Notornis, 2012, Vol. 59: 97-104
0029-4470

Sexual differences in vocalisations and playback-response behaviour of the Vanuatu petrel (*Pterodroma occulta*)

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Abstract Sexual differences in vocalisations of the Vanuatu petrel (*Pterodroma occulta*) are described. Qualitative differences in burrow calls could be used to sex adults with 63-100% accuracy in listening experiments. Males sounded "clear" and females sounded "hoarse". Higher accuracy is possible with the aid of spectrograms. Playback experiments demonstrated a male-bias in responses of incubating Vanuatu petrels to "war-whooping" and flight calls. Acoustic methods have practical and ethical advantages over handling breeding petrels and further studies of the vocal behaviour of gadfly-petrels are encouraged.

Totterman, S.L. 2012. Sexual differences in vocalisations and playback-response behaviour of the Vanuatu petrel (*Pterodroma occulta*). *Notornis 59(3&4): 97-104.*

Keywords Vanuatu petrel; *Pterodroma occulta*; vocalisations

INTRODUCTION

Most petrels (Procellariidae, Hydrobatidae and Pelecanoididae) are nocturnal at their breeding colonies and vocalisations are the primary channel for communication in the dark (Bretagnolle 1996). Calls are important in courtship, pair formation and in agonistic contexts.

Gadfly-petrels (*Pterodroma*) use aerial calling intensively at their colonies. These aerial callers are thought to be mainly unpaired petrels engaged in courtship (Bretagnolle 1996). Brooding petrels are generally silent except when disturbed and will actively defend their burrows against intruders of their own and other species (Warham 1990).

Larger gadfly-petrel species will also respond to human calls and call back when in flight, on the surface, and from within burrows (Warham 1988, Tennyson & Taylor 1990). "War-whooping" has been used in luring flying petrels to land and in finding burrows (Tennyson & Taylor 1990).

If acoustics are the primary channel for communication then calls should contain information about species, sexual and even individual identity (Bretagnolle 1996). Distinct male and female calls have been used for sexing petrels in the field (e.g., Bourgeois *et al*. 2007; Bretagnolle & Thibault 1995; Genevois & Bretagnolle 1995; Lo Valvo 2001). Although vocal dimorphism has been noted in the flight calls of several gadfly-petrel species (Bretagnolle 1995; Bretagnolle & Attié 1991; Grant *et al*. 1983; Simons 1985; Tomkins & Milne 1991), it has been difficult to catch and identify the sex of calling individuals. Quantitative studies of gadfly-petrel ground calls are almost unknown, except for McKown (2008), who reported sexual differences in

Received 10 Jan 2012; accepted 23 Jul 2012
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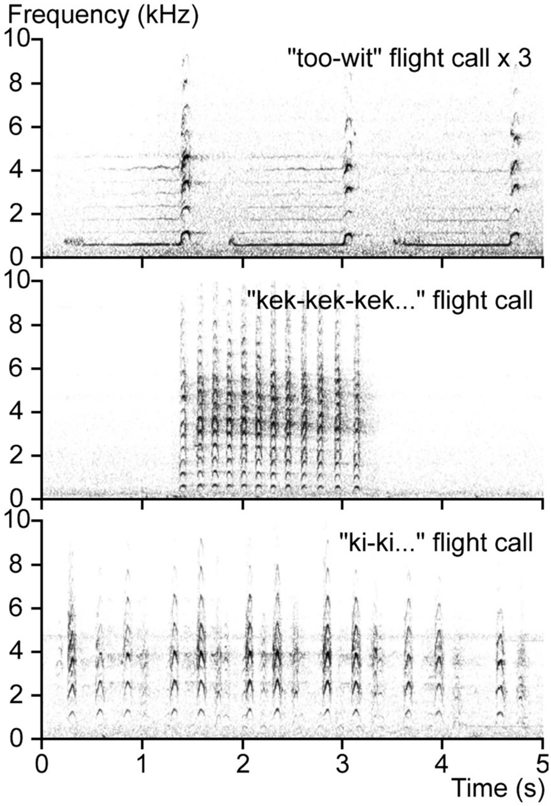

Fig. 1. Spectrograms of Vanuatu petrel flight calls used for playback.

burrow call frequency for the Juan Fernandez petrel (*Pterodroma externa*).

