

Sexually dimorphic vocalisations of the great spotted kiwi (*Apteryx haastii*)

JENNIFER M. DENT*

LAURA E. MOLLES

Department of Ecology, PO Box 85084, Lincoln University, Canterbury 7647, New Zealand

Abstract Kiwi (*Apteryx* spp.) are the most vocal of the ratites. Of the 5 *Apteryx* species only 2 have previously been subject to detailed vocal analysis: the North Island brown kiwi (*A. mantelli*) and the little spotted kiwi (*A. owenii*). This paper describes the vocalisations of the great spotted kiwi (*A. haastii*), the largest of the *Apteryx* species. Acoustic recorders were installed near the breeding den sites of 7 great spotted kiwi pairs residing in Hawdon Valley, Canterbury between November 2012 and March 2013. A total of 133 whistle vocalisations from 10 individuals were subject to detailed temporal and spectral analysis. Male and female syllables were found to be sexually dimorphic; syllables in male calls tended to be longer and more highly pitched than their female counterparts. Despite this dimorphism, patterns of intra-call variation were consistent between the sexes. It appears that intra-call variation is a trait which varies markedly within the *Apteryx* genus.

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INTRODUCTION

Kiwi (*Apteryx* spp.) are ratites, or palaeognaths (Struthioniformes: Apterygidae), endemic to New Zealand. Five species of kiwi are formally recognised: the North Island brown kiwi (*Apteryx mantelli*), rowi (*A. rowi*), tokoeka (*A. australis*), great spotted kiwi (*A. haastii*) and the little spotted kiwi (*A. owenii*) (Sales 2005; Holzapfel *et al.* 2008). All 5 species share a number of traits; they are flightless, nocturnal, highly territorial, occupy a generalist niche and have slow rates of reproduction (Fuller 1990; McLennan & McCann 1991; Sales 2005).

Kiwi are the most vocal of the ratite species worldwide (Davies 2002). They produce a variety of different sounds, the most prevalent being

the ‘whistle’ call which has a distinctive repetitive structure (Fuller 1990; Castro 2011). The whistle vocalisation is produced by both sexes and is thought to primarily function in territory defence and intra-pair communication (Colbourne & Kleinpaste 1984; Digby *et al.* 2013). Males tend to call more often than females (Digby *et al.* 2013). Taborsky and Taborsky (1992) determined that male North Island brown kiwi called at a rate of 0.85 calls/hour while females called at a rate of 0.35 calls/hour. Of the 5 recognised species of kiwi only 2 have been subject to detailed acoustical study: the North Island brown kiwi (Corfield *et al.* 2008) and the little spotted kiwi (Digby *et al.* 2013). Whistle calls of both species are composed of a series of highly repetitive multi-harmonic notes separated by periods of silence (Corfield *et al.* 2008; Digby *et al.* 2013). Although there are distinct differences in calls between species, both studies docu-

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*Correspondence: Jenny.Dent@lincolnuni.ac.nz

mented sexual dimorphism in calling. Males produce high frequency notes with a clear harmonic structure (Corfield *et al.* 2008; Digby *et al.* 2013). This gives the call a rather shrill, piercing sound (Fuller 1990; Castro 2011). Female calls are dominated by broadband, low frequency components (Corfield *et al.* 2008; Digby *et al.* 2013). Female calls sound more guttural than their male counterparts (Fuller 1990; Castro 2011).

The great spotted kiwi is the largest of the 5 kiwi species; females have a mean weight of about 3000 g while males reach a mean weight of about 2200 g (McLennan & McCann 2002). Aside from their size, great spotted kiwi are distinguished from other kiwi by their plumage which is predominantly mottled grey with a distinctive patch of chestnut on their back (Fuller 1990). Great spotted kiwi occupy subalpine and alpine habitats in the north west of the South Island and are most numerous in high rainfall, forested areas, 700-1000 m above sea level (Fuller 1990). There are 4 main populations remaining in the wild: in northwest Nelson, Nelson Lakes National Park, Paparoa Range and Arthur's Pass-Hurunui (McLennan & McCann 2002). Despite being the most vocal of the *Apteryx* species (Marchant & Higgins 1990); the vocalisations of the great spotted kiwi have not previously been subject to detailed acoustical study. Marchant and Higgins (1990) noted that, like other *Apteryx* species, their vocalisations appear to be sexually dimorphic. The aim of this study was to provide the first quantitative description of male and female great spotted kiwi vocalisations.

