

## A comparison of vocalisations between mainland tui (*Prosthemadera novaeseelandiae novaeseelandiae*) and Chatham Island tui (*P. n. chathamensis*)

Samuel D. Hill<sup>1\*</sup>, Weihong Ji<sup>1</sup>, Kevin A. Parker<sup>2</sup>, Christophe Amiot<sup>1</sup> and Sarah J. Wells<sup>1</sup>

<sup>1</sup>Human–Wildlife Interactions Research Group, Institute of Natural and Mathematical Sciences, Massey University, North Shore Mail Centre, Private Bag 102904, Auckland 1131, New Zealand

<sup>2</sup>The Ecology and Conservation Group, Institute of Natural and Mathematical Sciences, Massey University, North Shore Mail Centre, Private Bag 102904, Auckland 1131, New Zealand

\*Author for correspondence (Email: [S.Hill@massey.ac.nz](mailto:S.Hill@massey.ac.nz))

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**Abstract:** Vocalisations are important for territorial defence, mate attraction, and species recognition in many songbirds. Comparative studies on the songs of birds between islands and mainland populations provide insight into the evolution of vocal communication in terms of both ecological and social factors. We compared the vocalisations of tui (*Prosthemadera novaeseelandiae novaeseelandiae*), an endemic honeyeater from New Zealand’s mainland, with those of a subspecies from the remote Chatham Islands (*P. n. chathamensis*). Song spectral variables of male long-range ‘broadcasting’ songs differed between mainland and Chatham Island tui populations. Songs recorded from five mainland populations had significantly greater syllable diversity and produced a higher percentage of trills than those from the Chatham Islands. These characteristics have been revealed in past studies as being sexually selected traits positively correlated with male genetic diversity. The acoustic adaptation hypothesis could also help to elucidate the presence of a significantly higher percentage of trill components in the songs of the mainland population, as the mainland study sites in general contained more areas of open vegetation, where trills transmit more effectively than in dense forest, which dominated the sampling sites on the Chatham Islands. Future research into the variation of tui song complexity in relation to population size, geographic isolation, and habitat structure between different mainland sites would provide further insight into links between selective pressures and vocal complexity.

**Keywords:** diversity; island; song; syllable; trill; variation

### Introduction

Geographical variation in bird song is common in many species (Marler & Tamura 1962; Baker & Cunningham 1985). These differences can be on a microgeographic (Payne 1978; Leader et al. 2000) or macrogeographic scale (Benedict & Bowie 2009; Pitocchelli 2011). Geographical differences in bird vocalisations consist of variations in syllable (sound unit) and song structure (the patterns of song delivery), similar to regional dialects or accents in humans (Kroodsma 2005). In previous research, geographical variation of vocalisations has been observed in a wide number of species such as song sparrow (*Melospiza melodia*) (Peters et al. 2000), white-crowned sparrow (*Zonotrichia leucophrys*) (Derryberry 2011), blue tit (*Parus caeruleus*) (Doutrelant et al. 1999), and Eurasian nuthatch (*Sitta europaea*) (White 2012). New Zealand avian species have also been shown to exhibit regional variation in their vocalisations (bellbird *Anthornis melanura*, Brunton et al. 2008; hibi or stitchbird *Notiomystis cyncta*, Ranjard 2010; North Island saddleback *Philesturnus rufusater*, Parker et al. 2012; kōkako *Callaeas cinerea*, Brown et al. 2004, Rowe & Bell 2007; and kea *Nestor notabilis*, Bond & Diamond 2005).

Several hypotheses have been proposed to explain the evolution of regional song variation. These include the ‘local adaptation hypothesis’, which suggests females gain fitness advantages by breeding with birds from their natal regions rather than with birds from regions further away (Podos & Warren 2007). Dialects may function to induce birds to breed close to their natal areas as females are more attracted to males

that sing local dialect, thereby promoting assortative mating (Baptista & Morton 1982).

The ‘acoustic adaptation hypothesis’ proposes that birds inhabiting areas with similar vegetation type will share common song features (Date & Lemon 1993). This hypothesis suggests that the evolution of the acoustic properties of bird songs has been shaped by selection that is dependent upon habitat structure (Boncoraglio & Saino 2007). It predicts that songs that have on average lower frequency, narrower bandwidths, low-frequency whistles, long syllables, and long inter-syllable intervals are more likely to be produced in closed habitats such as rainforests that contain dense and complex vegetation (Nemeth et al. 2006). A more frequent production of high-frequencies, broader bandwidths, high-frequency modulations (trills), short syllables, and short inter-syllable intervals are expected to be produced in areas that are more open (Nemeth et al. 2006), in order to maximise the effective transmission of sound.

The ‘social adaptation hypothesis’ predicts that males gain fitness advantages by learning songs from dominant local males to maximise their chances of mating and breeding success (Payne et al. 2000). For example, young males of the highly promiscuous village indigobird (*Vidua chalybeata*) will mimic the songs of the older, dominant and reproductively successful male neighbours in order to attract female birds (Payne et al. 2000).

