

## Sexual and individual differences in wedge-tailed shearwater (*Puffinus pacificus*) burrow calls and vocal recognition

STEPHEN L. TOTTERMAN  
179 Reedy Creek Road, Empire Vale, NSW 2478, Australia

**Abstract** Calls and playback-response behaviour of breeding wedge-tailed shearwaters (*Puffinus pacificus*) were studied at Muttonbird Island, Coffs Harbour, New South Wales, Australia. Burrow calls were recorded from 45 females and 60 males. Male calls averaged higher in fundamental frequency and longer in note lengths than female calls, although ranges overlapped. Playback experiments demonstrated sexual recognition, with incubating females mostly responding to female playbacks. Males responded to both female and male calls. Ratios of between- to within-subject variation suggested that individual vocal signatures could be encoded in timing and some frequency parameters. Playback experiments demonstrated a “dear enemy” effect, where shearwaters in burrows were more responsive to stranger rather than neighbour calls. Wedge-tailed shearwater calls are informative and further studies are encouraged for other southern hemisphere breeding shearwaters.

Totterman, S.L. 2014. Sexual and individual differences in wedge-tailed shearwater (*Puffinus pacificus*) burrow calls and vocal recognition. *Notornis* 61 (3): 121-130.

**Keywords** dear enemy; neighbour-stranger discrimination; sex recognition; vocalisations; wedge-tailed shearwater

### INTRODUCTION

Most petrels (Procellariidae, Hydrobatidae and Pelecanoididae) are nocturnal at their breeding colonies and primarily use vocalisations to communicate in the dark (Shallenberger 1973; Bretagnolle 1996). Calls are important in courtship, pair formation and territorial interactions. Calls should then contain information about species, sexual and individual identity.

Nine *Puffinus* shearwaters studied have a single major call, used for both courtship and in territorial contacts and mostly given from the ground (Bretagnolle 1996). Major calls of males are typically

clearer than female calls, higher pitched and have longer note durations (e.g., Brooke 1978; James & Robertson 1985; Brooke 1988; Bretagnolle *et al.* 2000; Bourgeois *et al.* 2007). Individual signatures are usually encoded in timing parameters (e.g., Jouventin & Aubin 2000; Cure *et al.* 2009).

Playback experiments have been used to demonstrate both sexual and individual vocal recognition in petrels. Incubating *Puffinus* shearwaters typically respond only to same-sex calls, but sometimes will respond to their mates (e.g., Brooke 1978, 1988; Cure *et al.* 2009).

Experiments for individual recognition can be simplified by testing 2 non-equivalent categories (e.g., neighbour versus stranger). The “dear enemy” effect is when territorial animals respond more

frequently and with more aggression to displays of strangers than towards territorial neighbours (reviewed by Temeles 1994). Mackin (2005) reported that male Audubon's shearwaters (*P. lherminieri*) defending nest sites gave extended call responses towards playbacks of unfamiliar ("stranger") males versus playbacks of neighbours. Applying the relative threat hypothesis, prospecting birds ("real enemies") present a greater threat of burrow usurpation than established neighbours ("dear enemies"), which have little or nothing to gain by taking over another bird's burrow (Mackin 2005).

Sexual differences in wedge-tailed shearwater calls have, based on my literature searches, not previously been described. Gross *et al.* (1963) commented on between-individual variations in pitch, although they did not identify the gender of calling birds. A major study of vocal communication in wedge-tailed shearwaters by Shallenberger (1973) overlooked differences in female and male calls. Bretagnolle (1996) noted sexual differences in wedge-tailed shearwater calls as a *pers. obs.* and without any description.

This paper describes sexual and individual differences in burrow calls of breeding wedge-tailed shearwaters. Playback experiments were used to demonstrate sex and neighbour-stranger vocal recognition.

## METHODS

### Study site and general field methods

Breeding wedge-tailed shearwaters were studied from 9 December 2012 to 6 January 2013 on Muttonbird Island (13° 48' S, 167° 29' E), New South Wales, Australia. This 8 ha island supports the second largest colony of wedge-tailed shearwaters in NSW (after Broughton Island; Van Gessel 1978). Floyd & Swanson (1983) estimated 12,400 (95% c.i. 6,300–18,500) breeding pairs on Muttonbird Island in 1979–1980. During my field work, I encountered only wedge-tailed shearwaters on the ground. I heard single short-tailed shearwaters (*P. tenuirostris*) calling in flight on 9 nights and single black-winged petrels (*Pterodroma nigripennis*) on 2 nights. A few short-tailed shearwaters did breed on the island in the 1990s, but apparently failed to colonise (Lane 1997). Prospecting black-winged petrels were found in burrows in the 1970s although they did not breed (Holmes 1975). Based on these observations, Muttonbird Island was a single-species petrel colony in summer 2012–2013.

Wedge-tailed shearwaters on Muttonbird Island lay in the last week of November and first week of December. Hatching is in the last 2 weeks of January and young fledge at the end of April and in the first week of May (Swanson & Merritt 1974). This study was performed during the incubation phase, when

the majority of wedge-tailed shearwater nests are continuously attended by an adult (Garkaklis *et al.* 1998). Field work was at night, when wedge-tailed shearwaters are vocally active (Shallenberger 1973; Burger & Lawrence 1990).

