Notornis, 2014, Vol. 61: 165-169
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SHORT NOTE

Ultrasonic harmonics in the calls of rock wren (*Xenicus gilviventris*)

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Bird vocalisations are remarkably diverse and vary widely in complexity, intensity and frequency range (Bradbury & Vehrencamp 1998). The dominant frequency in most bird calls falls within the sonic range (20 Hz – 20 kHz), although a few species can also produce ultrasound (frequencies ≥ 20 kHz; Dooling *et al.* 2000). Ultrasonic vocalisations are well studied in echo-locating mammals which use them for navigation, hunting (Sales & Pye 1974), and communication (Wilson & Hare 2004; Kalcounis-Rueppell *et al.* 2006). However, in the few birds known to produce ultrasonic sound, its adaptive function remains speculation (Pytte *et al.* 2004; Brumm & Slabbekoorn 2005).

Ultrasonic sound has been recorded as harmonics in the song of the rufous-faced warbler (*Abroscopus albogularis*; Narins *et al.* 2004), and also as non-harmonic song components in the blue-throated hummingbird (*Lampornis clemenciae*; Pytte *et al.* 2004). The oilbird (*Steatornis caripensis*) and several species of swiftlets (*Aerodramus* and *Collocalia*) use audible echolocation (3-10 kHz) and in the process produce sound extending into the ultrasonic range, although it is not thought that these ultrasound signals are perceived and used for either navigation or communication (Price *et al.* 2004; Brinkløv *et al.* 2013). Short ultrasound harmonic components (0.1-0.2 seconds) have been reported in the calls of the New Zealand rifleman (tītipounamu) (*Acanthisitta chloris*), yet their adaptive function, if one exists, remains unknown (Krull *et al.* 2009).

Pytte *et al.* (2004) measured auditory brainstem responses (*i.e.*, sensory perception) of calls in the blue-throated hummingbird, yet found no response above 7 kHz. Brumm & Slabbekoorn (2005) suggested that the high frequency components in rufous-faced warbler vocalisations could help them stand out against the acoustic masking of low frequencies by water noise, yet acknowledged that it is unknown whether the birds can actually hear the high-frequency components. Perception of ultrasonic calls remains untested in other bird species in which ultrasonic acoustic components have been found, so communication remains a valid hypothesis.

In addition to intraspecific communication, 2 other explanations have been proposed to explain the presence of ultrasonic calls or song: (1) to flush ultrasound-hearing prey in insectivorous birds

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Received 24 June 2014; accepted 16 August 2014
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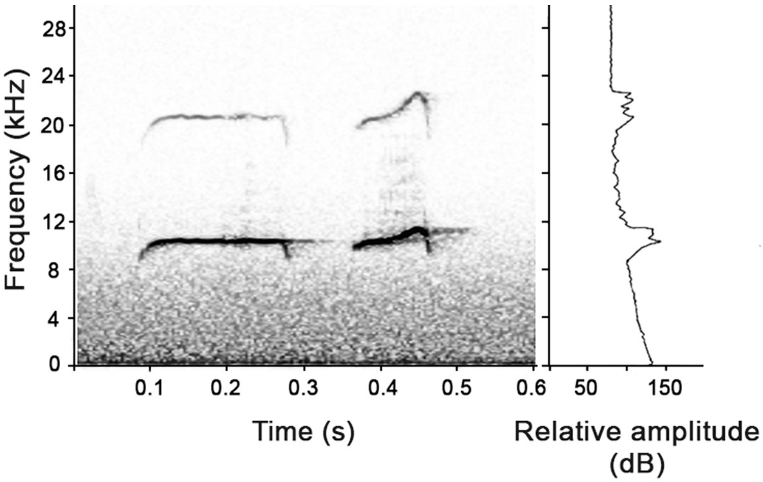

Fig. 1. Unamplified spectrogram and power spectrum of a male rock wren 3-note call with ultrasonic harmonics (1 note missing). The spectrogram and power spectrum were created using 512- point FFT's with 124 Hz resolution and 50% Hann window overlap.