Vocal properties may vary within different habitat types across regions, which in turn may coincide with changes in physiological and morphological features that underpin bird

song production, such as beak size and syrinx mass (Podos & Warren 2007). This phenotypic plasticity ultimately can contribute to the divergence of species (Slabbekoorn & Smith 2002).

Variation in avian vocalisations has also been previously observed between mainland and isolated island populations of singing honeyeaters (*Lichenostomus virescens*) (Baker et al. 2002), hwamei (*Garrulax canorus*) (Tu & Severinghaus 2004) and bush warblers (*Cettia diphone*) (Hamao & Ueda 2000). Island populations tend to have structurally simpler and less complex songs than their mainland congeners due to factors such as weaker selection pressures towards complex song for the acquisition of breeding partners and/or high quality territories (Hamao & Ueda 2000). Lowered song complexity in island subspecies might also be caused by founder effects, leading to reduced song diversity, as a result of a new population being established by a small number of founders from a larger population (Baker & Moeed 1987; Baker 1996; Parker et al. 2012). Indeed, evidence for a founder effect in song (cultural founder effect) has been observed in the Chatham Island population of chaffinch (*Fringilla coelebs*), an introduced European passerine (Baker & Jenkins 1987).

Song complexity is a sexually selected trait of fundamental importance to successful territory defence and mate attraction in songbirds (Briefer et al. 2010). Syllable repertoire size (syllabic diversity), the length of song, or the production of complex syllables can all be used to measure song complexity in birds (Boogert et al. 2008). Evidence suggests that this complexity is increased within mainland populations due to greater levels of male competition for resources, food, and mates than their island counterparts (Craig & Jenkins 1982). Complexity of vocalisations has also been positively correlated with parental ability (Buchanan & Catchpole 2000), reproductive success (Woodgate et al. 2012) and overall male quality (Buchanan & Catchpole 2000; Soma & Garamszegi 2010).

We examined geographical variation of the highly complex vocalisations of mainland tūi (*Prothemadera novaeseelandiae novaeseelandiae*) and an isolated subspecies, the Chatham Island tūi (*P. n. chathamensis*). The tūi is a honeyeater species 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 tūi (Driskell et al. 2007), the tūi being the larger and more dominant of the two species (Stewart & Craig 1985; Bergquist 1989).

Although common throughout the North Island, South Island, and Stewart Island of New Zealand, tūi are scarce on the east coast of the South Island (Gill et al. 2010). Tūi are also found in the subtropical Kermadec Islands and subantarctic Auckland Islands (Gill et al. 2010). The endangered Chatham Island subspecies (Miskelly et al. 2008) has been subject to recent translocation efforts that have resulted in the reestablishment of Chatham Island tūi onto the main Chatham Island (Bell et al. 2013). Very few recent studies have focused on tūi behavioural ecology, including their vocalisations. One previous study, however, suggested that tūi song exhibits sexual, regional, behavioural, and individual variation (Bergquist 1989).

The Chatham Islands are a volcanic archipelago formed just 3–4 million years ago (Stilwell & Consoli 2012), situated 800 km east of Christchurch, New Zealand. The islands are subject to high levels of endemism with 16 bird species being endemic to the Chatham Islands (Aikman et al. 2001).

Chatham Island tūi are larger and heavier, have paler feathers and longer white throat feathers compared with mainland tūi (Dilks & Kearvell 1996; Dilks 2004; Ballance

& Morris 2006). It is not known whether there are any behavioural differences between mainland and Chatham Island tūi, including their vocalisations. It was predicted that the larger overall mass of the Chatham Island subspecies might result in the production of lower frequency sounds (Pijanowski et al. 2011).

The aim of this study was to investigate differences in vocal characteristics between mainland tūi populations and Chatham Island tūi. Additionally, we predicted a lower syllabic diversity in Chatham Island tūi, resulting from geographic isolation, which presents tūi with a lesser scope for immigration and emigration as well as lower levels of male competition. We also predicted differences in frequency parameters between the mainland and the subspecies, due to morphological disparities and greater areas of closed habitats within the Chatham Islands. Acoustic adaptation theory predicts a greater percentage of trills would be produced by tūi on the mainland where there are more open areas of vegetation compared with the Chatham Islands study sites.

## Methods

Seven sites, two in the Chatham Island group and five on the mainland, were included in this study. Location sizes, a habitat description, and a list of dominant plant species is provided for each in Table 1.

### Chatham Islands

The two study sites on the Chatham Islands were the uninhabited and predator-free 219-ha Rangatira Island, or South East Island (44°34' S, 176°17' E), and the 40-ha predator-proof-fenced Ellen Elizabeth Preece Conservation Covenant (Caravan Bush; 44°28' S 176°17' E) (Table 1; Fig. 1a) on the east coast of Pitt Island. On both Rangatira and Pitt islands, flax (*Phormium tenax*), on which the tūi primarily feed during late spring and early summer, was flowering during the period of data collection. This ensured tūi were abundant. An estimated 45% of Rangatira, approximately 98 ha, is covered by forest (Nilsson et al. 1994). At Caravan Bush, all introduced mammals have been eradicated from the covenant apart from mice (*Mus musculus*).

