Seasonal variation in the song structure of tui (*Prosthemadera novaeseelandiae*)

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Abstract: Birdsong has evolved to help individual birds attract mates and defend territories. The breeding season is a critical period in the life history of many songbird species and previous studies indicate that bird vocal behaviour changes at the onset of breeding season. In this study, we compared the complex songs of a seasonal-breeding New Zealand honeyeater, the tui (*Prosthemadera novaeseelandiae*), between breeding and non-breeding seasons. We found that males' songs in the breeding season contained significantly greater proportions of trill components compared with songs in the non-breeding season. Trill rate and consistency may be related to individual quality and therefore might signal to rivals and potential mates the quality of the singer. This is the first study to show the differences in singing behaviour of tui between seasons and provides a basis for future studies to explore the drivers of this seasonal variation in song behaviour.

Keywords: birdsong, breeding season, non-breeding season, trills

Introduction

Song plays a vital role in communication in songbirds and is primarily for territorial defence and mate attraction (Catchpole & Slater 2008). Some species of birds, particularly in the tropics, may have year-round breeding, and may also sing throughout the year (Kunkel 1974; Stutchbury & Morton 2008). Other species, however, have more well-defined breeding seasons and so their song outputs may be confined to these times (Langmore 1998) – a critical period in the life history of many species (Johnston & Odum 1956). Alternatively, some species also sing throughout the year despite not breeding, but change their song properties between reproductive and non-reproductive periods. For example, the songs of wild male island canaries (*Serinus canaria*) were longer and had more syllable repetition in summer than in the non-breeding season (Leitner et al. 2001). Specifically, a decrease in whistle-type syllables and increases in rapid, frequency-modulated syllables was detected (known as trill syllables) (Leitner et al. 2001). Evidence suggests that male songs with more rapid rates of trill production are more sexually attractive to female canaries than songs with low trill rates and induce more female copulatory displays (reviewed in Podos et al. 2004). Trills are likely to be costly to produce and therefore may provide honest signals of physical and genetic quality of the singer (Hennin et al. 2009). Moreover, trill consistency or stereotypy is a vocal characteristic that has been linked with extra-pair success in male house wrens (*Troglodytes aedon*) (Cramer 2013). Therefore, trill production and consistency are likely to be sexually selected, and so should be produced at higher rates by individuals during the breeding season.

In many species, song complexity (measured by the number of different syllables produced; Boogert et al. 2008) is related to male attractiveness to females (Badyaev et al. 2002). Moreover, song complexity may reflect parental ability, reproductive success, and overall male quality (Buchanan & Catchpole 2000; Woodgate et al. 2011, 2012; Soma & Garamszegi 2011). For example, female common grackles (*Quiscalus quiscula*) prefer to breed with males that have large

song repertoires (Searcy 1992). In pied flycatchers (*Ficedula hypoleuca*) early arriving-males also sang more complex songs than later-arriving males (Alatalo et al. 1986; Lampe & Espmark 1994); suggesting that song complexity may be an indicator of male quality.

In some species, birds also produce songs in the non-breeding season. However, songs during this time may be different from those sung during the breeding season (e.g. quieter, in song sparrows *Melospiza melodia*; Maddison et al. 2012). The difference in songs between breeding and non-breeding season may be due to hormonally-mediated changes in anatomy (Riters et al. 2000). For example, seasonal variation in song can be attributed to the plasticity of song control nuclei, such as the high vocal centre (HVC), in songbird brains (Catchpole & Slater 2008). The volume of the HVC has been observed to change seasonally, and increased testosterone levels during the breeding season concomitantly increase the volume of the song nuclei (Ball et al. 2004). This in turn impacts the muscles of the syrinx (e.g. DeVoogd 1991) and subsequently birds' vocal behaviour. These seasonal changes in songbird neuroendocrinology play a key role in the seasonal differences of their song production (Ball et al. 2004).