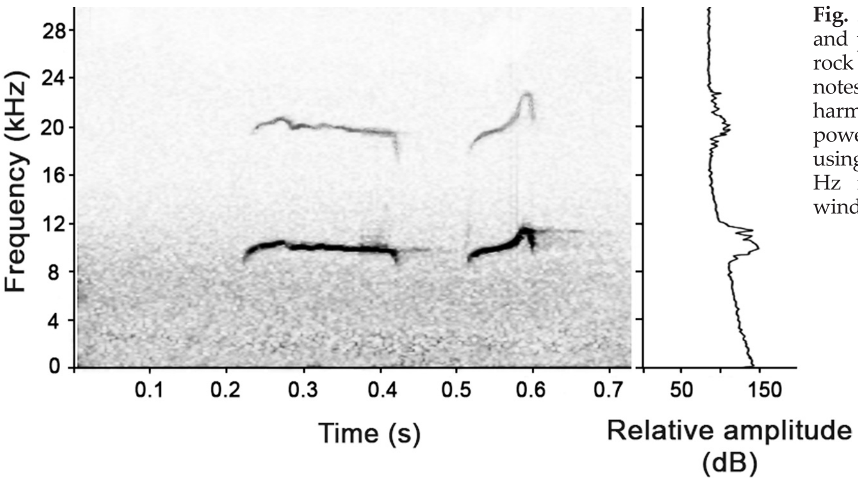

Fig. 2. Unamplified spectrogram and power spectrum of a female rock wren 3-note call (first 2 notes merged) with ultrasonic harmonics. The spectrogram and power spectrum were created using 512- point FFT's with 124 Hz resolution and 50% Hann window overlap.

(Hoy & Robert 1996; Jablonski & Lee 2006; Krull *et al.* 2009), and (2) that the production of ultrasound is an epiphenomenon (and thus no adaptive function) of sonic sound production (Pytte *et al*. 2004; Krull *et al.* 2009). Ultrasonic calls by insectivorous predators have been found to prompt flight responses, or mid-flight predator avoidance behaviour in prey insects that makes them more conspicuous and possibly easier to catch (Yager *et al.* 1990; Yager 2012). This could be an especially effective hunting strategy in diurnal birds where the response behaviour in insect prey evolved as an adaptation to nocturnal echo-locating predators such as bats (Conner & Corcoran 2012). Consequently, insectivores that feed close to the substrate and that are capable of fast prey pursuit could be expected to benefit most from prey-flushing using ultrasound (Jablonski *et al.* 2006).

In New Zealand, both the rifleman and rock wren (pīwauwau) (*Xenicus gilviventris*) are small endemic insectivores that fly infrequently, feed directly from substrates such as the ground and tree trunks (Hunt & McLean 1993), yet have fast flight (Higgins *et al.* 2001). They are the only extant members of the suborder Acanthisitti (Family Acanthisittidae; Barker *et al*. 2004; Gill *et al.* 2010). The rifleman is a forest-dweller (Higgins *et al.* 2001) whereas the rock wren inhabits alpine and subalpine rocky slopes and low vegetation (Michelsen-Heath & Gaze 2007). Both species have similar audible vocalisations consisting of high-pitched, repeated (especially in riflemen) '*ssip*' or '*zsipt*' calls (Higgins *et al.* 2001). High call repetition has been proposed as an adaptation for communication in habitats with considerable sound interference and background noise (Brumm & Slabbekoorn 2005). Both species have also been noted to feed on at least 4 orders of insect with species capable of ultrasonic hearing: flies (Diptera), weta (Orthoptera), beetles (Coleoptera) and moths (Lepidoptera; Yager *et al.* 1990; Libersat & Hoy 1991; Hoy & Robert 1996). Consequently, the communication, epiphenomenon and prey-flushing