### Mainland sites

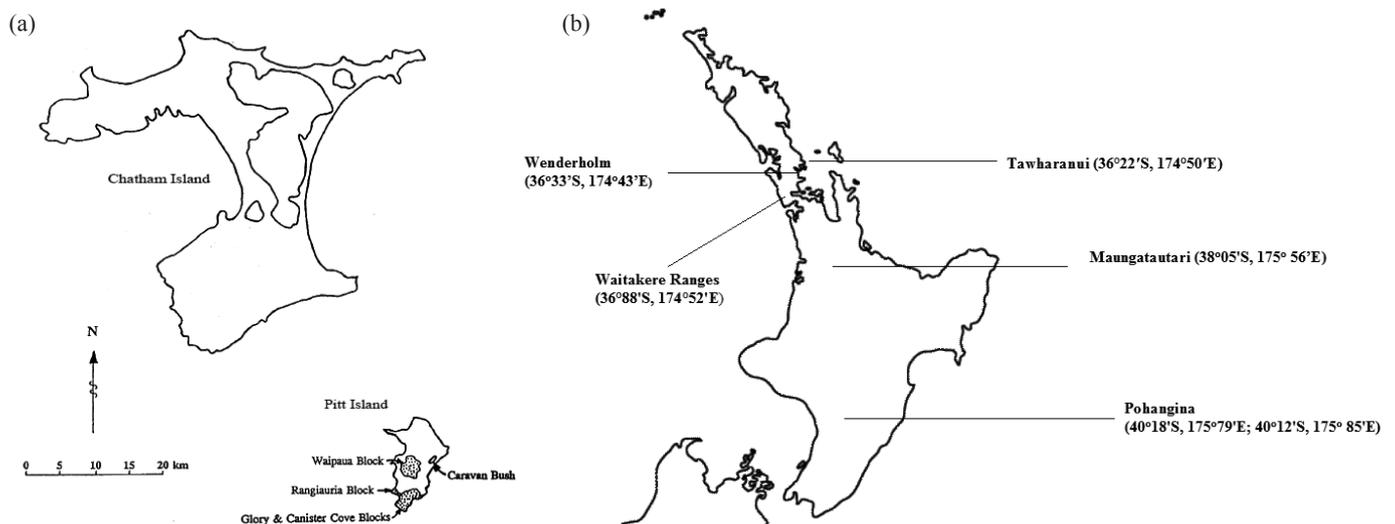
Sample sizes are reflective of the density of tūi at each of the five mainland sites (Table 1; Fig. 1b), at the time of recording. Sampling effort varied according to the size of each site, in order to record as many different individuals at each site as possible.

### Tawharanui Regional Park

Tawharanui Regional Park, 90 km north of central Auckland, New Zealand, is a 588-ha 'mainland island' located on the Tawharanui Peninsula. A fence was installed to exclude mammal predators and the coastal park became virtually predator-free in 2004, except for the presence of mice, following a successful poisoning and trapping programme (Brunton et al. 2008). Tawharanui Regional Park consists of predominantly grazed pasture (Auckland Council 2009). At least 50% of the tūi population were banded between 2009 and 2012 (S. J. Wells unpubl. data 2013).

**Table 1.** A broad description of the tūi vocalisation study sites including habitat complexity and dominant vegetation.