Other song parameters apart from trills may also be subject to sexual selection and therefore may vary between seasons. For example, maximum frequency (F_{max}) and frequency of maximum amplitude (FMA) have both been shown to be correlated with reproductive success and genetic quality in rock sparrows (*Petronia petronia*) (Nemeth et al. 2012) and zebra finches (*Taeniopygia guttata*) (Woodgate et al. 2012). Therefore, male songbirds may display seasonal variation in these traits in order to stimulate females to breed, and to maximise their reproductive success. Although seasonal changes in bird songs have been found in many species, few studies have quantitatively examined seasonal variation in song structure.

Bergquist (1989) found that winter songs of male tūī (*Prosthemadera novaeseelandiae*), a species that has highly complex vocalisations, generally consisted of a series of phrases that were repeated. During the breeding season male

songs were comprised of sequences of many loud phrases sung repeatedly, but with pauses, sporadic clicks, and whistles between phrases. Although these differences are noticeable to the human ear, there has been no detailed quantitative analysis of the seasonal variation of tūī songs. In this study, we examined the characteristics of tūī songs at the population level during breeding season and compared them to those in the non-breeding season. We predicted there would be a significant difference in song structure between seasons. Specifically, we predicted that tūī would produce a greater proportion of trills, a higher F_{max}, syllable diversity, and higher FMA in the breeding season than in the non-breeding season (after Woodgate et al. 2012, see above). Trills are costly to produce and may, therefore, be used to signal male quality during the breeding season.

Methods

Study species and site

Tūī are honeyeaters endemic to New Zealand. They are common throughout the three main islands, but are scarce on the east coast of the South Island (Gill et al. 2010). Tūī are also found in the subantarctic Auckland Islands and the subtropical Kermadec Islands (Gill et al. 2010). Breeding begins in September and finishes in February. Upon pairing the female starts building a nest (Heather & Robertson 2005). There are also extremely high levels of extra-pair paternity in this species (S. J. Wells, unpubl. data).

Male songs change noticeably at the start of the breeding season. From high vantage points tūī produce long-range-broadcast songs, which may function for territorial defence and mate attraction. Long-range tūī songs are complex and there is significant geographical variation among populations (Hill et al. 2013), and between sexes (Bergquist 1989). Tūī also produce short-range songs that often have aggressive contexts (Hill 2011), but long-range-song bouts in tūī are significantly longer than these short-range bouts (SDH unpubl. data).

Our study was conducted at Tāwharanui Regional Park (36°22' S, 174°50' E), a 588-ha predator-free sanctuary situated on the Tāwharanui Peninsula, 90 km north of central Auckland, New Zealand. Tāwharanui Regional Park consists of predominantly grazed pasture with patches of regenerating mānuka (*Leptospermum scoparium*) bush and some areas of mature coastal forest remnants (ARC 2009). The canopy tree species in these forest remnants include pōhutukawa (*Metrosideros excelsa*), kauri (*Agathis australis)* and puriri (*Vitex lucens*) (ARC 2009). Recordings were made at four locations within the park: Jones Bay, Anchor Bay, Ecology Bush, and Māori Bay (Fig. 1).

Recording procedure

We recorded tūī broadcast songs during the breeding season (October 2010 – January 2011) and non-breeding season (July–August 2010; August 2012 and May 2013). Songs were recorded between 0800 and 1500 hours in both seasons to standardise sampling times and sampling effort. We sampled tūī songs by walking slowly along marked tracks in one direction to locate tūī. We started a recording session when we located a singing male and ended it when the tūī either ceased singing or flew away. We stood between 4 and 10 m from a bird when we recorded it. For each recording, we noted the time, the bird's location, band combination (if it was banded), behaviour, and song type.

In order to minimise the chances of recording the same individual more than once in the same season, we recorded only one bird per location. Male tūī are highly territorial during the breeding season and sing largely within their own territories during this time. Therefore, recording birds in different locations was unlikely to result in recording the same bird twice. The minimum distance between recording locations was 300 m.

