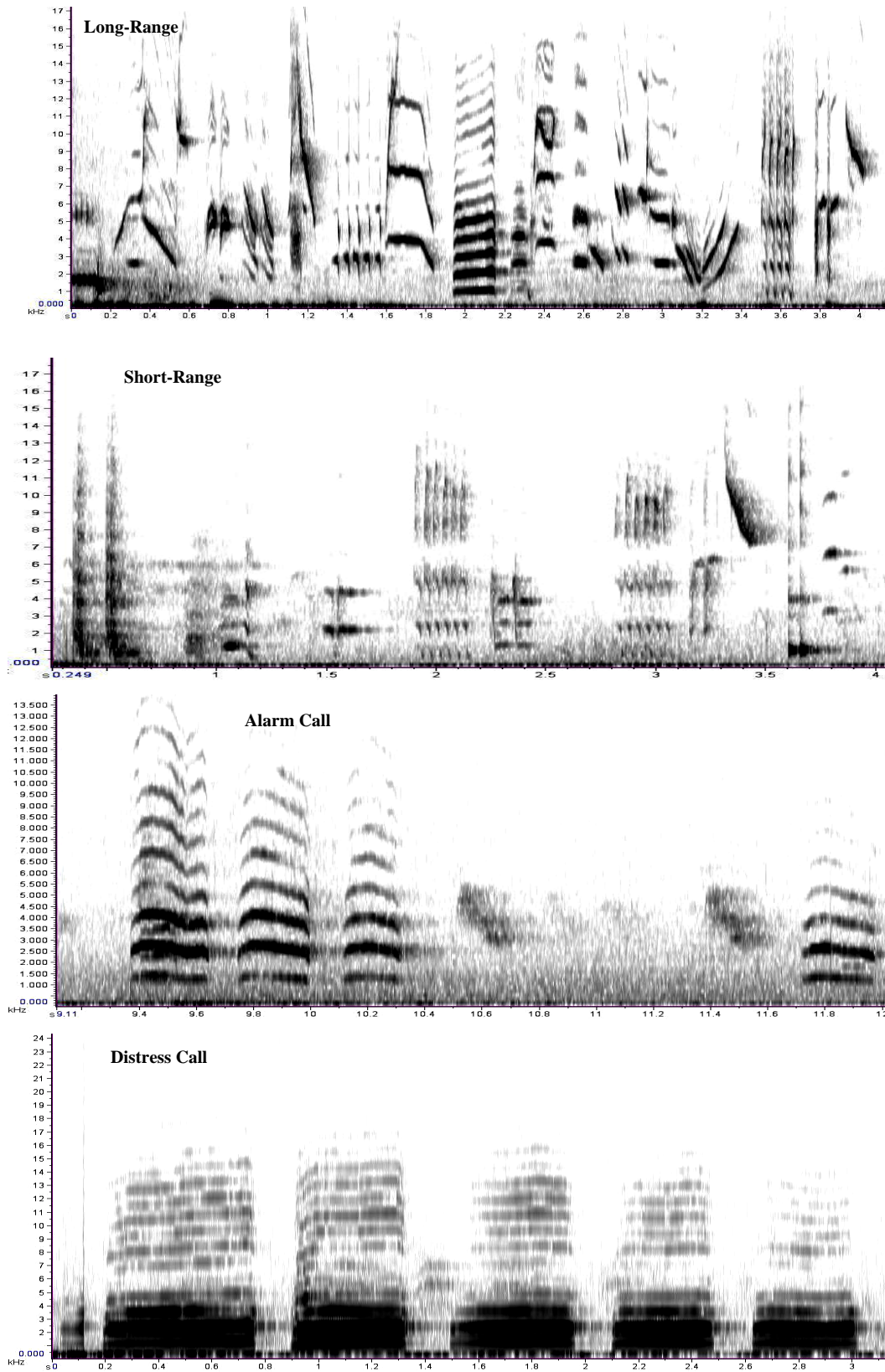


Figure 3.1: From top to bottom: spectrograms showing examples of a tui long-range song, a tui short-range song, an alarm call and a distress call, from Tawharanui Regional Park.

3.3.2 Population Syllable Repertoire

From the 30 randomly selected songs from 30 different individuals, 264 distinctly different syllables were recorded (see Appendix 2 for spectrogram images of these syllables). The accumulative number of syllables has not reached asymptote from 30 songs analysed and a total number of 552 syllables isolated from these 30 songs (Figures 3.4 and 3.5).

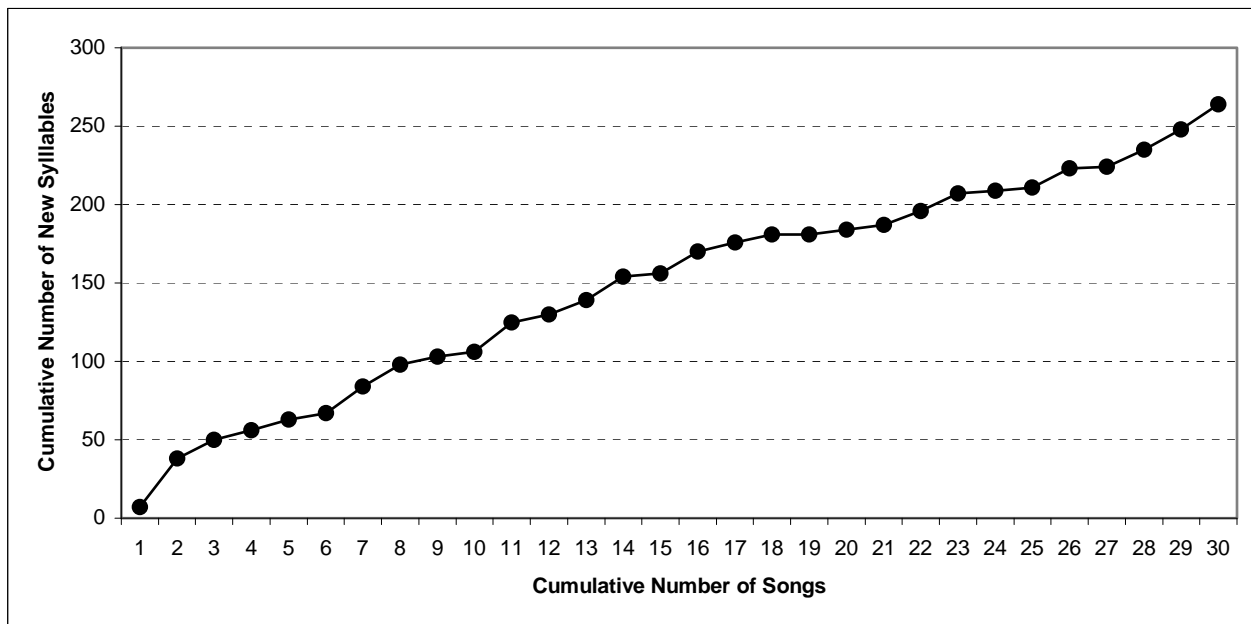


Figure 3.2: Accumulative number of new syllables encountered from the 30 tui songs analysed.

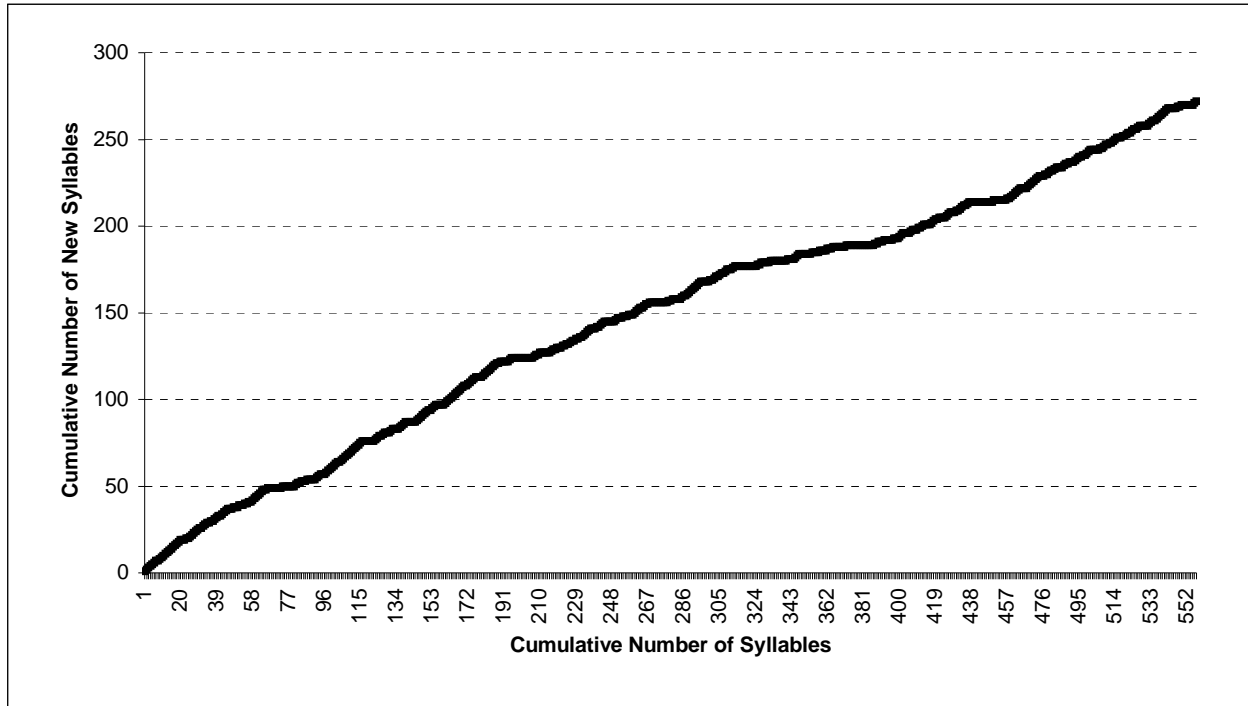


Figure 3.3: Accumulative number of new syllables encountered vs accumulative total number of syllables recorded from the 30 songs.

3.3.3 Syllable Frequency Distribution

From all songs collected, only 13 songs from different individuals in non-breeding season (February to August) were available. These 13 non-breeding season songs plus 13 songs randomly chosen from breeding season (September to January) were used for plotting the syllable frequency distribution. From these 26 songs a total of 379 syllables were recorded, among which 190 distinctly different syllables were observed. Of these 190 syllables, 114 different syllables (60% of the total) were recorded only once, and only 7% of these 190 syllables were recorded five times or more (Figure 3.4). The most commonly recorded syllable (repeated 13 times) was sung by 11 different individuals and the second most commonly recorded syllable (repeated 11 times) was sung by 9 different individuals (Figure 3.5; and the remaining most common syllables in Appendix 2) and the third most common syllable (repeated 9 times) was sung by 7 different individuals. These results highlight both the low repetition rate of syllables and large syllable repertoire within a tui population.

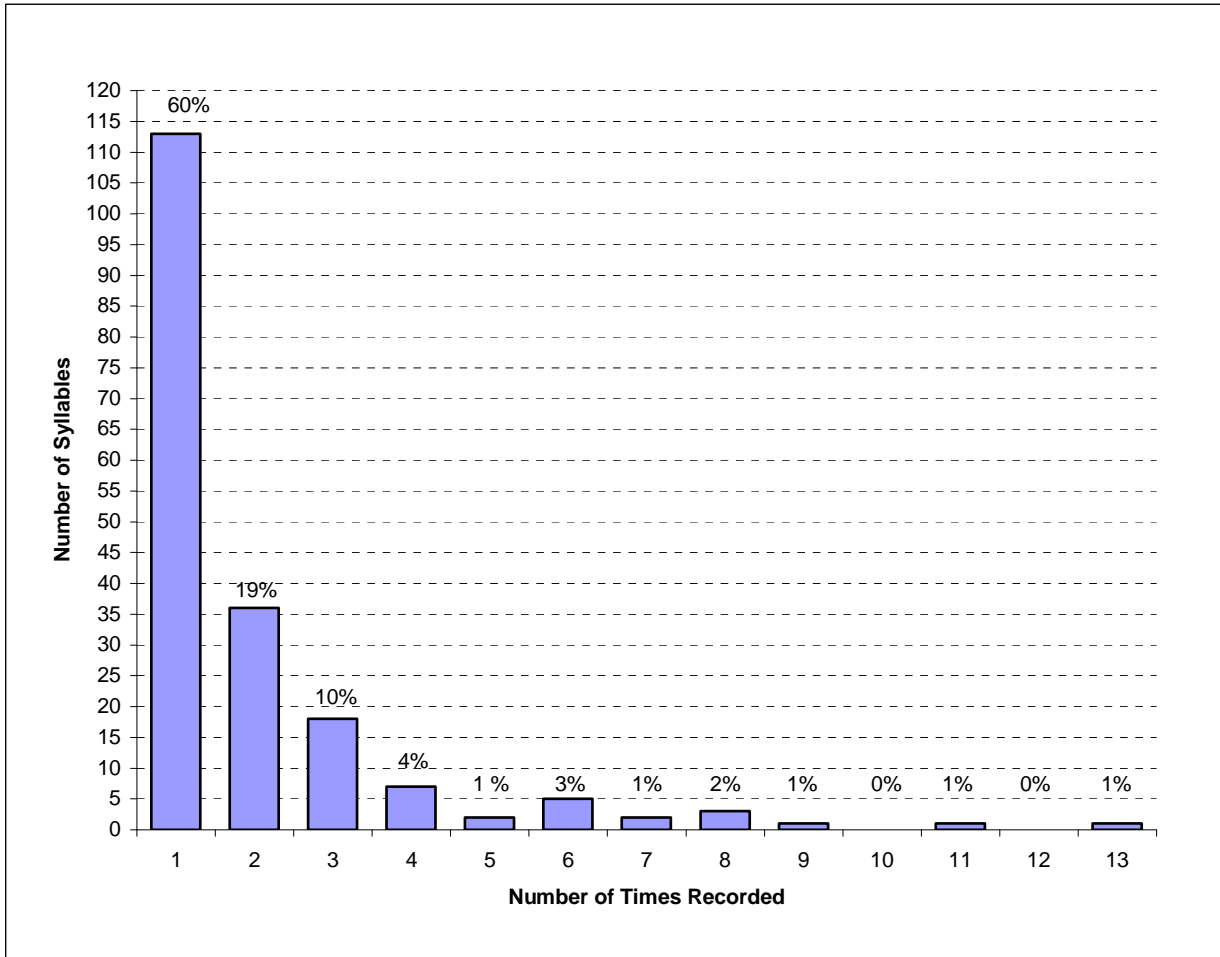


Figure 3.4: The syllable frequency distribution at Tawharanui Regional Park for 26 songs.

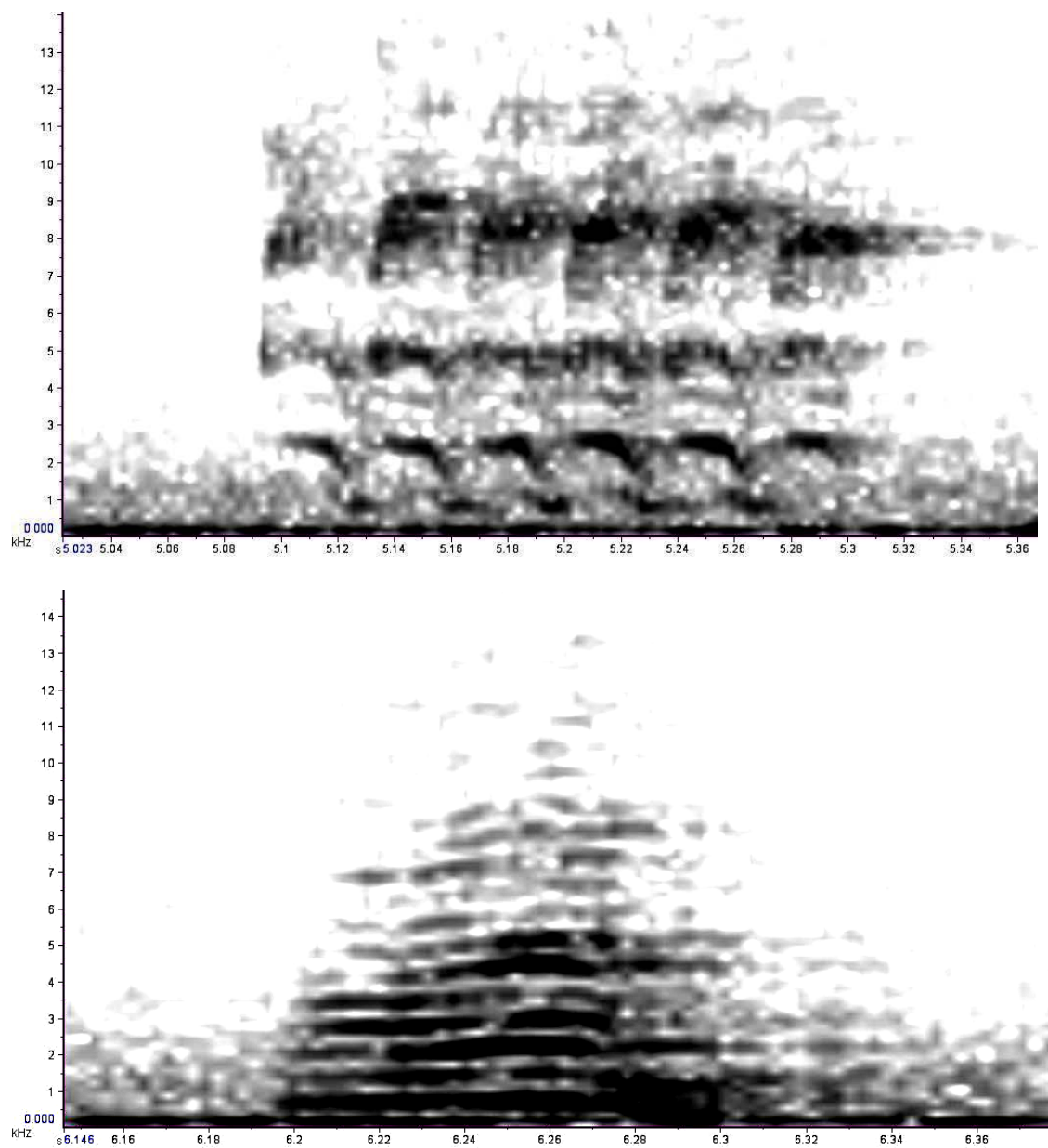


Figure 3.5: Spectrographic images of the two most common syllables within the songs recorded at Tawharanui. Most commonly repeated syllable (top) and the second most commonly repeated syllable (below).

3.3.4 Variation Between Long and Short-Range Songs

To explore the differences between long and short distance songs of tui. The following variables were extracted from a subset of 30 songs recorded: syllabic diversity, number of notes per song, song duration, overall mean frequency, maximum frequency, minimum frequency, FMA, bandwidth, FMA of the trill component, the proportion of song containing trill, interval between notes and the number of inflection points in the terminal note. The definition of these parameters are given in table 2.1 of Chapter two. Firstly, a test for correlations between these twelve variables was carried out. Syllabic diversity, maximum frequency, mean frequency and the number of notes per song were significantly correlated with two or more other variables (Table 3.1). These four variables were excluded from further analysis.

Table 3.1: Table showing the p-values based on the correlation coefficients for each variable. The figures in red denote significant correlations ($p = <0.05$) between particular variables, such as Fmax and bandwidth; and song duration and interval between notes.

	Bandwidth	FMA Song	FMA Trill	Fmax	Fmean	Fmin	Interval Between Notes	Inflection Points of Terminal Note	Number of Notes Per Song	Proportion of Song Containing Trill	Song Duration	Syllabic Diversity
Bandwidth												
FMA Song	0.4181											
FMA Trill	0.2263	0.2643										
Fmax	0.0000	0.4576	0.2417									
Fmean	0.0000	0.5005	0.2590	0.0000								
Fmin	0.0324	0.0944	0.2649	0.0872	0.2016							
Interval Between Notes	0.4273	0.2099	0.1073	0.4459	0.4661	0.3884						
Inflection Points of Terminal Note	0.5578	0.1991	0.0584	0.5185	0.4808	0.2160	0.2480					
Number of Notes Per Song	0.0020	0.2921	0.0022	0.0030	0.0046	0.0009	0.1352	0.5912				
Proportion of song containing trill	0.2851	0.4330	0.0065	0.2976	0.3116	0.4098	0.7699	0.0792	0.0000			
Song Duration	0.0032	0.1028	0.0041	0.0046	0.0067	0.0024	0.0000	0.1577	0.0000	0.0123		
Syllabic Diversity	0.0012	0.2447	0.0018	0.0020	0.0033	0.0002	0.1004	0.4567	0.0000	0.0000	0.0000	

PCA analysis of the eight chosen variables from long and short-range songs showed that Principal Component 1 or PC1 contributed 29.18% of the variance between song types and was significantly

correlated with song duration, bandwidth, proportion of song containing trill, interval between notes and minimum frequency (Table 3.2). PC2 contributed 19.27% of the variance between song types and was correlated with interval between notes, minimum frequency, FMA of the entire song and FMA of the trill component of song. Figure 3.6 shows a scatterplot from the PCA. The variables that had the highest correlation with PC1 and therefore contributed the greatest level of variation between the two song types were subsequently chosen for further statistical analysis. As the majority of the data exhibited nonparametric distribution, a Mann-Whitney U test was performed ($n = 18, 12$).

Table 3.2: Eigenvalues, variance explained and factor loadings of the eight variables following PCA analysis. Variables with factor loading values greater than 0.48 (or -0.48) are highlighted in bold.

