



## VOCALIZATIONS OF THE NORTH ISLAND BROWN KIWI (APTERYX MANTELLI)

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**ABSTRACT.**—Few studies have investigated the vocal communication of ratites, and none has investigated the spectral and temporal structure of vocalizations of *Apteryx*, the only extant ratite genus in New Zealand. We describe the long-range vocalization (whistle call) and vocal behavior of male and female North Island Brown Kiwi (*Apteryx mantelli*). Spontaneous calling by seven pairs was recorded in the field over a one-year period. Call notes produced by males were tonal in nature; the fundamental frequency was ~1.5 kHz, with overtones reaching up to ~13.0 kHz. Call notes produced by females contained a series of tightly packed, poorly defined harmonics and consisted of a fundamental frequency of ~0.1 kHz, with overtones reaching ≤7.0 kHz. The amplitude within notes of females was concentrated into two prominent formants. Some individuals of pairs exhibited duetting behavior that resulted in alteration of the inter-note interval after the onset of the call of their mate. Our findings draw attention to the uniqueness of the North Island Brown Kiwi's vocalizations, and we uncovered some unexpected structural features that call for further investigation. *Received 25 October 2006, accepted 3 June 2007.*

Key words: *Apteryx mantelli*, call structure, North Island Brown Kiwi, ratites, vocal communication.

### Vocalizaciones de *Apteryx mantelli*

**RESUMEN.**—Pocos estudios han investigado la comunicación vocal de las ratites, y ninguno ha investigado la estructura espectral y temporal de las vocalizaciones de *Apteryx*, el único género de ratite viviente de Nueva Zelanda. Describimos la vocalización de largo alcance (llamada de silbido) y el comportamiento vocal del macho y la hembra de *Apteryx mantelli*. Se grabaron en el campo las llamadas espontáneas de siete parejas a lo largo de un período de un año. Las notas de llamada producidas por los machos fueron de naturaleza tonal; la frecuencia fundamental fue de ~1.5 kHz, con sobretonos que alcanzaban más de ~13.0 kHz. Las notas producidas por las hembras contuvieron una serie de armónicos estrechamente empaquetados y pobremente definidos, y presentaron una frecuencia fundamental de ~0.1 kHz, con sobretonos llegando a ≤7.0 kHz. La amplitud dentro de las notas de las hembras se concentró en dos formantes prominentes. Algunos individuos de las parejas mostraron un comportamiento de dueto que produjo la alteración del intervalo entre las notas luego del comienzo de la llamada de su pareja. Nuestros hallazgos destacan la singularidad de las vocalizaciones de *Apteryx mantelli* y revelan algunos rasgos estructurales inesperados que requieren investigaciones futuras.

MOST BIRDS USE acoustic signals as a primary means of communication, and these can play an important role in their behavior, reproduction, and survival. Birds have evolved many adaptations associated with the production and performance of communication signals used to convey information to conspecifics. Structural features within a call or song have been found to contain information about the species, individual identity, habitat, predation pressures, body size, fitness, and vocal anatomy (e.g., Galeotti and Pavan 1991, Suthers 1994, Greene and Meagher 1998, Redpath et al. 2000, Bertelli and Tubaro 2002). Thus, describing the spectral and temporal structure of a call or song (through spectral analysis) is a crucial first step toward understanding vocal communication of any species. In the past, spectral analysis of avian vocal

signals has been focused largely on the songs of songbirds; now that the importance of vocal communication in other birds has become evident, more studies are focusing on other taxa. The vocal communication of ratites, however, has been largely ignored, despite the obvious uniqueness of this ancient lineage.

The ratite lineage consists of the kiwi (*Apteryx* spp.), Emu (*Dromaius novaehollandiae*), Ostrich (*Struthio camelus*), rheas (*Rhea* spp.), cassowaries (*Casuarius* spp.), and the extinct moa (Dinornithidae) and elephant bird (Aepyornithidae). Probably the most distinctive of the ratites are the kiwi, which have small bodies (2–4 kg), are highly territorial, maintain life-long pair bonding, and are nocturnal (Colbourne and Kleinpaste 1983, 1984; McLennan et al. 1987; Potter 1989; Marchant and Higgins 1990;

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Taborsky and Taborsky 1991, 1992). The taxonomic subdivision of kiwi has changed substantially in the past, and there are currently five recognized species: North Island Brown Kiwi (*Apteryx mantelli*); Okarito Brown Kiwi, or Rowi (*A. rowi*); Tokoeka (*A. australis*); Great Spotted Kiwi, or Roroa (*A. haastii*); and Little Spotted Kiwi (*A. owenii*) (Burbidge et al. 2003, Robertson and Colbourne 2003). The visual fields, eye, and visual areas in the brain are highly reduced in kiwi (Craigie 1930, Martin et al. 2007), which suggests that their vision is poor. In the absence of strong visual cues, kiwi require acoustic signaling to communicate with conspecifics. Thus, it is likely that kiwi have evolved a complex system of vocal communication associated with their nocturnal environment and their complex behavioral traits.

Kiwi are the most vocal of the ratites (Davies 2002), producing several distinctive sounds, the most prevalent of which is termed the “whistle call.” This vocalization is thought to be a long-range call and is produced by both sexes, either as a solo call, in response to the call of a neighbor or in response to the calls of a mate, which can sometimes overlap to form a duet (Colbourne and Kleinpaste 1984, Taborsky and Taborsky 1992, Corfield 2004). The social context of the whistle call is not well understood, but it is thought to have territorial and pair-communication functions (Colbourne and Kleinpaste 1984, Marchant and Higgins 1990). It may also be involved in breeding behavior, with calling-rate fluctuations corresponding to different breeding activities (calling rates are lowest during the incubation period and highest during the mating period (Colbourne and Kleinpaste 1984, Taborsky and Taborsky 1992, Miles et al. 1997).