MATERIALS AND METHODS

This study examined the vocal behaviour of a population of great spotted kiwi residing in Hawdon Valley, Canterbury, New Zealand (NZ260: K33 08250) which is located within Arthur's Pass National Park. The Hawdon Valley population falls within the wider Arthur's Pass – Hurunui grouping of great spotted kiwi (McLennan & McCann 2002). The density of birds in the Arthur's Pass – Hurunui region is known to be relatively low, about 2-3 per square kilometre (*c.* 3000 individuals in total) (McLennan & McCann 2002). At the time of this study 20-25 birds were fitted with 'diagnostic' transmitters (Wildtech, Hastings, New Zealand) which allowed their nest sites to be located by Department of Conservation (DOC) staff. All work was conducted under DOC research permit CA-34889-RES.

Call recording

Acoustic recorders were installed near (< 20 m) the breeding den sites of 7 great spotted kiwi pairs between November 2012 and March 2013. Recorders were installed during the incubation period or

shortly after egg hatching. Initial placement was done by, or in cooperation with, DOC staff familiar with the nest sites to ensure that nesting birds were minimally disturbed. Department of Conservation recording devices were employed at 5 of the sites. These devices were single channel (mono) and detect frequencies in the range of 0-4000 Hz. SoundCache recording units (Cornell Laboratory of Ornithology, Ithaca, NY, USA) were employed at the remaining 2 sites; these devices record across 2 channels (stereo) and were configured to detect frequencies in the range of 0-11000 Hz. All recorders were programmed to operate on a predetermined schedule. Recording began at 2000 h every night and ended at 0615 h the following morning (10 hours and 15 minutes duration of recordings per night). All recordings were digitised at 16-bit precision with a sampling rate of 8 kHz (DOC recorders) or 22 kHz (SoundCache recorders). The SoundCache recorders were set at a higher sampling rate in order to capture a broader range of harmonics for archival records.

Call processing

Recordings were first visualised as spectrograms using Raven Pro v. 1.5 (Bioacoustics Research Program 2012). These spectrograms were visually and aurally scanned for whistle vocalisations. In total, 303 whistle vocalisations were detected (262 individual calls and 41 duets). Poor quality and clipped recordings were discarded from further analysis, as were duets; this left a total of 133 calls from 12 individuals (7 males and 5 females). Following extraction, calls collected by SoundCache recorders were downsampled to 8 kHz in SoundStudio 3.5.2 (Kwok 2007) for consistency with sampling rates of DOC recorders. All calls were subject to background noise removal using Audacity v. 2.0.3 (Audacity Team 2013). A 5 second segment of background noise adjacent to the call was used to generate a noise profile; the noise profile was then used to subtract background noise from the rest of the call. The amount of volume reduction applied to the background noise was 24 dB with 150 Hz frequency smoothing, and 0.15 seconds attack/decay time. In order to test whether this noise reduction procedure was appropriate, it was tested on 25 randomly chosen calls. Frequency parameters (maximum, minimum, peak frequency) were measured before and after noise reduction. No change was detected so the procedure was applied to all calls. Background noise below 500 Hz and above 4000 Hz was also filtered out of the recordings prior to analysis.

Call measurement

The temporal and spectral parameters of calls were measured from spectrograms and power spectra produced by Raven Pro 1.5. Both the spectrograms