This paper describes sexual differences in the calls and playback-response behaviour of the Vanuatu petrel (*Pterodroma occulta*). The study focussed on burrow calls because petrels in burrows can easily be caught, marked and samples of blood or feathers collected for molecular analysis. The advantages and applications of acoustic methods in field studies of breeding petrels are discussed.

METHODS

Study site and field methods

Vanuatu petrels were studied in Mar 2011 at Mount Suretamatai (13° 48′S, 167° 29′ E) on Vanua Lava I, northern Vanuatu. Mount Suretamatai is the only known breeding site for the Vanuatu Petrel (Totterman 2009). Collared petrels (*Pterodroma brevipes*) have also been observed on Mount Suretamatai, but no nests have been found there to date (Tennyson *et al*. 2012).

The breeding biology of the Vanuatu petrel has not yet been studied. Knowledge of the breeding season is incomplete and the breeding population size has not been estimated. All breeding Vanuatu petrels found in Mar 2011 were incubating. Examination of 22 eggs, including 4 destructive examinations of egg development, indicated that Vanuatu petrels had laid around the end of Feb.

There were 2 stages in the field study: the 1st, from 5-10 Mar 2011, focussed on finding Vanuatu petrel nests and the 2nd, from 13-18 and 22-26 Mar 2011, focussed on nest monitoring and recording burrow calls. In stage 2, I inspected burrows on 9 days and recorded burrow calls on 7 nights.

Burrow searches employed “war-whooping” (Tennyson & Taylor 1990) at night to elicit call responses from burrow-holding petrels. Sixteen active burrows, where a Vanuatu petrel was incubating, were found in stage 1 and 2 additional nests were processed in stage 2. Each active burrow was numbered and marked with a flagging tape.

In stage 1, each breeding Vanuatu petrel was banded with a New Zealand Department of Conservation size Y band and marked with a white spot painted on the crown. In stage 2, each newly processed Vanuatu petrel painted had 2 white spots painted on the crown.

Samples for subsequent molecular analysis were collected from every Vanuatu petrel processed. Blood (*ca.* 1.0 ml) was taken from 13 breeding Vanuatu petrels, drawn from veins in the webs of the feet and preserved in lysis buffer (Seutin *et al.* 1991). Breast feathers were sampled from another 13 breeding petrels in lieu of blood.

Incubation changeover was confirmed when the burrow occupant was removed and found to have no band on its leg and no white spot on the crown. One changeover was confirmed in stage 1 of the study and 8 changeovers were confirmed in stage 2.

Calls were recorded with a Sony PCM-M10 digital recorder (16-bit, 44.1 kHz, uncompressed). The omnidirectional stereo microphones of the Sony PCM-M10 were adequate at close distances. To elicit call responses from Vanuatu petrels in burrows I used “war-whooping” and playback of flight calls that I had recorded in 2009. Three flight calls were played back through a small 12 V computer speaker in order: 1) “*too-wit*”; 2) “*kek-kek-kek*…”; and 3) a higher-pitched “*ki-ki*…” call (Fig. 1). Each call was played back repeatedly for 1 minute. I also played back burrow calls on occasion.