Descriptions currently available for vocalizations of kiwi, like those of most other ratites, are limited to transliterations of the call. For example, the call of male kiwi has been described qualitatively as a shrill “ah-eel,” and the call of females as a throaty “ah-eh” (Colbourne and Kleinpaste 1984). These descriptions are helpful but do not reveal the levels of complexity that may be perceived in these calls by conspecifics (Catchpole and Slater 1995). Here, we undertake a thorough description of the vocal behavior and spectrotemporal structure of the whistle call produced by male and female North Island Brown Kiwi. Through this process, we also aim to better understand the evolutionary pressures that have shaped the structure of kiwi vocalizations and gain insight into vocal communication in an avian species occupying a unique environmental niche.

## METHODS

**Study site.**—The study was conducted in Aponga Scenic Reserve, located 30 km north of Whangarei, North Island, New Zealand (36°23'S, 174°8'E). The area is a 33-ha reserve managed by the Department of Conservation. The site is a volcanic cone 365 m above sea level, flowing down into a broad valley with vegetation composed of mixed broadleaf–podocarp species. For further details on the study site, see Robertson et al. (1999). There were ~21 pairs of adult North Island Brown Kiwi in the reserve.

**Recording equipment and methods.**—Seven pairs of adult North Island Brown Kiwi were studied. Pairs had been identified by the Department of Conservation before the start of the study. Males were identified as M1 to M7, females as F1 to F7, and pairs as P1 to P7. All males and three of the females (F2, F3, and F6)

were fitted with transmitters. Each transmitter had a unique radio frequency, allowing for the use of telemetry equipment (Yagi directional aerial attached to a Telonics TR-4 receiver; Sirtrack, Havelock North, New Zealand) to identify and locate individual birds. Recordings were made within 20 m of the bird. Call recordings were restricted to radiotagged birds, except for F5, because she had been fitted with a transmitter previously and her call could be identified when she responded to her radiotagged mate. The probability of incorrectly identifying a bird was low, given the highly territorial nature of kiwi and the size of their territories (Colbourne and Kleinpaste 1983, Potter 1989). The identification of the caller could also be verified using spectral analysis (Corfield 2004). Calls were recorded from 5 May 2003 to 30 April 2004 using a Sennheiser ME66 directional microphone (Sennheiser, Wedemark, Germany; frequency response from 50 Hz to 20,000 Hz  $\pm$  2.5 dB) connected to a Sony digital audio tape (DAT) recorder (TCD-D8, Sony, Tokyo) with a sampling rate of 44.1 kHz with 16-bit precision. Recording commenced ~20 min after sunset and continued for 3–5 h. Once the target bird had called, the equipment was moved to a nearby bird that had not yet called that night, and recording continued.

**Analysis.**—Calls were digitized to computer at 44.1 kHz with 16-bit precision using RAVEN, version 1.0 (Cornell Laboratory of Ornithology, Ithaca, New York) and saved as WAV files. Quantitative analysis of vocalizations was done in RAVEN and in BAT-SOUND PRO, version 3.2 (Pettersson Elektronik AB, Uppsala, Sweden). A set of variables was used to describe the temporal and spectral structure of calls, each of which was measured from a spectrogram, waveform, or power spectrum produced by RAVEN or BAT-SOUND PRO. For calls of males, all measurements were made from the fundamental (f0), and for calls of females they were made from each of the two frequency components. Call variables measured from spectrograms were number of notes per call, highest frequency, and lowest frequencies. Call variables measured from waveforms were duration from the start of the first note to the end of the last note, duration of each note, and duration from the end of one note to the beginning of the next. The call variable measured from the power slice was the frequency with the highest amplitude. Spectrograms and power spectra were produced with a Fast Fourier Transformation (FFT) size of 1,024 points using a Hamming window and 50% overlap, which produced a frequency resolution of 56 Hz. Data were not distributed normally (Shapiro-Wilks W-test), so the median and the interquartile range (IQR) are described for each variable. Mann-Whitney U-tests were used to test for differences (1) in the temporal structure between sexes, (2) between the inter-note intervals of a duet compared with a solo call, and (3) between inter-note intervals in females' calls before and after the male's response call. Calls were defined as a response call if a bird responded to the call of its mate within 40 s of the start of the initiator's call.

## RESULTS

**Temporal structure.**—Whistle calls were composed of a series of notes separated by periods of silence (Fig. 1). Each call contained 13–36 notes and lasted 15.5–43.6 s (see Tables 1 and 2 for complete summary statistics). Note duration and inter-note interval increased steadily within a call and ranged in duration from 0.17 to 1.28 s and from 0.12 to 3.50 s, respectively.