	PC1	PC2
Eigenvalue	2.3	1.5
% of Variance	29.18	19.27
Song Duration (Sec)	0.79	-0.25
Bandwidth (KHz)	0.77	0.20
Proportion of Song Containing Trill (%)	0.68	0.11
Interval between notes (Sec)	0.59	0.49
Minimum Frequency (KHz)	-0.48	-0.65
FMA of Entire Song (KHz)	-0.12	0.78
FMA of Trill Component of Song (KHz)	0.13	0.38
The number of inflection points in the terminal note	0.16	-0.06
<i>n</i> = 18, 12		

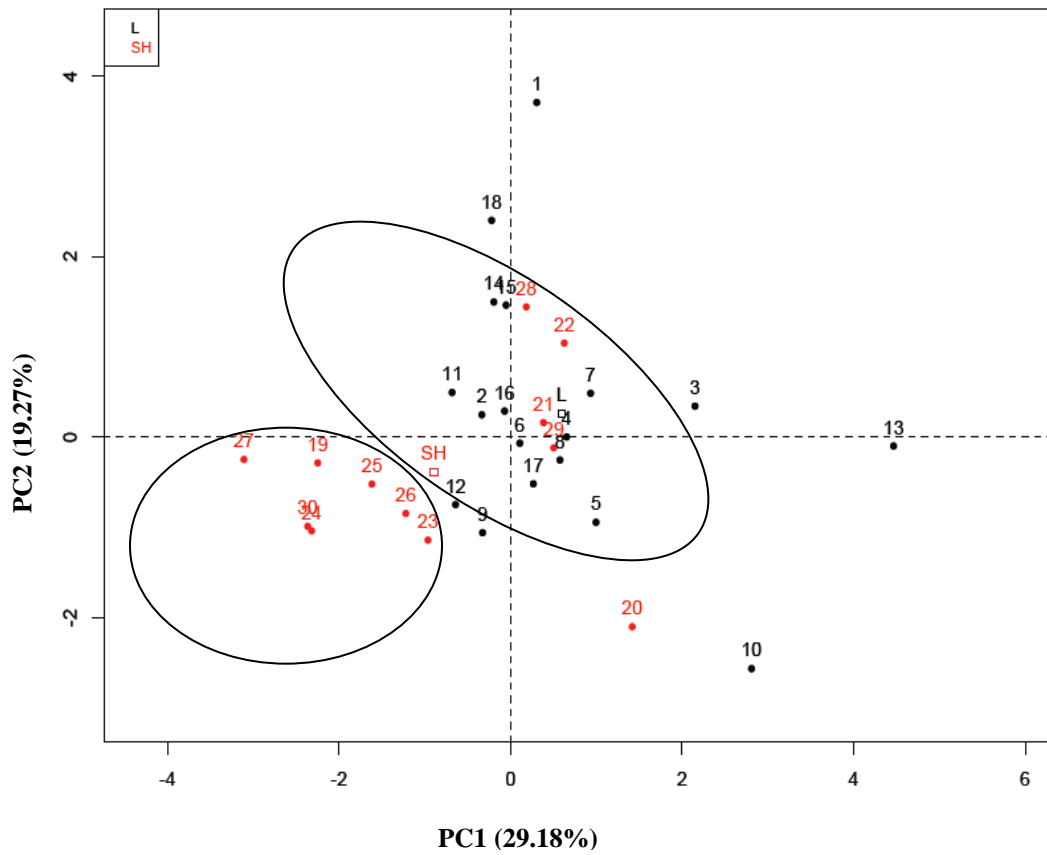


Figure 3.6: A PCA scatterplot with hand-drawn circles highlighting the main separation between long-range (L) and short-range songs (SH) at Tawharanui.

The results showed significant differences between song types in both the proportion of song containing trill ($p = 0.01031$) and minimum frequency ($p = 0.0276$) but no significant difference between song types in song duration ($p = 0.33$), bandwidth ($p = 0.0513$) and interval between notes ($p = 0.82$) (Table 3.3).

Table 3.3: Median value, the range of the song variables for short and long-range tui songs and the results of the Mann-Whitney U test.

Variable	Median		Range		Statistical Values from Mann-Whitney U Test	
	Long-Range Song	Short-Range Song	Long-Range Song	Short-Range Song	W	p
Proportion of Song Containing Trill (%)	51	12	75 Min: 18 Max: 93	90 Min: 0 Max: 90	186	0.001031
Minimum Frequency (KHz)	0.47	0.59	0.43 Min: 0.25 Max: 0.68	0.32 Min: 0.40 Max: 0.72	56	0.0276
Song Duration (Sec)	5.9	5.7	37.3 Min: 3.1 Max: 40.4	11.4 Min: 1.5 Max: 12.9	132	0.3252
Bandwidth (KHz)	14.6	10.4	11 Min: 10.9 Max: 21.9	19.5 Min: 2.2 Max: 21.7	154	0.0531
Interval Between Notes (Sec)	0.1	0.1	0.21 Min: 0.05 Max: 0.26	0.25 Min: 0.02 Max: 0.27	114	0.8159

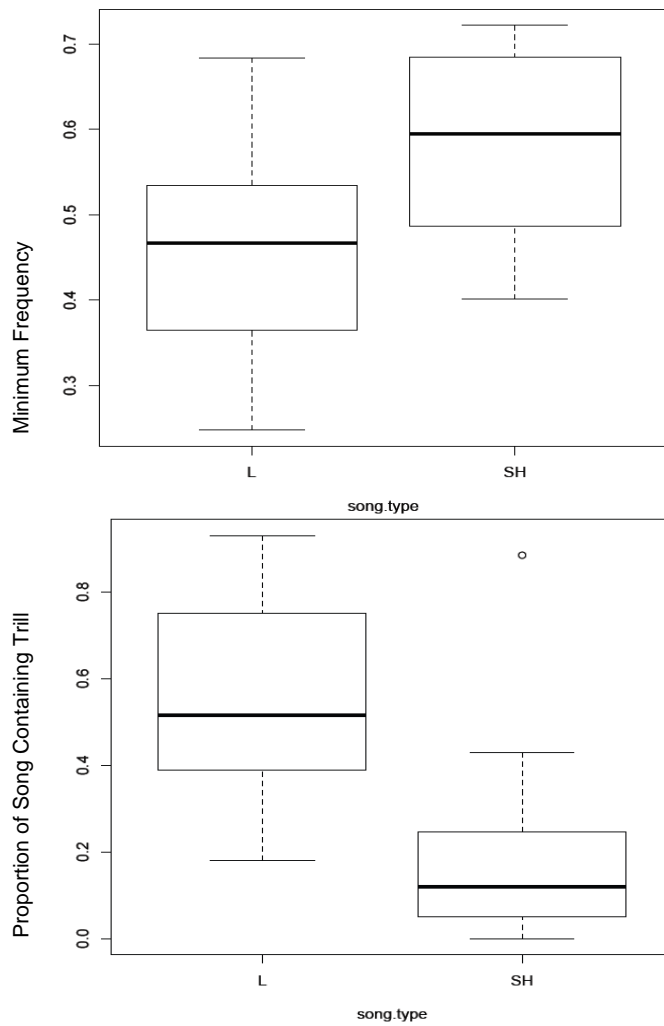


Figure 3.7: Boxplots showing the parameters that exhibited statistically significant differences between long and short-range songs at Tawharanui. Minimum frequency (top) and proportion of song containing trill (bottom). The median values are depicted by the black horizontal lines within the boxes.

3.4 Discussion

3.4.1 Song and Syllable Repertoire at the Population Level

Three hundred and seventy-three distinctly different songs were recorded in tui over a total of 48.5 hours of field sampling and 2.4 hours of recording. A study on songs of saddleback (*Philesturnus carunculatus*), another New Zealand bird species known for their diversity of songs, reported approximately 200 distinctly different songs, at multiple locations from 2,700 recordings (Parker, 2011). The white-plumed honeyeaters have a vocal repertoire of just three songs interspersed with whistles and calls and the repertoire of the New Holland honeyeater is small and limited due to the simple nature of its syllables which do not allow for a broad song variation (Jurisevic & Sanderson, 1994), whereas the song repertoire of a mainland population of singing honeyeater (*Meliphaga virescens*) in Australia has been recorded as 47 distinctive songs (Baker, 1995). It is therefore evident that the tui do indeed have very large song repertoires at the population level.

A large number of syllables have been recorded, as predicted. At a single locality, 264 distinctly different syllable types were obtained from 30 tui songs analysed. Plotting of the accumulative new syllables for the 30 songs analysed showed little evidence of saturation. The trendline suggests there are more syllables to be obtained within the population. Compared with a species such as the tree pipit (*Anthus trivialis*), which is considered also to have a large syllable repertoire, with a maximum of 82 distinctly different syllable types observed at a single location in one study (Petruškova et al, 2008), tui have a very large and highly complex repertoire of syllables. Repertoire has been described as being particularly difficult to estimate for bird species that produce many and highly variable songs (Peshek & Blumstein, 2011).

The syllable frequency distribution of tui within Tawharanui showed that the majority of syllables (175 of the 190 different syllables recorded) were recorded just four times or less, in 26 songs analysed. This low level of syllable repetition was predicted. Fifteen syllables (7%) were recorded five times or more. One could tentatively suggest that these more common syllables are signature syllables within this population, possibly facilitating tui species identification and syllable sharing. Syllable sharing has a territorial function in males and is more likely between close neighbours, as seen in Anna's hummingbird (*Calypte anna*) (Yang et al., 2007), in order to be able to differentiate

friend from foe (Briefer et al., 2009b), ensuring less time and energy are expended in needless physical confrontation (Molles & Vehrencamp, 2001; Catchpole & Slater, 2008).

A degree of syllable sharing within a population is also a signal of genetic similarity (Stewart & MacDougall-Shackleton, 2008). Furthermore, those males that share a greater number of syllables within a song with other males, have been shown in song sparrows to have larger testosterone-dependent traits such as cloacal protuberance, which is correlated with extreme sperm production as a result of sperm competition in Australian fairywrens (Aves: Maluridae) (Tuttle et al, 1996). Syllable sharing is also linked with fewer blood-borne parasites and lower levels of nutritional stress (Stewart & MacDougall-Shackleton, 2008).

It is possible, however, that the tui will ‘invent’ or improvise new syllables much like the song sparrow and American robin (*Turdus migratorius*) have been shown to do (Duke University, 2002; Beecher & Brenowitz, 2005; Johnson, 2006; Johnson, 2006; Parker, 2011). A large pool of syllables facilitates such improvisation and may be a contributory factor to such a large song repertoire in tui.

3.4.2 Variation Between Song Types

Four main song types have been recorded in this tui population: alarm calls, distress calls, short range songs and long range songs.

Alarm and distress calls are relatively short and simple, produced at high amplitude, spread over a broad range of frequencies and the majority of the sound energy was concentrated in the lower frequencies. These features help ensure the song is both heard and easily located by conspecifics both close by and much farther afield. The structures of tui alarm and distress calls have marked similarity to other honeyeater species such as the red wattlebird (Jurisevic & Sanderson, 1994). Tui alarm and distress calls have been observed to alert not only conspecifics but also other species such as bellbird and attracted a predator species on more than one occasion, the Australasian harrier (*Circus approximans*) (Pers. Obs. S. Hill, 2010). Alarm and distress calls show multiple harmonics reflecting the presence of a double syrinx.

There are two main classes to which bird song can be separated into. Those used over long distances and those used over shorter distances (Titus, 1998). Long-range songs are prominent, non-directional broadcasting signals habitually functioning as advertisements of male reproductive and territorial status to attract mates and repel rival males respectively (Wiley & Richards, 1982; Titus, 1998). Short-range songs on the other hand are often subtle and directed towards a specific individual close to the singing bird (Wiley & Richards, 1982) and are frequently used in aggressive male-male confrontations in conjunction with aggressive chases (Titus, 1998). Short-range songs are also habitually used in the breeding season during females' fertile period and used in pairbond maintenance (Titus, 1998).

In tui, long-range broadcasting songs are generally thought to be sung by more dominant birds, giving continuous information about their dominance or reproductive status (Bergquist, 1989). Furthermore, tui that sing from a higher vantage point have been shown to be more dominant than those singing from a lower point (Bergquist, 1989). Long-range broadcasting songs of tui may also be used to advertise territoriality or the disclosure of information about food sources, generally by male birds; short-range songs generally are directed towards a specific individual or group of individuals at close proximity to the singing bird. Short-range songs were observed in the context of aggressive confrontations between males, courtship, or close proximity singing by a male to a female and vice versa.

Differences between long-range and short-range tui songs at Tawharanui were detected as predicted. The long-range songs contained a higher proportion of trill and a lower minimum frequency compared to short-range songs, however there was not a significant difference in bandwidth between song types.

Long, high-frequency trill components in songbirds are designed for long-range transmission in open habitats, whereas low-frequency sounds are designed for long-range transmission in habitats with dense vegetation, because high-frequency trills suffer greater levels of reverberation than low-frequency sounds (Naguib, 2003; Patricelli et al, 2008). (Naguib, 2003; Patricelli et al, 2008). These high-frequency trills also travel more efficiently within open habitats than within denser vegetation in comparison to lower frequency syllables, due to the differing acoustic properties of the different habitat types (Naguib, 2003; Boncoraglio & Saino, 2007). High-frequency trills are less likely to suffer from rapid sound decay across open habitats (Blumstein & Turner, 2005).

Short-range songs of tui are directed to a neighbouring individual close by and often within vegetation such as trees or bush. Low frequency and low proportion of trill component would maximise sound transmission through vegetation. Female songbirds perceive rapid trill as a predictor of high male quality, such are the high energy demands of producing trill components (Ballentine et al, 2004; Hennin et al, 2009).

As they are costly to produce, trills are considered to convey the body condition and genetic quality of an individual and are important in mate attraction (Titus, 1998; Ballentine et al, 2004) and territory defence (Secondi et al, 2002) in males. Furthermore, high-frequency components such as trill are common characteristics in long-range songs as they are structurally designed to reduce the level of locatability by potential predators, or even brood parasites at the beginning of the breeding season (Boncoraglio & Saino, 2007).

As trill can serve as a signal to females of male quality in addition to being a signal of aggressive male territoriality, it is important for birds to relay trill to as many conspecifics as possible at the same time. Relaying trill to many conspecifics simultaneously can be achieved by singing long distance broadcast songs. Long-range songs of a tui are likely to be used for mate attraction and as signals of aggressive male territory defence. High proportions of trill would more efficiently advertise the quality of singers to potential mates, neighbours and rivals simultaneously, without the singer necessarily being seen. The trill component of tui song may also be the part of the song that contains ultrasound. During these 'trilly' bouts, on occasions no audible sounds were being emitted from the bird even though the bird was visibly continuing to assume its regular singing posture (Pers. Obs. S. Hill, 2010). However, our equipment could not detect sounds above 22.1 KHz.

Short-range songs of tui are usually sung to a close-by individual to augment physical intra-sexual aggression, as observed by Bergquist (1989) or inter-sexual interactions. When the bird can be seen by its opponent, physical appearance such as body size can signify its physical and genetic status, without the need to expend extra energy in their songs. Indeed, tui are often seen to erect their feathers to appear larger when singing to a bird in close proximity (Bergquist, 1989).

Lower frequencies are less affected by dense vegetation (Shy, 1983; Gorissen et al, 2002) and a higher proportion of low-frequency syllables are recorded in short-range songs. Lowering minimum frequency of song in birds is restricted by beak morphology (Huber & Podos, 2006).

Male Darwin's finches (*Geospiza fortis*) with longer, deeper and wider beaks will sing songs at significantly lower minimum frequency, which may facilitate assortative mating by females (Huber & Podos, 2006). Selection of low-frequency song by females during close interactions may also apply to tui. However this will need further investigation.

Structural differences between song types have also previously been documented in Galapagos finches (*Geospiza*) (Bowman, 1983). Individuals of this species have been shown to produce very high frequency (16 KHz) whistles towards their breeding partners, in short-range songs only. Very high frequencies do not travel far due to environmental degradation, however the finch will tend to use a higher amplitude, or level of volume, for these songs, illustrating the interchangeability of song structure to determine the range of transmission of the song (Titus, 1998).

The Eurasian blackbird (*Turdus merula*) will also alter the structure of its song according to the range at which it is transmitting the song (Dabelsteen & McGregor, 1996). Short-range songs will contain quieter, faster and lower frequency sounds than their long-range songs, whilst longer-range songs will contain syllables, or individual sound units, more suited for transmission across a wider area and a longer distance (Dabelsteen & McGregor, 1996).

Dark-eyed juncos (*Junco hyemalis*) will alter their song structure when singing short-range songs (Titus, 1998). In order to maximise efficient transmission of the song's information, a dark-eyed junco will change particular song components, for example short-range songs tend to have a greater degree of complexity than long-range songs and their notes will span a greater frequency bandwidth than long-range songs in addition to reduced immediate syllable repetition (Titus, 1998). Both of these song properties would be ineffective at long-range transmission due to degradation of the syllables before reaching their long-range target (Titus, 1998).

It is likely that the altered proportion of trill and minimum frequency when tui switch between song types is in order to maximise the effective transmission of their song to the desired recipient.

Chapter Four: Individual, Gender and Seasonal Variation in Tui Vocalisation within a Mainland Population



Tui in a flame tree (Photograph: S. Wells).

4.1 Introduction

4.1.1 Individual Variation in Bird Song

Individual Repertoire

With their very well adapted vocalisation mechanisms, songbirds tend to have complex vocalisations. An individual can have a high diversity of songs or song ‘types’. The different song types by an individual is known as its song repertoire. In some highly vocal avian species, such as the brown thrasher (*Toxostoma rufum*), song repertoire of an individual can number over 1,100 different songs (Boughey & Thompson, 1981). The repertoire of an individual can give much information on their biological and social status (van Herpt, 2009).

Previous studies have proposed many hypotheses on the evolution of the song repertoires in songbirds (Krebs, 1977), four of which will be discussed here:

1. One such hypothesis regarding the evolution of song repertoire is that large song repertoires are products of sexual selection (Nottebohm, 1972). Large song repertoires in male red-winged blackbirds (*Agelaius phoeniceus*) have been shown to be positively correlated with their reproductive experience (Yasukawa et al., 1980). Furthermore, large song repertoires increase success in territorial conflicts, allowing males to maintain high quality territories and females to preferentially choose to mate with them (Yasukawa et al., 1980). The size of the song repertoire of a songbird can also be assessed by the number of different syllables it uses (Briefer et al., 2009b). Similarly to large song repertoires, large syllable repertoires have been demonstrated to be products of sexual selection. The great reed warbler (*Acrocephalus arundinaceus*) is perhaps the most well documented bird species that has shown to sexually favour a large syllable repertoire over a small repertoire (Nowicki et al., 2000). Female individuals are more likely to solicit copulations and choose to breed with those males with larger syllable and song repertoires (Hasselquist et al., 1996; Forstmeier & Leisler, 2004). Moreover, males with larger repertoires will attract more mates and produce more young (Catchpole, 1986). In addition, a significant number of males with small repertoires will not mate at all (Catchpole, 1986; Catchpole et al., 1986).

Evidence suggests that sexual selection will favour those individuals who have a better immune system than those with smaller repertoires. Studies have shown that large song repertoires are

positively correlated with the size of spleen, an organ of fundamental importance in immune defence, relative to body size (Moller et al., 2000), presumably due to the reproductive advantages of choosing a male breeding partner with high levels of immunocompetence.

Early egg-laying in female song sparrows has also been correlated positively with the large song repertoires of their breeding partner, thereby facilitating a greater chance of multiple broods per season and possibly increased chance of successful fledging of young (Reid et al., 2004). Furthermore, large song repertoires are associated with males who will provide greater parental care in terms of nest building and feeding young in red-winged blackbirds (Read & Weary, 1992). Greater male viability has also been shown to be strongly correlated with large song repertoires, benefitting the female breeding partner (Moller et al., 2000). In addition, song repertoire size has been shown to have positive correlations with genetic diversity in the sedge warbler (*Acrocephalus schoenobaenus*) (Marshall et al., 2003), therefore presumably is related to their fitness

2. A second hypothesis to the evolution of song repertoires in males is that it increases the chances of successful territorial defence through the ability to song match with rival males (Krebs, 1977). In many territorial avian species, an individual defending a territory will match the song of an intruding individual. The wider the range of songs, the more bird songs the host will be able to match and stave off the threat of losing territory to another male. It was also found that song matching was used by rival birds to avoid aggression from a territory holder. A bird unable to match songs of a territorial male, will be aggressively chased away as seen in the tufted titmouse (*Baeolophus bicolor*), (Kroodsma, 2005). Song matching allows assessment of the position and the distance of competing individuals (Ranjard, 2009).

3. A third hypothesis ‘the antiexhaustion hypothesis’ is another possible explanation to the evolution of song repertoires in songbirds. In a study on great tits (*Parus major*), it was found that birds would prevent exhaustion by regularly switching song types, thereby alternating muscle contraction patterns, thus developing a larger song repertoire (Lambrechts & Dhondt, 1988).

The production of song repertoires may also be a way of preventing habituation in intruding birds (Dawson, 1982). The anti-monotony principle states that songs, designed to keep would-be intruders away from territory and to attract potential breeding partners, are frequently switched, thus ensuring they remain effective and stimulate a desired response from the target individual (Krebs, 1976; Dawson, 1982).

4. Finally, the Beau Geste hypothesis proposes that song repertoires evolved in the context of population density assessment (Krebs, 1977). The presence of a large song repertoire will give the illusion of a large population density thereby inhibiting the influx of new individuals into the area (Krebs, 1977; Yasukawa, 1981).

4.1.2 Gender Variation in Bird Song

Previous studies have demonstrated differences in male and female songs in songbirds. In the only other New Zealand honeyeater, the bellbird (*Anthornis melanura*), females have been shown to sing complex songs that parallel male songs (Brunton & Li, 2006). Female song sparrows, in contrast, sing less complex and shorter songs than males. Both sexes, however, will sing during intrasexual conflicts (Arcese et al., 1988; Wingfield, 1993) and females sing more often in areas of high population densities (Arcese et al., 1988). Gender differences in vocalisation have also previously been demonstrated in eastern whipbirds (*Psophodes olivaceus*) (Mennill & Rogers, 2006). Syllables within the songs of male whipbirds were seen to remain consistent in different geographic regions within Australia, but syllables in female songs significantly varied (Mennill & Rogers, 2006), suggesting the sexual selection of syllable consistency in males, a trait previously shown to be positively correlated with dominance status, age and brain integrity in tropical mockingbirds (*Mimus gilvus*) (Botero et al., 2009).

4.1.3 Seasonal Variation in Bird Song

The breeding season is a critical period of the year for all animal species. Brenowitz et al. (1997) demonstrated that in temperate zones, birds exhibit higher rates of mating and territorial songs during the breeding season, dropping sometimes to zero songs during the non-breeding season. Birds in tropical and equatorial regions, however, generally sing to defend territory all year round (Langmore, 1998), due in likelihood to the plentiful year-round availability of food in tropical regions.

A study on wild island canary (*Serinus canaria*) found that during the breeding season, male songs were on average longer and syllable repetition rate greater than in the non-breeding season (Leitner et al., 2001). The composition of the bird's repertoire changed seasonally. In male birds, there was

a decrease in whistle-type syllables and an increase in fast-frequency modulated syllables, or trill syllables. Trill has been demonstrated to be sexually attractive to female songbirds (Bolhius & Gahr, 2006), as they are very costly to produce and therefore can only be produced by high-quality individuals (Hennin et al., 2009).

During the non-breeding season, songs can be shorter, sung with less amplitude and less frequently sung, furthermore a heightened auditory sensitivity to songs outside of the breeding season has been observed in white-crowned sparrows (*Zonotrichia leucophrys gambelii*) (Caras et al., 2010). It is hypothesised that this heightened auditory sensitivity may serve as a roosting signal in birds that form large social groups outside the breeding season (Caras et al., 2010).