Most study burrows were located along the southern and northern edges of the colony, away from a public walking path across the island. Fifty non-adjacent burrows were selected and each was marked with a plastic tent peg and reflective numbered marker. Some nests failed during the study and 19 burrows were added near the end of the study to increase sample sizes.

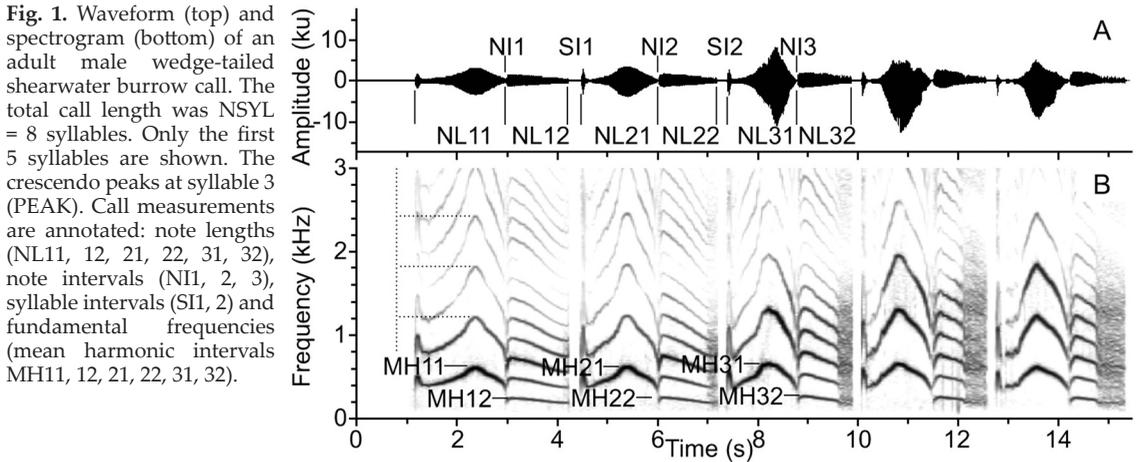
All study birds were marked to enable identification in subsequent playback experiments and recording. The first bird processed from each burrow was marked with a single white spot of paint on the forehead and a few millimetres were clipped from the left, outermost tail feather (non-permanent marking). The second bird was marked with 2 spots and clipped on the right side of the tail. Subjects were thus uniquely identified by their burrow number and markings.

Burrow calls were recorded during burrow searching and playback experiments. A Sony PCM-M10 digital recorder (16-bit, 22.05 kHz, uncompressed digital audio) and Sennheiser ME-64 directional microphone were used. To elicit call responses I played wedge-tailed shearwater calls from a MP3 player through a battery-powered speaker. To minimise disturbance, I approached burrows with a low intensity headlamp setting (3 lumens), avoided illuminating the burrow entrance and switched off the headlamp during playbacks and recording.

### Gender identification

Correct assignment of gender is critical for studies of sexual differences. Wedge-tailed shearwaters were sexed in the field by cloaca size, where breeding female petrels show an enlarged cloaca associated with the passage of the large egg (Serventy 1956). These preliminary results were useful for classifying recordings for playback experiments. However, cloacal sexing for petrels is not error-free (Roberts *et al.* 1974; Boersma & Davies 1987; O'Dwyer *et al.* 2006) and molecular tests were used for final results.

A few breast feathers for molecular analyses were sampled from every study bird. Sex was determined by polymerase chain reaction (PCR) methods sensitive to markers on the CHD gene. The primary laboratory was at the University of Queensland, where the primer pair P2/P3 was used, followed by restriction enzyme digestion with HaeIII (Norris-Caneda & Elliott 1998). A duplicate verification sub-sample was analysed at another laboratory, Gribbles Veterinary Australia, Clayton



**Fig. 1.** Waveform (top) and spectrogram (bottom) of an adult male wedge-tailed shearwater burrow call. The total call length was NSYL = 8 syllables. Only the first 5 syllables are shown. The crescendo peaks at syllable 3 (PEAK). Call measurements are annotated: note lengths (NL11, 12, 21, 22, 31, 32), note intervals (NI1, 2, 3), syllable intervals (SI1, 2) and fundamental frequencies (mean harmonic intervals MH11, 12, 21, 22, 31, 32).

and with primers P2/P8 (Griffiths *et al.* 1998). Results were also checked for heterosexual social monogamy within breeding pairs (Warham 1990). There were 2 PCR amplification failures, which fortunately occurred in breeding pairs where both birds were sampled. The complementary sex was assumed for each of these missing results.

Having marked all study burrows, marked all study birds and identified the birds in all recordings used for analyses and playbacks, molecular results could be matched to every single bird and every single recording.

### Acoustic analysis

Playbacks of same-sex calls to incubating wedge-tailed shearwaters would often result in vigorous responses ("defence calls" in Shallenberger 1973). These major calls consist of repeated 2-note units ("syllables"; following the terminology of Thompson *et al.* 1994) that sound like "ooh-ah" or "kooh-ah" (Fig. 1). Exhalant note 1s are louder, higher-pitched and longer than inhalant note 2s. Successive syllables increase in volume and pitch to a peak and then decline towards the end of a call. Late syllables and especially inhalant notes can be noisy (Shallenberger 1973).