Calls were not used to sex Vanuatu petrels. Instead, responses were matched to individuals and then later to molecular tests of gender. The identity of callers could usually be established by simultaneous observation of marks or was known from regular burrow inspections. A fence of twigs was planted across the burrow entrance and if the fence was intact then the occupant had not left the burrow since the last inspection. Whenever

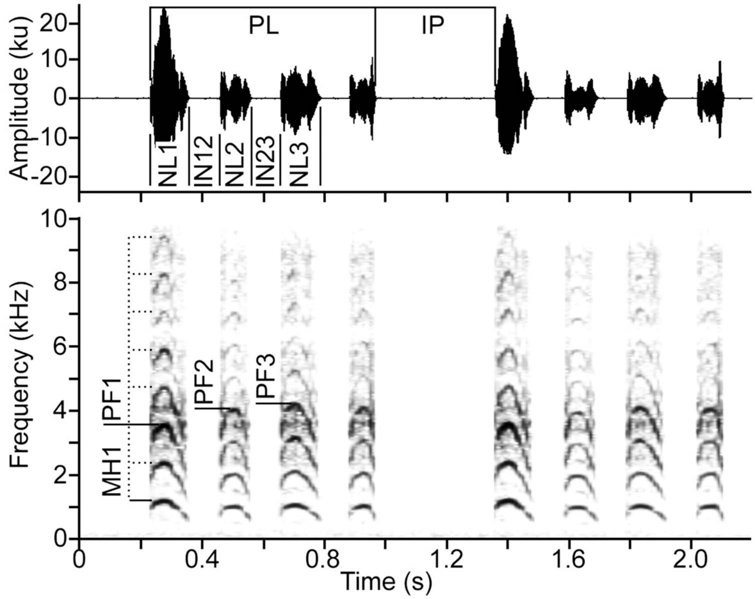

Fig. 2. Waveform (top) and spectrogram (bottom) of 2 phrases of an adult male Vanuatu petrel burrow showing the call properties examined: note lengths (NL1, 2, 3), note intervals (IN12, 23), phrase length (PL), inter-phrase spacing (IP), peak frequencies (PF1, 2, 3 = darkest part of the spectrogram) and note 1 mean harmonic interval (MH1 = mean of all clear overtones on note 1). These measurements were repeated on every phrase.

the occupant was not confidently identified, those recordings and playback-response results were excluded from the analyses.

Molecular tests of sex

The sex of all Vanuatu petrels in this study was determined by molecular tests, which were assumed to be 100% accurate. Analysis of blood and feather samples was performed at Massey University, Palmerston North, New Zealand, using a polymerase chain reaction (PCR) method that exploits genetic markers on the CHD gene (Norris-Caneda & Elliott 1998).

I assumed strict heterosexual monogamy in breeding petrels (Warham 1990). The new occupant found in a breeding burrow after incubation changeover was assumed to be the partner of the previous bird. Molecular tests were performed for only 1 member of each pair and the opposite sex was assumed for the partner.

Acoustic analysis

"War-whooping" and call-playback often produced vigorous call responses from burrow-holding Vanuatu petrels. Their major burrow calls had a simple structure, consisting of 2-12 distinct phrases with 2-6 "*eh*" notes per phrase (Fig. 2). The 1st note in each phrase was usually emphasised. Phrases appeared similar within calls and individuals did not appear to modify their calls when responding to different stimuli. On 1 occasion I was fortunate to record the calls of a breeding pair together in a burrow and from that point on recognised 2 different call types: "clear" and "hoarse".

Burrow-holding Vanuatu petrels often responded immediately during playback or "war whooping". I did not have a separate audio player and had to stop the playback first and disconnect the audio output to the speaker before recording a response. Most call recordings were incomplete as a result, and the burrow call analysis examined phrases within calls (McKown 2008). Some individuals did not call with greater than 3 notes per phrase and the analysis focussed on notes 1, 2 and 3.