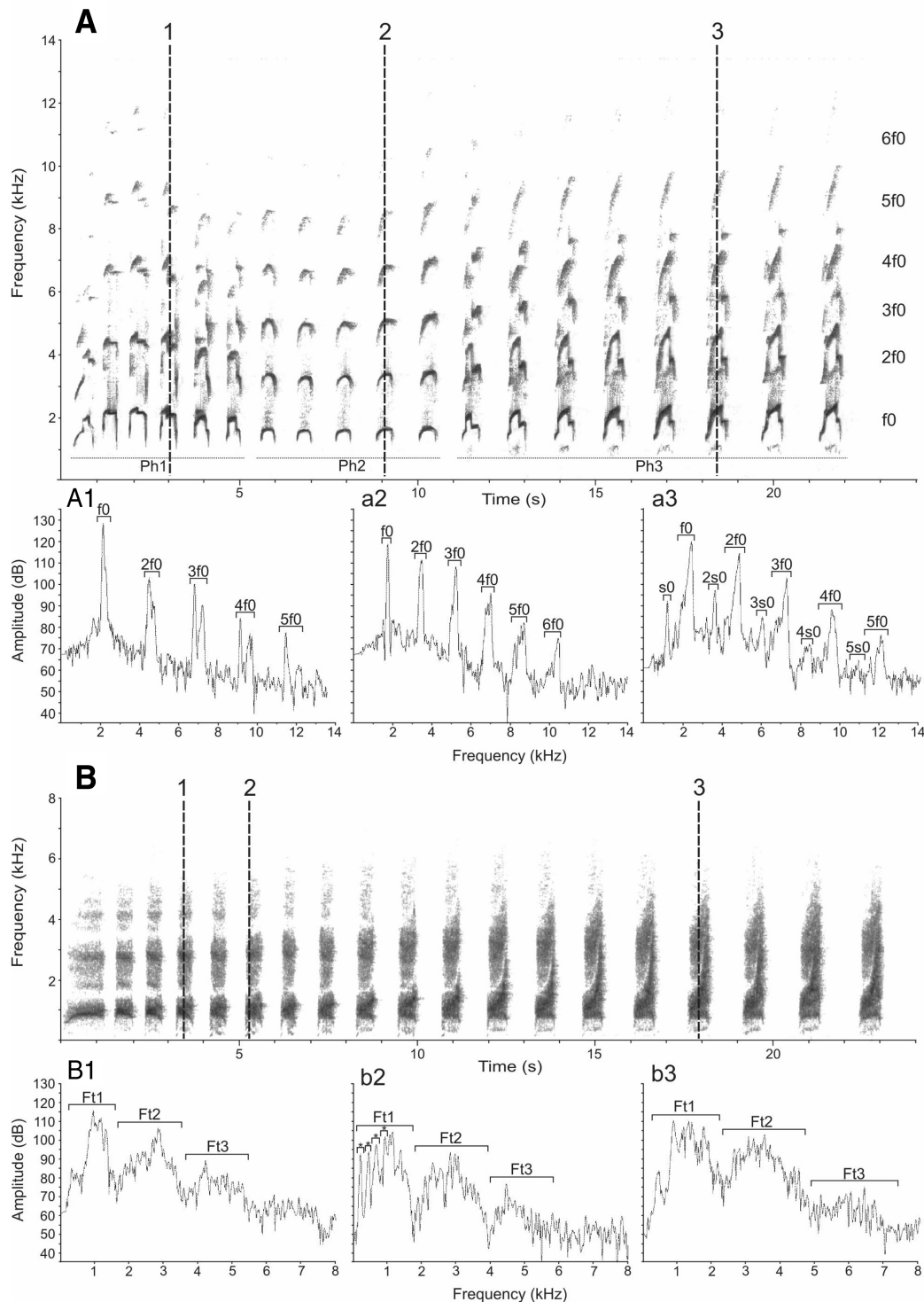


FIG. 1. Spectrograms and power slices of (A) a call of a male and (B) a call of a female North Island Brown Kiwi (Fast Fourier Transformation [FFT] = 1,024 points, 50% overlap, frequency resolution = 56 Hz). Calls of males contained a clear harmonic structure ( $f_0$ – $6f_0$ ), whereas calls of females contained a series of tightly packed, poorly defined harmonics. In calls of males, notes could be grouped into phrases (Ph1, Ph2, Ph3). Power slices from Ph1, Ph2, and Ph3 are represented by a1, a2, and a3, respectively. Phrase-three notes contain an additional low-amplitude peak within each harmonic ( $s_0$ – $5s_0$ ). In calls of females, amplitude is concentrated into two or three prominent formants (Ft1, Ft2, Ft3). Formants are well defined near the start of a call (b1) and become merged and less apparent in notes near the end (b3). Constant frequency components (CFC) are obvious only at the start of some notes and at the lower frequencies of a note (b2; asterisk indicates obvious CFC).

TABLE 1. Summary statistics for temporal and spectral variables measured from calls of male North Island Brown Kiwi. Data are presented as median, interquartile range (in parentheses), and range (below).

Bird	Temporal Variables				Spectral Variables			<i>n</i>
	Tdur (s)	Nnote	Notedur (s)	INI (s)	Fmax (kHz)	Highfreq (kHz)	Lowfreq (kHz)	
M1	26.7 (5.3)	21.5 (2.5)	0.52 (0.16)	0.67 (0.35)	2.0 (0.5)	2.2 (0.7)	1.4 (0.2)	6
	20.8–29.8	18.0–29.0	0.25–0.96	0.20–2.39	1.5–2.6	1.7–2.8	0.6–1.5	
M2	32.8 (18.6)	32.0 (11.8)	0.53 (0.12)	0.64 (0.23)	1.8 (0.2)	1.9 (0.2)	0.8 (0.3)	7
	21.0–30.4	22.0–26.0	0.37–0.98	0.19–1.09	1.5–2.3	1.5–2.4	0.5–1.3	
M3	29.2 (5.7)	25.0 (2.0)	0.57 (0.18)	0.52 (0.32)	1.7 (0.3)	1.8 (0.3)	1.2 (0.2)	6
	17.1–41.1	21.0–36.0	0.25–0.77	0.12–1.57	1.3–2.2	1.3–2.4	0.7–1.5	
M4	25.9 (4.6)	22.0 (2.5)	0.51 (0.06)	0.70 (0.35)	1.8 (0.1)	2.1 (0.3)	1.0 (0.5)	8
	23.3–33.6	21.0–25.0	0.30–0.88	0.22–1.61	1.5–2.1	1.6–2.7	0.4–1.5	
M5	33.5 (4.1)	26.0 (4.0)	0.52 (0.25)	0.84 (0.17)	1.7 (0.2)	1.7 (0.2)	1.3 (0.1)	8
	23.0–36.5	19.0–30.0	0.17–0.70	0.25–1.65	1.3–2.3	1.3–2.4	1.0–1.5	
M6	27.8 (3.8)	22.0 (2.0)	0.62 (0.10)	0.68 (0.27)	2.0 (0.3)	2.2 (0.3)	1.4 (0.8)	6
	15.9–29.9	14.0–24.0	0.43–0.82	0.21–1.85	1.6–2.3	1.6–2.6	0.5–1.8	
M7	34.5 (6.6)	28.0 (2.5)	0.59 (0.16)	0.65 (0.31)	1.8 (0.2)	2.0 (0.2)	1.5 (0.2)	7
	20.4–40.3	19.0–34.0	0.17–0.77	0.16–3.18	1.4–2.4	1.4–2.9	1.1–1.7	
	29.1 (8.9)	24.0 (6.0)	0.54 (0.13)	0.66 (0.33)	1.8 (0.3)	1.9 (0.4)	1.2 (0.4)	48
	15.9–41.1	14.0–36.0	0.17–0.98	0.12–3.18	1.3–2.6	1.3–2.9	0.4–1.8	