The acoustic analyses focussed on syllables 1-3. Measurements were made in Raven Pro 1.3 (Cornell Laboratory of Ornithology 2008, Ithaca, <http://www.birds.cornell.edu/raven/>). Temporal-domain measurements from call waveforms were note lengths (NL), note intervals (NI) and syllable intervals (SI) (Fig. 1a). Frequency-domain measurements from spectrograms were peak mean harmonic intervals of each note (MH) (Fig. 1b). Mean harmonic interval estimates fundamental frequency. The spectrogram 3 dB filter bandwidth was 16 Hz. Two syntactic features were measured: the total number of syllables per call (NSYL) and the syllable number at the crescendo peak (PEAK).

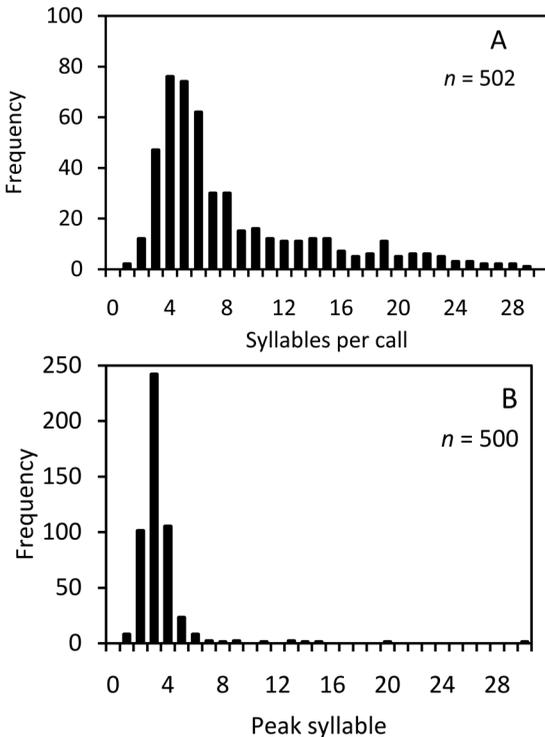
### Sex recognition playbacks

For the sex vocal recognition experiment, there were 2 playback tests: (1) stranger female, and (2) stranger male. These were performed at each study burrow on different nights. Three different calls were played in each test and calls were rotated between burrows. The playback sample contained 13 female and 20 male recordings. Sexual identity of these recordings was later verified by molecular results. The speaker was placed on the ground, facing the burrow entrance and the sound volume was approximately matched by ear to the intensity of natural calls. The presence/absence of a call response to any of the 3 playbacks was noted. The burrow occupant was then captured and identified.

### Neighbour-stranger recognition playbacks

For the neighbour-stranger vocal recognition experiment, I counted the number of shearwaters calling before and after playbacks. There were 4 playback tests: (1) neighbour-male (= study burrow male), (2) stranger male, (3) neighbour female (= study burrow female), and (4) stranger female. The experiment was limited to sites where both the female and male in a study burrow had been recorded. Different tests were performed on different nights and stranger calls were rotated between sites. The speaker was held at chest height and the broadcast volume was about twice the natural volume. I avoided testing in windy conditions, where the wind can interfere with playbacks and hearing.

Calling locations (*i.e.*, individual shearwaters) were counted rather than the total number of calls, which can include repeated calls from the same birds. No distance limit was applied when counting. Spontaneous calling varied through the night and I counted background calls for 2 minutes before playback. I then played a short recording, edited to 10-16 s duration, twice and counted response calls for 2 minutes inclusive of the playback



**Fig. 2.** Distributions of syllables per call (A) and crescendo peak syllable (B) for wedge-tailed shearwaters, sexes combined. Both histograms are truncated at 30 syllables. Maximum syllables per call was 93 and the maximum peak syllable was 38. Single syllable calls cannot crescendo ( $n = 2$ ).

duration. I also noted if the response included the study burrow. Molecular results revealed that the playback sample contained 31 female and 32 male recordings. Playback results could then be re-assigned to the correct groups where field sexing results were in error.

Response counts were adjusted by subtracting the study burrow response. This accounts for differences between occupied and unoccupied burrows (which generally were failed nests). Secondly, study burrow occupants may respond to mate calls (e.g., Brooke 1978, Cure *et al.* 2009) and playbacks of their own calls (Shallenberger 1973), which is not neighbour-stranger discrimination.

### Statistical analyses

Statistical computations were performed with R version 3.0.1 (R Development Core Team 2013). Acoustic measurements were first screened for outliers using boxplots by subject. Any non-representative calls were removed (e.g., short, 3-syllable calls with weakly expressed terminal notes). Sexual differences were evaluated using 2-sample *t*-tests. To remove pseudo-replication (multiple calls per subject), subject means were used.

These were computed by taking the mean of calls within-nights and then the mean of nights within-subjects. Boxplots by sex were used to evaluate homogeneity of variance and quantile-quantile plots to evaluate normality (Zuur *et al.* 2010).

Individual signatures were investigated using coefficient of variation (CV) ratios and one-way ANOVAs (e.g., Jouventin & Aubin 2000). The CV-ratio of variation between-subjects (calculated from subject means) to mean variation within-subjects (calculated from calls) provides a measure of effect size. The one-way ANOVA *F*-ratio similarly measures variance between- to variance within-groups, however mean squares are influenced by sample sizes. The *F*-ratio was used for statistical testing. ANOVA assumptions were checked using linear model diagnostic plots.