Acoustic measurements were made using Raven Pro 1.3 (Cornell Laboratory of Ornithology 2008, Ithaca, http://www.birds.cornell.edu/raven/). Spectrogram settings were: window size = 1024 samples, window type = Hann, overlap = 50%. With these settings, 3 dB filter bandwidth was 62 Hz. Temporal properties measured from call waveforms were note lengths (1, 2, 3), note intervals (1-2, 2-3), phrase length (PL), inter-phrase spacing, and notes per second (Fig. 2). Frequency properties measured from spectrograms were peak frequencies (1, 2, 3), inter-quartile frequency ranges (1, 2, 3), and mean harmonic interval of note 1 (Fig. 2). Inter-quartile frequency range is a measure of bandwidth (Cortopassi 2006). Mean harmonic interval estimates fundamental frequency. One syntactic property was measured: the number of notes per phrase (NN). Notes per second is a derived quantity (= NN/PL). Some notes had no clear harmonic structure and fundamental frequency could not be measured. In a few calls, adjacent notes coalesced towards the middle or end of some phrases and these indistinct notes were discarded from the analysis.

Table 1. Properties of burrow calls for breeding Vanuatu petrels. Mean ± *SD* and range in brackets. Differences between male and female distributions tested with Kolmogorov-Smirnov 2-sample tests. *P*-value adjustment for multiple comparisons (*e.g.*, Rice 1989) is overly conservative when sample sizes are small and not recommended for exploratory studies (Moran 2003).

	Males $n = 5$	Females $n = 6$	K-S test	
			D	*P*
Note 1 peak (Hz)	2541 ± 395 [2173, 3173]	2639 ± 546 [2084, 3566]	0.33	0.82
Note 2 peak (Hz)	1739 ± 479 [1230, 2250]	1739 ± 758 [790, 2543]	0.33	0.82
Note 3 peak (Hz)	1756 ± 529 [1028, 2288]	1755 ± 815 [962, 2792]	0.33	0.82
Note 1 bandwidth (Hz)	1528 ± 230 [1253, 1882]	1880 ± 600 [1171, 2550]	0.50	0.36
Note 2 bandwidth (Hz)	1710 ± 349 [1398, 2272]	1742 ± 579 [885, 2523]	0.33	0.82
Note 3 bandwidth (Hz)	1622 ± 136 [1495, 1828]	1638 ± 422 [1023, 2101]	0.33	0.82
Note 1 fundamental (Hz)	1065 ± 53 [1020, 1153]	934 ± 137 [725, 1070]	0.67	0.11
Note 1 length (ms)	113 ± 24 [88, 149]	125 ± 20 [103, 151]	0.43	0.59
Note 2 length (ms)	102 ± 24 [73, 128]	104 ± 33 [65, 148]	0.33	0.82
Note 3 length (ms)	106 ± 34 [64, 157]	106 ± 46 [59, 186]	0.17	1.00
Note 1-2 interval (ms)	114 ± 34 [88, 174]	113 ± 40 [77, 186]	0.33	0.82
Note 2-3 interval (ms)	99 ± 25 [82, 141]	91 ± 34 [48, 145]	0.33	0.82
Phrase length (ms)	778 ± 156 [579, 986]	613 ± 187 [385, 943]	0.63	0.18
Phrase interval (ms)	577 ± 115 [484, 776]	575 ± 94 [497, 754]	0.30	0.90
Notes per phrase	4.6 ± 0.8 [3.2, 5.2]	3.4 ± 0.7 [2.5, 4.6]	0.63	0.22
Notes per second	6.0 ± 0.8 [5.1, 7.1]	5.7 ± 0.6 [4.8, 6.6]	0.30	0.90

Individual sample sizes were variable and for equal weighting of calls and individuals, I computed call means, individual means and finally grand means for each sex (Barbraud *et al*. 2000). Frequency distributions cannot be identified from small samples (Fowler *et al.* 1998) and normal distributions could not be assumed *a priori*. I applied distribution-free Kolmogorov-Smirnov 2 sample tests to evaluate statistical differences between male and female calls. The Kolmogorov-Smirnov statistic measures the distance between empirical distribution functions of 2 samples and is sensitive to differences in shape, location and scale. All statistics were computed in R version 2.13.0 (R Development Team 2011).