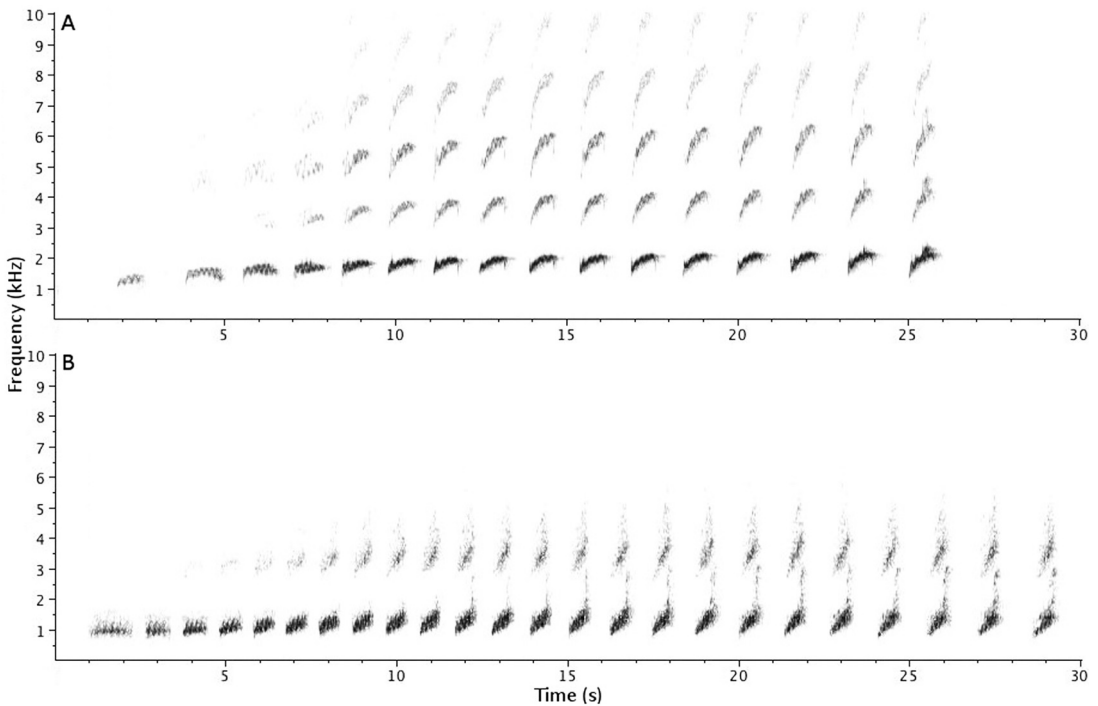


Fig 1. Spectrograms of male (a) and female (b) great spotted kiwi vocalisations.

and power spectra were generated using a 512-sample Hann window with a 50% overlap and a frequency resolution of 15.6 Hz. Measurements were taken at a whole call and individual syllable level. For individual syllable measurements, 3 syllables were measured from the start (first 3 syllables), middle (central 3 syllables) and end (last 3 syllables) of each call. Corfield *et al.* (2008) noted that male calls had 3 distinct phases; by sampling 3 distinct sections within the call we hoped to capture any potential variation without being biased by the total number of syllables. Digby *et al.* (2014) further suggested that syllables changed gradually throughout the call duration. The inclusion of 3 syllables from each call section also reduces the influence of any within-phase variation.

Temporal variables

The temporal variables that we measured were: total duration of call, the number of syllables per call and syllable duration. Call and syllable duration were derived from the signal energy distribution. Duration was defined as the interval containing 90% of the signal energy in each spectrogram selection (separate selections were generated to encompass each individual syllable and the entire call) (Bioacoustics Research Program 2012). This definition provided a consistent measure of duration

despite substantial variation in background noise and amplitude.

Spectral variables

Zollinger *et al.* (2012) suggested that, due to variation in background noise and amplitude, uncalibrated spectrograms were unsuitable for making accurate and repeatable measurements of frequency. Zollinger *et al.* (2012) employed an alternative methodology whereby maximum frequency, minimum frequency and bandwidth were measured from the power spectrum at a set number of decibels (20 dB) below the peak amplitude. Peak amplitude and peak frequency were calculated automatically for this study based on the spectrogram selections (as described for temporal variables). It should be noted that all spectral variables were derived from the fundamental harmonic only. This was easily identified on the power spectrum as it corresponds to the first peak in the sound profile.

Statistical analysis

Prior to analysis, syllable parameters were averaged according to their position within the call (beginning, middle, and end sections of the call). This merging of syllables formed 3 variants of each parameter (*e.g.*, duration at beginning, middle and end). The averaging of syllables was justified as

Table 1. Comparison of temporal and spectral syllable parameters within great spotted kiwi vocalisations. Values are reported as averages and displayed alongside the standard error of the mean and range (in parentheses). Beginning, middle and end refer to the position of the syllable within the call.

	Male (<i>n</i> = 81)			Female (<i>n</i> = 52)		
	Beginning	Middle	End	Beginning	Middle	End
Duration (sec)	0.65 ± 0.01 (0.37-1.03)	0.48 ± 0.01 (0.37-0.60)	0.49 ± 0.01 (0.4-0.6)	0.57 ± 0.01 (0.4-0.73)	0.42 ± 0.01 (0.4-0.53)	0.41 ± 0.01 (0.33-0.53)
Maximum Frequency (Hz)	1960 ± 23 (1462-2444)	2417 ± 25 (1895-2882)	2546 ± 24 (2069-3069)	1353 ± 10 (1207-1598)	1758 ± 24 (1386-2160)	1839 ± 27 (1423-2327)
Minimum Frequency (Hz)	1565 ± 18 (1158-1822)	1766 ± 16 (1429-2005)	1778 ± 16 (1460-2065)	869 ± 12 (714-1021)	1012 ± 6 (903-1115)	1006 ± 7 (911-1140)
Peak Frequency (Hz)	1792 ± 21 (1226-2143)	2240 ± 24 (1755-2594)	2364 ± 23 (1849-2810)	1087 ± 9 (966-1257)	1270 ± 11 (1130-1521)	1331 ± 11 (1164-1544)
Bandwidth (Hz)	395 ± 9 (278-689)	651 ± 15 (348-982)	782 ± 20 (399-1107)	484 ± 9 (375-663)	746 ± 25 (490-1188)	833 ± 31 (530-1388)