The neighbour-stranger experiment dataset was examined using analysis of covariance with linear mixed-effects models for repeated measures in the R package lme4 version 0.99999911-5 (Bates *et al.* 2013). Data evaluation included conditional boxplots to identify potential outliers and evaluate homogeneity of variance, scatterplots to explore relationships between response and predictor variables and coplots to explore interactions (Zuur *et al.* 2010). Models of varying complexity were compared using Akaike's information criterion (AIC; Akaike 1974). Model fit and assumptions were checked using linear model diagnostic plots.

## RESULTS

### Sexual differences in calls and sex recognition

A total of 502 burrow calls were recorded from 45 female and 60 male shearwaters. The most frequent number of syllables was 4 and the crescendo peaked most frequently in syllable 3 (Fig. 2). Acoustic analyses therefore focussed on syllables 1-3. There were 471 good quality recordings with 3 or more syllables. Male calls averaged significantly higher in frequencies and longer in note lengths than female calls ( $t \geq 6.5$ ,  $df = 103$ ,  $P < 0.001$ ; Table 1), although ranges overlapped (Fig. 3). Mean differences for exhalant notes were 86-118 Hz and 0.25-0.45 s. Mean differences for inhalant notes were 31-38 Hz and 0.30-0.36 s.

To test sex vocal recognition, female calls were played back at 42 active study burrows in the first pass and male calls at 35 burrows in the second (7 nests failed in between). All males responded to male calls, versus only 11% of females responded to male calls (Fisher exact test,  $P < 0.001$ ; Table 2). Both sexes responded to female playbacks.

### Individual differences in calls and neighbour-stranger recognition

Variance computations require multiple calls per subject and were restricted to wedge-tailed

**Table 1.** Comparison between-sexes of wedge-tailed shearwater burrow call acoustic measurements (mean  $\pm$  SD and range). Mean differences assessed using *t*-tests (all  $df = 103$ ). Effect sizes are provided as mean differences with 95% confidence intervals (Nakagawa & Cuthill 2007). Acoustic measurements are defined in Fig. 1.

	Females <i>n</i> = 45	Males <i>n</i> = 60	Male–Female mean difference	
			95% c.i.	<i>t</i> , <i>P</i>
MH11 (Hz)	448 $\pm$ 34 [393, 528]	534 $\pm$ 42 [459, 647]	86 [71, 101]	11.3, < 0.001
MH12 (Hz)	201 $\pm$ 13 [175, 224]	232 $\pm$ 17 [201, 271]	31 [25, 37]	10.2, < 0.001
MH21 (Hz)	505 $\pm$ 49 [441, 629]	623 $\pm$ 52 [528, 735]	118 [98, 137]	11.8, < 0.001
MH22 (Hz)	211 $\pm$ 11 [182, 236]	249 $\pm$ 16 [218, 284]	38 [32, 43]	13.7, < 0.001
MH31 (Hz)	550 $\pm$ 62 [456, 703]	668 $\pm$ 55 [543, 778]	118 [95, 141]	10.3, < 0.001
MH32 (Hz)	212 $\pm$ 15 [167, 244]	248 $\pm$ 16 [200, 286]	36 [30, 42]	11.7, < 0.001
NL11 (s)	1.79 $\pm$ 0.28 [1.21, 2.35]	2.23 $\pm$ 0.30 [1.62, 2.94]	0.45 [0.33, 0.56]	7.8, < 0.001
NL12 (s)	0.92 $\pm$ 0.21 [0.37, 1.45]	1.27 $\pm$ 0.22 [0.71, 1.73]	0.36 [0.27, 0.44]	8.3, < 0.001
NL21 (s)	1.34 $\pm$ 0.20 [0.99, 1.83]	1.59 $\pm$ 0.19 [1.12, 2.05]	0.25 [0.17, 0.33]	6.5, < 0.001
NL22 (s)	0.82 $\pm$ 0.18 [0.31, 1.28]	1.12 $\pm$ 0.19 [0.65, 1.55]	0.30 [0.23, 0.37]	8.2, < 0.001
NL31 (s)	1.27 $\pm$ 0.22 [0.87, 1.76]	1.56 $\pm$ 0.23 [1.19, 2.16]	0.30 [0.21, 0.39]	6.8, < 0.001
NL32 (s)	0.85 $\pm$ 0.20 [0.29, 1.27]	1.15 $\pm$ 0.18 [0.71, 1.55]	0.30 [0.23, 0.37]	8.1, < 0.001
NI1 (s)	0.04 $\pm$ 0.03 [0.01, 0.16]	0.03 $\pm$ 0.03 [0.01, 0.13]	-0.01 [-0.02, 0.00]	-1.3, 0.20
NI2 (s)	0.04 $\pm$ 0.03 [0.01, 0.18]	0.03 $\pm$ 0.03 [0.01, 0.11]	-0.01 [-0.02, 0.01]	-1.0, 0.32
NI3 (s)	0.05 $\pm$ 0.04 [0.01, 0.23]	0.04 $\pm$ 0.03 [0.01, 0.15]	-0.01 [-0.02, 0.00]	-1.6, 0.11
SI1 (s)	0.16 $\pm$ 0.04 [0.07, 0.25]	0.17 $\pm$ 0.04 [0.06, 0.27]	0.01 [-0.01, 0.03]	1.3, 0.20
SI2 (s)	0.14 $\pm$ 0.04 [0.06, 0.24]	0.15 $\pm$ 0.03 [0.10, 0.23]	0.01 [0.00, 0.03]	1.8, 0.07
NSYL	10.1 $\pm$ 6 [3, 36]	9.1 $\pm$ 5.4 [3, 27]	-1.0 [-3, 1]	-0.9, 0.36
PEAK	3.6 $\pm$ 0.8 [2, 6]	3.4 $\pm$ 1.5 [2, 11]	-0.2 [-1, 0]	-0.8, 0.45