Listening experiments were conducted to assess the ability of people to sex recorded Vanuatu petrel burrow calls. I prepared 5 sets of 10 short recordings of identified adult petrels. Each set contained 5 different males, 5 different females and an interpreted reference recording of a pair calling in a burrow. The calls and sequence of individuals were randomised. These 5 sets of recordings were distributed between 2 experienced and 3 less-experienced observers. Less-experienced observers had not previously studied petrel calls. Each person was asked to classify the 10 unknown calls by comparison to the reference and by comparisons between calls. Calls were classified as type I (which was male), type II (female) or unsure. Each listening evaluation was performed without help from others.

Playback and "war-whooping" response analysis

Playback experiments were haphazard. When individual Vanuatu petrels were subject to playbacks on 2 nights I only used results from the 1st trial. However, responses on repeat nights were consistent. Excluded was 1 trial where a pair called from the burrow because the 1st response may stimulate the partner to call (Taoka *et al*. 1989a).

For each stimulus, sexual differences in frequency of response were evaluated with Fisher exact tests. The Fisher exact test is preferable to

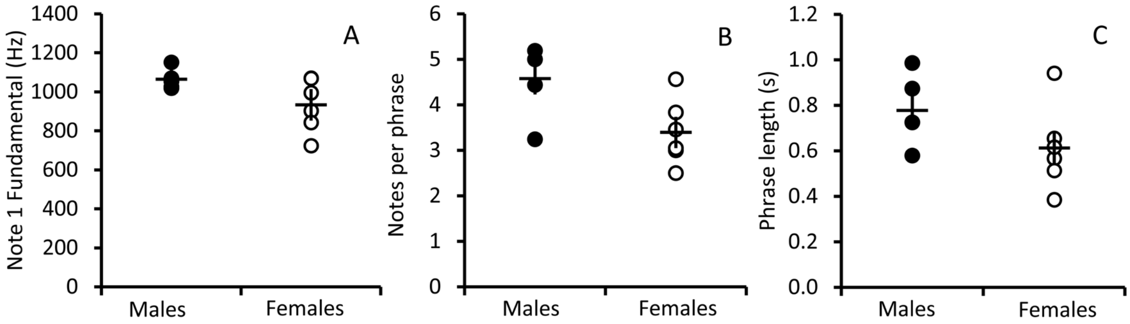

Fig 3. Sexual differences in burrow call properties of adult Vanuatu petrels. Males are plotted with solid circles (n =5), females with open circles (n = 6) and means are plotted as crosses. Males averaged higher in fundamental frequency and notes per phrase.

chi-square analysis for 2 x 2 contingency tables and small sample sizes (Zar 1999). Responses of individuals in widely-separated burrows can be assumed independent. Statistical comparisons of response rates between-stimuli were not attempted because responses may not be independent when different calls are played back one after the other (Taoka *et al.* 1989b).

RESULTS

A total of 58 Vanuatu petrel burrow calls and 145 phrases from 5 identified males and 6 identified females were examined. Individual sample sizes were 3-11 calls. With overlapping ranges, there was no obvious separation between sexes in burrow call measurements (Table 1). Sample sizes were small and Kolmogorov-Smirnov statistics suggested weak differences in fundamental frequency ($D = 0.67$, $n_1 = 5$, $n_2 = 6$, $P = 0.11$), phrase length ($D = 0.63$, $n_1 = 5$, $n_2 = 6$, $P = 0.18$) and notes per phrase ($D = 0.63$, $n_1 = 5$, $n_2 = 6$, $P = 0.22$). Mean fundamental frequency of male calls was 131 Hz higher than females (Fig. 3a). Males also averaged 1.2 more notes per phrase than females (Fig. 3b) and mean phrase length was 165 ms longer (Fig. 3c).