less variation is found within syllable subsets than between calls of the same bird (Dent 2013). Unless otherwise stated all analyses treated males and female calls separately and were conducted using SPSS v 22.0 (IBM corp. 2013). Each call was treated as a separate data point throughout the analysis. One-way repeated measures ANOVAs were used to examine intra-call variation in both spectral and temporal parameters. This analysis was chosen as it allows for examination of correlated, within subject effects. In cases where the initial ANOVA was significant ($P < 0.05$), a Fisher's Least Significant Difference (LSD) post hoc test with a Greenhouse-Geisser correction was applied. As the tests violated the assumption of sphericity, a Greenhouse-Geisser correction was applied to normalise the variances. In addition to single-sex analyses, one-way ANOVAs were conducted for all call and syllable parameters to examine the extent to which male and female vocalisations differ ($\alpha = 0.05$). Unequal group size was accounted for by applying a Welch's correction.

RESULTS

There was no significant difference between male and female calls in terms of total duration ($F = 1.16$, $df = 1, 112$, $P = 0.283$: male = 25.5 ± 0.3 sec, female = 26.2 ± 0.5 sec) and syllable count ($F = 3.4$, $df = 1, 115$, $P = 0.068$: male = 18.1 ± 0.3 syllables, female = 18.8 ± 0.3 syllables). However, male and female calls differed significantly across all measured syllable parameters (Appendix 1). Male syllables were

longer and contained higher frequency elements (minimum frequency, maximum frequency, peak frequency) than their female counterparts (Table 1; Fig. 1a). Female syllables contained lower frequency elements and had greater bandwidth than male syllables (Table 1; Fig. 1b).

Repeated measure ANOVA tests indicated that there was a significant degree of intra-call variation across the 3 call sections for all temporal and spectral syllable parameters. Despite differences in absolute values the patterns of intra-call variation were consistent between sexes. In both sexes, syllables at the start of calls were significantly longer than all other syllables (male: $F = 113.19$, $df = 1.19, 92.93$, $P < 0.001$; female: $F = 202.75$, $df = 1.48, 73.89$, $P < 0.001$). There was no significant difference between middle syllable duration and end syllable duration (Table 2). Maximum frequency (male: $F = 773.56$, $df = 1.52, 118.2$, $P < 0.001$; female: $F = 252.13$, $df = 1.65, 82.64$, $P < 0.001$), peak frequency (male: $F = 840.1$, $df = 1.70, 132.4$, $P < 0.001$; female: $F = 175.69$, $df = 1.65, 82.64$, $P < 0.001$) and bandwidth (male: $F = 242.13$, $df = 1.67, 230$, $P < 0.001$; female: $F = 133.52$, $df = 1.66, 83.01$, $P < 0.001$) all increased significantly throughout the duration of the whistle call (Table 2). For each of these parameters, the change was most pronounced between the beginning and middle of the call. Syllables at the start of calls had the lowest values of minimum frequency (male: $F = 300.09$, $df = 2, 156$, $P < 0.001$; female: $F = 253.94$, $df = 1.55, 77.57$, $P < 0.001$; Table 2). There was no significant difference between middle syllable duration and end syllable duration (Table 2).

Table 2. Summary of intra-call variation in great spotted kiwi vocalisations. Values are *P*-value scores from LSD pairwise comparisons. B denotes beginning syllables, M denotes middle syllables and E denotes end syllables. * indicates a significant result ($P < 0.05$).