shearwaters recorded on at least 2 nights and with at least 2 calls per night. A total of 353 calls from 23 female and 34 male shearwaters were used. Log-transforms were applied to note intervals and the number of syllables to improve normality and homogeneity of variances for ANOVAs.

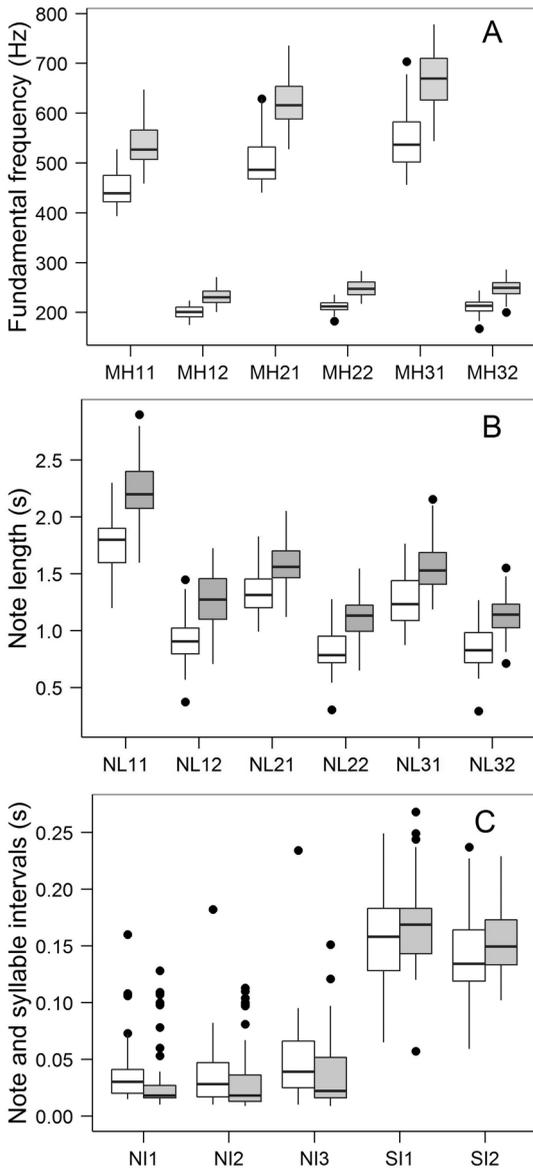
One-way ANOVAs indicated significant between-subject variation in all acoustic measurements for both females ( $F \geq 4.1$ ,  $df_1 = 22$ ,  $df_2 = 109$ ,  $P < 0.001$ ) and males ( $F \geq 3.0$ ,  $df_1 = 33$ ,  $df_2 = 187$ ,  $P < 0.001$ ; Table 3). There was a strong correlation between female and male CV-ratios ( $r_s = 0.70$ ,  $n = 19$ ,  $P < 0.001$ ). Large CV-ratios  $\gg 1$  suggest reliable between-subject differences. The highest CV-ratios were for syllable intervals (maximum 3.0), inhalant note lengths (maximum 3.1) and some inhalant note frequencies (maximum 2.4).

Neighbour-stranger playbacks were performed at 30 study burrow sites, with  $30 \times 4 = 120$  tests. These tests were performed over 6 consecutive full-moon nights, with moonrise occurring later on successive nights (1917 h on the first night, 2219 h on the last). Supplementary observations did not indicate

any effect of moonlight (some early evening tests occurred before moonrise), cloud cover, wind and day on wedge-tailed shearwater activity patterns during the course of the experiment, except that the number of flying birds increased with wind speed. Meteorological variables and day were therefore not included in the statistical model. More noticeable were the nightly peaks in calling after dusk and just before dawn as shearwaters arrived and departed the colony.

There was a strong correlation between playback response counts and background counts ( $r = 0.71$ ,  $t = 10.92$ ,  $df = 118$ ,  $P < 0.001$ ), with some influence from playback sex (female/male) and playback identity (neighbour/stranger). A few burrow-sites had consistently higher counts than others and linear mixed models were used to account for within-site correlations (*i.e.*, repeated measures).

The maximal response count model included fixed-effect predictors for playback sex, playback identity, background counts and all 2-way and 3-way interactions (8 fixed effects in all). The burrow-site effect was modelled using correlated



**Fig. 3.** Sexual differences between female (open boxes,  $n = 45$ ) and male (filled boxes,  $n = 60$ ) wedge-tailed shearwater burrow calls in frequency (A), duration (B) and timing (C). Acoustic measurements are defined in Fig. 1. Boxes show the medians, first and third quartiles. Whiskers are 1.5 times the inter-quartile range. Data outside the whiskers are shown as dots.

random intercepts and slopes. Model simplification eliminated 4 fixed effects with small  $t$ -statistics and random slopes for the site effect. Estimates were stable for various candidate models (Table 4). The minimum AIC model was:

$$R = 3.0 + 0.8(B) + 0.3(B \times S) - 0.2(B \times M) + Si(0, 0.8^2) + Re(0, 1.5^2)$$

**Table 2.** Response frequencies (positive + and negative -) of incubating wedge-tailed shearwaters to call playbacks.  $P$ -values from Fisher exact tests.