Despite only small measured differences, spectrograms showed qualitative differences between adult Vanuatu petrel male and female burrow calls (Fig. 4). Male calls sounded "clear" and showed strong harmonic structure on all notes. Females sounded "hoarse" and spectrograms typically showed weak or no harmonic structure. In listening experiments, people could identify the sex of Vanuatu petrel burrow call recordings with 63-100% accuracy overall (n = 5). Experienced observers were more successful (100% accuracy, n = 2) than others (63-89% accuracy, n = 3).

Sexual differences in responses of breeding Vanuatu petrels to war whooping and call playbacks were observed (Table 2). Males were significantly more likely to respond to "war whoops" (Fisher exact test, $P < 0.01$) and "*ki-ki*…" flight calls ($P < 0.01$) than were females. Both males and females responded to "*kek-kek-kek*…" flight calls.

DISCUSSION

Vocal behaviour of Vanuatu petrels

There have been few descriptions of burrow calls for gadfly-petrels. Hoarse, raspy or gruff female burrow calls have been reported for white-headed petrel (*P. lessonii*; Warham 1967), Juan Fernandez petrel (McKown 2008: "slightly hoarse") and now Vanuatu petrel. White-naped petrels (*P. cervicalis*) also gave dimorphic clear and hoarse burrow calls although recorded birds were not sexed (Alan Tennyson, *unpubl. data, pers. comm.*).

Vanuatu petrel burrow calls were similar in structure to those of Juan Fernandez petrels studied by McKown (2008). Sexual differences in notes per phrase and phrase length were consistent. However, McKown (2008) observed that note 1 fundamental frequency of female Juan Fernandez petrels was distinctly higher than males whereas Vanuatu petrels females were slightly lower-pitched than males. It is not unexpected that sexual identity can be expressed differently in different petrel species and even within the same genus (*e.g.* Taoka *et al*. 1989b).

During field work I learnt to recognise sexual differences in Vanuatu petrel burrow calls. In listening experiments, 5 other observers were mostly less accurate in sexing burrow call recordings although given brief call descriptions and no training. Not all petrel species show strong sexual signatures in their calls (*e.g.*, Taoka *et al*. 1989a) and human listeners may then fail to detect differences between sexes. Regardless of an observer's confidence in identifying calls by ear, field recordings should be acquired as evidence for acoustic sexing and for spectral analysis (Bourgeois *et al.* 2007). A sixth observer in the listening experiments voluntarily produced spectrograms