Syllable Repertoire as a Reliable Measure of Song Complexity

Syllable repertoire size is a reliable measure of song complexity, this can be within-song complexity, the number of different syllables sung per song, or between-song complexity, the number of different syllables within an entire repertoire. Different species can have a large within-song syllable repertoire and a small between-song syllable repertoire or vice versa (Read & Weary, 1992).

Syllable consistency in tropical mockingbirds (*Mimus gilvus*) has been shown to be a trait possessed by older, more dominant and reproductively successful males holding good, quality territories within breeding season. Furthermore, syllable consistency has been linked with brain function integrity (Botero et al., 2009).

4.1.4 Variation in Tui Vocalisation

Previous research has demonstrated seasonal, sexual and individual variation in tui vocalisation (Bergquist, 1989).

Song variation occurs between males and female tui (Bergquist, 1989). In previous studies on gender variation in tui song, both sexes have been shown to sing loud, complex songs all year round, however it was suggested that female songs were more complex than male songs, in terms of the frequency of occurrence at which the syllables were sung. It was also observed that males will sing longer songs than females (Bergquist, 1989) and that males were the most regular, dominant singers within a population. No obvious statistical comparisons, however, have been carried out on tui vocalisation, data generally limited to being merely observational and qualitative.

Unsurprisingly, male and female interaction during the breeding season is greater than at any other time of the year. Studies by Thorpe (1963) showed that both female and male duetting is common in birds within the breeding season. Ecological functions of this synchronised singing can be attributed to location and maintenance of mate contact (Thorpe, 1963), establishment and maintenance of pair bond (Diamond & Terborgh, 1968; Payne & Skinner, 1970), mate guarding (Sonnenschein & Reyer, 1983) and sexual recognition in monomorphic species (Hooker & Hooker, 1969). It has also been documented that tui song continued all year round, but it has been shown to change seasonally, such as during the breeding season (Bergquist, 1989).

Gaining knowledge on individual birds' vocalisations is a crucial tool in obtaining information on life-history traits such as whether or not the bird has developed within a stable or unstable environment (McGregor & Peake, 1998; McGregor et al., 2000). Knowledge of vocalisation at both the individual and population level can highlight behavioural traits that can determine or alter conservation value of particular sections of a population in terms of time and effort, such as individuals' dominance statuses reflecting reproductive success (McGregor & Peake, 1998) and can help differentiate floaters or residents. Floating individuals in a population could, for example, be selected for translocation to areas where that species is rare, as they may show breeding success if moved to a favourable habitat (Smith & Arcese, 1989). Vocalisation knowledge also generates input data for conservation models and can be used as a tool to monitor the success of an individual or a whole population over time (Terry et al., 2005).

4.1.5 Research Aims and Hypotheses

I predict the following:

1. Considering the large song repertoire recorded in the population, there will be a large number of syllables within each individual tui's repertoire and a large number of songs within each individual's song repertoire.
2. I predict a variation in the diversity of songs and syllables between individuals, reflecting the variation in genetic diversity of individuals within the population. A large syllable repertoire, for example, is a reliable measure of song complexity and song complexity has been demonstrated to be linked to high genetic diversity (Read & Weary, 1992; Gil & Gahr, 2002). Therefore an individual with a large syllable repertoire is likely to have higher genetic diversity than an individual with a smaller syllable repertoire.
3. I also predict significant differences between male and female songs. I predict that male tui will sing more frequently, sing longer songs and have a higher song complexity, measured by syllabic diversity, or higher number of different syllables per song, than females. I also predict the use of different syllable types between the sexes, for example, males will use more complex syllable types than females.
4. I predict differences in tui songs between breeding season and non-breeding season. Songs will contain a larger proportion of trill in breeding season compared to non-breeding season since trill is a trait reflecting male quality and this advertisement is more likely to be advertised in the breeding season.

4.2 Methods

For Study Site and Recording Methods, please refer to Chapter Two.

4.2.1 Individual Song Repertoire and Gender Variation of Songs

Data collection

Songs of five male tui and five females recorded during breeding season between December and March were used for investigating individual and gender variations in syllable repertoire. All five males were banded (band combinations: BM-OO, YM-RY, YM-LbG, YM-WO and GO-WM). Only one female was banded, YM-WB, and the other four tui were chosen from different locations of Possum Gully and Home Bush (Mid and Upper levels, see Figure 2.1 in Chapter Two). The total number of songs recorded from each of the males varied between 5 and 38 and females between 4 and 7. The first five recorded songs were selected from each bird for analysis of the gender differences in syllable repertoire.

Parameters

Accumulative new syllables were plotted (a saturation curve) for each of the ten birds, in order to establish syllable repertoire of each individual and to determine whether or not all syllables within the individuals' repertoire have been recorded within the first five songs. When the saturation curve reaches an asymptote, we assume the majority of syllables in an individual's song repertoire have been recorded.

For five banded male individuals (BM-OO, GO-WM, YM-WO, YM-GR, M), saturation curves for song repertoire were also plotted using thirty songs from each bird, apart from BM-OO for which only 24 songs were available. Note that two of the five banded males in this song repertoire section differ from the five banded birds from the syllable analysis, which was due to lack of availability of 30 songs from the two males YM-LbG and YM-RY. A different song was defined as a song that contained different syllables and/or sequences of syllables from any other song seen previously in that individual's repertoire.

Parameters used for comparing gender variation in songs include:

1. Syllable diversity: measured by number of different syllables per song and total number of different syllables in five songs;
2. Song frequency: number of songs recorded during a five minute sampling unit;
3. Song duration: duration of song, from first note to last note. A song is defined as a series of notes and syllables preceded by and followed by an interval of three seconds or more.

Gender Variation in Song Structure Data Analysis

The mean values of song duration and syllabic diversity (both repeated and unrepeated syllables) between songs of the aforementioned five males (25 songs) and five females (22) at Tawharanui, were tested for any statistical differences in song structure between the sexes. As the majority of the data were non-parametric i.e. non-normally distributed data, a Mann-Whitney U test (Mann & Whitney, 1947), was performed.

Syllable Type Frequency Distribution

Due to the large syllable repertoire of the tui, syllables were categorised into five main syllable types using established aural and spectrogram visual syllable analysis techniques (Ranjarad & Ross, 2008).

Syllable Type Frequency Distribution Data Analysis

Principal Component Analysis (PCA) was performed to investigate variation and trends between the common male and female syllable types. Where possible, for each of the 10 individuals, five songs were analysed for syllable repetition frequency analysis. In total, there were 25 songs analysed for the males and 22 songs analysed for the females, all from the breeding season only. A Mann-Whitney U test (Mann & Whitney, 1947), was then performed to test the differences. Boxplots were created to visualise the data (Figure 4.8).

4.2.2. Variation of Songs between Breeding Season and Non-Breeding Season

Thirteen songs each from both the breeding season (September to February, 13 males) and non-breeding season (March to August, 10 males and 3 females) were randomly chosen to analyse the differences of songs between breeding and non-breeding season, aside from song structure analysis (Section 4.3.3). Thirteen songs were chosen because there were only thirteen songs from the non-breeding season available for analysis. Methods for song structure analysis were described in Sections 2.3 and 2.4 of Chapter 2 and Section 3.3.4 of Chapter 3. Female songs were removed from the statistical tests.

All statistical tests were performed using software R 2.12.2 (© R Foundation for Statistical Computing, 2010) and Microsoft (Redmond, USA) Excel. The PCA was performed using package FactomineR. All statistical tests were two-tailed and the alpha was set at 0.05, which is a 95% confidence interval. Therefore, p values = <0.05 were interpreted as significant.

Parameters used for comparison included song structure, song type (long and short range songs), syllable frequency distribution and frequency of singing.

Syllable frequency distribution is defined as the number of times each syllable were repeated in the 26 songs analysed, 13 from the breeding and 13 from the non-breeding season.

Frequency of singing was measured by the number of songs recorded during a 3 minute period. For both the breeding season and non-breeding season, a total of 30 minutes of recordings from each season was carried out at two different locations within Tawharanui Regional Park: Ecology Bush (6 x 3 minutes) and Jones Bay (4 x 3 minutes). Mann-Whitney U test was used to determine if there was a significant difference in the frequency of singing between the two seasons.

4.3 Results

4.3.1 Individual Variation in Syllable and Song Diversity

The median number of different syllables recorded per song varied between individuals from 5 to 10 for males and from 4 to 5 for females (Table 4.1) The median duration of the songs varied between individuals: BM-OO: 5.2 seconds (sec); YM-RY: 7.3; YM-LbG: 4.3; YM-WO: 6.9; GO-WM: 4; Female 1 (4 songs): 5.5; Female 2: 3; Female 3: 4.1; Female 4: 3.6; YM-WB (3 songs): 4.

Table 4.1: Summary of the ten individual tui analysed for syllable analysis.

Individual	Sex	Tarsus length	Weight	Total No of songs recorded	Median duration (range) of each song (Sec)	Median Number (Range) of syllables per song*
BM-OO	Male	48	141	24	5.2 (2.7 - 14.5)	10 (6 - 30)
YM-RY	Male	45	110	33	7.3 (4.3 - 17.1)	6 (4 - 20)
YM-LbG	Male	46	121	22	4.3 (1.6 - 12.3)	6 (1 - 14)
YM-WO	Male	46.7	115	39	6.9 (2.2 - 22.5)	6 (1 - 36)
GO-WM	Male	47.4	117	38	4 (1.5 - 5.0)	5 (2 - 14)
Female 1	Female	-	-	4	5.5 (1.9 - 6.9)	4 (2 - 9)
Female 2	Female	-	-	7	3 (1.2 - 7.8)	4 (1 - 7)
Female 3	Female	-	-	5	4.1 (1.4 - 5.1)	5 (2 - 9)
Female 4	Female	-	-	6	3.6 (1.1 - 7.1)	4 (2 - 5)
YM-WB	Female	41.2	76	3	4 (1.8 - 6.6)	4 (2 - 12)

* Maximum 5 songs were used for extracting syllables from each bird.

The number of *different* songs recorded ranged from 14 to 30 for five males. Male ‘BM-OO’ had only 24 songs available for analysis, of which all 24 were different songs. The accumulative new songs recorded did not reach an asymptote in 30 songs (24 for BM-OO) for most males (Figure 4.1) therefore the size of song repertoire could not be determined and compared between individuals. Saturation curves for females were not created, due to small sample size. However, the general pattern for female songs is that they also sang generally different songs per song encountered, as males.

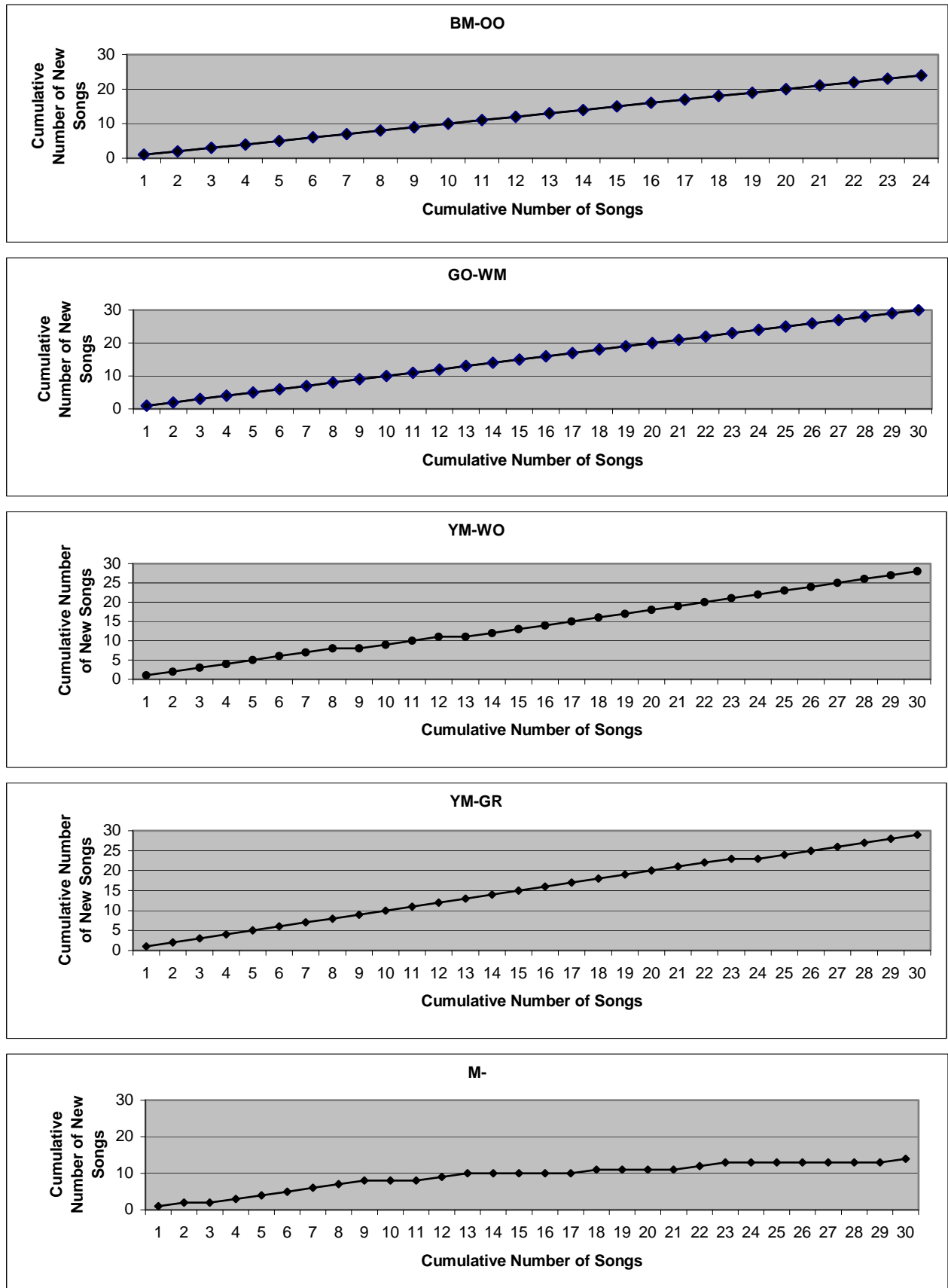


Figure 4.1: Saturation curves for song repertoire of five banded tui.

4.3.2 Gender Variation

Song Duration, Syllable Diversity and Frequency of Singing

Males did not sing significantly longer songs compared to females ($n = 5$, $n = 5$; $u = 5$; $p = 0.150794$), and did not produce a significantly greater number of different syllables per song than females ($p = 0.222222$), however males *did* produce a significantly greater number of new syllables in each consecutive song than females ($u = 0.5$; $p = 0.007937$) (Table 4.2, Figure 4.2), suggesting larger male syllable repertoire. The female songs did however show a trend of being simpler and shorter than the male songs, containing fewer syllables.

In the five banded males in five songs, there was a range of 45 to 101 cumulative syllables, 33 to 62 of which were new syllables that were not repeated syllables (Figure 4.3). All females had a low number of accumulative new syllables than the male birds (Figure 4.3 and Figure 4.4), with a range of 19 to 37 cumulative syllables in five songs, 18 to 28 of which were new syllables that were not repeated syllables. Asymptote of the curve was not reached for any of the females indicating that the full repertoire of female syllables had not been obtained.

The results from the 5-minute song sampling did not show significant differences in the frequency that males and females sang ($p = 0.15$).

Table: 4.2: Summary of statistical analysis on syllable diversity of male and female tui.

Variable	Median		Range		Statistical Values from Mann-Whitney U Test	
	Male	Female	Male	Female	U	P
Number of Different Syllables per Song	12	5	32 Min : 4 Max : 36	10 Min : 2 Max : 12	6	0.222222
New Syllables per Song	8	5	7 Min : 6 Max : 13	2 Min : 4 Max : 6	0.5	0.007937
Song Duration (Sec)	6.8	4	5.8 Min : 3.3 Max : 9.1	1.4 Min : 3.4 Max : 4.8	5	0.150794

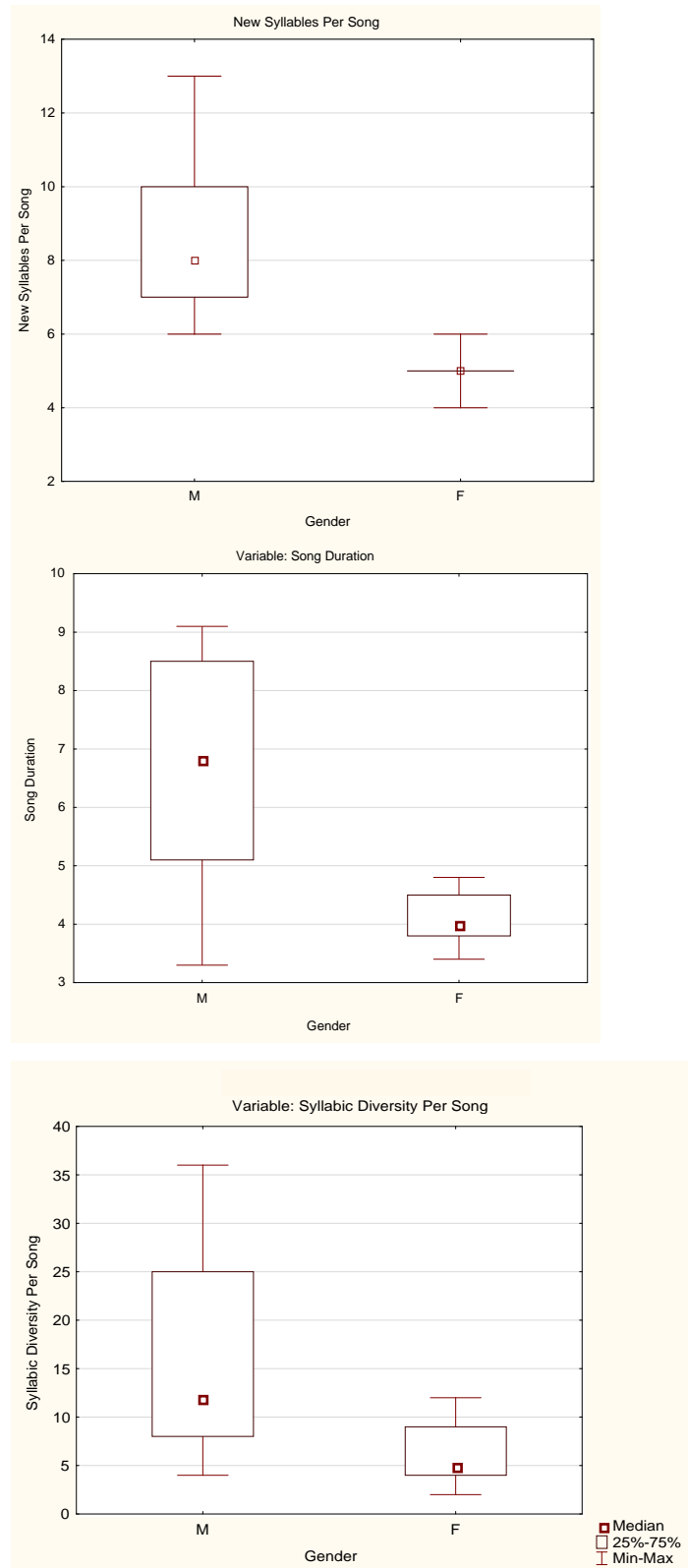


Figure 4.2: Boxplots showing the medians and distribution of the parameters that were tested for significant differences between male and female tui following a Mann-Whitney U test.

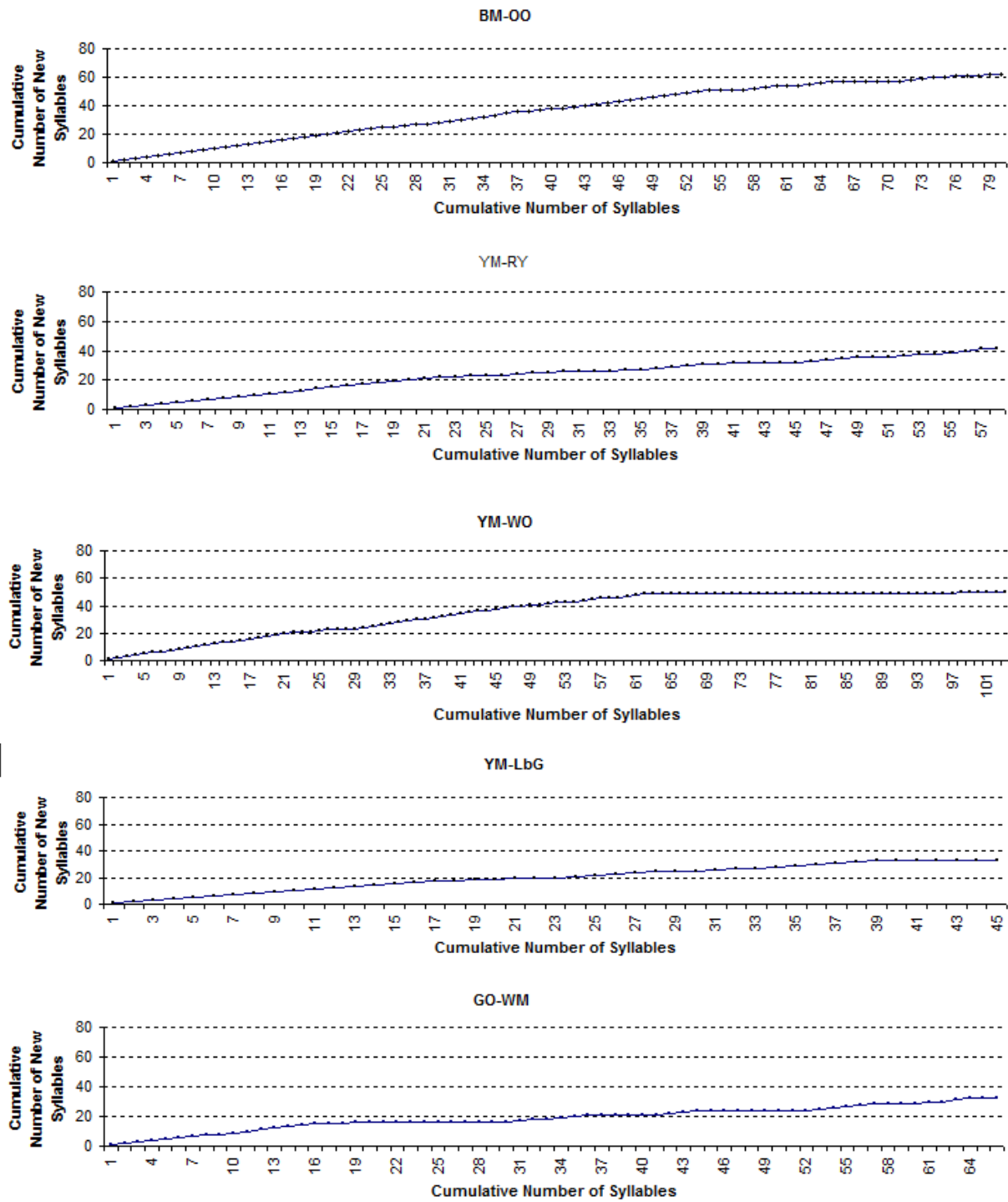


Figure 4.3: Saturation curves for the syllable repertoire of each male individual in five songs.