Burrow occupants	Female playback		Male playback	
	+	-	+	-
Females	28	2	2	16
Males	12	0	17	0
	$P = 1$		$P < 0.001$	

where  $R$  is response,  $B$  is background count,  $S$  is stranger (0 if neighbour),  $M$  is male playback (0 if female),  $S_i$  is site random intercept ( $SD = 0.8$ ) and  $Re$  is residual variance ( $SD = 1.5$ ). Multiplication ( $\times$ ) represents interactions. Although responses were counts, the linear model with normal errors was a satisfactory fit. The model is plotted in Fig. 4.

**DISCUSSION**

This study provides the first quantitative description of sexual differences in wedge-tailed shearwater calls. Playback experiments were used to show that incubating birds are responsive to sexual and individual signatures in call playbacks.

**Sexual differences in calls**

In 25 field nights, I did not learn to recognise differences between male and female wedge-tailed shearwater burrow calls. Acoustic analysis revealed that male calls averaged up to 118 Hz higher than females in fundamental frequency and 0.45 s longer in note length. It is difficult for human listeners to detect these small effects during a crescendo.

Wedge-tailed shearwaters apparently do not have distinct female and male calls, unlike Manx shearwater (*P. puffinus*; Brooke 1978), Yelkouan shearwater (*P. yelkouan*; Bourgeois *et al.* 2007), Audubon’s shearwater (*P. herminieri*; Bretagnolle *et al.* 2000) and little shearwater (*P. assimilis*; James & Robertson 1985). Wedge-tailed shearwater calls were more similar to great shearwater (*P. gravis*), for which Brooke (1988) reported that male calls had higher mean note 1 frequencies and longer mean syllables than females, with overlapping ranges. Great shearwater calls also crescendo in pairing and agonistic contexts. The larger southern-hemisphere breeding shearwaters form a distinct phylogenetic clade (Kuroda 1954; Wragg 1985; Austin 1996) and quantitative studies of vocal behaviour are required from other members of this group.

**Sex vocal recognition**

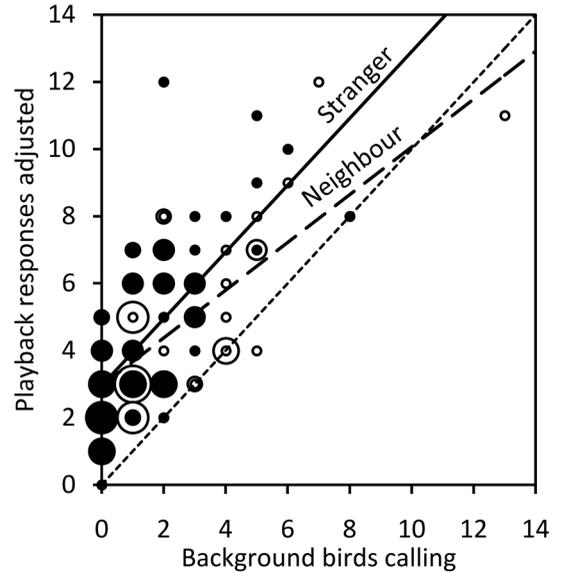
Incubating wedge-tailed shearwater females responded almost exclusively to female playbacks whereas males responded to both female and male calls. Female selectivity agreed with results for Manx shearwater (Brooke 1978), Yelkouan

**Table 3.** Between-subjects variation in wedge-tailed shearwater burrow calls measured using CV-ratios and tested using one-way ANOVAs. Log-transforms were applied to note intervals and number of syllables. All *F*-ratios were significant ( $P < 0.001$ ). Acoustic measurements are defined in Fig. 1.

	Females		Males	
	CV-ratio <i>n</i> = 23	<i>F</i> -ratio <i>df</i> = 22, 109	CV-ratio <i>n</i> = 34	<i>F</i> -ratio <i>df</i> = 33, 187
MH11 (Hz)	1.1	5.1	1.2	8.1
MH12 (Hz)	2.4	29.2	2.1	22.8
MH21 (Hz)	2.0	14.6	1.3	8.5
MH22 (Hz)	1.9	17.9	2.2	24.8
MH31 (Hz)	1.8	15.2	1.2	7.6
MH32 (Hz)	2.0	17.9	1.5	10.6
NL11 (s)	1.2	7.4	1.3	9.3
NL12 (s)	3.1	47.3	2.2	24.2
NL21 (s)	1.7	15.7	1.5	12.3
NL22 (s)	3.1	57.8	2.6	30.7
NL31 (s)	1.7	14.6	1.3	7.3
NL32 (s)	2.9	44.4	1.7	14.7
log(NI1)	1.7	8.9	1.2	13.0
log(NI2)	2.0	10.8	1.5	19.8
log(NI3)	1.9	13.3	1.6	21.5
SI1	2.6	23.2	1.9	26.8
SI2	3.0	41.7	2.2	27.0
log(NSYL)	0.9	5.9	1.4	7.0
PEAK	1.1	4.1	1.9	3.0

shearwater (Cure *et al.* 2009) and great shearwater (Brooke 1988). These responses to same-sex calls are likely defensive, to prevent usurpation of the burrow (Brooke 1978).