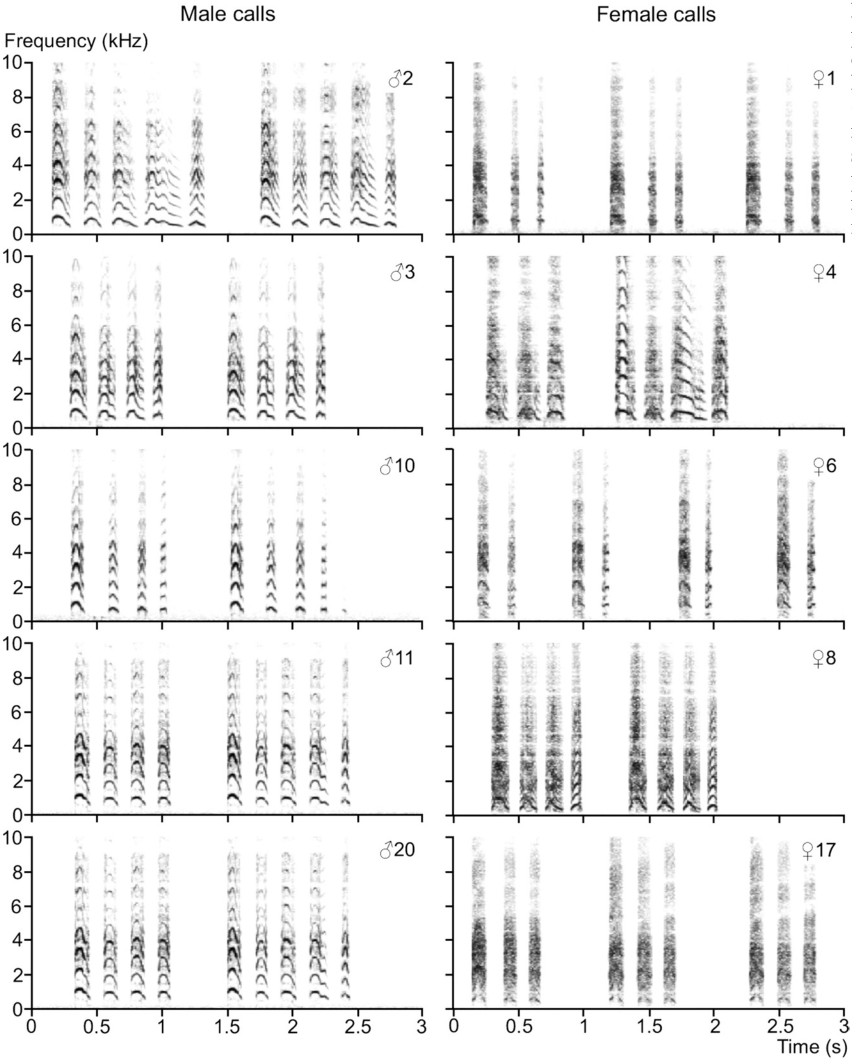

Fig. 4. Spectrograms comparing Vanuatu petrel burrow calls of 5 breeding males (on left) and 5 breeding females (on right). Nest numbers are indicated. Female 4 shows some harmonics and most people experienced difficulty in identifying the sex of this recording.

and achieved 100% accuracy in identifying the sex of Vanuatu petrel burrow calls.

Burrow-holding petrels are more likely to respond to same-sex burrow and flight calls (Bretagnolle 1989; Brooke 1978; Brooke 1998; McKown 2008; Taoka *et al*. 1989a; Taoka *et al*. 1989b). Assuming this generalisation holds, play-back results for Vanuatu petrels suggest that the particular "*kek-kek-kek…*" call played back (Fig. 1) was a female call. One of the females which landed during war-whooping also gave a "*kek-kek-kek…*" call on the surface but was not recorded. The final note of the "*too-wit*" call I played back has a high fundamental frequency like the "*ki-ki…*" call and these 2 are possibly male calls (Fig. 1). More playback experiments are required to confirm the sexual identity and function of Vanuatu petrel flight calls.

Male grey-faced petrels (*Pterodroma macroptera*) in burrows respond more strongly to "war-whooping" than do females (Tennyson and Taylor 1990). In flight, mostly female grey-faced petrels land in response to "war-whoops", contrary to Tennyson and Taylor (1990) who realised this sexual bias soon after publishing their paper (A. Tennyson & G. Taylor, *pers. comm.*). The behaviour of Vanuatu petrels was similar to grey-faced petrels including 3 females which landed during "war-whooping". I also agree with Tennyson and Taylor's (1990) observation that major calls given by burrow-holding gadfly petrels often serve an aggressive or a territorial function. During playback experiments, incubating Vanuatu petrels would often turn to face the burrow entrance and some moved towards the speaker. On 1 occasion a female Vanuatu petrel came

Table 2. Response frequencies (positive + and negative −) of breeding Vanuatu petrels to "war whooping" and call playbacks. Fisher exact tests computed for 2 × 2 contingency tables. The burrow call playback sample size was too small for testing. Average response rates calculated by dividing the number of individuals that responded by the number of individuals tested. An average response rate of 1.00 indicates that males/females always responded.