Abbreviations: Tdur = total duration of call, Nnote = number of notes per call, Notedur = duration of each note, INI = duration from the end of one note to the beginning of the next, Fmax = frequency with the highest amplitude in the fundamental harmonic, Highfreq = highest frequency reached in the fundamental harmonic, and Lowfreq = lowest frequency reached in the fundamental harmonic.

There was little difference between sexes in the temporal variables (Tables 1 and 2), and none of these differences was statistically significant (Tdur:  $Z = -0.85$ ,  $P = 0.412$ ; Note:  $Z = -1.424$ ,  $P = 0.164$ ; Notedur:  $Z = -0.53$ ,  $P = 0.648$ ; and INI:  $Z = -0.712$ ,  $P = 0.527$ ), which suggests that the temporal structure of calls was similar between sexes. Variation among calls of each bird was high, in both total call duration and number of notes per call, for

both sexes. For example, one male produced a call with a duration of 17.1 s, containing 21 notes, and another lasting 41.1 s and containing 36 notes. All individuals in the study exhibited this high level of variation among calls.

**Spectral structure: Males.**—The males produced notes with a clear harmonic structure (Fig. 1A). The fundamental frequency was ~1.5 kHz, with a series of overtones reaching up to ~13 kHz.

TABLE 2. Summary statistics for temporal and spectral variables measured from calls of female North Island Brown Kiwi. Data are presented as median, interquartile range (in parentheses), and range (below).

Bird	Temporal Variables				Spectral Variables				<i>n</i>
	Tdur (s)	Nnote	Notedur (s)	INI (s)	Fmax (kHz)		Highfreq (kHz)	Lowfreq (kHz)	
					LFC	UFC			
F2	25.6 (0.9)	20.5 (0.5)	0.53 (0.08)	0.62 (0.34)	1.3 (0.3)	3.2 (0.4)	4.1 (0.9)	0.1 (<0.1)	2
	24.7–26.5	20.0–21.0	0.44–1.13	0.21–3.31	0.9–2.6	2.6–4.8	1.7–5.3	0.9–0.3	
F3	30.3 (0.5)	28.5 (0.5)	0.47 (0.16)	0.63 (0.25)	1.9 (0.6)	3.8 (0.8)	0.3 (0.1)	5.2 (0.9)	2
	29.8–30.8	28.0–29.0	0.25–0.64	0.23–1.08	1.3–2.2	2.8–4.3	3.8–6.7	0.1–0.5	
F5	26.7 (2.4)	21.5 (1.5)	0.60 (0.15)	0.69 (0.27)	2.0 (0.6)	4.5 (1.2)	5.1 (0.4)	0.2 (0.1)	5
	15.4–30.3	13.0–23.0	0.42–0.86	0.29–1.17	1.5–2.7	2.9–5.3	4.6–6.6	0.9–0.7	
F6	30.4 (13.4)	19.0 (7.0)	0.66 (0.11)	0.63 (0.36)	1.7 (0.3)	3.2 (0.7)	5.0 (1.1)	0.2 (0.1)	5
	19.2–43.5	16.0–29.0	0.42–1.28	0.28–3.50	1.1–2.7	2.2–4.3	3.0–6.6	0.1–0.4	
	27.3 (5.2)	21.0 (6.0)	0.60 (0.15)	0.64 (0.32)	1.8 (0.5)	3.6 (1.1)	5.0 (0.7)	0.2 (0.1)	14
	15.5–43.6	13.0–29.0	0.25–1.28	0.21–3.50	0.9–2.7	2.2–5.3	1.7–6.7	0.1–0.7	

Abbreviations: Tdur = total duration of call, Nnote = number of notes per call, Notedur = duration of each note, INI = duration from the end of one note to the beginning of the next, Fmax = frequency with the highest amplitude in the lower frequency component (LFC) and upper frequency component (UFC), Highfreq = highest frequency reached in the upper frequency component, and Lowfreq = lowest frequency reached in the lower frequency component.