We recorded tūī songs using a Sony MZ-NHF800 Portable High-Definition MiniDisc Recorder (Sony, Park Ridge, NJ) or a Marantz PMD620 solid-state digital recorder (Marantz, Kanagawa, Japan), which were both paired with a Sennheiser ME67 shotgun long-range directional microphone (Sennheiser, Old Lyme, CT). All songs were recorded at a sampling frequency of 44.1 kHz at a resolution of 16 bits. The frequency response range of the long-range microphone was 40 Hz to 20 kHz. MiniDisc sound files were converted to wave (.wav) files using the software 'Sonic Stage' (Sony Corporation, Tokyo, Japan).
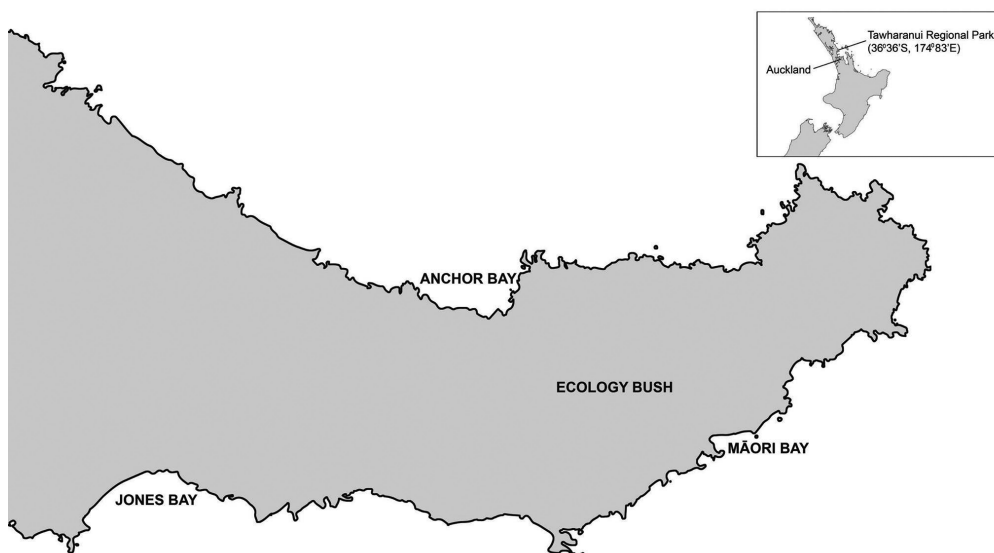

Figure 1. Map of Tāwharanui Regional Park with the four recording locations of Anchor Bay, Jones Bay, Ecology Bush, and Māori Bay, and (inset) a map of New Zealand's North Island showing the location of Tāwharanui in relation to Auckland City.

Comparison of spectral characteristics between seasons

One representative long-range song with a clean, high quality recording was analysed per individual. The song spectrograms were digitised and parameters measured using Raven Pro 1.4 Beta Version software (Cornell Lab of Ornithology, Ithaca, NY, USA). For all recordings, spectrograms were created by Discrete Fourier Transform (DFT) with a Hann window. The frame length was set at 256 points. Additionally, a 50% frame overlap with hop size of 2.9 milliseconds was used. Frequency grid spacing of 172 Hz was also employed and the bandwidth was set at 3 dB. To investigate the variation of song spectral characteristics of male tūī between seasons, we used Raven Pro to extract 10 variables for analysis (Table 1; Fig. 2). These variables have been employed for characterising variation in bird songs in previous studies (Mennill & Rogers 2006; Hennin et al. 2009).