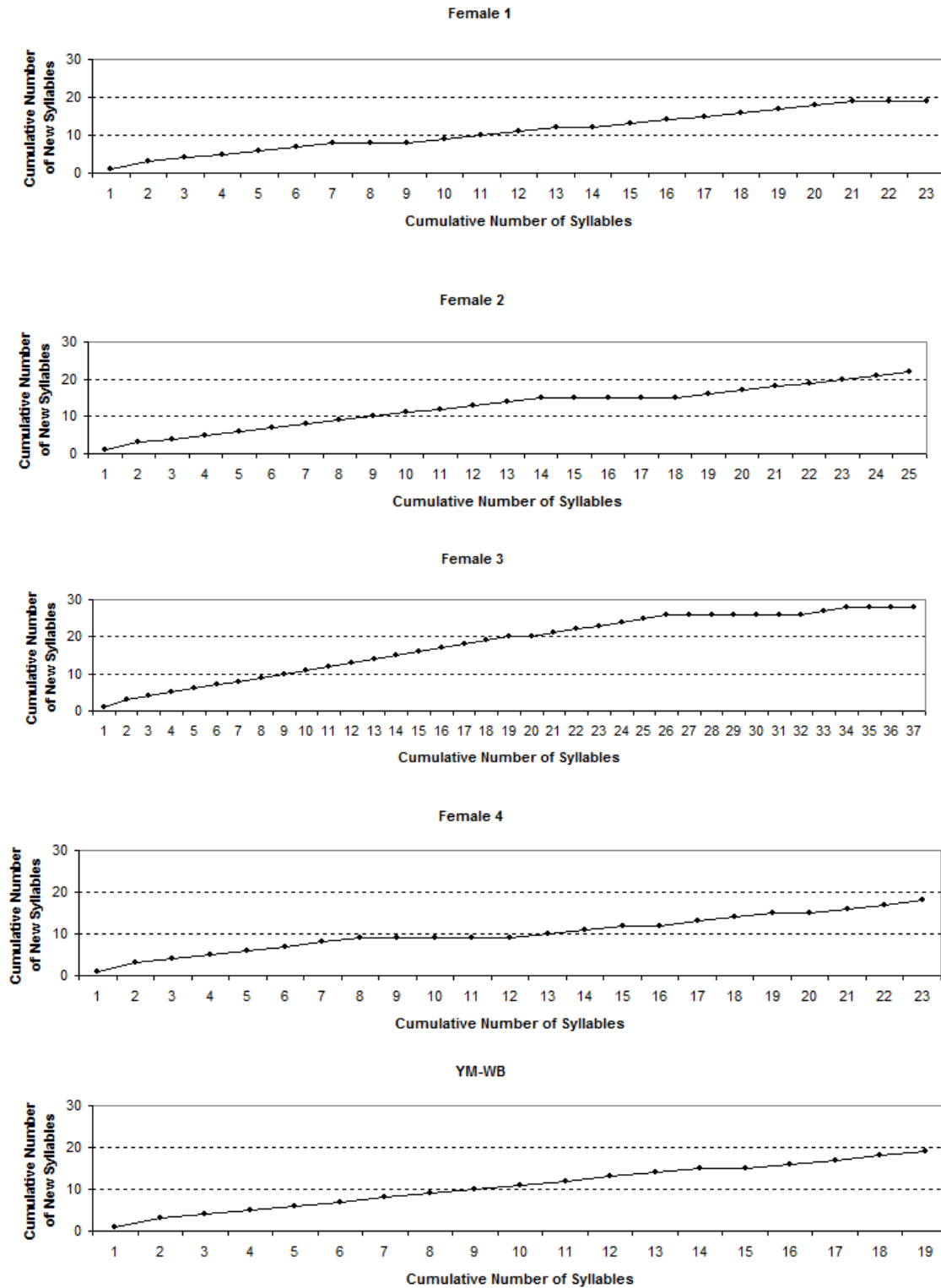
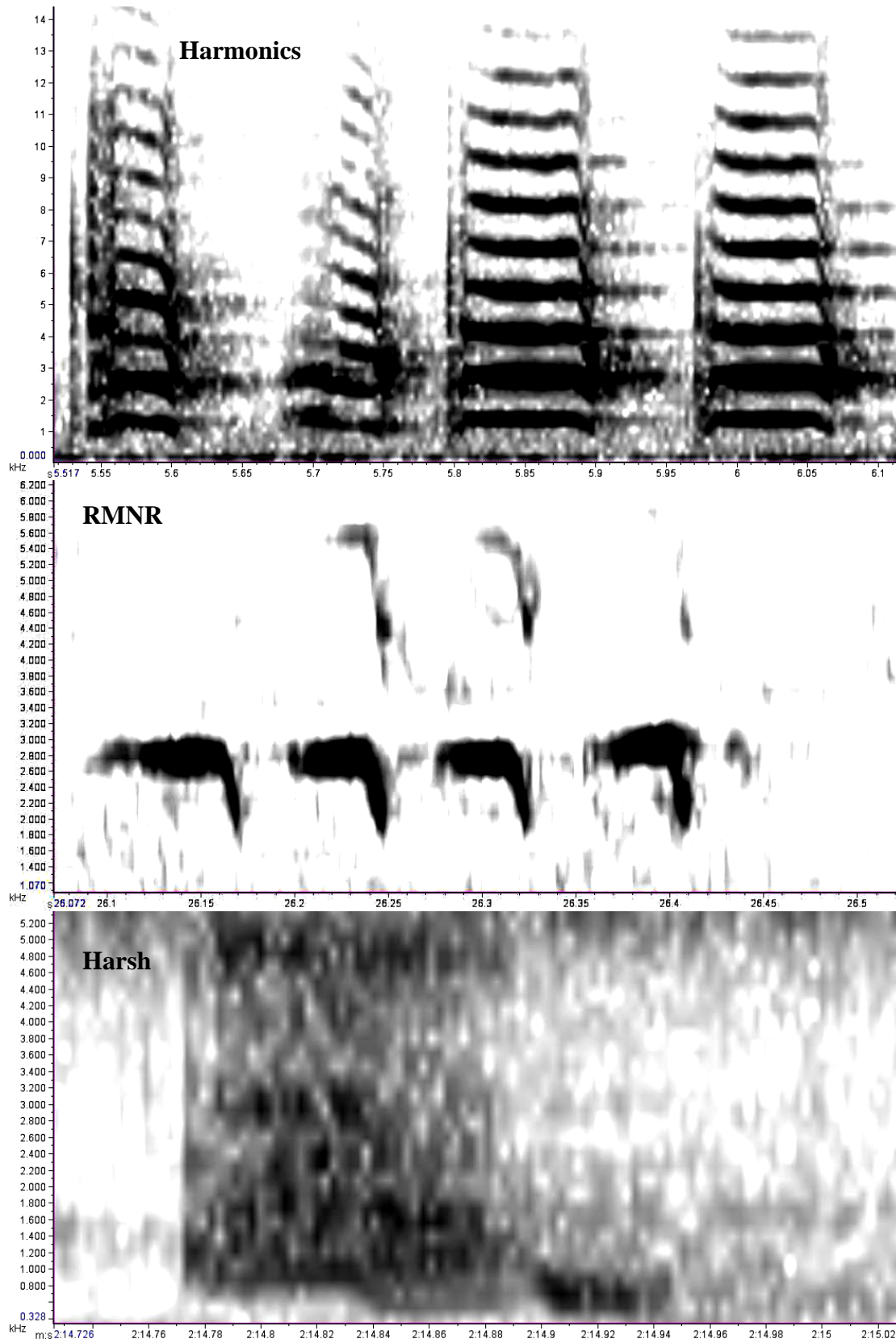


Figure 4.4: Saturation curves for the syllable repertoire of each female individual in five songs, where applicable.

Syllable Type Frequency Distribution

Due to the extreme diversity of syllables in tui songs, it is difficult to categorise the type of syllables. However five main groups of syllables were heard relatively frequently. These were harmonic syllables (those spanning many frequencies), rapid multiple note repetition (RMNR) syllables, harsh or throaty syllables, rapid frequency modulation or trill-type syllables and very low frequency syllables (syllables sung below 1KHz). These syllables made up 37% of all syllable types used. A large number of syllables (63%) are difficult to categorise due their variability and complex nature. These were used infrequently and some were rare, such syllables were included in the group named 'Others'. Figure 4.5 gives examples of each syllable type.

The frequency of each syllable type used by each of the individuals is shown in Table 4.3. Figure 4.6 shows the proportion of syllable type in the repertoire of each individual, including the rarer 'Others' syllables.



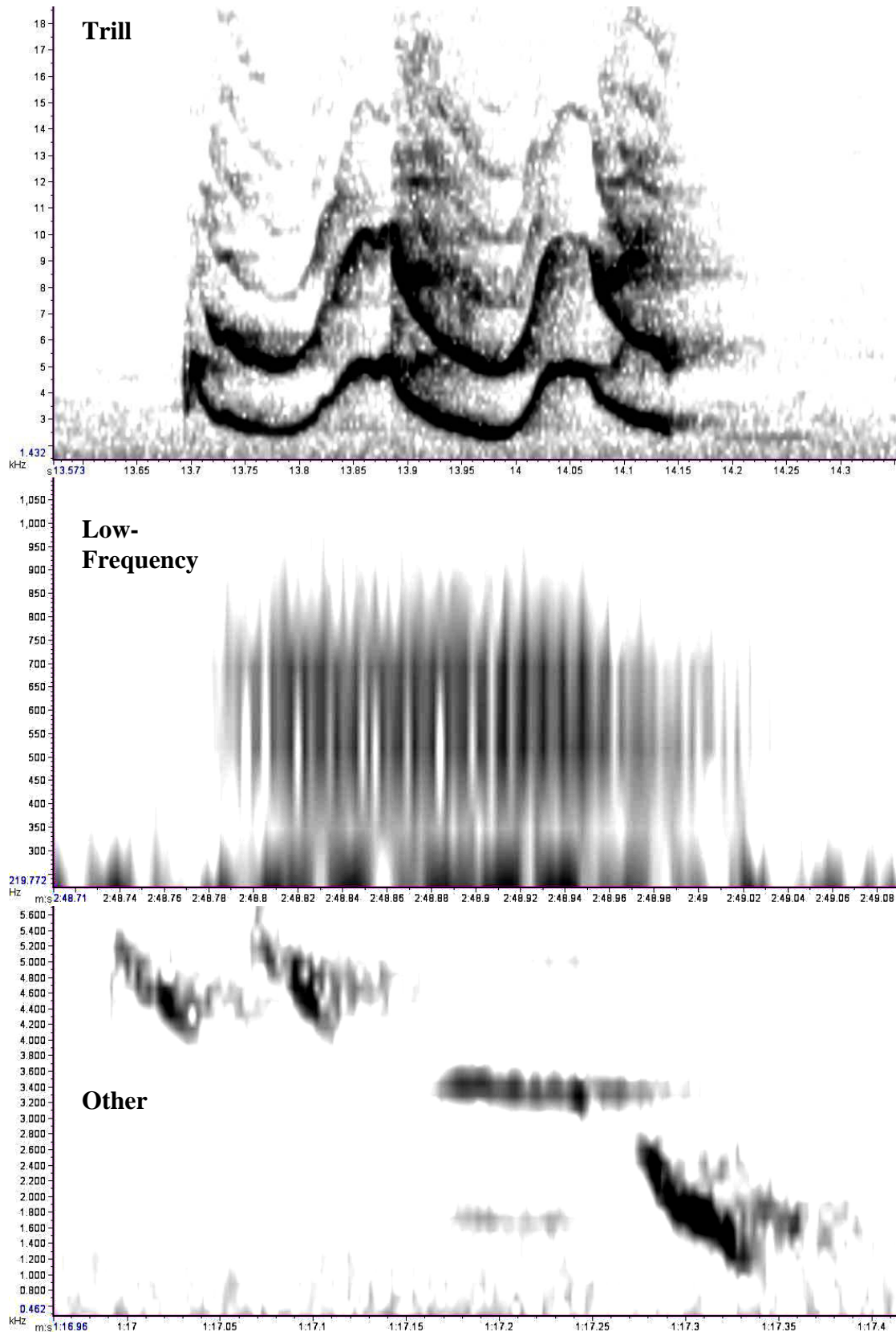


Figure 4.5: Examples of each syllable type that were most commonly heard from ten specific individuals within Tawharanui Regional Park. These syllables, aside from the ‘Other’ category, constituted 37% of all syllables heard.

Table 4.3: Showing the frequency of each syllable type used for each of the ten individuals.

Syllable Categories	BM-OO	YM-RY	YM-LbG	YM-WO	GO-WM
Harsh Syllables	1	2	7	9	1
Harmonics	17	7	0	14	7
Low-Frequency Syllables	6	0	3	5	6
Rapid Frequency Modulation Syllables (Trill)	1	3	0	14	6
Rapid Multiple Note Repetition (RMNR)	8	7	6	7	3
Others	39	22	23	1	9

Syllable Categories	Female 1*	Female 2	Female 3	Female 4	YM-WB**
Harsh Syllables	4	3	1	1	1
Harmonics	0	1	0	2	0
Low-Frequency Syllables	6	2	3	1	4
Rapid Frequency Modulation Syllables (Trill)	0	0	1	2	1
Rapid Multiple Note Repetition (RMNR)	1	2	1	2	1
Others	8	14	22	10	12

* Only 4 songs recorded

**Only 3 songs recorded

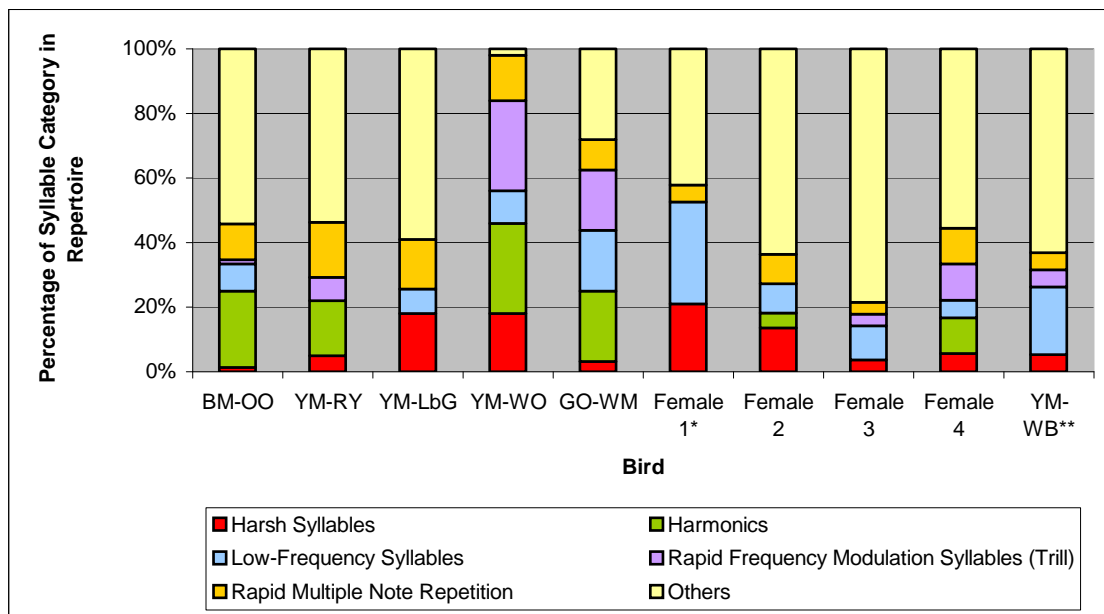


Figure 4.6: The proportion of different syllable types by each of the birds from five of their songs each, following categorisation. This shows the proportion of syllable type in the repertoire of each individual, including the less commonly repeated ‘Others’ category.

*Only sang four songs in a five-minute sampling spell.

**Only sang three songs in a five-minute sampling spell

Principal Component Analysis of syllable types showed that PC1 was significantly correlated with harmonic syllables, RMNR syllables and rapid frequency modulation syllables or trill (Table 4.4, Figure 4.7). PC1 contributed 51.09% of the variance between sexes syllable types (Table 4.4). PC2 contributed 19.94% of the variance between sexes and was correlated with low frequency syllables but exhibited no significant contribution to the variance between sexes. Figure 4.7 shows a scatterplot from the PCA.

Further analysis on the three syllable types exhibiting the highest correlation with PC1 showed that males sang a significantly higher proportion of rapid multiple note repetition (RMNR) than females ($p = 0.01066$). There were no significant difference in harmonic syllables ($p = 0.06601$) or the frequency of trill syllables between males and females ($p = 0.1988$) (Table 4.5, Figure 4.8).

Table 4.4: Eigenvalues, variance explained and correlation coefficients of the five syllable types following PCA analysis. Variables with factor loading values greater than 0.48 are highlighted in bold. See Figure 4.8 for the scatterplot for the correlation of all variables.

	PC1	PC2
Eigenvalue	2.55	0.99
% of Variance	51.09	19.94
Harmonic Syllables	0.86	0.15
Rapid Multiple Note Repetition	0.81	-0.34
Rapid Frequency Modulation Syllables	0.80	-0.02
Low Frequency Syllables	0.39	0.88
Harsh Syllables	0.60	-0.31
$n = 5, 5$		

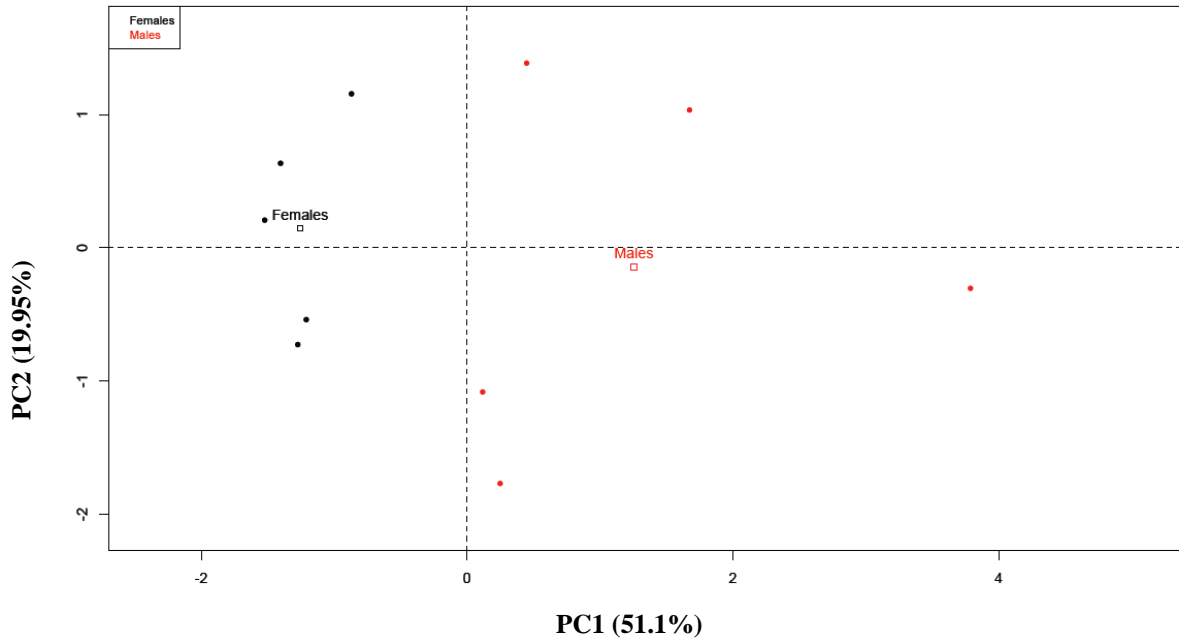


Figure 4.7: PCA plot showing the level of variation between male and female syllable types. The scatterplot shows clear variation between the sexes, highlighting a strong degree of variance between the syllable type frequency and a high degree of correlation between PC1 and harmonic and RMNR syllables.

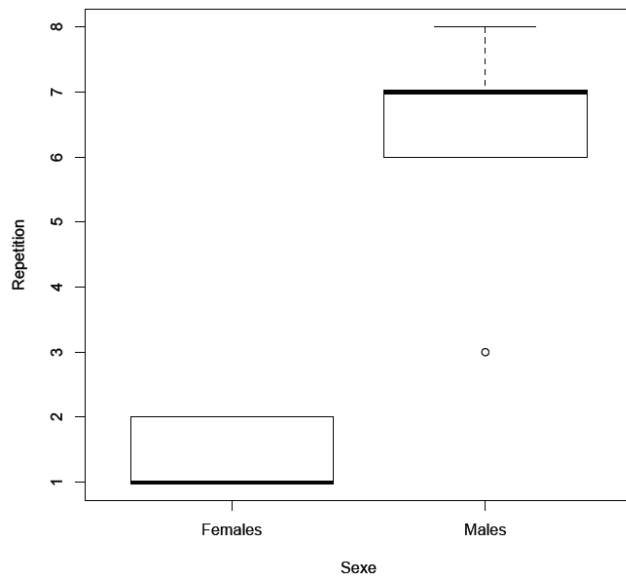


Figure 4.8: Boxplot of the syllable type (RMNR syllable) that showed significant difference in frequency of occurrence between the sexes.

Table 4.5: The descriptive statistics and Mann-Whitney U test results when comparing syllable type frequency between males and females at Tawharanui.

Variable	Median		Range		Statistical Values from Mann-Whitney U Test	
	Male	Female	Male	Female	U	P
RMNR Syllables	7	1	5 Min : 3 Max : 8	1 Min : 1 Max : 2	0	0.01066
Harmonic Syllables	7	0	17 Min : 0 Max : 17	2 Min : 0 Max : 2	3.5	0.06601
Rapid Frequency Modulation Syllables (Trill)	3	1	14 Min : 0 Max : 14	2 Min : 0 Max : 2	6	0.1988
Harsh Syllables	2	1	8 Min : 2 Max : 19	3 Min : 1 Max : 4	9	0.5038
Low Frequency	5	4	6 Min : 0 Max : 6	3 Min : 1 Max : 4	9.5	0.5959

4.3.3 Seasonal Variation

Song structure

Parameters of song structure from long-range songs of males (all female songs were removed) were used for the comparison of song structure between the breeding and non-breeding seasons using PCA. PC1 was significantly correlated with proportion of song containing trill, inflection points within the terminal note, song duration and FMA of the trill component. PC1 contributed 24.67% of the variance between song types (Table 4.4). PC2 contributed 23.27% of the variance between song types (Table 4.4). Figure 4.9 shows a scatterplot from the PCA. The variables exhibiting the highest correlation with PC1 were subsequently chosen for further statistical

analysis using the Mann-Whitney U test (Mann & Whitney, 1947). The results showed that there was a far greater proportion of trill in breeding season songs (51%) compared to non-breeding season songs (23%) ($P = <0.05$, Figure 4.10). There were no significant differences between seasons in inflection points in the terminal note ($p = 0.058$), song duration ($p = 0.86$) or FMA of the trill component ($p = 0.31$) (Table 4.7).