Site name	Size (ha)	Predator status	Habitat complexity	Dominant species	References
Rangatira Island	219	Predator-free island	High	<i>Phormium tenax</i> , <i>Muehlenbeckia australis</i> , <i>Pteridium esculentum</i> , <i>Plagianthus regius chathamicus</i> , <i>Myoporum laetum</i> , <i>Olearia traversii</i> , <i>Myrsine chathamica</i> , <i>Coprosma chathamica</i> , <i>Melicytus chathamicus</i> , <i>Pseudopanax chathamicus</i> , <i>Macropiper excelsum</i> , <i>Ripogonum scandens</i>	Nilsson et al. 1994; Dilks 2004; Roberts et al. 2007
Caravan Bush, Pitt island	40	Predator-proof fence	High	<i>Rhopalostylis sapida</i> , <i>Phormium tenax</i> , <i>Muehlenbeckia australis</i> , <i>Pseudopanax chathamicus</i> , <i>Corynocarpus laevigatus</i> , <i>Corokia macrocarpa</i>	Miskelly & Emberson 2008
Tawharanui	588	Predator-proof fence	High	<i>Leptospermum scoparium</i> , <i>Metrosideros excelsa</i> , <i>Agathis australis</i> , <i>Vitex lucens</i> , <i>Beilschmiedia tarairi</i> , <i>Rhopalostylis sapida</i>	Auckland Council 2009; S. D. Hill pers. obs
Wenderholm	134	Predator-controlled	Medium	<i>Metrosideros excelsa</i> , <i>Beilschmiedia tarairi</i> , <i>Kunzea ericoides</i> , <i>Sophora microphylla</i> , <i>Corynocarpus laevigatus</i> , <i>Cordyline australis</i> , <i>Rhopalostylis sapida</i>	James & Clout 1996; Lovegrove et al. 2002
Ark in the Park, Waitakere	1100	Predator-controlled	High	<i>Dacrydium cupressinum</i> , <i>Agathis australis</i> , <i>Metrosideros robusta</i> , <i>Podocarpus totara</i> , <i>Dacrycarpus dacrydioides</i> , <i>Dicksonia</i> spp., <i>Kunzea ericoides</i>	Fraser & Hauber 2008; Derraik 2009
Maungatautari Southern Enclosure	65	Predator-proof fence	High	<i>Dacrydium cupressinum</i> , <i>Beilschmiedia tawa</i> , <i>Ixerba brexioides</i> , <i>Weinmannia racemosa</i> , <i>Quintinia serrata</i>	Watts et al. 2011
Pohangina Wetlands	7.2	Predator-controlled	Low	<i>Dacrycarpus dacrydioides</i> , <i>Podocarpus totara</i> , <i>Phormium tenax</i> , <i>Cordyline australis</i> , <i>Clianthus puniceus</i>	S. D. Hill pers. obs
Totara Reserve, Pohangina	340	Predator-controlled	Medium	<i>Podocarpus totara</i> , <i>Dacrydium cupressinum</i> , <i>Metrosideros robusta</i> , <i>Prumnopitys taxifolia</i> , <i>Dacrycarpus dacrydioides</i> , <i>Rhopalostylis sapida</i>	S. D. Hill pers. obs

**Figure 1.** Map showing the location of Caravan Bush (44°28' S, 176°17' E) (a) (adapted from Walls et al. (2000), with permission from the Department of Conservation) and a map of New Zealand's North Island showing the locations of all of the mainland tūi study sites (b).

*Wenderholm Regional Park*

Wenderholm Regional Park, 46 km north of Auckland, is a 134-ha mainland reserve. The park is bounded by two tidal estuaries and consists of an 80-ha hilly forested headland. Wenderholm also consists of a partly forested spit of open coastal pastureland and consolidated sands and wetlands bordering one of the surrounding estuaries (Lovegrove et al. 2002).

*Ark in the Park, Waitakere Ranges Regional Park*

Ark in the Park, within the Waitakere Ranges Regional Park, approximately 30 km west of Auckland, is a conservation area consisting of 1100 ha of forest.

*Maungatautari Ecological Island*

Maungatautari Ecological Island, 37 km south-east of Hamilton, Waikato, New Zealand, is a 3400-ha mainland island and an extinct andesitic volcanic cone. The Southern Enclosure of Maungatautari is 65 ha and is where recording took place. The reserve is surrounded by farmland.

*Pohangina, Manawatu*

Two sites in the Pohangina Valley, 30 km north-east of Palmerston North, Manawatu, were chosen. The first was the Pohangina Wetlands, a 7.2-ha nature reserve surrounded by farmland. The second site was the 340-ha Totara Reserve Regional Park located adjacent to large areas of farmland.

**Sound recordings**

Data collection of tūī songs on both the Chatham Islands and the mainland was carried out during the tūī breeding season (October–January). This occurred in 2010/11 (both sites) and 2012/13 (mainland only). During sampling sessions we walked slowly one way along marked tracks to locate tūī, and at all sites we attempted to cover as much area as possible. When a tūī was located, recording was initiated and ended when the tūī either ceased singing or flew away. During each recording, the location, time, the band combination of the tūī

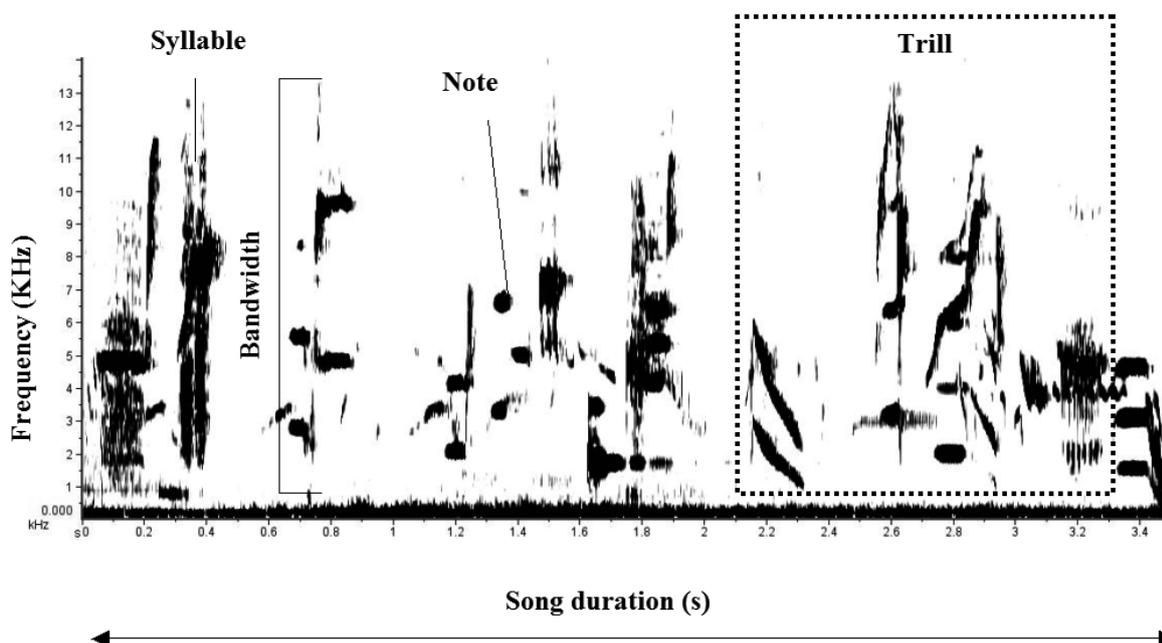
(if applicable), behaviour, and song type were also recorded.