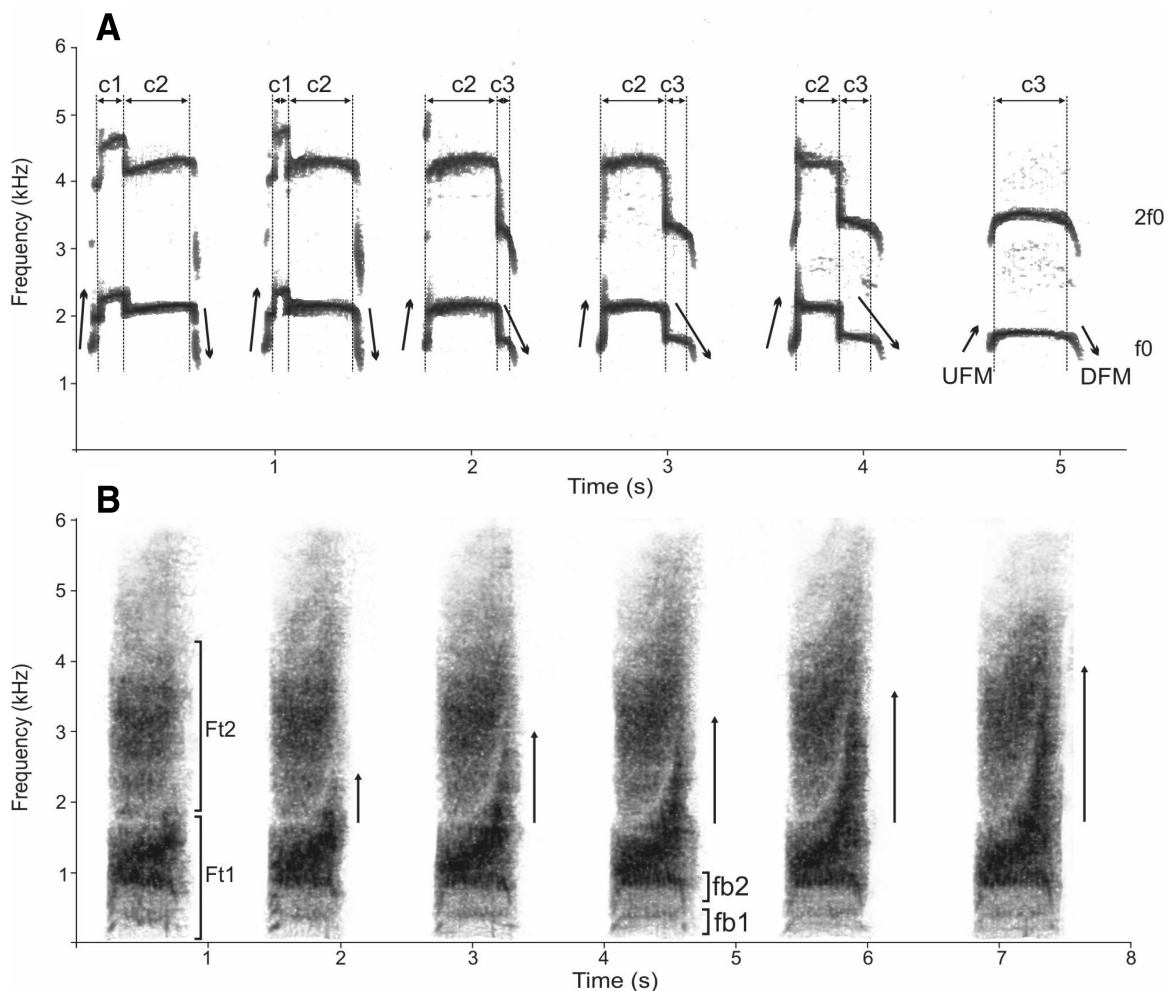


FIG. 2. (A) Spectrogram of a section of phrase 1 ( $f_0$  and  $2f_0$ ) of a call of a male and (B) spectrogram of a section of the middle of a call of a female North Island Brown Kiwi (Fast Fourier Transformation [FFT] = 1,024 points, 50% overlap, frequency resolution = 56 Hz). Notes from calls of males are composed of up to three constant frequency components (CFC); c1 indicates the upper CFC, c2 the middle CFC, and c3 the lower CFC. Each note also has an upward frequency modulated (UFM) component at the start and a downward frequency modulated (DFM) component at the end. Phrase-one notes gradually shift from the upper CFCs to the lower CFC. Notes from calls of females gradually add a UFM near the end of a note, causing the frequency components to overlap (indicated by arrows). Only two harmonic-like structures can be seen in notes from calls of females (fb1, fb2).

Amplitude generally decreased across harmonics, dropping at least 5 dB between harmonics (Fig. 1A: 1–3). Peak amplitude within the fundamental ( $f_0$ ) was produced within a frequency range of 1.3–2.6 kHz, and frequencies within this harmonic spanned a range of 0.4–2.9 kHz (see Table 1 for complete summary statistics). The spectral structure of a note was primarily composed of one, two, or three constant frequency components (CFC) and always contained an upward frequency modulation (UFM) at the start and a downward frequency modulation (DFM) at the end of a note (Fig. 2A). The CFCs were either close to pure tones or were slightly modulated frequency sweeps. Although variable among birds, the frequency of the lowest CFC was generally within the range of 1.5–1.8 kHz, the middle CFC was within 1.8–2.3 kHz, and the upper CFC was >2.3 kHz. Frequency modulations (FM) at the start and end varied in frequency range and slope within calls, with some notes

consisting of very steep UFM or DFM. Birds modified the structure of a note by altering which CFCs they produced or by altering the duration, or degree of modulation, of a CFC.

In calls of males, notes could be grouped into “phrases” (Fig. 1A), defined as groups of notes similar in structure and degree of FM. Calls contained three phrases, the first in the first quarter, the second in the second quarter, and the third in the last half. Phrase one was characterized by high CFCs and large, sharp FMs, the degree of which varied between consecutive notes (Fig. 1A). Phrase two was characterized by small FMs and was composed entirely of a low CFC (Fig. 1A). Phrase three was characterized by constant high FMs and two CFCs (Fig. 1A). Phrase three also consisted of an additional structural feature, whereby additional CFCs were produced below the fundamental frequency and within each of the harmonics. These additional CFCs were