Analysis

For each season, we tested whether there was a difference between morning and afternoon song, using a one-way permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001). PERMANOVA is a non-parametric distance-based analysis of variance that uses permutation procedures to test hypotheses. In this case, the Euclidean distance measure was used. In order to remove skewness, we used a $ln(x) + 0.01$ transformation for five variables: number of notes, song duration, trill duration, FMA, and syllable diversity. The 10 variables from the breeding and non-breeding seasons were examined using one-way PERMANOVA to detect whether song structure between seasons was significantly dissimilar. PERMANOVA was also used to detect any significant differences between morning song (0800–1200 hours) and afternoon song (1200–1500

Table 1. Definition of the 10 variables employed to compare songs of tūī between seasons.

| Song variable	Definition
Number of notes	Number of individual notes (fundamental sound units) per song. A note alone without a repeat is considered a syllable. Multiple notes repeated consecutively are considered one syllable
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 repeated, high-frequency-modulation portions per song
Trill percentage	Percentage of each song that contains rapid, repeated, high-frequency-modulation notes. Computed by dividing song duration with the amount of time (seconds) trills are produced within a song
Frequency of maximum amplitude (FMA) (kHz)	Frequency of the time point within the song that contains the highest level of energy
Syllable diversity	Number of *different* sound unit complexes (syllables) per song. Syllables can be comprised of several notes
Maximum frequency (kHz)	The highest pitch produced in a song
Minimum frequency (kHz)	The lowest pitch produced in a song
Mean frequency (kHz)	Overall average pitch of sounds per song
Bandwidth (kHz)	The difference between maximum and minimum frequency
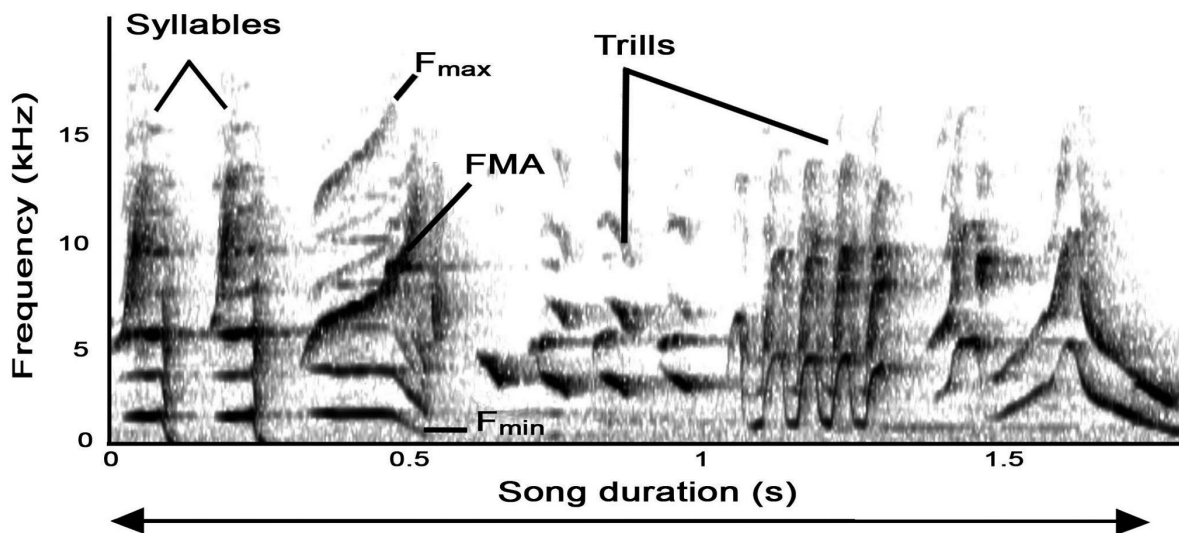
Figure 2. A spectrogram of the long-range song of a mainland male tūī (*Prosthemadera novaeseelandiae*), showing the variables employed in this study.

hours) and within the same season (breeding season: September–February; non-breeding season: March–August). This allowed us to assess whether all data from the same season could be pooled for further analysis. The conservative Bonferroni correction for multiple testing was used for all multivariate analyses. PERMANOVA was performed using PAST software (version 2.17b) (Hammer et al. 2001).