Recordings were collected from banded tūī whenever possible. For unbanded birds, only one individual was recorded at any one time to avoid recording the same bird twice in any given sampling location, hence no individual was used more than once in song analysis. During the breeding season, when both nests and flowering plants are being guarded, male tūī will remain strictly within their respective territories, which helped avoid pseudoreplication. Furthermore, the highly territorial and habitual nature of tūī (i.e. individual males only singing on particular perches, S. D. Hill pers. obs.) also minimised the chances of pseudoreplication. All songs included in the analysis were recorded between 0800 and 1400 hours at a distance of between 2 m and 5 m from the bird.

A Sony Portable High-Definition MiniDisc Recorder (Sony, Park Ridge, NJ, USA) and a Marantz PMD620 Solid-State Digital Recorder (Marantz, Kanagawa, Japan) were used to record songs, along with a Sennheiser ME67 shotgun long-range directional microphone (Sennheiser, Old Lyme, CT). The uncompressed MiniDisc sound files were converted to wave files using Sony SonicStage software (Sony, NJ, USA). All songs were recorded at a sampling frequency of 44.1 KHz and at a resolution of 16-bits. The frequency response range of the long-range microphone was 50 to 20 000 Hz. The song spectrograms were digitised and song variables measured using the Raven Pro 1.4 Beta Version software (Cornell Lab of Ornithology, Ithaca, NY, USA) (discrete fourier transform (DFT) = 256, Hann window, 2.9 ms, 50% frame overlap, bandwidth = 3dB).

**Song variables**

To compare the spectral characteristics of tūī vocalisations between all mainland sites and Chatham Island tūī, eight song variables were extracted from each tūī song for analysis (Table 2; main variables are depicted in Fig. 2). These variables have been employed in previous studies for characterising bird songs (Mennill & Rogers 2006; Hennin et al. 2009).



**Figure 2.** Diagrammatic representation of the variables employed in this study. The spectrogram presented here is part of a mainland male long-range tūī song.

**Table 2.** A summary and definition of the eight variables employed in this study to compare vocalisations between mainland and Chatham Island tūi (*Prosthemadera* spp.).

Song variable	Definition
Number of notes	The number of individual notes (fundamental sound units) per song
Song duration (seconds)	Time from the beginning of the first note to the end of the terminal note of each chosen song
Trill duration (seconds)	Cumulative total length of high-frequency modulation portions per song
Trill percentage	Percentage of each song that contains high-frequency modulation notes
Syllable diversity	The number of <i>different</i> sound unit complexes (syllables) per song. Syllables can be comprised of several notes
Maximum frequency (KHz)	The highest pitch produced in a song
Mean frequency (KHz)	Overall average pitch of sounds per song
Bandwidth (KHz)	The difference between maximum and minimum frequency

### Comparison of song variables between mainland and Chatham Island tūi

Song variables described above were extracted from male long-range (broadcasting from a perch in a tree) songs and were explored using principal component analysis (PCA) with VARIMAX orthogonal rotation. This rotational procedure is designed to simplify the interpretation of calculated factors by changing the factor loadings, which represent correlations of each factor with the original variables, to be as maximally correlated with each principal component as possible, with the total amount of variance explained by the factors remaining unchanged (Hanson et al. 2002). Three variables, one from each principal component with factor loadings greater than 0.8, were selected for further Mann–Whitney–Wilcoxon tests, as the data distribution was not normal. The variable ‘syllable diversity’ was selected for further testing based on its significance noted by previous research (Boogert et al. 2008). Boxplots were created to visualise the data. Statistical tests were performed using SPSS software (version 20.0; SPSS, Chicago, IL, USA). All statistical tests were two-tailed and  $P$  values  $< 0.05$  were interpreted as significant.