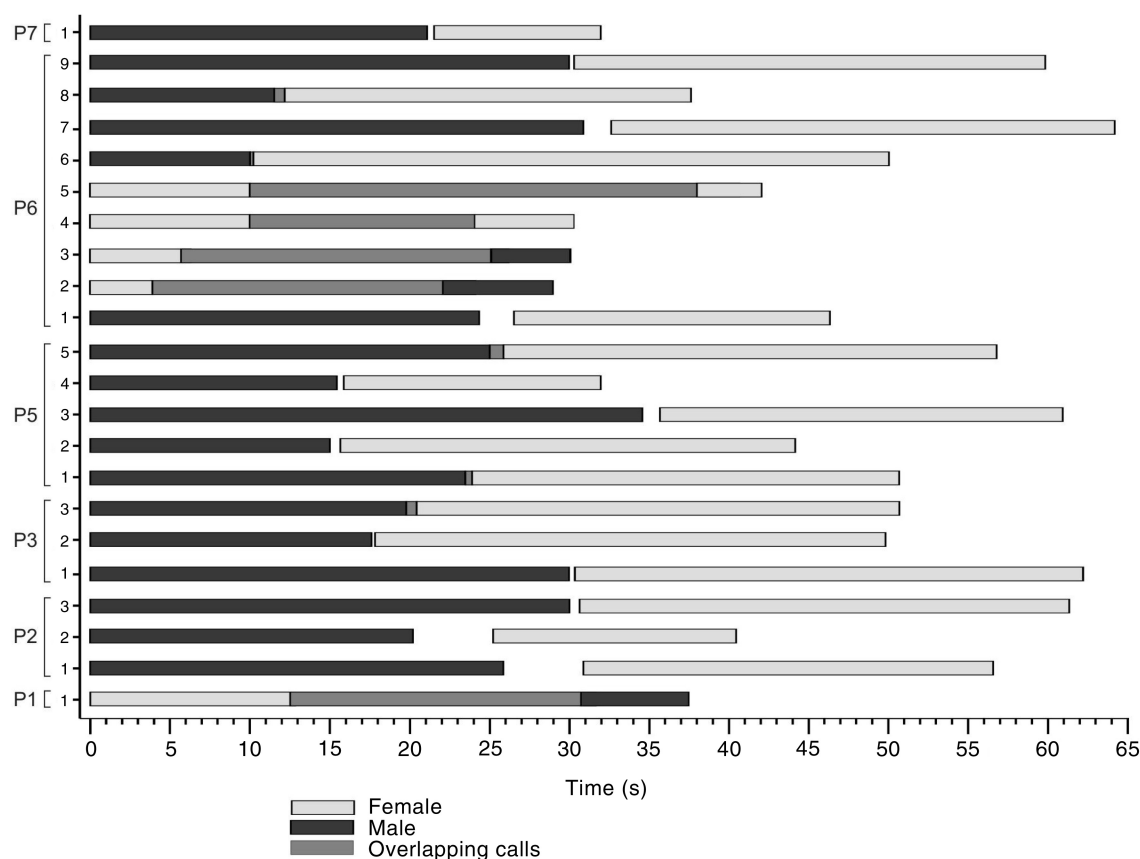


FIG. 3. Calling behavior of the seven pairs of North Island Brown Kiwi recorded in the present study (F4 was not recorded during the study). P1, etc., indicates the pair corresponding to the duet. Three different calling behaviors were observed: (1) females responded to the call of their mate shortly after he had finished calling; (2) females responded during their mate's call, causing a stop to the male's call; and (3) males responded to their mate's call, and both birds called together, producing overlapping calls.

produced at around 1.5, 3.5, 6.0, and 8.0 kHz and at much lower amplitude than the harmonics.

**Spectral structure: Females.**—The structure of calls from females consisted of a fundamental frequency ( $f_0$ ) of  $\sim 0.1$  kHz, with overtones reaching  $\leq 7.0$  kHz (Fig. 1B). Harmonics were present, though tightly packed, and each spanned a narrow frequency range, which made them difficult to detect. The harmonic structure was obvious in only a few calls, normally in the lower harmonics and in a small area at the beginning of each note (Fig. 1B, 2B). Within notes, energy was distributed among harmonics to form two obvious broad frequency components, each containing a series of approximately eight harmonics (Fig. 1B: 1–3). Harmonics reached peak amplitude near the center of each component, with amplitude decreasing in harmonics on both sides. A third broad frequency component was detected in a small number of calls. The lower frequency component was produced from about 0.1 to 3.0 kHz, and the upper frequency component was produced from about 2.0 to 6.0 kHz. Amplitude within the lower frequency component peaked at a frequency of 0.9–2.7 kHz, and the upper frequency component peaked between 2.2 and 5.3 kHz (Table 2). The degree of FM varied greatly between notes, with a UFM near the

end of a note gradually being added, causing the frequency components to overlap (Fig. 2B).

**Pair communication behavior.**—Females produced a response to the call of their mate within 35 s of the start of their call (Fig. 3). Females either waited for their mate to stop calling or interrupted his call, causing him to stop (i.e., to finish the note he was on and then stop calling). Males responded to the calls of their mate within a much shorter period, within 13 s of the start of the female's call. When the male responded, the female continued to call, causing the two calls to overlap. No obvious patterns occurred with respect to alternation, or overlapping, of notes within these possible duets. There was, however, some alteration of the inter-note interval after the onset of the mate's call. Females paused after the onset of the call of their mate, and this pause was considerably longer than any of the inter-note intervals before their mate's response call (Fig. 4). After the onset of a male's call, within these duets, the inter-note interval of the calls of their mate also became highly variable, with long irregular pauses that were not present before the male's response call (Fig. 5). There was a large difference between inter-note intervals before and after the onset of the male's calls ( $Z = -2.31$ ,  $P = 0.03$ ), but this result may