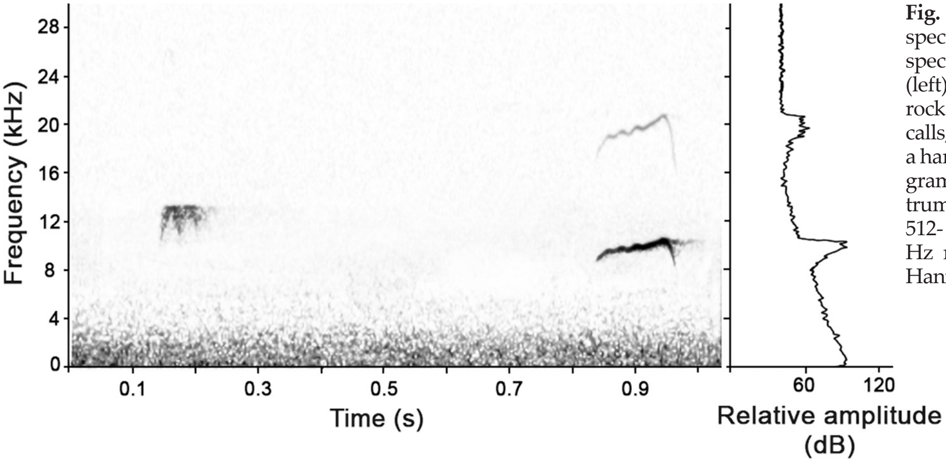

Fig. 3. Unamplified spectrogram and power spectrum of a female (left) and male (right) rock wren single-note calls, with and without a harmonic. The spectrogram and power spectrum were created using 512- point FFT's with 124 Hz resolution and 50% Hann window overlap.

hypotheses are all potential explanations for the use of ultrasound by riflemen.

Here I present evidence for ultrasonic harmonics in rock wren and compare them with those found in the rifleman (Krull *et al.* 2009). I made recordings of 1 adult male and 1 adult female rock wren on 29 March 2014 in the Otira Valley, Arthur's Pass, New Zealand (42° 53'47.5 S, 171° 32'12.5 E) from a distance of 4-6 m for 35 minutes. All recordings were of birds continuously vocalising as they foraged near the Otira River. The relative positioning of the birds suggested they were paired and sex of the vocalising individual was noted while recording. Video recordings were also made between sound recording bouts to supplement my field notes.

Audio recordings were made with a ME66 Sennheiser highly directional microphone (Sennheiser, Wademark-Wennebostel, Germany) with a frequency response of 40–20,000 Hz ± 2.5dB (it is frequency sensitive beyond 20,000 Hz but without the same amplitude sensitivity). The microphone was fitted with a Rycote windshield (Rycote Microphone Windshields Ltd, U.K.), and recordings were stored on a Sony PCM D50 portable solid-state digital recorder (Sony Inc., Japan) with a 96 kHz sampling rate as 48-bit WAV files. All recordings were analysed and visualised using the sound analysis programme Raven Pro v1.4 (Cornell Lab of Ornithology, Ithaca). Measures of maximum frequency (the frequency at which maximum amplitude occurs within a sound component) were made for both the fundamental and harmonic of each syllable recorded. This is a measure robust to repetition and observer bias (Krein *et al.* 2009).

Two different rock wren calls were identified from the acoustic recordings and behavioural observations. Primarily made by the male, the first vocalisation was the common '3-note call' (Higgins *et al.* 2001), although 1 note was frequently omitted or 2 notes merged (Fig. 1, 2), and the second was a high single-note call (Michelsen 1982), made by both the male and female as they moved among the boulders feeding (Fig. 3). Ultrasonic harmonics were identified in both calls, and while some 3-note calls had no harmonic, they were present in most single-note calls (see Fig. 3 for contrast with and without ultrasonic harmonics). The rock wrens were separated by a distance of 3-10 m for the entire observational period while they moved under and around boulders, making it possible to record each separately. Three-note calls were consistently given from a conspicuous perch whereas single-note calls were regularly made from nearer the substrate while moving or perching on low rocks. When the caller was perched, the single-note calls were almost always accompanied by vigorous bobbing of the body interspersed with wing flicks. During both call types, in both sexes, the head was often tilted to one side and quick sallying flights often followed the single-note calls.

The highest fundamental frequency in either call was 12.4 kHz from 51 calls made by both individuals. Of these, 22 had harmonics (43%) with a highest harmonic frequency of 22.3 kHz in male calls ($n = 10$) and 22.1 kHz in female calls ($n = 12$). The average peak in the ultrasonic harmonics was 20.6 kHz ($n = 22$, SD = 870 Hz), and most harmonics started below the ultrasonic boundary (20 kHz), peaked above it and then dropped below again (*e.g.*, Fig. 1). As in the rifleman, only 1 harmonic was ever present in any call (Krull *et al.* 2009), and the dominant frequency was always the fundamental, with no stand-alone ultrasonic sounds.