The 100% response rate for male wedge-tailed shearwaters towards stranger female playbacks was much higher than the 36% reported for Manx shearwater (Brooke 1978), 27% for Yelkouan shearwater (Cure *et al.* 2009), and 0% for great shearwater (Brooke 1988). Experiments were performed on incubating birds in all of these studies. Given the importance of vocalisations in pairing, it is unlikely that male wedge-tailed shearwaters fail to differentiate between female and male calls. Male responses to female playbacks could be territorial, as males are more vocal and more active than females in burrow defence (Shallenberger 1973). Alternatively, stranger female calls could result in a courtship response. For short-tailed shearwaters,



**Fig. 4.** Relationship between counts of wedge-tailed shearwaters responding to playbacks and counts of background calling preceding the playbacks ( $n = 120$  tests at 30 burrows). Open circles indicate neighbour (= study burrow) call playbacks and solid circles are stranger playbacks. Circle diameters are proportional to frequency (range: 1-6). The solid line shows the female and male average stranger playback response predicted by the minimum AIC model (conditional  $R^2 = 0.60$ ; Table 4). The dashed line shows the average predicted neighbour playback response. The dotted line indicates a 1:1 relationship. Removing the possible influential point (13, 11) did not change model results.

genetic analyses detected extra-pair paternity in 11% of 83 nests from 2 colonies (Austin & Parkin 1996). Further investigations are required to identify the motivation for wedge-tailed shearwater male responses to stranger females.

**Individual differences in calls**

Ratios of between- to within-subject CVs for wedge-tailed shearwater burrow call measurements were largest for syllable intervals (maximum 3.0), inhalant note lengths (maximum 3.1) and some inhalant note frequencies (maximum 2.4). These ratios are similar to 2.7 for syllable interval and 1.8 for inhalant length in Shallenberger (1973), even though he did not account for sexual differences and apparently did not match syllables by rank. He suggested that inhalant notes were more reliable because birds exercise less vocal control during inhalation. For Yelkouan shearwaters, Cure *et al.* (2009) reported large CV-ratios  $\geq 2$  for inhalant note duration (maximum 3.8), exhalant note duration (maximum 3.3), inhalant note second quartile frequency (maximum 2.4) and exhalant note third quartile frequency (maximum 2.3). For

**Table 4.** Six candidate linear mixed-effects models for wedge-tailed shearwater neighbour-stranger playback response counts: A = minimum AIC model; B = without sex effect; C = without neighbour-stranger effect; D = without sex and neighbour-stranger effects; E = maximal model including 4 additional fixed effects and 1 additional random effect which are not presented; F = null model with only a site effect. Fixed effect predictors are the intercept, background count (Bkg.), stranger playback (0 if neighbour) and male playback (0 if female). Multiplication ( $\times$ ) represents interactions. Site *SD* represents a random intercept for each study burrow site and Residual *SD* is unexplained residual variance. 95% confidence intervals were estimated by deviance profiling.  $\Delta$ AIC is computed by subtracting the minimum AIC. As a rule of thumb, models with  $\Delta$ AIC  $\leq 2$  have similar levels of support (Burnham & Anderson 2002). Marginal  $R^2_m$  (which considers fixed effects only) and conditional  $R^2_c$  (with both fixed and random effects) were calculated using the methods of Nakagawa & Schielzeth (2013).

	Intercept	Bkg.	Bkg. $\times$ Stranger	Bkg. $\times$ Male	Site <i>SD</i>	Residual <i>SD</i>	$R^2_m$	$R^2_c$	$\Delta$ AIC
A	3.0 [2.5, 3.5]	0.8 [0.6, 1.0]	0.3 [0.1, 0.5]	-0.2 [-0.4, -0.03]	0.8 [0.3, 1.3]	1.5 [1.3, 1.7]	0.48	0.60	0.0
B	3.0 [2.5, 3.5]	0.7 [0.5, 0.9]	0.3 [0.1, 0.5]	-	0.8 [0.3, 1.3]	1.5 [1.3, 1.8]	0.46	0.59	3.0
C	3.0 [2.5, 3.6]	0.9 [0.7, 1.1]	-	-0.2 [-0.5, -0.04]	0.8 [0.3, 1.3]	1.5 [1.3, 1.8]	0.45	0.58	5.1
D	3.1 [2.6, 3.6]	0.8 [0.6, 0.9]	-	-	0.8 [0.3, 1.3]	1.6 [1.4, 1.8]	0.43	0.56	8.4
E	3.0 [2.1, 3.8]	0.9 [0.6, 1.2]	0.2 [-0.3, 0.6]	-0.2 [-0.6, 0.2]	1.0 [0.5, 1.8]	1.5 [1.2, 1.7]	0.46	0.64	10.5
F	4.5 [3.9, 5.2]	-	-	-	1.6 [1.0, 2.2]	1.9 [1.7, 2.3]	-	0.39	74.6

male short-tailed shearwaters, Jouventin & Aubin (2000) reported large *CV*-ratios for exhalant note maximum amplitude frequency (2.2) and inhalant note duration (2.0). In all 3 of these shearwaters, large between-subject variation in burrow calls was found in both temporal and frequency parameters. High frequencies are strongly attenuated by the environment however, and background noise in petrel colonies can be high. Jouventin & Aubin (2000) showed that male short-tailed shearwaters in their burrows were sensitive to playback calls modified in the temporal domain and insensitive to modifications in the frequency domain. They explained that simple timing encoding of individual identity and repeated syllables for redundancy are adaptations for reliable communication of territorial messages.