	"War-whooping"			"*too-wit*" call playback			"*kek-kek-kek*…" call playback			"*ki-ki*…" call playback			Same-sex burrow call playback		
	+	−	Rate	+	−	Rate	+	−	Rate	+	−	Rate	+	−	Rate
Males	6	1	0.9	4	1	0.8	4	1	0.8	5	0	1.0	2	0	1.0
Females	0	6	0.0	2	7	0.2	7	2	0.8	1	8	0.1	2	1	0.7
Odds ratio	Infinite			11.0			1.13			Infinite			N/A		
P	0.005			0.09			1.00			0.003			N/A		

outside of her burrow and attacked the speaker in response to same-sex burrow call playbacks.

Acoustic methods

Field researchers should beware of any sexual bias in gadfly-petrel responses to "war-whooping". When searching for grey-faced petrel and Vanuatu petrel burrows using "war-whooping", repeat visits are necessary because silent females can be overlooked. Black-winged petrels (*Pterodroma nigripennis*) behave differently however, and both sexes respond to "war-whooping" (G. Taylor, *pers. comm.*).

Some petrels (*e.g.,* storm-petrels and some larger shearwaters) are sensitive to handling, which can result in nest abandonment, broken pair bonds, burrow shifts, temporary nest neglect, delayed hatching and reduced hatching success (Carey 2009). Three of 18 Vanuatu petrel nests (16%) in this study were abandoned after the incubating bird was handled. Imber (1971) reported that 5-10% of incubating grey-faced petrels deserted the nest after handling. O'Dwyer *et al.* (2006) reported 9 failures (egg broken or desertion) in 25 Gould's petrel (*Pterodroma leucoptera*) nests (36%) where incubating adults were handled every 7-10 days.

Playback-response methods can reduce disturbance to burrowing petrels, potential injury to the birds, accidental egg breakage and burrow damage. Sexing petrels from calls can be faster and easier than capturing and inspecting the birds. Breeding petrels in burrows can be sexed at any breeding stage, if they can be stimulated to call. Sex determination by cloacal inspection is effective mostly from around 3 weeks before laying to 4-5 weeks into incubation (Serventy 1956). Playback-response methods are also useful in determining burrow occupancy (*e.g.,* Ambagis 2004; Burger & Lawrence 2001) and in luring petrels out of burrows (*pers. obs.*).

There are some limitations to playback-response methods. Some individuals remain silent, at least on some visits (Ambagis 2004; Berrow 2000). Negative responses can be minimised when appropriate calls are played back (both male and female burrow calls are suggested). Secondly, playback methods in this study were applied exclusively to burrow-holding petrels. Birds on the surface and unpaired birds may respond with different calls or not at all (Tennyson and Taylor 1990), and their sex may remain indeterminate. Thirdly, possible age-dependent variation in calls should be investigated. Identifying the sex of Vanuatu petrels from burrow calls is therefore best applied to breeding adults.

The call behaviour of gadfly-petrels has been neglected and this is evident in the paucity of published studies. Most field workers stop at "war-whooping". Known-sex call recordings do not exist for most gadfly-petrel species. This is disappointing since calls are key to understanding the behaviour of nocturnally-active breeding petrels (Bretagnolle 1996). Hopefully this paper will encourage more researchers to record and investigate gadfly-petrel calls and to develop useful applications for the vocal behaviour of petrels.

ACKNOWLEDGMENTS

Alan Tennyson and Colin Miskelly (Museum of New Zealand Te Papa Tongarewa) volunteered expert field skills in getting the first stage of the field study underway. My adoptive family in Lalngetak village, Vanua Lava I, provided essential field support. Meriam happily looked after us on the coast. Manman was our lead guide. Alex, John Ala and Ben were helpful assistants. From the Vanuatu Department of Environmental Protection and Conservation, Anaclet Philip was enthusiastic and helpful in the field. Michelle Fremaux-Houston at Massey University is thanked for the laboratory work. Bo Totterman provided helpful reviews of 2 draft manuscripts. I also thank Alan Tennyson, Colin Miskelly, Graeme Taylor, Paul Scofield, Bo Totterman and Les McPherson for listening to the burrow calls.

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