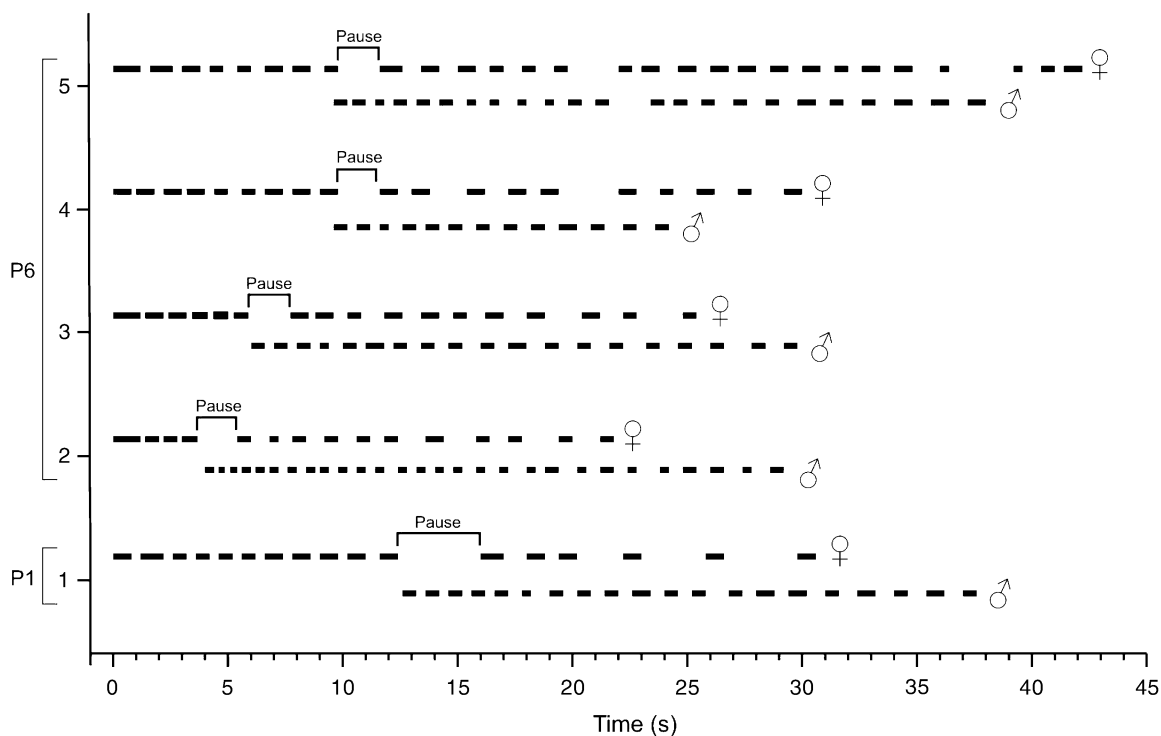


FIG. 4. Temporal structure of the calls of male and female North Island Brown Kiwi when part of a duet. No obvious patterns with respect to note alternation or overlapping occurred within these duets. However, females paused for considerably longer after the onset of the male's response call than before it.

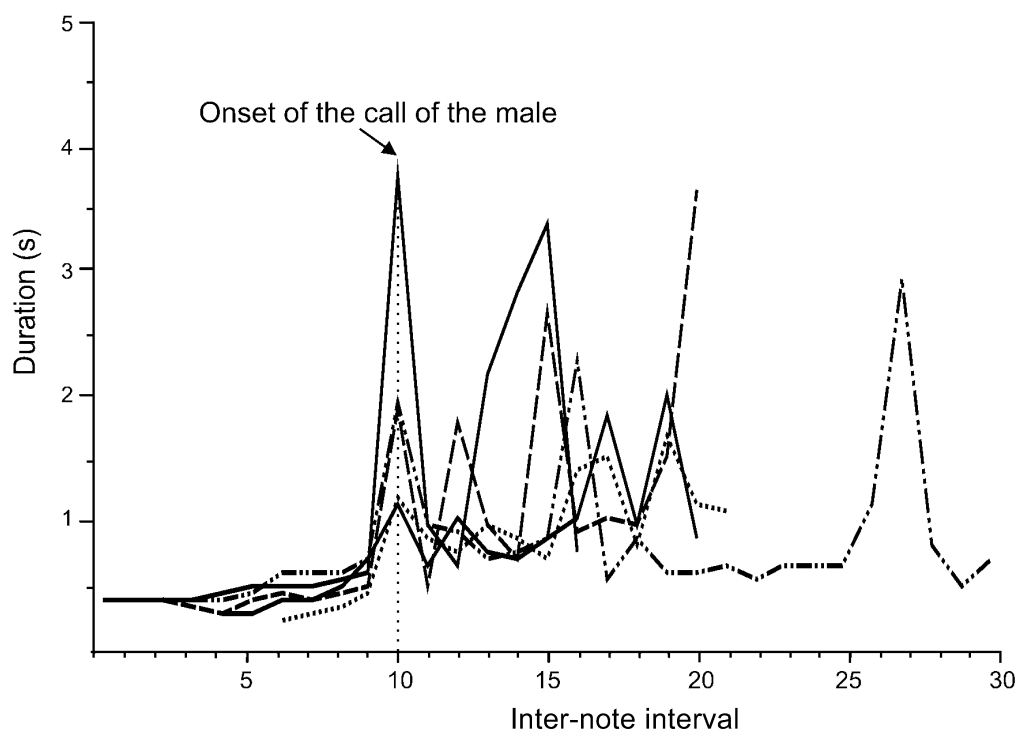


FIG. 5. Duration of the inter-note interval in individual calls of female North Island Brown Kiwi that are part of a duet with their mate. The figure has been normalized so that the onset of calls by males occurs at the same time during each female's call. After the onset of the call of the male, the inter-note interval becomes much more variable, with long erratic pauses between notes.

have been influenced by the increasing inter-note interval over the duration of a call. The inter-note intervals of calls that were part of a duet were similar to those that were not (non-duet median = 0.64, duet median = 0.62,  $Z = -0.29$ ,  $P = 0.89$ ). The inter-note interval in calls of males did not appear to change when they were part of a duet (non-duet median = 0.68, duet median = 0.64,  $Z = -0.58$ ,  $P = 0.69$ ).