### Analysis of similarity between mainland and Chatham Island tūi

The variables described above were examined for normality and the following were transformed to  $\ln(x) + 0.01$  to remove skewness: number of notes, song duration, trill duration, trill percentage, syllable diversity, and maximum frequency. The variables from the mainland and the Chatham Islands were then examined by analysis of similarity (ANOSIM, 9999 permutations) following standardisation to z-scores (i.e. normalisation). ANOSIM is a non-parametric multivariate test based on, in this instance, Euclidean distance measure, using the rank order of dissimilarity values to test whether the overall song structure differed between the mainland and Chatham Island populations. ANOSIM was performed using PAST software (version 2.17b) (Hammer et al. 2001).

## Results

### Comparison of overall song structure between the two sites

There was no significant difference in the ranked distance within mainland sites (ANOSIM,  $n = 61$ ;  $R = -0.155$ ,  $P = 0.982$ , 9999 permutations) allowing data from all mainland sites to be pooled (Tawharanui:  $n = 37$ ; Wenderholm:  $n = 14$ ; Waitakere:  $n = 3$ ; Maungatautari:  $n = 3$ ; Pohangina:  $n = 4$ ; Total:  $n = 61$ ).

There was a significant difference in the ranked distance between mainland tūi and the Chatham Island population (ANOSIM,  $n = 61, 44$ ;  $R = 0.131$ ,  $P < 0.001$ , 9999 permutations).

### Comparison of song variables between mainland and Chatham Island tūi

Principal component analysis with VARIMAX rotation was performed in male long-range songs between all mainland sites and Chatham Island tūi ( $n = 61, 44$ , Table 1; Fig. 3). The first three principal components (PCs) cumulatively explained 94.59% of the variance between the mainland and Chatham Island populations. PC1 was correlated with maximum frequency, mean frequency, and bandwidth. PC2 was correlated with the number of notes, song duration and syllable diversity, and PC3 with trill duration and trill percentage (Table 3).

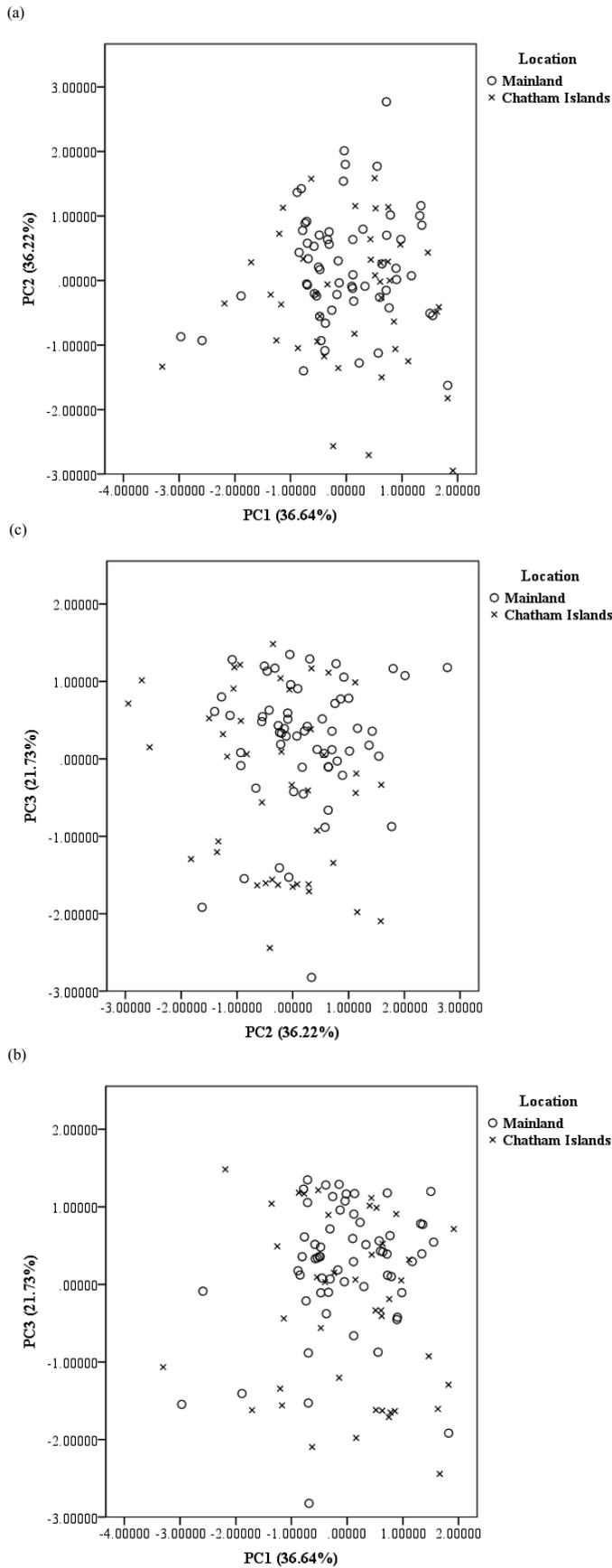
The mean frequency of songs did not differ between the mainland and Chatham Island populations ( $P = 0.885$ ). However, mainland tūi had a significantly greater syllable diversity ( $P = 0.038$ ) and contained a higher percentage of trills ( $P = 0.009$ ) than the Chatham Island population (Table 4; Fig. 4).