Table 4.6: Eigenvalues, variance explained and correlation coefficients of the eight variables following PCA analysis. Variables with factor loading values greater than 0.48 are highlighted in bold. See Figure 4.9 for the scatterplot for the correlation of all variables.

	PC1	PC2
Eigenvalue	1.97	1.86
% of Variance	24.67	23.27
Proportion of Song Containing Trill	0.73	-0.04
Inflection Points Within the Terminal Note	0.66	-0.50
Song Duration	0.53	0.78
FMA of the Trill Component	0.52	0.01
Interval Between Notes	0.46	0.63
Bandwidth	-0.40	0.53
Minimum Frequency	0.29	-0.48
FMA of the Entire Song	-0.03	-0.28
<i>n</i> = 18, 12		

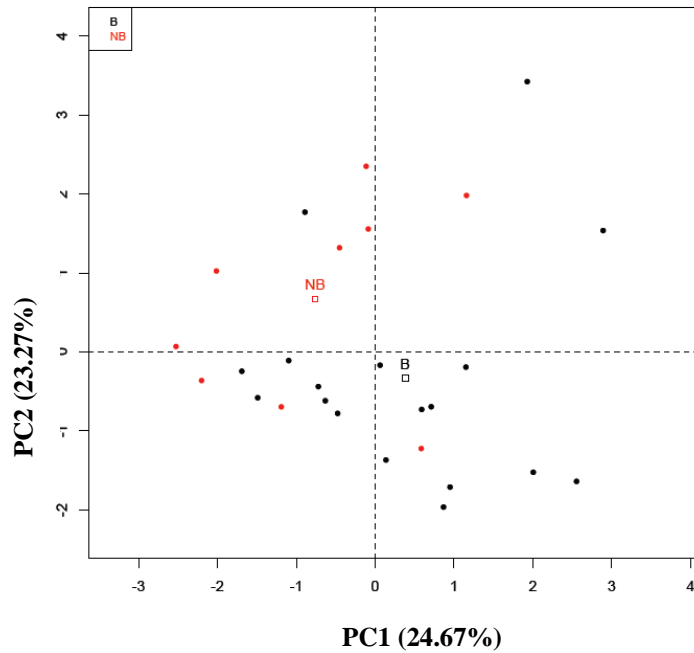


Figure 4.9: A PCA scatterplot highlighting the separation between breeding season (B) and non-breeding season (NB) at Tawharanui. In conjunction with the correlation values in Table 4.6, it can be seen that proportion of song containing trill and FMA of the trill component are the variables most strongly correlated with PC1 (Dimension 1). Song duration and inflection points within the terminal note also showed correlation with PC1.

Table 4.7: The descriptive statistics and Mann-Whitney U test results on song parameters of tui between seasons at Tawharanui.

Variable	Median		Range		Statistical Values from Mann-Whitney U Test	
	Breeding Season	Non-Breeding Season	Breeding Season	Non-Breeding Season	W	P
Proportion of Song Containing Trill (%)	51	23	75 Min: 18 Max: 93	61 Min: 0 Max: 61	130	0.01257
Inflection Points in the Terminal Note	1	0	4 Min: 0 Max: 4	2 Min: 0 Max: 2	113	0.0585
Bandwidth (KHz)	14.56	18.07	11 Min: 10.9 Max: 21.9	17.2 4.6 21.8	54.5	0.1811
Interval Between Notes (Sec)	0.09	0.12	0.19 Min: 0.05 Max: 0.26	0.19 Min: 0.05 Max: 0.26	57	0.2266
FMA of the Entire Song (KHz)	1.68	1.51	5.41 Min: 1.04 Max: 6.45	0.53 Min: 1.03 Max: 1.56	101	0.3158
Song Duration (Sec)	5.9	7.2	37 Min : 3.1 Max: 40.1	18.7 Min : 1.2 Max : 19.6	77	0.8599

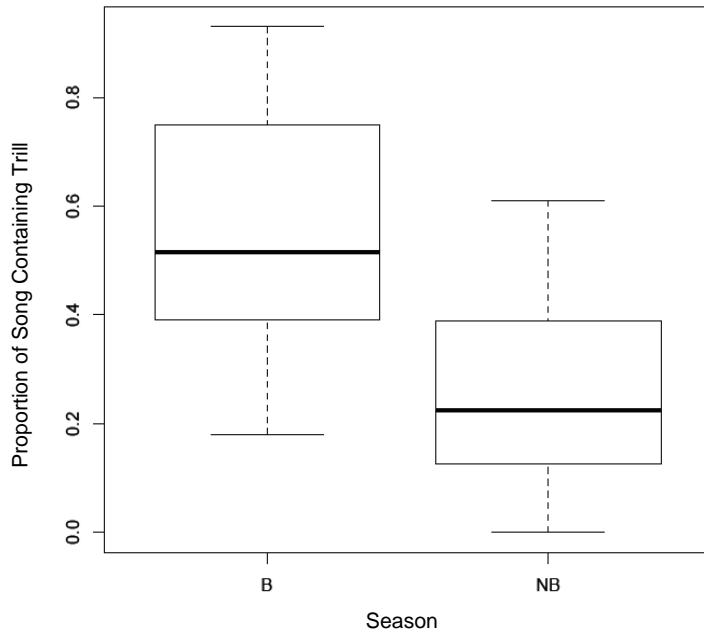


Figure 4.10: Boxplot displaying a significantly greater percentage of each song containing trill in the breeding season compared to the non-breeding season.

Song Type Frequency Distribution

Of the 26 songs analysed from both the breeding and non-breeding season (13 songs from each season), in total 18 were long-range broadcast songs (62%) and 8 were short-range interactive songs (38%). Within the breeding season, of 13 songs, 7 were long-range songs (53%) and 6 were short-range songs (47%). Within the non-breeding season, of 13 songs, 10 were long-range songs (77%) and 3 were short-range songs (23%).

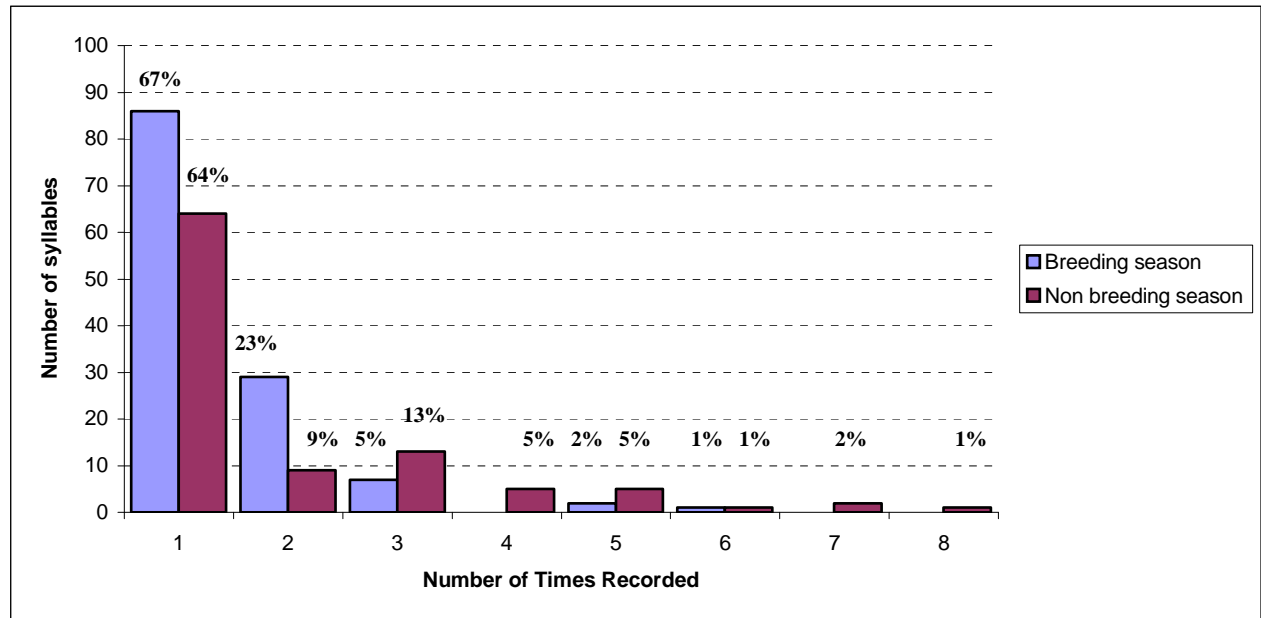


Figure 4.11: The syllable frequency distribution of breeding season and non-breeding season.

Syllable Frequency Distribution

In total, 190 different syllables were encountered in both the breeding and non-breeding season. Of these syllables, 128 were recorded during the breeding season compared to 100 in the non-breeding season. (Figure 4.11). The majority of syllables were recorded just once for both seasons. However, a greater percentage of once and twice-recorded syllables were recorded in the breeding season suggesting lower repetition of syllables within the breeding season.

Frequency of Singing

From 30 minutes of recordings (10 x 3 minute samples) at two separate locations (6 samples at Ecology Bush and 4 samples at Jones Bay) during each season, 172 songs were recorded in the breeding season and 227 songs were recorded in the non-breeding season, at the population level. A Mann-Whitney U test ($u = 21$; $p = 0.028806$) showed that there was a significantly greater number of songs sung during a 3 minute period in the non-breeding season than the breeding season (Figure 4.12).

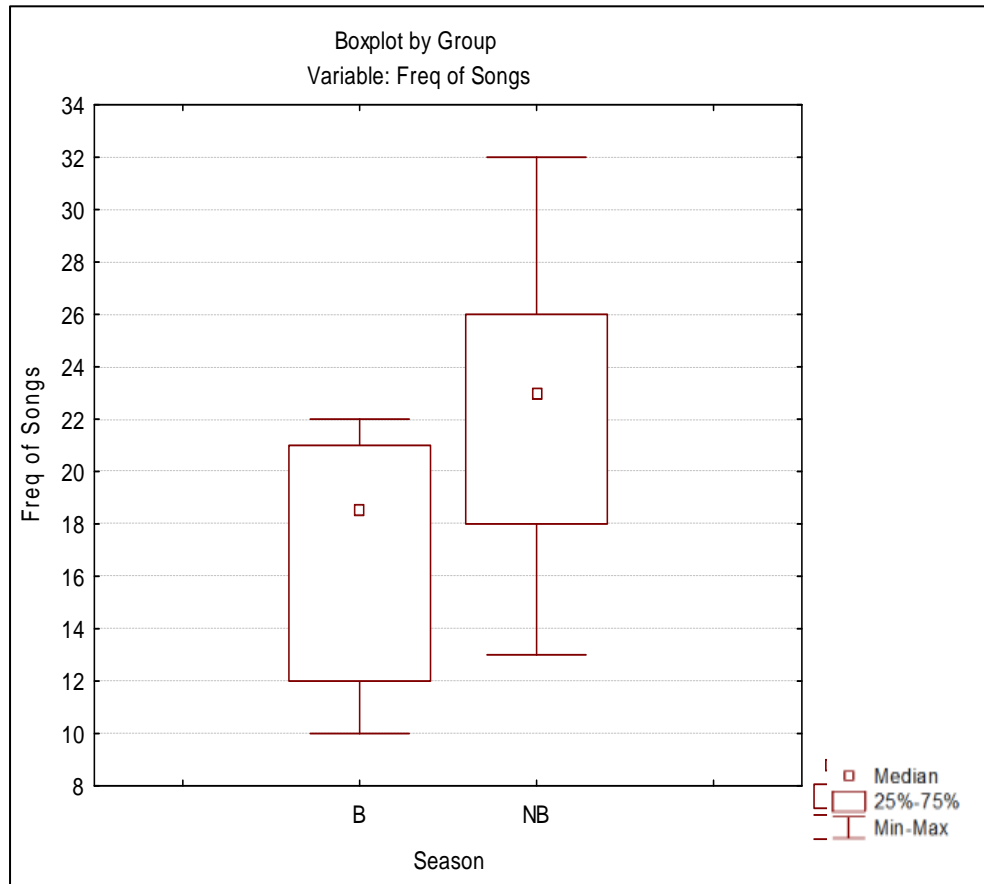


Figure 4.12: Boxplot displaying a significantly greater frequency of songs in the non-breeding season compared to the breeding season.

4.4 Discussion

4.4.1 Individual Variation

Syllable and Song Repertoire

A degree of individual variation in vocalisation between five banded male tui was observed. In 30 consecutive songs analysed, YM-WO sang just one song that was an exact repeat of any other song within its 30. In the individual 'M' (a single metal band on the right leg), over half of its 30 songs were repeated (16). This male individual had a simple repertoire of syllables and had limited variation in the sequence of these syllables. The individual BM-OO, the largest male among the five, sang 62 different syllables within five songs. Each of the 24 songs analysed were new songs. For most males, the number of new songs did not reach the asymptote suggesting that these tui have large song repertoires and that many more songs are needed to study their song repertoire. The females also generally sang different songs per song encountered. However due to the small number of female songs recorded, it was difficult to draw conclusions on the individual variations in song diversity.

The number of syllables recorded in five songs also varied between individuals. Two of the five males showed a trend of saturation of new syllables from the five songs, YM-WO at 51 syllables and YM-LbG at 33. New syllables were still recorded in the fifth song for the other three males with the largest number of syllables recorded for the largest male BM-OO (62). Two females showed a trend of saturation of new syllables from the five songs. Female 1 at 19 syllables and Female 3 at 28 syllables. New syllables were still recorded in the final song of the other three females and Female 3 produced the largest number of syllables out of the five. Although there was a trend of larger tui tending to have a higher number of syllables, analysis could not be carried out to investigate the correlation between song diversity and morphological measurements due to small sample size,

A study on the other New Zealand honeyeater, the bellbird, on Tiritiri Matangi Island, revealed a repertoire of 10 different songs and three different calls for males and a maximum of 21 different songs for females (Brunton & Li, 2006). Compared to bellbird, tui may have much larger song

repertoires. However, this can only be confirmed once the song repertoire is known for the bellbird populations on the mainland. Singing honeyeaters (*Meliphaga virescens*) have been found to have a repertoire of 47 distinctive songs (Baker, 1995), whereas white-plumed honeyeaters have a repertoire of just three songs (Jurisevic & Sanderson, 1994).

The variation in song and syllable diversity gives a basis for sexual selection. The presence of special syllables, within a male's repertoire, that are attractive to females, could also explain the sexual selection of males with large repertoires. Female canaries have been shown to be highly sexually responsive to male canaries that sing special trill-type syllable types. In the water pipit (*Anthus spiniletta*), the presence of a special buzz-type syllable within the male's repertoire has also shown to trigger high levels of sexual response from females. The larger a male's song repertoire, the higher the probability of them containing these syllables (Gil & Gahr, 2002).

Large song repertoires in males are also linked to genetic quality (Suter et al., 2009). In red-winged blackbirds, females have been shown to select males with larger song repertoires as breeding partners. These males tend to provide a greater amount of food for young birds (Buchanan & Catchpole, 2000; Buchanan & Catchpole, 2004) aiding offspring success by increasing offspring weight or condition at time of fledging, which are both key factors in post-fledging survival (Magrath, 1991).

Sexual selection for large song repertoires have also been found in stonechats (*Saxicola torquata*) (Greig-Smith, 1982). In both cases, large song repertoires were also linked to males who possess large territories (Yasukawa et al, 1980; Greig-Smith, 1982; Searcy & Yasukawa, 1996), which would increase foraging success, therefore increase chances of successful brooding. Male sedge warblers with large song repertoires were found to be healthier and less likely to carry diseases such as avian malaria (Buchanan et al, 1999). Furthermore in the great reed warbler, it was shown that males with larger repertoires are more likely to survive to breeding age than those males with smaller repertoires (Hasselquist et al, 1996).

From the syllable type distribution, the common syllable types comprised on average 37% of each bird's repertoire (Figure 4.6). The 'Other' syllable type group made up the remainder of each repertoire are those that are sung less often and/or are syllables difficult to categorise. The

repertoire of tui 'YM-WO' consisted of 99% of the most common syllable types such as harmonics and rapid frequency modulation syllables or trill. Within five songs, this male individual sang a very large amount of syllables.

There was less consistency of syllable types in the repertoire of the other nine birds. The five main syllable types comprised between 41 and 99% of male syllable repertoire and between 21 and 58% of the female syllable repertoire. In tropical mockingbirds it has been found that syllable consistency is positively correlated with age, breeding success and level of dominance (Botero et al, 2009). It could then be hypothesised that YM-WO is of high dominance and/or an older bird, but further testing would be needed to be conclusive.

4.4.2 Gender Variation

Females tended to have a smaller syllable repertoire than the male birds from their five songs analysed, however, there were no statistically significant differences in syllable diversity between genders, but the general trend did suggest that females had smaller syllable repertoires than males. Males did however produce a significantly greater number of new syllables per consecutive song than females, suggesting a larger male syllable repertoire. This is consistent with the findings from other studies such as in the crescent honeyeater (*Phylidonyris pyrrhoptera*) (Clarke & Clarke, 1999) and the canary (Nottebohm & Arnold, 1976) and consistent with the hypothesis that large syllable repertoires in male birds have evolved through female choice (Nottebohm & Arnold, 1976; Clarke & Clarke, 1999).

In a previous study on tui vocalisation, it was suggested that female tui will sing more complex songs than males (Bergquist, 1989), which was not the case in this study. Within this research, song complexity was measured by the number of different syllables within a song, whereas in the previous study on tui vocalisation, the level of song complexity was determined by the number of different frequencies at which the syllables were sung (Bergquist, 1989). In the other New Zealand honeyeater, the bellbird, females have also been shown to sing complex songs that parallel male songs (Brunton & Li, 2006), which was not the case in this study on tui.

The trends observed in this study are consistent with those of Arcese et al. (1988) who documented that the songs of the female song sparrow were structurally less complex than those of males and

that female singing was rare. Males in another honeyeater species, the crescent honeyeater, however, sing multiple syllable songs, whereas the female sings just a single syllable call (Clarke & Clarke, 1999) and in the canary, males sing longer, more complex songs than females (Nottebohm & Arnold, 1976). High levels of syllabic diversity, or song complexity, is a costly trait (Espmark, 1999; Hennin et al, 2009) and has been found to be a sexually-selected trait functioning to both attract mates and repel rivals (Searcy & Nowicki, 2000 & 2005), mostly in males, resulting in a higher song diversity in males than females.

Five-minute song sampling did not yield significant differences in the frequency of male and female singing ($p = 0.15$). Bergquist (1989) found that females sang less than males and when females did sing in the presence of males it was often a case of song matching or duetting with a male. The results of this, however, suggest that females will sing just as frequently as males. Further research with a larger sample size of females is required.

Female songs were not significantly shorter in duration nor simpler in terms of syllabic diversity, than male songs. The trends did however suggest that female songs were in general shorter and more simple than male songs. The lack of statistically significant differences in song duration and syllabic diversity is possibly due to small sample size and again further research with a larger sample size is required. These trends are consistent with the study on tui by Bergquist (1989). Previous research has shown that long song bouts by males are sexually-selected traits by females (Ball et al., 2006). In male birds, long song duration was found to correlate with overall genetic quality (Lambrechts & Dhondt, 1988; Forstmeier & Leisler, 2004; Leadbeater et al., 2005) and the ability to hold on to high-quality territories (Lampe & Espmark, 2003). Song duration has previously been observed to increase during aggressive confrontations in male ocelated antbirds (*Phaenostictus mcleannani*) (Araya-Ajoy et al., 2009). Female starlings for example will spend a greater amount of time listening to long male song bouts than to shorter ones and will preferentially track the position of longer bouts coming from different locations, highlighting the importance of song duration in male songs (Ball et al., 2006).

Male tui sang a significantly greater amount of rapid multiple note repetition (RMNR) syllables than females. RMNR syllables are complex, a further example of the greater level of song complexity exhibited by males over females. Complex syllables such as these are reliable signals

of male quality and are therefore favoured by sexual selection (Hofstad et al., 2002; Garamszegi et al., 2005). Sexual selection theory for the preferential selection of males that sing more complex syllables and songs, suggests that singing complex songs has additional costs, which only high quality males can afford to expend. Complex songs are controlled by elaborate pathways in the brain, so it has been theorised that those individuals that produce complex syllables have a larger brain capacity, therefore have a greater number of neurons and have a higher degree of quality (Marler & Slabbekoorn, 2004). In the sedge warbler, for example, it was shown that those males with larger and more complex song repertoires did indeed have a larger high vocal centre (HVC), the main song nucleus in songbirds (Airey et al, 2000).

4.4.3 Seasonal Variation

As predicted, there was a significantly greater proportion of trill in male songs in breeding season than non-breeding season. Trill is defined as a series of rapid frequency modulated syllables (Bolhius & Gahr, 2006).

Trill is highly costly to produce and therefore is an honest signal advertising the good physical and genetic condition of the callers that may be older and have high breeding success (Ballentine et al., 2004; Ballentine, 2009; Sewall et al., 2010). The breeding season is a crucial time for males to attempt to attract mates for purposes of reproduction, hence presenting a probable reason for higher proportion of trill in male songs during the breeding season (Ballentine et al., 2004; Hennin et al., 2009). Males with songs containing higher proportion of trill have been demonstrated to obtain a greater number of mating opportunities (Bolhius & Gahr, 2006).

The higher proportion of song containing trill during the breeding season could be a signal of unpaired males advertising their genetic quality to potential female breeding partners. In other songbird species such as the island canary, birds will alter their songs during the breeding season so that they contain more trill (Leitner et al., 2001).

In male nightingales (*Luscinia megarhynchos*), it has been demonstrated that trills, particularly those with broad bandwidth are signals of aggression and that songs containing trill stimulated

stronger responses from rival males. Trill was also shown to be a reliable predictor of the quality of the males responding to songs containing trill and their likelihood of obtaining a breeding partner within that season. Males that remained unpaired for the entire season decreased defensive territorial behaviour with increased amounts of trill in a simulated male opponent. Whereas males that became paired during the season increased the intensity of response to increased trill in the simulated opponent (Schmidt et al, 2008).