In the rock wren, ultrasonic harmonics were slightly longer than those found in riflemen, with some lasting up to 0.25 second compared to 0.15 second in riflemen (Krull *et al.* 2009). They also reached a higher maximum frequency than those in riflemen (20.75 kHz; Krull *et al.* 2009); however, overall harmonic frequency range is similar. Few studies have compared sonic vocalisations in the Acanthisittidae despite their unique taxonomy and contrasting habitat; thus, I conducted a preliminary comparison of the fundamental frequencies of both species and found no significant difference in maximum frequency between species (*unpubl. data*). The key body of work on rock wren vocalisations (Michelsen 1982) was conducted with equipment that would have made it hard to record ultrasound, and so ultrasonic (or any) harmonics may have simply remained undetected until now.

Overall, my recordings show that both single-note calls and the common 3-note calls in rock wren can contain ultrasonic harmonics. This suggests that harmonics in rock wren could have an adaptive function in increasing the communication signal-to-noise ratio (Brumm & Slabbekoorn 2005), because the 3-note call is the primary call involved in intraspecific communication (Higgins *et al.* 2001). My recordings were made under noisy circumstances (see power spectra on Fig. 1 to 3), and rock wren and riflemen both live in environments where selection pressures on signal transmission may be high (Krull *et al.* 2009). It must be noted that in both species, the sonic fundamental frequency was always of greater power than the ultrasonic harmonic. However, until it is shown otherwise, the use of ultrasound to increase signal efficacy cannot be discounted as a function in either species.

Prey-flushing is an alternative functional adaption for ultrasound in birds (Nairn *et al.* 2004). Rapid wing-flushing in riflemen disturbs insect prey (Higgins *et al.* 2001), and rock wrens are also known for vigorous bobbing and wing flicking while perched (Michelsen 1982; Higgins *et al.* 2001). During sound recording, both wing flicking and bobbing were observed, and both the male and female made numerous sallying flights off low perches. These behaviours while calling suggest that rock wren may use a mixed foraging strategy that combines gleaning for cryptic or hidden items (Jablonski 2002), with prey-flushing and sallying prey-pursuit behaviour (Galatowitsch & Mumme 2004; Jablonski & Lee 2006; Mumme 2014). Ultrasonic harmonics may function in conjunction with other prey flushing behaviour such as wing-flicking to increase foraging success near the substrate. However, whether the success of prey captures increases with the use of ultrasonics by rock wren needs further study.

Finally, it is possible that the ultrasonic sounds of rock wren may simply be an epiphenomenon, similar to that proposed for the blue-throated hummingbird (Narins *et al.* 2004), yet this does not satisfactorily explain why they are present in some calls but not others. One possibility is that sonic harmonics evolved for prey-flushing or optimised communication, and the propagation of sound beyond 20 kHz is simply an epiphenomenon, thus providing an explanation for why some calls lack harmonics. Communication and prey-flushing are also not necessarily opposing selective forces on vocal adaptations (Ryan & Brenowitz 1985), therefore if high frequency sounds are perceived by rock wrens, then ultrasonic harmonics in calls while foraging could be multifunctional. Ultimately, none of the rock wren vocalisations recorded can be considered purely ultrasonic, yet the power in the harmonics along with the associated bobbing, wing-flicking and sallying behaviour all favour a functional rather than epiphenomenal explanation. Prey-flushing appears the most likely explanation for ultrasonic harmonics in rock wren, yet further research is needed to better understand this phenomenon.

ACKNOWLEDGEMENTS

I thank James V. Remsen Jr., David Moyer, Ximena Nelson and an anonymous reviewer for helpful comments on the manuscript. I also thank Laura Azzani for useful discussion, Shera Moyer for commenting on an early draft, Jim Briskie for the use of recording equipment, Nyil Khwaja for his Kaikoura rifleman recordings and Neil Robertson for sharing rock wren footage used for behavioural comparison.

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Keywords rock wren; *Xenicus gilviventris*; rifleman; ultrasonic harmonics; prey-flushing behaviour