## Discussion

### Song variation

Consistent with our prediction, song spectral variables of male long-range ‘broadcasting’ songs differed between the mainland and Chatham Island tūi populations. Moreover, Chatham Island tūi had a significantly smaller percentage of song that contained trills in addition to a lower syllable diversity than their mainland conspecifics. These variables have been demonstrated as being sexually selected traits linked to male genetic diversity (van Buskirk 1997; Nowicki et al. 1998; Ballentine et al. 2004). With greater geographic isolation, Chatham Island tūi experience a lesser degree of emigration and immigration than mainland tūi (Dilks & Kearvell 1996; Department of Conservation 2001). The limited opportunities for dispersal in the Chatham Island subspecies may have contributed to lower genetic diversity. The observed differences in song characteristics from this population may be a reflection of this. However, further studies on genetic diversity in tūi are required to confirm such a relationship.

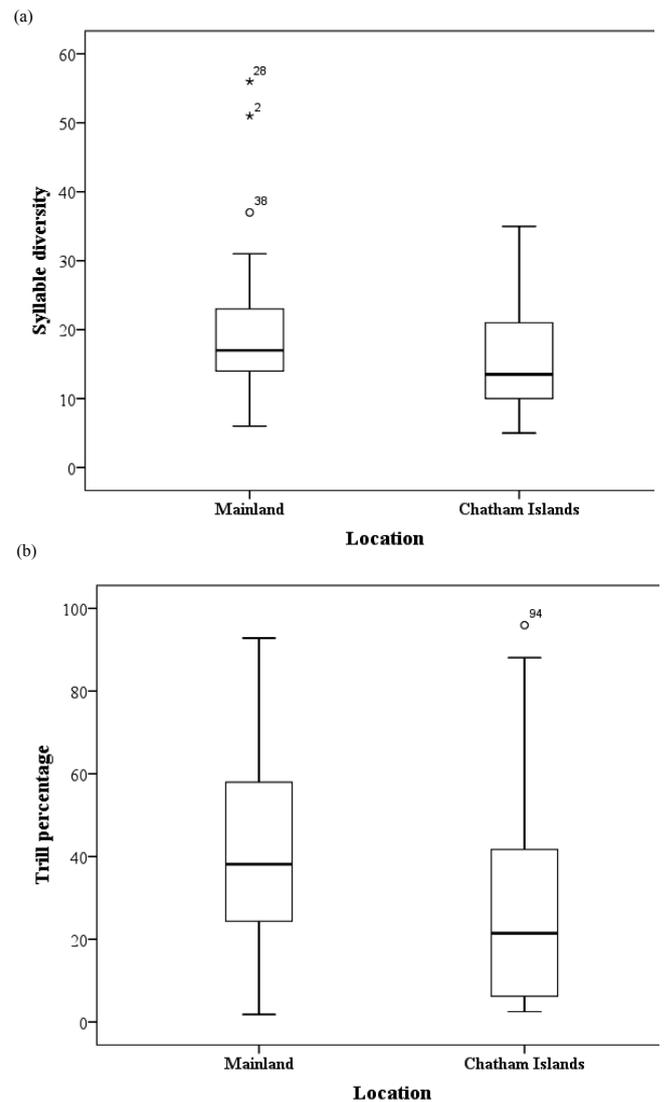
Contrary to our prediction, there were no significant differences in frequency parameters between the populations. Lower-frequency shifts attributable to habitat and morphological differences (Pijanowski et al. 2011) have been shown in past



**Figure 3.** VARIMAX-rotated PCA (principal component analysis) scatterplots (PC1 and PC2 (a); PC1 and PC3 (b); PC2 and PC3 (c)), showing the principal component scores for each individual from mainland and Chatham Island tū defined by PC1, PC2 and PC3, obtained from eight variables.

**Table 3.** Eigenvalues, variance explained and factor loadings of the eight variables following principal component (PC) analysis for male long-range songs between the mainland and Chatham Island tū ( $n = 61, 44$ ). Those variables with factor loading values greater than 0.8 are shown in bold.

	PC1	PC2	PC3
Eigenvalue	2.93	2.90	1.74
% of variance	36.64	36.22	21.73
Number of notes	0.08	<b>0.93</b>	0.18
Song duration	0.18	<b>0.91</b>	0.09
Trill duration	0.11	0.54	<b>0.82</b>
Trill percentage	0.01	0.06	<b>0.99</b>
Syllable diversity	0.16	<b>0.91</b>	0.17
Maximum frequency	<b>0.96</b>	0.17	0.09
Mean frequency	<b>0.99</b>	0.12	0.02
Bandwidth	<b>0.98</b>	0.13	0.02



**Figure 4.** Boxplots of variables with statistically significant differences between the mainland and Chatham Island tū populations in male, long-range songs. Syllable diversity (a), and percentage of song containing trills (b).