Four variables – trill percentage, F_{max}, syllable diversity and FMA – were compared between seasons. These four variables were chosen as these song characteristics have been linked with reproductive success in other songbird species. We used non-parametric Mann–Whitney-Wilcoxon tests, as the data were non-normally distributed, to test our hypotheses that tūī would produce a (1) greater proportion of trills, (2) higher F_{max}, (3) higher syllable diversity, and (4) higher FMA in the breeding season than in the non-breeding season. These tests were conducted using SPSS (version 20.0; SPSS, Chicago, IL, USA). All statistical tests were two-tailed and P values < 0.05 were interpreted as significant.

Results

In total, 27 birds were recorded (14 in the breeding season and 13 in the non-breeding season). Five of the birds we recorded during the breeding season were banded, while only a single banded bird was recorded in the non-breeding season.

Within-season variation in tūī song structure

Results from a one-way PERMANOVA test (9999 permutations) showed no significant difference in song structure between songs recorded in the morning and those in the afternoon for both the breeding season ($n = 6, 8$; Pseudo $F_{3,14} = 0.5314$, $P = 0.743$) and non-breeding season ($n = 9, 4$; Pseudo $F_{2,13} = 0.589$, $P = 0.612$). Therefore the data obtained from the mornings and afternoons were pooled for further analysis.

The PERMANOVA test (9999 permutations) showed no significant difference in song structure within seasons for either the breeding season ($n = 14$; Pseudo $F_{3,14} = 0.473$, $P = 0.982$) or non-breeding season ($n = 13$; Pseudo $F_{2,13} = 1.42$, $P = 0.257$). Therefore the data within a season were pooled for further analysis.

### Between-season variation in tūī song structure

A one-way PERMANOVA test revealed a significant difference in the ranked distance in tūī song structure (using all ten variables) between the breeding season and the non-breeding season ($n = 14, 13$, Pseudo $F_{16,27} = 2.856$, $P = 0.044$, 9999 permutations). This suggested that tūī alter their song structure at the onset of the breeding season.

The results of the Mann–Whitney-Wilcoxon tests showed that there was a significantly greater proportion of trills in breeding season songs compared to non-breeding season songs ($W = 98$, $P = 0.001$) (Table 2; Fig. 3). However, there were no significant differences between seasons in F_{max}, syllable diversity, and FMA (Table 2).

Table 2. Descriptive statistics of four tūī song variables between seasons at Tāwharanui.

Variable	Median; Interquartile range		Range		Statistical values from Mann–Whitney–Wilcoxon tests	
	Breeding season	Non-breeding season	Breeding season	Non-breeding season	W	P
Proportion of song containing trills (%)	56; 39–75	24; 7–38	18, 93	0, 61	98	0.001
FMA (kHz)	1.60; 1.47–1.72	1.54; 1.31–1.55	1.37, 1.86	1.03, 1.72	98	0.069
Syllable diversity	18; 16–26	15.5; 6–28	14, 56	2, 31	156.5	0.220
F_{max} (kHz)	15.11; 12.41–18.90	15.36; 11.16–18.46	11.50, 19.96	4.95, 19.84	193.5	0.905