	Male			Female		
	B-M	B-E	M-E	B-M	B-E	M-E
Syllable duration (Sec)	< 0.001*	< 0.001*	0.33	< 0.001*	< 0.001*	0.22
Maximum frequency (Hz)	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*
Minimum frequency (Hz)	< 0.001*	< 0.001*	0.47	< 0.001*	< 0.001*	0.19
Bandwidth (Hz)	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*
Peak frequency (Hz)	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*

DISCUSSION

Male and female whistle vocalisations in great spotted kiwi are the same length and contain a similar number of syllables. The syllables themselves, however, appear to be sexually dimorphic. Male syllables were longer and higher pitched than their female counterparts. Female syllables were characterised by lower spectral elements and had greater bandwidth than male syllables. Sexual dimorphism in calling has also been noted in little spotted kiwi and North Island brown kiwi (Corfield *et al.* 2008; Digby *et al.* 2013). Ballintijn *et al.* (1997) suggested that sexually dimorphic vocalisations could arise in 1 of 3 ways: both males and females have similar vocal structures but use them differently, males and females have different vocal anatomy, or males and females differ in both anatomy and production. In many species, vocal dimorphism has been linked to differences in body size (Martin *et al.* 2011). Larger individuals produce calls with lower frequency spectral features owing to larger vocal structures (Bradbury & Vehrencamp 1998), although this does not appear to be case in *Apteryx* species (Digby *et al.* 2013). Digby *et al.* (2013) proposed an alternative hypothesis whereby dimorphism is linked to divergent vocal tract morphology. They further suggest that this may have arisen due to selection for vocal cooperation and/or intersexual differences in call function. We have not examined great spotted kiwi size in relation to call frequency. This and the functionality of great spotted kiwi calls are potential areas for future investigation.

Despite the striking vocal dimorphism apparent in great spotted kiwi, temporal and spectral intra-call trends were consistent between sexes. Syllable duration and minimum frequency showed least intra-call variation; variation in these parameters

was restricted to the beginning of the call. On the other hand, maximum frequency, bandwidth and peak frequency all increased throughout the duration of the call. Intra-call variation was also noted in the calls of male North Island brown kiwi (Corfield *et al.* 2008). The variation in this species was to such an extent that it was necessary to divide the syllables into 3 distinct phases, each phase defined by its own unique structure (Corfield *et al.* 2008). Interestingly, such variation does not extend to the female of this species.

Intra-call variation is a trait which varies substantially within the *Apteryx* genus. While the North Island brown kiwi (male) vocalisations demonstrate substantial intra-call variation, Digby *et al.* (2013) noted that syllables in little spotted kiwi calls were uniform and did not show significant structural variation. Quantitative comparisons of syllable structure and call complexity have not been conducted for *Apteryx* species; however, based on the findings of his study, it appears that the vocalisations of great spotted kiwi are more comparable to those of little spotted kiwi. Although there was some intra-call variation in the temporal and spectral extent of syllables, the overall syllable structure appears to be more or less consistent throughout the duration of the whistle call. In other contexts, differences in syllable diversity and vocal complexity have been linked to differences in population density, habitat, social behaviour and genetic diversity (van Buskirk 1997; Hamao & Ueda 2000; Hill *et al.* 2013). *Apteryx* vocalisations are unlikely to be learned (Kroodsmma 2005); it has therefore been suggested that inter-specific differences in call structure may relate to genetic diversity (Digby *et al.* 2013). Further study into the functionality of whistle calls is required in order to determine the underlying basis of inter-specific differences in intra-call variation.

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Appendix 1. One-way ANOVA with Welch correction for comparison of male and female syllable parameters in great spotted kiwi vocalisations. B denotes beginning syllable parameter, M denotes middle syllable parameter and E denotes end syllables parameter.* indicates a significant result ($P < 0.05$).

	Adjusted <i>F</i> statistic	<i>df</i>	<i>P</i>
Duration (B)	14.11	1, 118	< 0.001*
Maximum frequency (B)	1029.75	1, 109	< 0.001*
Minimum frequency (B)	603.81	1, 94	< 0.001*
Peak frequency (B)	61.77	1, 108	< 0.001*
Bandwidth (B)	946.02	1, 95	< 0.001*
Duration (M)	30.50	1, 118	< 0.001*
Maximum frequency (M)	1730. 71	1, 86	< 0.001*
Minimum frequency (M)	373.07	1, 118	< 0.001*
Peak frequency (M)	11.789	1, 82	< 0.001*
Bandwidth (M)	1370. 86	1, 95	< 0.001**
Duration (E)	62.12	1, 119	< 0.001*
Maximum frequency (E)	1930.14	1, 96	< 0.001**
Minimum frequency (E)	382.26	1, 107	< 0.001*
Peak frequency (E)	5.90	1, 80	< 0.001*
Bandwidth (E)	1583.49	1, 98	< 0.001**