**Table 4.** The descriptive statistics and Mann–Whitney–Wilcoxon test results on the three tested song variables of tūi populations on the mainland and on the Chatham Islands.

Variable	Mean $\pm$ SD		Range		Statistical values from Mann–Whitney–Wilcoxon Test		
	Mainland	Chatham Islands	Mainland	Chatham Islands	d.f.	W	P
Percentage of song containing trills	41 $\pm$ 24	31 $\pm$ 28	91 Min: 2 Max: 93	93 Min: 3 Max: 96	103	1793	0.009
Syllable diversity	19 $\pm$ 9	16 $\pm$ 7	50 Min: 6 Max: 56	35 Min: 1 Max: 36	103	1875.5	0.038
Mean frequency (KHz)	8 $\pm$ 2	8 $\pm$ 2	9 Min: 2 Max: 11	10 Min: 1 Max: 11	103	3150.5	0.885

research; however, in vocal studies across a wide range of habitats in chaffinches (Williams & Slater 1993) and orange-tufted sunbirds (*Nectarinia osea*) (Leader et al. 2008), the acoustic adaptation hypothesis has not been supported. Frequency characteristics, such as bandwidth, may be stable features of tūi vocalisations across their wide geographical range, or perhaps in tūi, social adaptation pressures dominate. Future studies focusing on frequency variation across a larger suite of geographical areas and habitat types are needed to confirm this.

Songs on the mainland contained a significantly greater percentage of trills than in the Chatham Islands, which could, at least in part, be explained by the acoustic adaptation hypothesis. Across the mainland sites the habitat, in general, contained a large proportion of open, mainly agricultural pastureland whereas sampling sites on the Chatham Islands were largely covered by dense vegetation (Roberts et al. 2007).

Complex trill notes are highly costly to produce and may be a female selected-trait that indicates male quality (Ballentine et al. 2004; Nowicki & Searcy 2004). Evidence also suggests that females will use acoustic cues such as trills to select males that are more suited to the particular habitat (Slabbekoorn & Smith 2002). The observed differences in song structure may also be a result of physiological and anatomical differences between the mainland and Chatham Island populations. A study of Lincoln's sparrows (*Melospiza lincolnii*) has suggested that alterations in bill morphology can directly affect the production and rate of trill components (Sockman 2009) in song. Future research is required to investigate the possible correlations between morphological variables and song structure and complexity in tūi.

### Syllable diversity

Significantly greater syllabic diversity per song, another indicator for song complexity (Boogert et al. 2008), was identified in the mainland populations as predicted. This result is consistent with findings in a previous study on the singing honeyeater (Baker et al. 2002), a phylogenetic relative of the tūi. 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 in terms of number of syllables has been previously found to be correlated with larger population density (Hamao & Ueda 2000) and greater levels of male competition for resources, food, and mates (Craig & Jenkins

1982), both of which may apply to the mainland populations.

Another possible reason for a lowered song complexity in island subspecies is the founder effect. A reduced degree of genetic variation as a result of a new population being established by a small number of individuals has been recorded (Baker & Moeed 1987). Indeed, evidence for founder effect in song (cultural founder effect), where simpler songs and smaller repertoires are learned by young birds and ultimately passed down through generations, has been observed in North Island saddlebacks, as a result of serial translocations (Parker et al. 2012). Founder effect has also been demonstrated in the Chatham Island chaffinch (Baker & Jenkins 1987). The volcanic Chatham Islands have been separated from mainland New Zealand for approximately 60 000 years (Worthy & Holdaway 2002) giving rise to isolation and thus limiting the migration of avian species. The small number of founders for the Chatham island tūi population may have also contributed to their limited syllable repertoire.

Research into variation of the complexity of tūi song in relation to population density, habitat structure, and individual breeding success, between different mainland sites, would give further insight into links between selective pressures and vocal complexity. Future studies incorporating phylogenetic data across the Meliphagidae family will provide deeper insight into the effect of population insularity on vocal complexity. Furthermore, these studies will help to investigate the genetic and environmental contributions to song evolution.

The differences found in vocalisations of tūi between mainland and Chatham Island populations further indicates the divergence of these two subspecies and confirms the Chatham Island tūi as an ecologically significant unit for conservation management. Although endangered, population augmentation using mainland tūi should not be carried out. In some areas on the mainland, tūi are rare and subject to population reintroduction. Although no differences were found in song spectral variables among mainland tūi populations, differences in syllables and singing patterns (dialect) may exist. Assortative mating by song dialect was observed in North Island kōkako translocated from different source populations (Rowe & Bell 2007), which can potentially reduce the breeding potential of the establishing population (Brown et al. 2004). Further studies on geographical variation of tūi singing patterns and the role of song in their mate choice should provide more information in terms of taking vocal communication into account in the conservation management of this important native honeyeater.

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Editorial Board member: Kevin Burns

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