Figure 3. Trill percentage ($P = 0.001$) in songs of male tūī (*Prosthemadera novaeseelandiae*) in the breeding season compared with the non-breeding season at Tāwharanui Regional Park. On average, the trills were sung at twice the rate in breeding-season songs than in non-breeding-season songs.
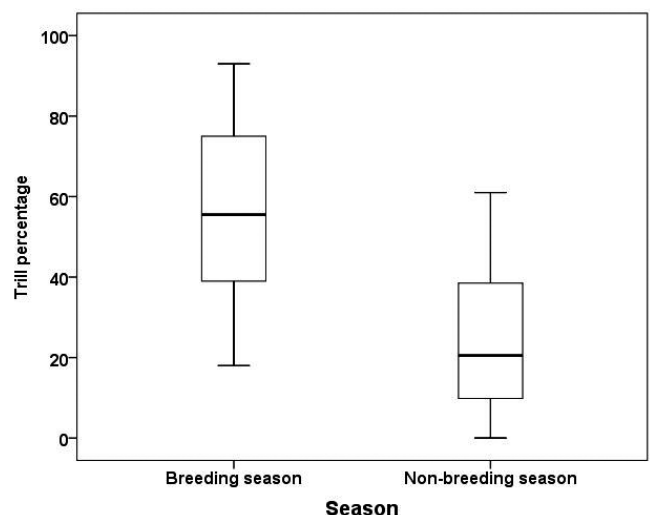
Discussion

We found a significantly greater proportion of trills in male tūī songs in the breeding season than the non-breeding season, which is consistent with our hypothesis, but no difference in FMA, syllable diversity or F_{max} between seasons (Table 2). That males produced a higher proportion of trills in the breeding season suggests this song characteristic may be sexually selected. Trills are complex, rapidly repeated syllables that are costly to produce (Suthers & Goller 1998), and are considered honest signals of male phenotypic quality and may advertise the physical and genetic condition of callers (Ballentine et al. 2004; Ballentine 2009; Sewall et al. 2010). Males that produce a higher number of trills during the breeding season may therefore be demonstrating their phenotypic quality and suitability as mates to females. For example, swamp sparrows (*Melospiza georgiana*) that included a higher proportion of trills within their songs have been shown to have greater breeding success than other males (Ballentine et al. 2004). Furthermore, in island canaries, males altered their songs during the breeding season so that they contained more trills (Leitner et al. 2001). Therefore, it is possible that males in our study population were using trills to advertise their quality to potential mates.

Trills may also signal aggressive intent in birds and may elicit more aggressive responses from rival males. For example, male nightingales (*Luscinia megarhynchos*) that produced trills with broad bandwidths elicited greater aggressive responses from rival males than those who produced trills with narrower bandwidths (Schmidt et al. 2008). In males that became paired during the breeding season, there was also a positive correlation between increased trill production (from a simulated model) and increased aggression (Schmidt et al. 2008). Therefore, we encourage further research to assess the significance of trills in reproductive and territorial contexts in New Zealand passerines (including tūī).

Although male tūī produced more trills in the breeding season, there were no differences in the other frequency parameters (FMA and F_{max}) recorded between seasons. This lack of difference in frequency parameters might indicate the tūī in our study were subject to physical or energetic constraints. For example, silvereyes (*Zosterops lateralis*) increased the F_{max} and F_{min} during the dawn chorus on days when they had access to supplementary food (Barnett & Briskie 2007). This suggests that the quality of bird songs may be related to the birds' energy levels. However, the relationships between birds' energy levels and specific song parameters within species require further research.

The seasonal difference in birds' song was likely to be mediated hormonally. For example, blood titres of testosterone have been directly correlated with levels of competition in birds and are increased during the breeding season, for example in canaries (Bolhius & Gahr 2006). Furthermore, studies in zebra finch and male grey partridge (*Perdix perdix*) show that testosterone can affect specific features of bird vocalisations, which may enable females to assess male quality (Fusani et al. 1994). Future studies could experimentally investigate the individual differences in birds' endocrinological profiles and the quality of their song displays and relate this to individual reproductive success.

In conclusion, we found that male tūī songs contained a greater proportion of trills in the breeding season compared with their songs in the non-breeding season – the first study to have shown how tūī songs change between seasons. These seasonal vocal changes may be related to male resource-holding potential and mate choice. However, we encourage further studies to investigate the adaptive significance of seasonal variations in tūī songs.

Acknowledgements

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