## DISCUSSION

The present study provides the first detailed description of the spectral and temporal features of the “whistle call” of male and female North Island Brown Kiwi. According to our current understanding of vocal signals and kiwi behavior, kiwi vocalizations should be optimized for long-range signaling in a nocturnal, temperate forest environment and, thus, characterized predominantly by low frequencies and long simple notes spanning a narrow frequency range (Morton 1975, Sorjonen 1986, Wiley 1991, Badyaev and Leaf 1997, Bertelli and Tubaro 2002). The results presented here, however, show that North Island Brown Kiwi, especially males, produce calls that do not conform to this assumption. Males produced a complex call consisting of  $\leq 36$  multiharmonic notes that are frequency-modulated and broadband, with a high-frequency component. Indeed, the vocalizations of kiwi are very unlike the booming and grunting of the Emu, Ostrich, rheas, and cassowaries (Davies 2002), which are dominated by low frequencies ( $< 300$  Hz) and well suited to traveling long distances. The vocalizations of North Island Brown Kiwi appear to be more characteristic of short-range signals and open environments (Smith 1991, McGregor and Dabelsteen 1996, Titus 1998). Although a possible explanation may be that the relatively small size of the kiwi (2–4 kg; Marchant and Higgins 1990) limits their ability to produce a low-frequency signal at a sufficient amplitude (e.g., Walliscläger 1980, Ryan and Brenowitz 1985, Tubaro and Mahler 1998, Bertelli and Tubaro 2002), many other species of a similar size, such as Capercaillie (*Tetrao urogallus*; Moss and Lockie 1979, Moss 1983) and Great Bittern (*Botaurus stellaris*; Puglisi et al. 1997), have developed the means to produce a low-frequency, long-range call. The call structure of North Island Brown Kiwi, however, may have been influenced by its unique behaviors. Kiwi, unlike any other ratites, are highly territorial and maintain and defend a 30- to 40-ha area against neighbors and wandering conspecifics (Potter 1989). They are also socially monogamous, each member of the pair occupying close, overlapping territories (Taborsky and Taborsky 1991, 1992). Therefore, the calls of North Island Brown Kiwi are likely to be directed primarily at immediate neighbors, mates, and unknown kiwi intruding on their territory. Thus, conveying information over long distances may not be advantageous for kiwi, as it is for the other nomadic, nonterritorial, and polygamous ratites (Davies 2002).

It is likely that, as with many other nonpasserines, the kiwi call is shaped by the resonances in the vocal tract (Fant 1960). This is most obvious in calls of females, which show a structural feature consistent with formants. Formants are thought to be an information-bearing element within a call and have been found to accurately indicate body size in Rhesus Macaques (*Macaca*

*mulatta*; Fitch 1997) and dogs (*Canis familiaris*; Riede and Fitch 1999) and to provide an acoustic cue for individual recognition in the Oilbird (*Steatornis caripensis*; Suthers 1994). Whooping Cranes (*Grus americana*) have also been found to perceive changes in formant frequencies (Fitch and Kelley 2000). Formants are only one of a number of possible cues for conveying information to conspecifics. Therefore, it is reasonable to assume that male kiwi—confronted with a nocturnal environment and needing to pronounce ownership of a territory and to distinguish between intruders, neighbors, and mates—have made use of other frequency, amplitude, and temporal elements of calls to obtain information from conspecifics (e.g., the low-amplitude CFCs in phrase 3).

It was surprising to find such a high degree of structural difference between the sexes, each producing calls with completely different structural features. Males produced relatively high-frequency notes with a clear harmonic structure, compared with the low-frequency, broadband-frequency components in the notes of females. It is possible that these differences in the structure of calls are simply attributable to differences in body size between the sexes (females are larger than males; Marchant and Higgins 1990) and the consequent differences in size of the sound-producing organ (Ballintijn et al. 1997) and length of the trachea (Hinds and Calder 1971).

It has been suggested that kiwi pairs duet (e.g., Colbourne and Kleinpaste 1984, Taborsky and Taborsky 1992), but the present study is the first to describe the temporal structure of these apparent duets. There are no well-defined parameters for defining a duet, but the general consensus is that duetting is a joint acoustic display by paired individuals such that their elements within bouts have a degree of temporal precision (Farabaugh 1982, Hall 2004). Although temporal precision like that described by Farabaugh (1982) and Hall (2004) was not found with regard to note alternation or overlap within duets of North Island Brown Kiwi, changes in the inter-note interval occurred after the onset of the call of a mate. This suggests that kiwi may be using auditory feedback to alter the temporal structure of their calls during duets. Further studies are needed to uncover how this feedback influences the temporal pattern of calls. Because these possible duets occur only between pairs that share a territory, it is possible, as suggested by Colbourne and Kleinpaste (1984), that they are used to maintain pair bonds or to guide displaced kiwi back to their territories. It is also likely that kiwi duets have cooperative territorial-defense and mate-guarding functions similar to those found in other taxa (Wickler 1980, Sonnenschein and Reyer 1983, Levin 1996, Langmore 1998). Both functions would be of use to kiwi in their nocturnal habitat. However, behavioral experiments are needed to explore this function further.

The present study shows that North Island Brown Kiwi have evolved a call structure and vocal communication system unlike those of other ratites or other species living in a nocturnal forest environment. Clearly, kiwi have adopted a unique call structure to convey information to conspecifics. In describing the call of the North Island Brown Kiwi, we are beginning to understand the evolutionary pressures that have led to such an odd bird (flightless, nocturnal, territorial, monogamous). Ultimately, this will further our understanding of the evolution of avian vocal communication.



## ACKNOWLEDGMENTS

We are very grateful to the Department of Conservation, and in particular to S. Bell and C. Gardner, for assistance in working with kiwi. Thanks also to F. Kubke, M. Hauber, M. Wild, and several anonymous referees for comments that improved an earlier version of the manuscript.

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- Associate Editor: A. M. Dufty, Jr.*