Furthermore, male swamp sparrow songs with a larger rate of trill with a broad bandwidth will elicit a greater number of copulation solicitation displays from females (Ballentine et al, 2004). Other complex syllables that are considered high-performance syllables have been shown to stimulate copulation displays in female canaries, suggesting that females assess the quality of males by the syllables they produce and will sexually favour those that produce syllables that are on the border of physical limits (Vallet et al, 1998; Gil & Gahr, 2002).

There could also be a hormonal basis to high levels of trill in breeding season songs. Levels of plasma testosterone are directly correlated with levels of competition in birds. Testosterone regulates avian song behaviour during the breeding season (Hau et al., 2000) and levels are increased during breeding season (Bolhius & Gahr, 2006), furthermore testosterone can affect specific features of bird calls as seen in studies in zebra finch (*Taeniopygia guttata*) and male grey partridge (*Perdix perdix*) songs, enabling females to assess male quality and their sexual motivation (Fusani et al., 1994). In Lincoln's sparrows (*Melospiza lincolni*), arginine vasotocin, a hormone involved with reproductive function in birds (Seth et al., 2004), has been shown to be increased in breeding season, in response to high-quality songs being sung during periods of mate attraction, particularly in the beginning of the breeding season. This increase in the hormone induces the counter-production of high-quality songs in response to higher levels of competition. These high-quality songs contain a large proportion of trill (Sewall et al., 2010). Indeed, the link between increased levels of testosterone during the breeding season and the production of trill within a male's song has been demonstrated in wild-living canaries (Bolhius & Gahr, 2006). Approximately 50% of trill syllables that were lost after one breeding season, were not sung again until the following breeding season when testosterone levels increased, supporting the theory that trill syllables are used as a tool for mate attraction, whose production is controlled by altering hormonal levels (Bolhius & Gahr, 2006).

Seasonal changes in tui song found in this study are consistent with earlier findings, songs in the non-breeding season were more uniform across a population than songs in the breeding season (Bergquist, 1989). However an increase in trill levels in the breeding season were not reported in previous studies. Prior research also showed that tui will sing different types of songs in the non-breeding season than in the breeding season furthermore playback experiments have shown that a non-breeding season song played in the breeding season will stimulate the singing of the same non-breeding season song (Bergquist, 1989). This response could, however, be attributed to the instinctive territorial function of song-matching, a crucial aspect of vocalisation in maintaining territory, especially during the breeding season.

At the population level, there was a greater diversity of syllables during the breeding season than in the non-breeding season. The majority of syllables were sung just once for both seasons. However, a greater percentage of once and twice-heard syllables were recorded in the breeding season, suggesting lower repetition of syllables within the breeding season. This greater diversity of songs during the breeding season suggests they play a role in mate choice. Large syllabic diversity, which is associated with high song complexity, may indicate a higher level of quality of the singer, because it is costly to allocate energy and time into this advertising (Gil & Gahr, 2002).

Seasonal differences in the frequency distribution of song types were found in the tui. In the breeding season, short-range interactive songs (43%) were more prevalent than in the non-breeding season (23%). In the non-breeding season, long-range songs were more prevalent than in the breeding season. For more accurate comparisons of song type frequency distribution between seasons in the future, song frequency data should be collected using standard sampling effort such as fixed time units song counts (i.e. songs per 5 minutes) in both seasons.

Short-range songs are most likely to be aggressive, territorial male to male confrontations and these encounters were observed especially at the beginning of the breeding season, when male tui were fighting to establish and maintain breeding territories. In other songbird species, aggressive male to male singing contests have also been shown to be most common at the start of the breeding season (Mennill et al., 2002). Short-range songs between male and female breeding partners are also most likely during the breeding season, mainly for pair-bonding and communication between

each other but also due to females actively soliciting copulations (Mennill et al., 2002) and parent-offspring communications.

Testosterone levels have been shown to be at their highest during the nest-construction phase of breeding season in zebra and Bengalese finches (*Lonchura striata*), which in turn increases the number of short-range, directed songs (Ritschard et al., 2010). This could also help explain why in the non-breeding season, long-range tui songs were more likely to be heard than short-range songs. Long-range broadcast songs in tui, have been previously shown to be more prevalent in the non-breeding season, when birds have a propensity to move around in large, family groups than in the breeding season (Bergquist & Craig, 1988).

Long-range broadcast songs are more common than short-range songs in general because tui are highly territorial songbirds. Even in the non-breeding season, by personal observations and in previous studies (Bergquist, 1989), tui will often guard an area of territory containing rich sources of nectar and/or fruit, from potential intruding conspecifics by singing regular long-range broadcast songs. These songs are designed to relay territoriality to as many rival individuals in the area as possible.

When comparing song frequency between the breeding and the non-breeding season, a significantly larger number of songs were recorded during the non-breeding season than in the breeding season. This is due possibly not to the reduction of number of songs each individual sang, but rather a decrease in the density of birds in the area, as most individuals tended to remain within their own territory within the breeding season, due to stronger territorial behaviour during this period, rather than feed in close proximity to many other individuals as they did in the non-breeding season. For example, in the non-breeding season, a single flame tree will be occupied by up to eight feeding tui (Pers. Obs. S. Hill, 2010) but during breeding season will be occupied most of the time by just one nesting pair. It has been previously shown in tropical regions that birds will sing all year round, due to plentiful year-long food availability (Langmore, 1998), which is likely to apply to northern New Zealand, a region of subtropical climate (Bolland et al., 2006), where this study was conducted.

The lower frequency of songs during the breeding season could also be attributed to both parents having a shift in priorities away from mate attraction and rival repulsion, especially once eggs have hatched, where the priority lay with chick-rearing.

Chapter Five - Regional Variation in Tui Vocalisation – Mainland Tui (*Prothemadera novaeseelandiae*) and Chatham Island Tui (*Prothemadera novaeseelandiae chathamensis*)



Chatham Island tui on flax, Rangatira Island (Photograph: S. Hill).

5.1 Introduction

Regional differences in vocalisations are common in avian species (Baker & Cunningham, 1985). Many New Zealand avian species have been shown to exhibit regional variation in vocalisation (bellbird (*Anthornis melanura*), Brunton et al, 2008; hihi or stitchbird (*Notiomystis cyncta*) Ranjard, 2009; tīeke or North Island saddleback (*Philesturnus rufusater*), Parker, 2010, and kokako (*Callaeas cinerea*), Brown et al, 2004).

Regional variations or dialects in bird song can be described as differences in songs of separate populations of the same species (Marler & Tamura, 1962). It can also be termed ‘geographical variation’ in songs of populations in different locations (Searcy et al., 1997). Regional dialects develop due to individuals copying and imitating the vocalisations of parents or neighbours (Gill, 2007). Differing dialects consist of variations in syllable (sound unit) and song structure (the patterns of song delivery), similar to the regional accents in humans (Gill, 2007).

There have been several hypotheses proposed to explain the evolution of regional song dialect:

1. *Local Adaptation Hypothesis*

This hypothesis proposes that females will gain fitness advantages when they breed with birds from their natal regions, rather than birds from other regions (Podos & Warren, 2007). Dialects may function to induce birds to breed near their natal areas as females are more attracted to males that sing local dialect, thereby promoting assortative mating (Baptista & Morton, 1982).

2. *Social Adaptation Hypothesis*

The social adaptation hypothesis suggests that males will gain fitness advantages by learning similar songs to those of dominant local males to maximise mating and breeding success. Young males, for example, of the highly promiscuous village indigobird (*Vidua chalybeata*) will mimic the songs of their older, dominant and reproductively-successful male neighbours in order to attract female birds (Payne et al, 2000).

3. *Colony Password Hypothesis*

Similar to the social adaptation hypothesis, this proposes that dialects serve the function of allowing the immediate recognition of intruders with foreign dialects into a population (Podos & Warren, 2007).

4. Vocal Convergence Hypothesis

The vocal convergence hypothesis proposes that regional dialects are long-term survival features kept stable by a combination of the preferential learning of local song or call types by immigrants and the purifying against selection of foreign songs or calls into the local population (Wright et al, 2008). Regional dialects are maintained through the generations via the processes of cultural evolution, where young birds will learn the local dialects from their parents and neighbours (Luther & Baptista, 2009).

5. Male Exclusion Hypothesis

The male exclusion hypothesis states that male songbirds will aggressively drive away individuals from adjacent foreign dialect areas, thereby preventing the settling of alien male conspecifics into the local territory, maintaining common local dialect and preventing dialect mixing (Baker & Cunningham, 1985). Male white-crowned sparrows (*Zonotrichia leucophrys*) generally will react most strongly, in terms of aggression or rate of singing, towards those individuals from immediately adjacent dialect areas, followed by those male rivals with local dialects and males would respond the weakest to those with distant dialects (Baker et al, 1981). The strength of a male's response was seen to be directly related to the degree of difference between the local dialect and the song being sung by a rival (Tomback et al, 1983). The level of response of white-crowned sparrows was therefore seen to decrease, with increased differences from the local song. This difference in response level is due to either nonrecognition of distant dialect as being from a conspecific by the male bird, or due to the lower sexual rivalry a distant bird poses due to the lower sexual response of a local female to a distant dialect. Conversely, the stronger response level to adjacent males is likely due to the greater genetic threat males from adjacent dialect areas pose to local males (Baker et al, 1981; Baker & Cunningham, 1985).

6. Acoustic Adaptation Hypothesis

Birds inhabiting areas with similar vegetation type will share common song features (Date & Lemon, 1993), which can be perceived as dialects. The acoustic adaptation hypothesis (AAH)

proposes that the evolution of the acoustic properties of bird songs has been shaped by selection that is dependent on habitat structure (Boncoraglio and Saino, 2007). The AAH predicts that songs that have on average lower frequency, narrow bandwidths, low-frequency whistles, long syllables and inter-syllable intervals are more likely to occur in habitats containing dense and complex vegetation including rainforests (Nemeth et al, 2006), that is to say habitats that are closed. Whereas high-frequencies, broader bandwidths, high-frequency modulations (trills), short syllables and short inter-syllable intervals are expected in areas with more herbaceous coverage or areas that are more open (Nemeth et al, 2006).

Low-frequency songs in habitats containing dense and complex vegetation may have evolved through the following evolutionary pressures: 1. closed-habitat species may have evolved low-frequency songs as they are stronger than high-frequency songs in enclosed habitat areas and therefore allow the song to travel further and be heard further away, 2. narrower bandwidth may have evolved in areas with greater density of vegetation, as energy has to be concentrated in smaller bands of frequency to maintain strong transmission signals, 3. high-frequency sounds have a greater propensity for blurring or ‘reverberation’, within closed habitats. No such restrictions occur in more open habitat. Maximum and minimum frequencies within songs would also be different in different habitats, due to the selective pressures for a reduced bandwidth for birds populating closed habitats (Boncaraglio and Saino, 2007).

Regional variation of bird song has long been of interest to ecologists, who wish to further understand the relationship between regional differences and the process of speciation (Payne, 1999; Podos and Warren, 2007). Speciation can ultimately occur due to alterations in habitat-dependent acoustic signals females use in mate choice. These acoustic labels can be used to judge a male’s fitness to the female’s habitat. Effective vocal transmission is dependent on habitat type. Vocal properties may vary in different habitat types found in different regions, which in turn may contribute towards changes in physiological and morphological aspects that underpin bird song production, such as beak size and syrinx mass (Podos & Warren, 2007). This phenotypic plasticity ultimately will result in the divergence of species (Slabbekoorn & Smith, 2002).

The study of bird song dialect has been useful in determining the source population of immigrations. For example, a study was carried out to determine the source population of a self-introduced population of bellbird at Tawharanui Regional Park. This study found that their songs

were most closely matched tui songs from Little Barrier Island, confirming the immigration of bellbird from Little Barrier Island (Brunton et al., 2008).

Studies of song dialect are also potentially important for conservation management. Female North Island kokako (*Callaeus cinerea wilsoni*), for example, will preferentially choose to breed only with those males with local dialect. This highly selective song choice in breeding partner of female kokako could potentially result in the lack of breeding success of newly translocated kokako and hinder the efforts to re-establish self-sustaining populations (Brown et al, 2004).

Tui are common throughout the North Island, South Island and Stewart Island of New Zealand but scarce on the east coast of the South Island (Robertson & Heather, 1999). Tui are also found in the Kermadec and Auckland Islands and a tui subspecies is found in the Chatham Islands (Robertson & Heather, 1999). Very little is known about the ecology of the tui, including their vocalisation.

Chatham Island tui (*Prosthemadera novaeseelandiae chathamensis*) are very similar to the mainland species, however, they are, on average, one-fifth larger and one-fifth heavier, have paler feathers and have longer white throat feathers than their mainland relatives (Canterbury University Press in association with the Dept. of Conservation, 1996; Dilks, 2004; Morris & Ballance, 2006).

Following the extinction of the Chatham Island bellbird (*Anthornis melanocephala*) in the early 20th century, the tui is the only extant honeyeater on the Chatham Islands (Dilks et al, 1998; Morris & Ballance, 2006). Chatham Island tui were almost extinct from the main Chatham Island in the early 1990s (DoC, 2001) and breeding of tui on the main island has not been recorded since (DoC 2001). To re-establish tui populations on the main Chatham Island, 14 tui were translocated from Rangatira to a small conservation covenant on the main island in 2009 (DoC, 2009) and a further 40 tui translocated in the summer of 2010 (Molles, 2010, July). Chatham Island tui are ranked as Category A, the highest priority classification for conservation management (Molloy & Davis, 1994) and are classified as Endangered by the IUCN Red List Categories (IUCN, 1994). Before human colonisation, the Chatham Island tui were widespread and common on the main Chatham Island and Pitt Island, Rangatira and Mangere but has suffered a continual decline in the last 50 years (DoC, 2001). The decline in Chatham Island tui can be attributed to the introduction of predators in particular cats, rodents and possums as well as extensive habitat loss by fire and conversion into farmland. The Rangatira population is threatened by interspecific competition for food resources mainly from starlings (*Sturnus vulgaris*) (DoC, 2001).

5.1.1 Research Aims and Hypotheses

Due to morphological differences, the Chatham Island tui is regarded as a subspecies of the mainland tui. The effect of the isolation of Chatham Island tui from the mainland tui population in terms of their vocalisation is not known. The aim of this study was to investigate the regional differences in song between a mainland population of tui, at Tawharanui Regional Park, and Chatham Island tui.

Such knowledge is important for understanding the evolution of songs in tui. It provides baseline information for further investigations in the role of vocalisation on mate choice and fitness. Understanding the role of songs in mate choice can potentially improve the conservation management of endangered Chatham Island tui by taking the song dialect into consideration when planning further translocations.

I predict the following differences in their songs between the two populations:

1. Significant overall difference in the spectral characteristics of both short-range and long-range song structure between the two populations due to the isolation of Chatham Island tui and mainland tui.
2. A proportion of identical syllables between the two populations, but a larger proportion of syllables would be unique to either population.
3. Tui in the Chatham Islands to have less variation within their songs, smaller song repertoire and lower syllabic diversity due to smaller population size and lack of gene flow compared to the mainland tui populations.
4. Shorter song duration, lower proportion of song containing the complex, higher frequency trill component and the number of inflection points in the terminal note are predicted in the Chatham Islands population compared to the mainland population, for the reasons described in 3.

5.2 Methods

5.2.1 Study Sites

There were two study sites for this chapter, Chatham Islands and Tawharanui Regional Park. Details about these sites are given in Chapter Two.

The Chatham Islands trip was made at the start of the breeding season, so tui were territorial and remained mainly within their territories for the duration of the sampling period. This enabled the sampling of each individual target multiple times with confidence, despite the lack of individual identification for many of the tui.

5.2.2 Recording Methods and Song Variables

Recording methods and song variables used in this study were consistent with those used in Chapter 3 and 4. Song variables include number of notes, song duration, trill duration, proportion of song containing the trill component, FMA of entire song, syllabic diversity, FMA of trill, F_{\max} of song, F_{mean} of song, bandwidth of song. For details of recording methods and variable definitions please refer to Chapter Two.

5.2.3 Overall Song Variation Between Populations

Multivariate statistical analyses were used to investigate further the differences between the two populations in the overall (both long-range and short-range songs) dispersion of the spectral characteristics as well as the overall variation of structure of male tui songs between the two populations, using the parameters described in Section 2.3 of Chapter 2.

The song variables derived from male tui songs, recorded on the Chatham Islands ($N = 40$) and Tawharanui ($N = 33$) were examined for normality and extreme outliers. Six outliers were removed from the data set (2 from the Chatham Islands population, 4 from Tawharanui population) and the following variables were transformed to $\ln(x)+0.01$ to remove skewness: number of notes, song duration, trill duration, FMA of entire song). A resemblance matrix based on Euclidean

distance was then calculated and the patterns of relationship were visualised by 2D and 3D non-metric multi-dimensional scaling (MDS) ordination plots (each with 25 random iterative starts) (Figure 5.1). Heterogeneity in spectral characteristics of male short-range and long-range songs from the Chatham Islands and Tawharanui was then examined using the distance-based test of multivariate dispersions (PERMDISP, 9999 permutations) (Anderson, 2006) following standardisation to z-scores (i.e. normalisation). Finally, a non-parametric multivariate analysis of variance was conducted (PERMANOVA, 9999 permutations) (Anderson, 2001). These song analyses were performed using the PRIMER v6 computer program (Clarke and Gorley, 2006) with the PERMANOVA+ add-on package (Anderson et al., 2008).

5.2.4 Comparison of Short and Long-Range Song Parameters between Populations

Differences in dialects are often subtle and can only be demonstrated using statistical analysis to compare parameters such as number of inflection points and sequences within trill (Marler, 1956). Song parameters described in Section 2.3 in Chapter 2 extracted from short and long range songs were explored separately using PCA and compared between the two populations using Mann-Whitney U tests as the majority of the data exhibited nonparametric distribution (Mann & Whitney, 1947).

Boxplots were then created to visualise the data (Figure 5.4). All statistical tests were performed using software R 2.12.2 (© R Foundation for Statistical Computing, 2010) and Microsoft (Redmond, USA) Excel. All PCA procedures were performed using package FactomineR.

All statistical tests were two-tailed and the alpha was set at 0.05, which is a 95% confidence interval. Therefore, p values = <0.05 were interpreted as significant.

5.2.5 Song and Syllable Repertoire

For analysis of comparison of song repertoire between the Chatham Island and Tawharanui tui populations, 72 minutes (1.2 hours) of song recording was collected from a total of 9.3 hours recordings on Chatham Islands. To standardise the sampling for comparison, a subsample of 72 minutes (1.2 hours) worth of recordings data, from a total of 15.3 hours of recording effort at Tawharanui Regional Park during breeding season, was also used in this study.

Song repertoire was measured by the number of different songs recorded during the recording period. Songs that sounded similar but had subtle differences, such as the addition of an extra syllable or the subtraction of syllables, were considered to be different songs.

To compare the syllabic diversity between the two populations, firstly, 30 breeding season songs (all from different individuals) were randomly selected, using simple random sampling, from both populations, from the 9.3 hours and 15.3 hours of recordings on Chatham Islands and at Tawharanui respectively. Secondly, the number of *different* syllables in each population's repertoire, encountered within the above-mentioned 30 songs of each population, were counted using Raven Pro 1.4 Beta Version (Cornell Lab of Ornithology, Ithaca, NY, USA). Thirdly, a Mann-Whitney U test was performed to test for statistically significant differences in syllabic diversity between the two populations, using STATISTICA data analysis software (Statsoft, Inc). Time constraints limited the number of songs that could be analysed to 30 per population, for this part of the study.

Due to time constraints, the first 200 non-trill syllables encountered from these 30 songs from each population were used to compare the diversity and similarity of syllables between Chatham Island and Tahwaranui tui songs. Trill syllables were excluded from this analysis due to their high complexity, making visual and audio comparisons of large number of syllables difficult and extremely time consuming. Syllables with a harmonic structure, for example, but dissimilar sound were regarded to be not similar and those with similar sound but dissimilar structure were also regarded to be not similar.

5.3 Results

5.3.1 Comparison of Overall Song Variation between the Two Sites

The number of different songs recorded in a total of 72 minutes (1.2 hour) recording time was 79 songs for the Chatham Island population (Appendix 5) and 103 songs for the Tawharanui population (Appendix 1). Statistical tests of song diversity between the two sites were not carried out due to the differences in sampling effort for individual birds.

There were no significant differences in multivariate dispersion of spectral characteristics (PERMDISP, $F = 0.17$, $P = 0.68$, 9999 permutations) evident when male tui songs, both long-range and short-range, from the Chatham Islands ($N = 40$ songs from 40 individuals) were compared with male tui songs, both long-range and short-range, from Tawharanui ($N = 33$ songs from 33 individuals) but there was a significant difference in multivariate location (PERMANOVA, pseudo- $F_{1, 71} = 4.07$, $P = 0.002$). That is to say, there was a significant overall difference in the multiple variables in short and long-range songs between the two populations (Figure 5.1).

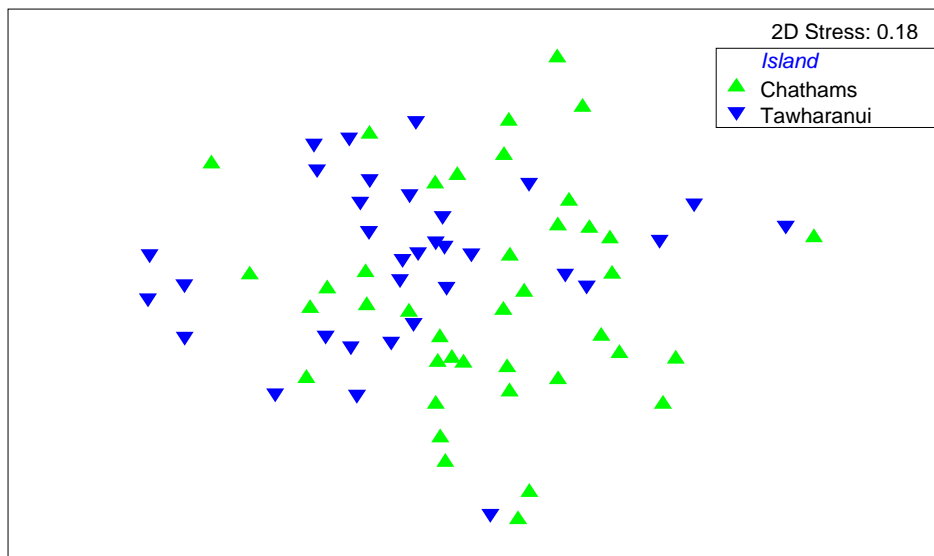


Figure 5.1: An unconstrained non-metric MDS ordination of multivariate differences in song variables measured from male tui song recorded on the Chatham Islands and at Tawharanui Regional Park.

5.3.2 Variation of Song Types between Populations

Firstly, the correlations between the twelve variables described in Section 2.3 were tested. Due to their significant correlation with two or more other variables, syllabic diversity, maximum and mean frequencies and the number of notes per song were extracted from further analysis (Table 3.1 in Chapter Three).

Male short-range songs ($n = 20, 12$) were compared between the two populations initially and there was no significant variation found, however male, long-range songs ($n = 28, 17$) between the populations were compared and significant variation was found.

Male short-range and male long-range, breeding season songs were compared between the two populations to test for variation. The PCA showed which of the remaining eight variables were contributing the greatest amount of variation between male short-range and male long-range songs between the two populations.

When comparing male *short*-range songs between the two populations, Principal Component 1 (PC1) was correlated with song duration, interval between notes, FMA of the trill component, the number of inflection points in the terminal note, bandwidth and minimum frequency. PC1 contributed 35.38% of the variance between the Chatham Islands and the Tawharanui population. PC2 contributed 18.63% of the variance between the two populations and was correlated with FMA of the entire song, percentage of song containing trill, bandwidth and FMA of the trill component (Table 5.1, Figure 5.2). However, no trends of difference were detected in short-range songs for further analysis.

Principal component analysis of *long*-range songs showed that PC1 was correlated with song duration, inflection points in the terminal note, proportion of song containing trill, FMA of the trill component, interval between notes and minimum frequency. PC1 contributed 22.00% of the variance between the Chatham Islands and the Tawharanui population (Table 5.2). PC2 contributed 19.02% of the variance and was correlated with FMA of the trill component, FMA of the entire song, song duration, interval between notes and bandwidth, but exhibited no significant contribution to the variance between populations. Figure 5.3 shows a scatterplot from the PCA, which highlights the separation between the two populations. The variables that had the highest correlation with PC1 and therefore contributed the greatest level of variation between the two populations were subsequently chosen for further statistical analysis.

Table 5.1: Eigenvalues, variance explained and factor loadings of the eight variables following PCA analysis for *short*-range songs. Variables with factor loading values greater than 0.48 are highlighted in bold.

	PC1	PC2
Eigenvalue	2.83	1.49
% of Variance	35.38	18.63
Song Duration	0.90	-0.02
Percentage of Song Containing Trill	0.12	0.67
Inflection Points in the Terminal Note	0.50	-0.29
FMA of the Trill Component	0.62	0.37
Interval Between Notes	0.83	-0.09
Minimum Frequency	-0.63	0.14
Bandwidth	0.47	0.43
FMA of the Entire Song	-0.24	0.77
<i>n</i> = 20, 12		

Table 5.2: Eigenvalues, variance explained and factor loadings of the eight variables following PCA analysis for *long*-range songs. Variables with factor loading values greater than 0.48 are highlighted in bold.

	PC1	PC2
Eigenvalue	1.76	1.52
% of Variance	22.00	19.02
Song Duration	0.71	-0.45
Proportion of Song Containing Trill	0.70	0.25
Inflection Points in the Terminal Note	0.57	0.18
FMA of the Trill Component	0.45	0.61
Interval Between Notes	0.38	-0.47
Minimum Frequency	-0.31	0.18
FMA of the Entire Song	-0.04	0.60
Bandwidth	-0.06	-0.49
<i>n</i> = 28, 17		

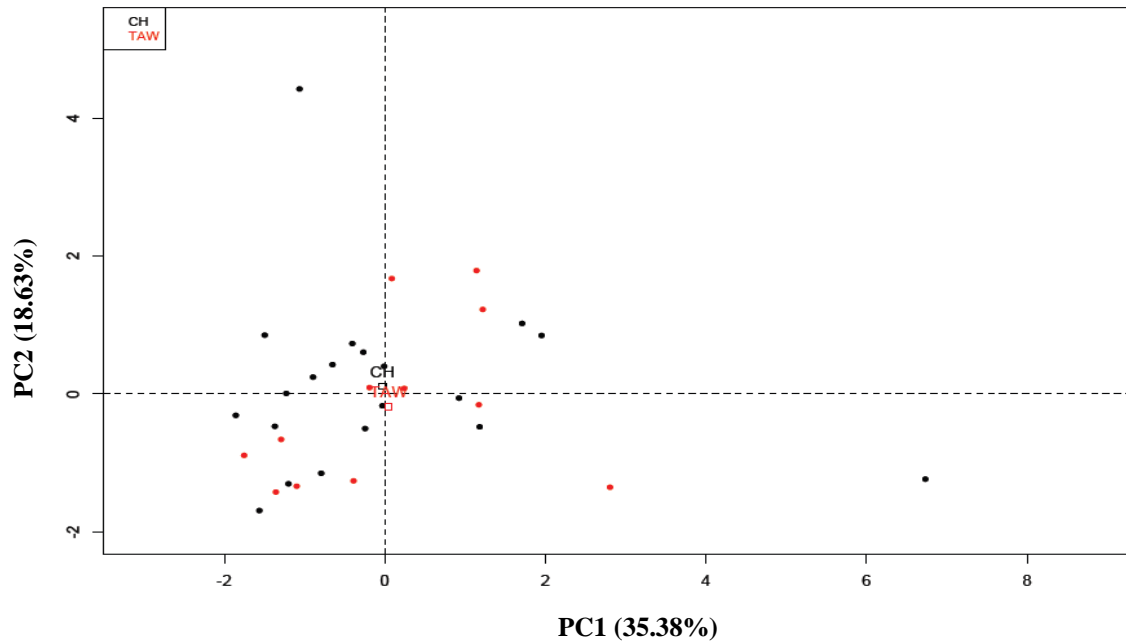


Figure 5.2: A PCA scatterplot highlighting the lack of significant separation of short-range songs at the Chatham Islands (CH) and Tawharanui (TAW) populations.

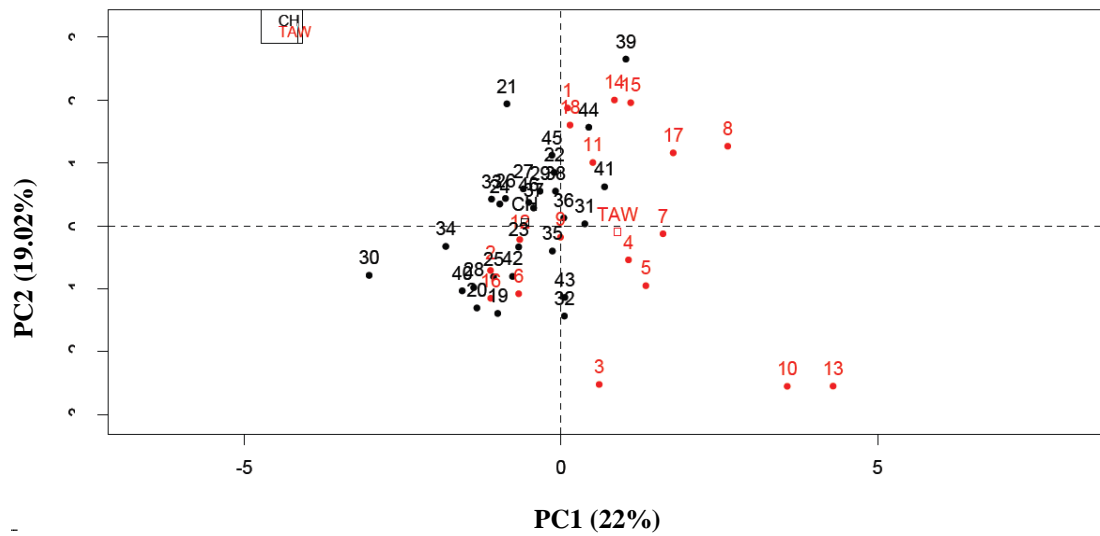


Figure 5.3: A PCA scatterplot highlighting the separation between long-range songs at the Chatham Islands (CH) and Tawharanui (TAW) populations.

The Mann-Whitney U test results showed significant differences between the two populations in song duration, proportion of song containing trill and the number of inflection points in the terminal note (Table 5.2, Figure 5.4).

Table 5.3: The descriptive statistics and Mann-Whitney U test results on song parameters of tui populations at Chatham Islands and Tawharanui.

Variable	Median		Range		Statistical Values from Mann-Whitney U Test	
	Chatham Islands	Tawharanui	Chatham Islands	Tawharanui	W	p
Song Duration (Sec)	4.4	5.9	7.9 Min: 1.5 Max: 9.4	37.3 Min: 3.1 Max: 40.4	119	0.00227
Proportion of Song Containing Trill (%)	26	51	75 Min: 18 Max: 93	96 Min: 0 Max: 96	135.5	0.009016
Inflection Points in the Terminal Note	0	1	2 Min: 0 Max: 2	4 Min: 0 Max: 4	160	0.00895
FMA of the Trill Component	4.1	5.9	8.4 Min: 0 Max 8.4	7.9 Min: 0.7 Max: 8.6	209	0.3424
FMA of the Entire Song	2.07	1.67	4.12 Min: 0.86 Max: 4.98	5.41 Min: 1.04 Max: 6.45	286	0.4508
Interval Between Notes	0.08	0.11	0.16 Min: 0.05 Max: 0.21	0.6 Min: 0.05 Min: 0.65	213.5	0.3923
Minimum Frequency	0.58	0.47	0.88 Min: 0.16 Max: 1.04	0.43 Min: 0.25 Max: 0.68	328	0.0892

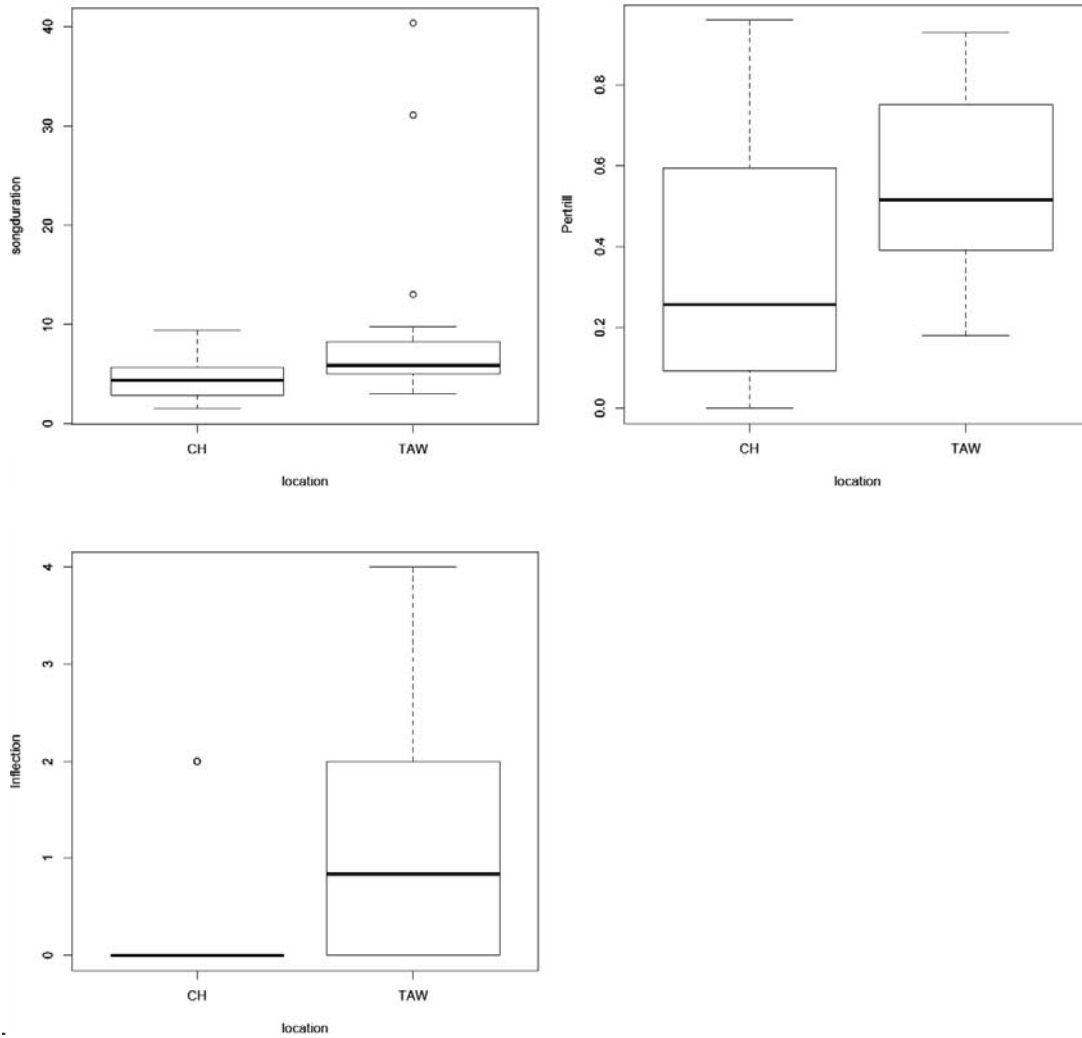


Figure 5.4: Boxplots showing the parameters that exhibited statistically significant differences between the two populations in male, long-range songs: song duration, proportion of song containing trill and number of inflection points in the terminal note. The median values are depicted by the black horizontal lines within the boxes and the circles depict outliers from the normal 75% of the population.

5.3.3 Syllabic Diversity and Syllable Sharing

From 30 songs, the number of different non-trill syllables found in the Chatham Islands population was 241 (a median of 7 new syllables per song) (Appendix 3). From 30 breeding season songs in the Tawharanui population, the number of different non-trill syllables found was 356 (a median of 10 new syllables per song) (Appendix 2). The number of syllables per song was significantly larger in the Tawharanui population than the Chatham Islands population ($U = 313$, $p = 0.042362$) (Figure 5.5).

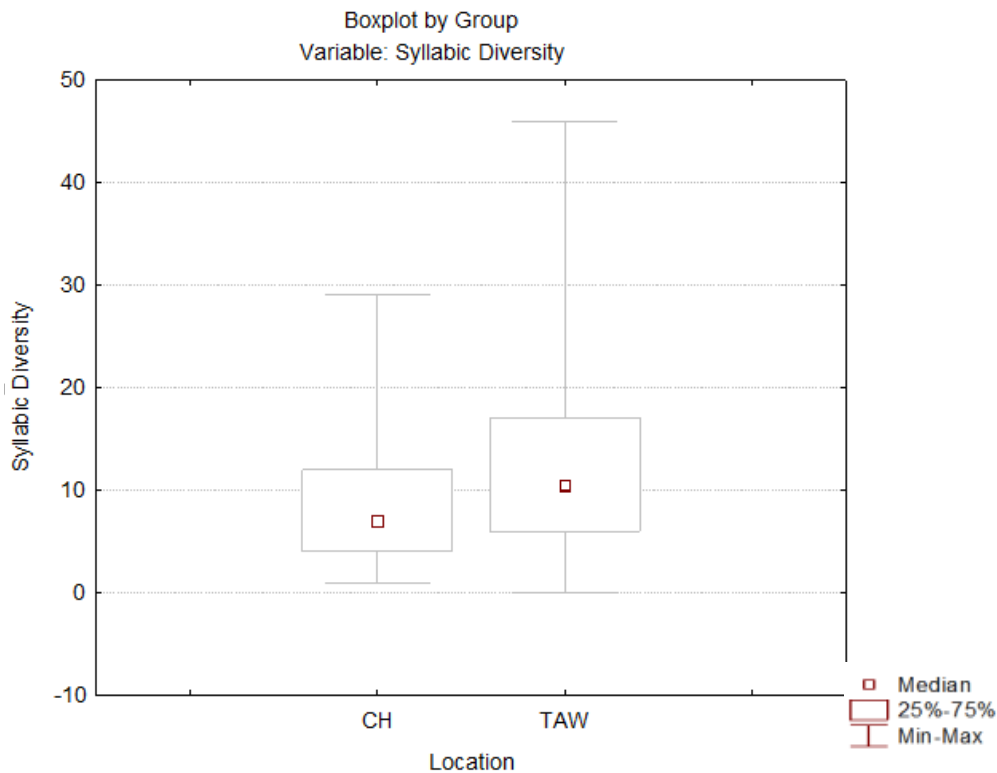


Figure 5.5: Boxplot displaying a significantly greater number of different syllables per song at Tawharanui compared to Chatham Islands.

It was also found that from the first 200 non-trill syllables from each population within the same data set, 15 (7.5%) of the syllables shared high similarity both in sound and structure between the two populations. These 15 syllables can be seen in Appendix 4.

Within each population, 28.5% of syllables were shared between individuals in the Tawharanui population and 35% in the Chatham Island population.

5.4 Discussion

5.4.1 Song Variation between Populations

There were no significant differences in the structure of short-range songs between the two tui populations. The lack of significant differences in short-range songs is presumably because in both populations these song types tended to be confrontations and/or aggressive encounters, whereas long-range songs, which did show significant differences between the populations, functioned as advertisements of information such as genetic diversity, body size and strength and were not directed towards any specific individual (Wiley & Richards, 1982). It has been suggested that long-range tui songs are sung by more dominant birds, giving continuous information about their dominant status (Bergquist, 1989). It is possible, therefore, that in short-range songs, a tui will rely principally on visual cues, such as feather ruffling, to create the illusion of increased body mass, to transmit its intent or status, rather than the more complex, vocal cues used in long-range songs. Furthermore, compared to long distance songs, effective transmission of short-distance songs are less likely to be under the constraints of habitat type, therefore structure of short-range songs would be expected to be more homogeneous in both populations than long-range songs.

Unsurprisingly, statistically significant difference was found in the overall song structure, for both long and short-range songs, between the two locations. Chatham Island tui had significantly shorter song duration, a lower proportion of song containing trill and fewer inflection points in the terminal note than their mainland counterparts, as predicted. These have all been demonstrated as being sexually-selected traits linked to male genetic diversity (van Buskirk, 1997; Nowicki et al, 1998; Ballentine et al., 2004). These results indicate a lower genetic diversity in this island population. However, this lower genetic diversity will need to be confirmed with genetic data.

In male birds of some species, song duration is directly linked with mating success (European starling, Hamao, 2008) and male quality (great tit, Lambrechts & Dhondt, 1987); immunocompetence (European starling, Ball et al, 2006), longevity (great reed warbler, Forstmeier & Leisler, 2004); and survival rates (great tit, Lambrechts & Dhondt, 1987). The Rangatira and Pitt Island population was estimated to be 278 ± 62 in 1999 (Dilks, 2004; P. Dilks, personal communication, September 29, 2011). Although a population survey has not been carried out at the Tawharanui site, from Oct 2009 to Jan 2011, 393 tui have been colour banded (Sarah Wells,

unpublished data) and a significantly greater number of unbanded tui were sighted in the park, indicating a significantly larger tui population size compared to that on the Chatham Islands. A greater level of intraspecific competition on the mainland could explain why mainland tui sing significantly longer songs than their island counterparts. Song length has been shown to reflect male physical strength and aggressiveness in the hoopoe (*Upupa epops*) (Martín-Vivaldi et al., 2004).

At Tawharanui, the habitat is generally more open and contains less dense vegetation than at either of the two study sites on the Chatham Islands, particularly on the uninhabited Rangatira. The acoustic adaptation hypothesis, which proposes that song characteristics are driven by habitat type to maximise transmission (Boncoraglio & Saino, 2007), helps to explain why long-range songs at Tawharanui contained a significantly greater proportion of trill than long-range Chatham Islands songs. Bird song trills transmit more effectively in open habitats than in habitats containing a greater density and complexity of vegetation, due to the interference caused by the vegetation and reverberation that blurs the distinction between notes (Doutrelant et al., 1999; Nemeth et al., 2006; Boncoraglio & Saino, 2007; Grant & Grant, 2010).

Trill is highly costly to produce and may be perceived by female birds as an indicator of male quality (Ballentine et al., 2004). These high levels of vocal performance were found to reflect a male's phenotype (Nowicki & Searcy, 2004). Evidence also suggests that females will use acoustic cues such as trill to select those males more suited to the female's particular habitat (Slabbekoorn & Smith, 2002). Higher proportion of trill found in tui songs on the mainland may also be a result of stronger intra and inter-sexual selection on the mainland due to a greater density of conspecifics, therefore a greater number of male competitors and potential breeding partners.

The greater proportion of trill within the long-range songs of Tawharanui tui could also have an anti-predatory function. There is evidence supporting the idea that long-range bird songs are structurally designed to reduce the level of locatability by potential predators or even brood parasites at the start of the breeding season (Boncoraglio & Saino, 2007). High-frequency trill components will reduce the level of locatability of the signaller (Boncoraglio & Saino, 2007). There are a far greater number of potential predators on the mainland than in the Chatham Islands population, hence a greater motive to incorporate song structural features such as trill to help evade predation during long-range broadcast transmission.

Less trill could also simply imply lesser genetic diversity of males at Chatham Islands than at Tawharanui. The geographic isolation of populations such as Chatham Island tui inevitably leads to increased levels of inbreeding, reducing fitness and genetic diversity and replenishment (Frankham, 1997; Hedrik & Kalinowski, 2000) and may result in limiting the production of energy costly song characteristics such as trill.

The number of inflection points, defined as the number of frequency modulation slopes in a note or syllable within a song, is a reflection of bird song complexity (van Buskirk, 1997). It has been suggested that the number of inflection points in the terminal note of a song could also distinguish between the sexes. Song complexity is linked to genetic variation in male birds (Nowicki et al., 1998b; Hasselquist, 1998). It would be predicted that females would have lower inflection points than males, as it is likely a female selected trait linked to reproductive viability. The higher number of inflection points in tui song in mainland population may indicate a greater level of genetic variation, in the mainland population compared to that in the Chatham Islands.

The Chatham Island tui population will have a lesser degree of emigration and immigration (Waitakere City Council, n.d; Dilks & Kearvell, 1996; DoC, 2001) as well as a likely smaller population compared to the mainland tui populations. The level of song variability would be expected to be lower in the island population. Contrary to the prediction, however, there were no significant differences in the multivariate dispersion of the song spectral characteristics between the mainland and the island population. This may indicate the strong selection on song diversity through its function in mate choice and resource defence. Nevertheless, it should be acknowledged that the lack of statistically significant differences in multivariate dispersion between the songs of the two populations could be an effect of small sample size. Further analysis with a larger sample size is required before a firm conclusion can be drawn.

5.4.2 Syllabic Diversity

In 30 songs analysed, the syllabic diversity of the mainland population was found to be significantly greater than the Chatham Island population ($p < 0.05$), as predicted.

This result is consistent with findings in a previous study on the singing honeyeater. Isolated island populations of singing honeyeater were found to have a lower syllabic diversity than mainland and other less isolated island populations (Baker et al., 2002).

Greater song complexity was found to be correlated with larger population size (Hamao & Ueda, 1999) and greater levels of male competition for resources, food and mates (Craig & Jenkins, 1982). These factors result in stronger sexual selection pressures towards the possession of complex songs (Collins et al., 2009), which are reliable indicators of genetic quality to female birds (Hasselquist, 1998; Marshall et al., 2003), overall condition (Nowicki et al., 2000) and parental ability (Buchanan & Catchpole, 2000). High quality males generally will have high quality territories and food sources, which are key factors in female mate choice and subsequent reproduction.

As predicted, a small proportion (7.5%) of syllables had high similarity between the two populations and the majority of syllables were unique to each population. It was expected that the two populations would have a degree of similarity in their syllable composition, as they are related subspecies and share similar physiological and morphological traits that related to song production. In the Puget Sound White-crowned sparrow (*Zonotrichia leucophrys pugetensis*), it was observed that identical syllables were produced in several separate populations in a range spanning approximately 480 kilometres, in USA and Canada. For example, two identical syllable types were observed in 14 separate populations of Puget Sound White-crowned sparrow across this range. Furthermore, identical complex syllables were observed in up to nine separate populations of this species (Baptista, 1977).

Greater syllable diversity predicts a higher level of song diversity. Indeed a larger number of different songs were recorded within the mainland population than the Chatham Island population, as predicted. Microgeographic dialects have also been noted in both populations with more local dialects heard in Tawharanui Regional Park. However, due to data insufficiency, these aspects cannot be tested statistically as yet and need to be further investigated.

Chapter Six – Conclusions, Future Research and Implications



Chatham Island tui on Rangatira Island (Photograph: S. Wells).

6.1 Conclusions and Scope for Future Research

Song Complexity

This is the first in-depth investigation into the vocalisation of tui. The results showed that tui used various types of calls (alarm calls, distress calls) and songs (short-range songs, long range songs). Their large, diverse and complex array of syllables have provided the basis for a large and complex song repertoire which put tui at the top end of song complexity among honeyeaters. Notwithstanding, it is most likely that the full repertoire of tui song has not been reached in this study, the number of tui songs (303) recorded is larger than that of the singing honeyeater (47) (Baker, 1995), which was considered to have a large song repertoire among honeyeaters. Further study is required to obtain more complete tui song repertoire in order to better evaluate of the complexity of tui vocalisations and to investigate the possibility of infinite repertoires within the tui. In previous studies, species such as the sedge warbler have been assigned as having infinite song repertoires, even though their syllable repertoire is little larger than 60 syllables (Gil & Gahr, 2002).

Individual, Gender and Seasonal Variation

Males produced a significantly larger number of complex syllables than females and showed a trend of singing longer songs and a greater syllabic diversity. These are all sexually-selected traits that linked to genetic quality and reproductive potential. Indeed, a variation is observed among individuals, especially among males, in syllable diversity, song repertoire and song duration, providing the basis for sexual selection. However the sample size in this study was too small for statistical tests on individual variations. Such variations should be further investigated using a larger sample size. Future long term studies should also be carried out to investigate these song aspects of individual tui and relate these to their fitness in order to further understand the function of songs and their role in sexual selection.

In terms of seasonal differences, compared to the non-breeding season, a greater proportion of trill were recorded in male tui songs during the breeding season. Evidence suggests that trill syllables

are costly to produce and that the production of trill within a song is a sexually-selected trait. Between seasons, there was also a greater frequency distribution of less common syllables in the breeding season, likely due to a greater need, at this critical period, for individuals to advertise their quality and fitness to potential breeding partners, by singing a wider range of syllables. There was also a trend that a higher proportion of long-range songs were produced in non-breeding season compared to breeding season. Further studies with appropriate sampling methods are required to investigate whether such differences are statistically significant.

This research can also lead to further studies investigating the relationship between the variability in song and the levels of fitness and genetic quality of different individuals. Enhancing our knowledge of tui vocalisation could also be crucial in determining individuals' reproductive potential, past breeding success and gender differentiation, factors which all have implications in terms of the conservation of tui, especially in areas where tui are rare and require management such as translocation.

Regional Variation

A significantly greater syllabic diversity was observed in the population at Tawharanui than in the Chatham Islands. Differences in song structure were only detected in male long-range songs between populations. Chatham Island tui had significantly lower song duration, lower proportion of song containing trill and fewer inflection points in the terminal note than the mainland population. These spectral parameters have all been demonstrated as being sexually-selected traits positively correlated with male genetic diversity (van Buskirk, 1997; Nowicki et al, 1998; Ballentine et al., 2004), suggesting that the mainland population has an overall higher level of genetic diversity than the island population. Geographical isolation, greater chances of inbreeding and lower emigration and immigration on the island population could help explain this possibility. Further studies on the genetics of these two populations will help to test this hypothesis.

Bird song trills transmit more effectively in open habitats than in habitats containing a greater density and complexity of vegetation, this acoustic adaptation hypothesis could also explain the higher proportion of trill component in the mainland population. The habitat at Tawharanui is generally more open and contains less dense vegetation than at either of the two study sites on the

Chatham Islands, particularly on the uninhabited Rangatira. Trill also has lower locatability than other syllable types (Boncoraglio & Saino, 2007), which could thus facilitate both the successful transmission of long-range songs whilst at the same time not jeopardising exact location to would-be predators. There are a greater number of predators on the mainland than in the Chatham Islands population, giving greater cause to produce trill in long-range broadcast transmission. However all these hypotheses require further testing.

Tui are known to have regional dialects. Further study is required to collect data from different locations on the mainland to understand the degree of regional variation in tui vocalisation. Long term data collected from the same individuals or locations will help understanding the song change over time.

6.2 Implications to Conservation Management

This study has provided baseline data of song type, individual, gender, seasonal and regional differences in tui vocalisation. Enhanced knowledge is important to develop our understanding of communication in tui. Development of our knowledge of tui vocalisations can help in determining individuals' reproductive potential, past breeding success and may enable us to differentiate between sexes using songs. These factors all are of high importance in terms of conservation of tui, particularly in those areas where tui are scarce and require more conservation efforts and management such as translocation projects.

Song dialect can effect breeding success of newly translocated populations of bird species, if birds were from different sources. North Island kokako, as mentioned, have been shown to preferentially choose mates originating from their local population (Brown et al, 2004), consistent with the local adaptation hypothesis (Ranjard, 2009). Indeed, following the kokako translocation project at Kapiti Island, when pairing successes between translocated and local individuals did take place, it was predominantly young local birds who mated with the translocated kokako, who presumably had learned at least part of their songs (Brown et al., 2004).

Female saddlebacks will also discriminate against males from other populations potentially limiting and reducing the effective population size of this species (Parker et al, 2010).

It is as yet unknown whether or not translocated tui face potential reproductive barriers. However in the planning of future translocation projects it would seem sensible to choose birds from as few original populations as possible (Brown et al, 2004) in order to maximise breeding success and subsequently increase the chances of establishing a self-sustaining population.

The number of different songs heard within populations could be used as a population density estimation method (Wilson & Bart, 1985). Dawson & Efford (2009) combined sound information collected in the field using four microphones, with statistical analysis methodology called 'spatially explicit capture-recapture'. They found that using acoustic signal methods were more accurate than mist-netting for estimating population density. These techniques were also advantageous as they are non-invasive, causing far less stress to birds and involved far less field-effort than mist-netting and other ecological practices. These methods were suitable for a wide range of songbirds, particularly those with easily distinguishable individual characteristics (Dawson & Efford, 2009). This may be a potential technique suitable for tui population survey and should be explored.

The results of the study on regional variation in tui song suggests that the vocalisation of the Chatham Islands and mainland population of tui were significantly different. The Chatham Island tui has a current conservation status of 'Endangered' by the IUCN Red List Categories (IUCN, 1994) and has morphological differences to the mainland tui so is considered a subspecies. The Chatham Island tui needs to be conserved to prevent extinction.

Small populations combined with limited immigration enriching the genetic diversity could potentially lead to population bottlenecks and even extinction (Amos & Balmford, 2001; Kennedy, 2009), which is why it is important to continue monitoring vulnerable populations such as the Chatham Island tui for genetic diversity and population fluctuations. Long-term genetic studies on the Chatham Island tui are currently underway with the overall aim of acquiring important information as regards to their genetic diversity relative to the mainland species. Subsequently, conclusions can be drawn as to the levels of inbreeding and potential genetic bottlenecking in the island population. Strategies to counter these problems can then be planned and implemented accordingly.

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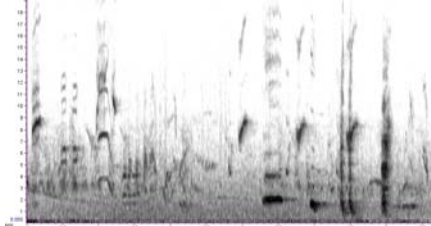
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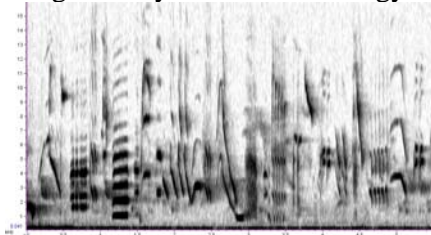
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Appendix 1: Sample of 5 songs from a total of 302 from Tawharanui Regional Park. The remainder on CD-ROM.

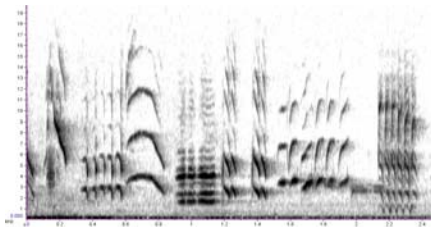
Song 41. July 29th 2010. Anchor Bay, Tawharanui. Male.



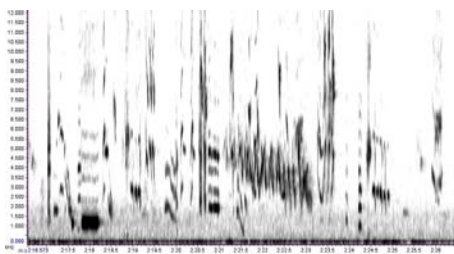
Song 46. July 30th 2010. Ecology Bush, Tawharanui. YM-RY (Male).



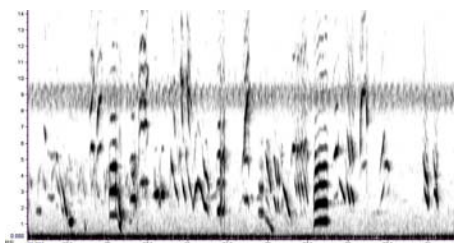
Song 50. July 30th 2010. Ecology Bush, Tawharanui. YM-RY (Male).



Song 227. November 30th 2010. Jones Bay, Tawharanui. GO-WM (Male).

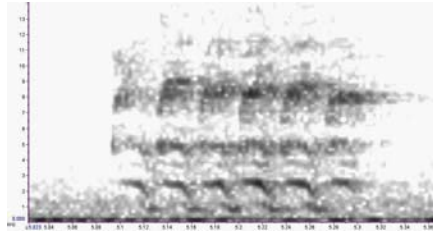


Song 296. December 15th. Jones Bay, Tawharanui. BM-OO (Male).

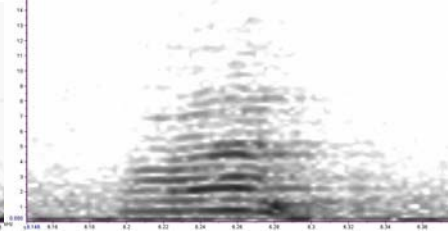


Appendix 2: Sample of 10 syllables from the 264 syllables in 30 breeding and non-breeding season songs from Tawharanui Regional Park. The remainder on CD-ROM.

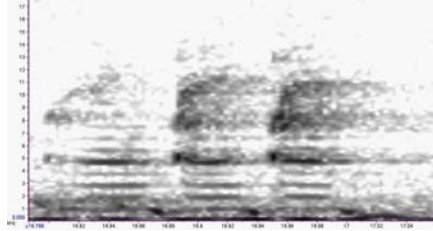
Syllable 3.



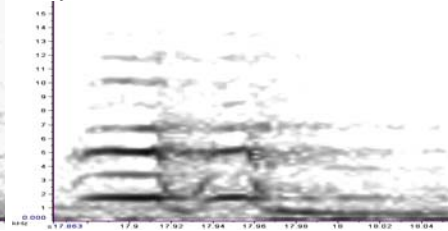
Syllable 6.



Syllable 12.



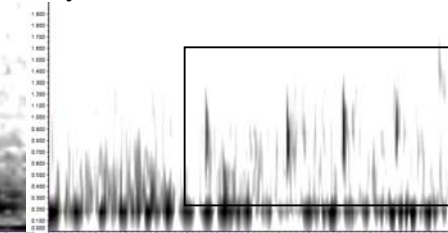
Syllable 14



Syllable 36.



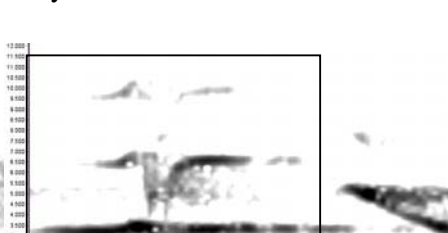
Syllable 37.



Syllable 35.



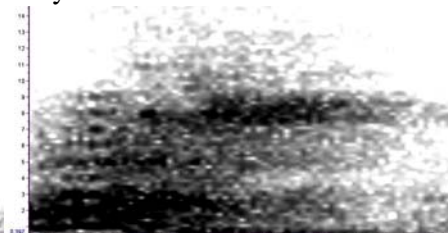
Syllable 47.



Syllable 79.

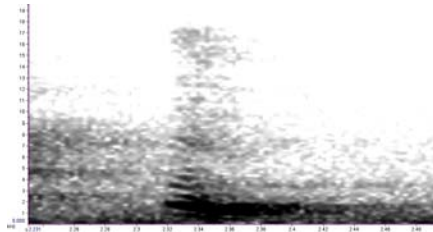


Syllable 82.

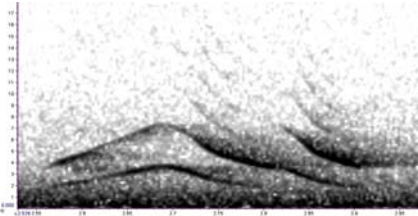


Appendix 3 : Sample of 10 syllables from the 241 syllables in 30 songs from Chatham Islands. The remainder on CD-ROM.

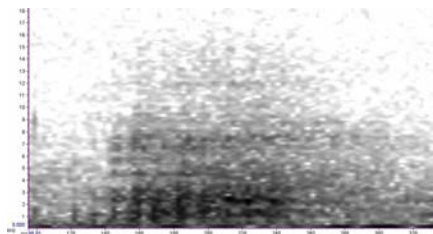
Syllable 4.



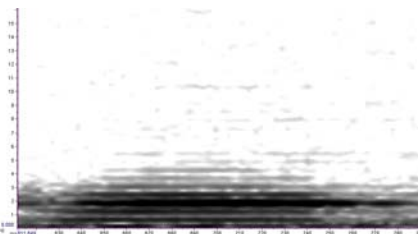
Syllable 5.



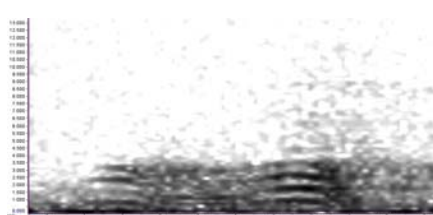
Syllable 12.



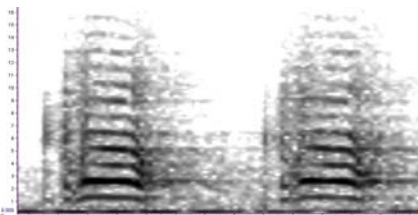
Syllable 13.



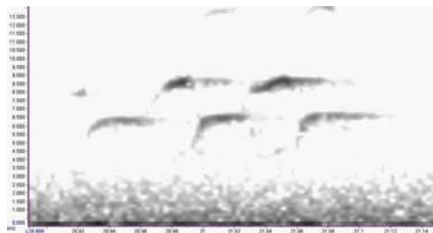
Syllable 15.



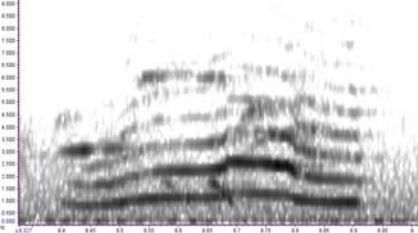
Syllable 25



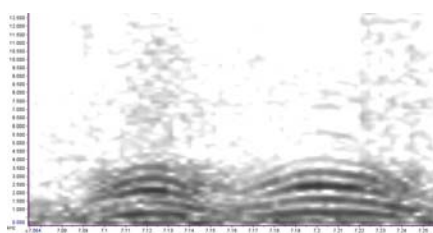
Syllable 39.



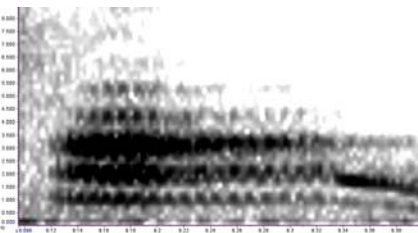
Syllable 50.



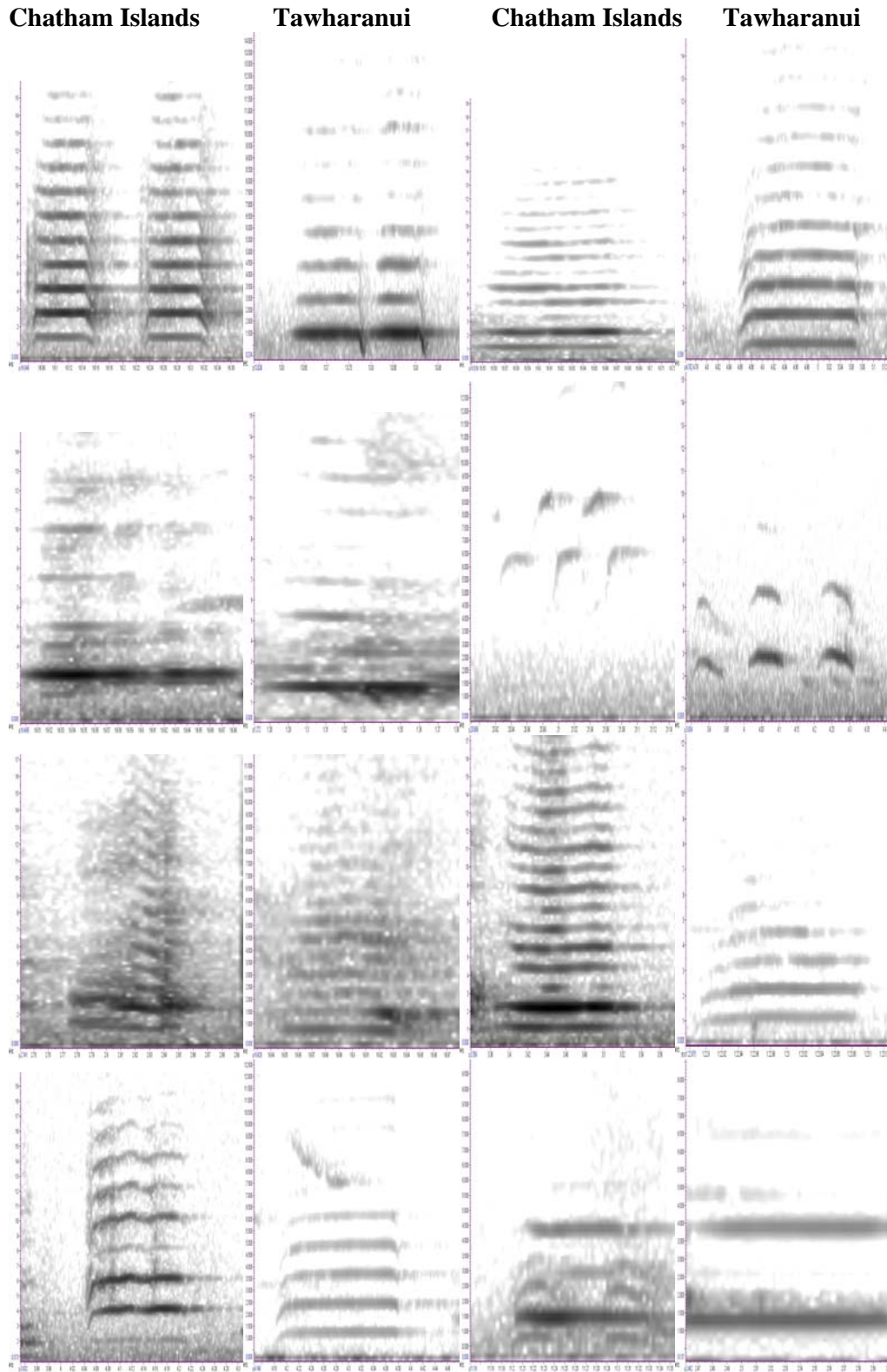
Syllable 57.



Syllable 60.

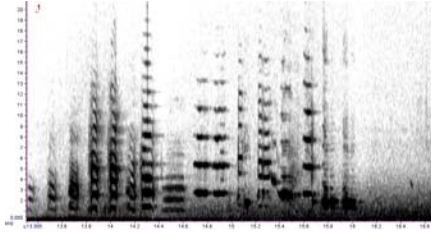


Appendix 4: Similar syllables from the two populations. The remainder on CD-ROM.

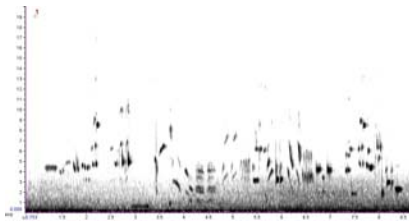


Appendix 5: Sample of 5 songs from a total of 79 from Chatham Islands. The remainder on CD-ROM.

Song 15. October 23rd 2010. West Landing, Rangatira, Chatham Islands. Male.



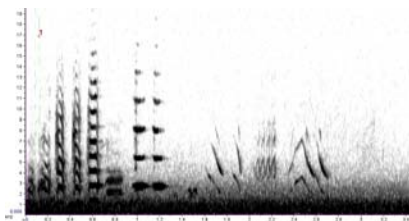
Song 25. October 24th 2010. West Landing, Rangatira, Chatham Islands. Male.



Song 39. October 25th 2010. West Landing, Rangatira, Chatham Islands. Male.



Song 44. October 25th 2010. West Landing, Rangatira, Chatham Islands. Male.



Song 54. October 26th 2010. West Landing, Rangatira, Chatham Islands. Male.