### Neighbour-stranger recognition

Statistical modelling was used to interpret counts of wedge-tailed shearwaters responding to call playbacks. Useful predictor variables were background counts, followed by burrow-site, neighbour-stranger identity and sexual identity.

Playback response counts were approximately proportional to background counts, which provide a measure of colony activity and burrow density. The common intercept for the minimum AIC model suggests no differences in responsiveness to different playbacks (neighbour/stranger or female/male) when background counts are zero, *i.e.*, during

quiet periods any call playback is stimulating. Scatter around the intercept could result from variation in burrow density (number of birds available to respond) and was modelled with different intercepts for each burrow-site. The additional 22% variance explained with the site effect indicates a substantial burrow density signal in the data.

Stranger playbacks increased the slope of the response-background relationship, *i.e.*, a “dear enemy” effect. The minimum AIC model predicts a +31% average increase in response counts at the maximum observed background count = 13. Shallenberger (1973) similarly observed that wedge-tailed shearwaters appeared to be more responsive to stranger playbacks than to neighbour calls, although he did not test neighbour-stranger recognition in the field.

Male playbacks decreased responsiveness. The minimum AIC model predicts a -19% average decrease in response counts at the maximum observed background count = 13. Assuming a balanced sex ratio in burrows, the expected decrease could be nearer -50% since females mostly did not respond to stranger males in the sex vocal recognition experiment. The wide confidence interval for the background  $\times$  sex interaction allows for a stronger effect. Alternatively, some females may have been responding to neighbours rather than directly to the male playbacks.

Although the minimum AIC neighbour-stranger playback response model is reasonable, there are

several caveats. Conditional  $R^2 = 0.60$  means that 40% of the variation was unexplained and there could be other and more useful predictors. I expect that response counts are proportional to burrow density at each site, which was not measured. Secondly, only a few sites with high burrow densities and background counts were sampled. The effective area sampled was also not fixed and could vary with topography, vegetation, burrow lengths and weather conditions, all of which affect sound propagation and reception, although most responses were near to the playback sites. Jouventin & Aubin (2000) found that short-tailed shearwaters did not respond to playbacks at distances > 8 m. However, call disturbances can propagate radially through a petrel colony (Warham 1996) and Mackin (2005) reported that Audubon's shearwaters at distances > 3 m usually responded to other neighbours rather than directly to playbacks. Finally, spatial co-ordinates of burrow locations were not measured and the analysis did not consider spatial autocorrelation. Most individual burrows were widely-spaced however (10s of metres), and spatial autocorrelation effects might have been small.

This study examined the numerical response of wedge-tailed shearwaters to neighbour-stranger playbacks. Mackin (2005) evaluated response intensity for Audubon's shearwaters as measured by call duration. These 2 approaches are complementary and both should indicate a "dear enemy" effect, although they have not yet been combined in a single study.

Playback methods have useful field applications. Burger & Lawrence (2001) played back duet calls to estimate burrow occupancy for wedge-tailed shearwaters. The mean time to respond was 33 s (range 1-120 s) for playbacks at night and they recommended 120 s long playbacks. Ground calls of large shearwaters are usually much shorter, around 5-15 s (Warham 1996). Playback of same-sex or female agonistic calls in the present study was a powerful stimulus, with virtually all birds responding during the first few syllables (within 7-9 s). Statistical modelling showed that counts of birds responding to playbacks are predictable to some extent and further research into developing playback-response methods for estimating population size is suggested.

#### ACKNOWLEDGEMENTS

Work on Muttonbird Island was permitted under Scientific License 101052, authorised by the NSW Office of Environment and Heritage, and Animal Research Authority 12/4839, authorised by the NSW Department of Primary Industries. I am thankful to Ann Walton, Coffs Coast Ranger and Glenn Storrie, Area Manager, National Parks & Wildlife Service, for their support and advice. Deanne Waine from the University of Queensland and Dr Richard McCoy from Gribbles Veterinary are thanked

for their efficient genetics laboratory work. Colin Miskelly and Bo Totterman gave helpful pre-submission reviews of this paper. Hadley Wickham is also thanked for the ggplot2 graphics package for R (Wickham 2009).

#### LITERATURE CITED

- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716-723.
- Austin, J.J. 1996. Molecular phylogenetics of *Puffinus* shearwaters: preliminary evidence from mitochondrial cytochrome *b* gene sequences. *Molecular Phylogenetics and Evolution* 6: 77-88.
- Austin, J.J.; Parkin, D.T. 1996. Low frequency of extrapair paternity in two colonies of the socially monogamous short-tailed shearwater *Puffinus tenuirostris*. *Molecular Ecology* 5: 145-150.
- Bates, D.; Maechler, M.; Bolker, B.; Walker, S. 2013. lme4: Linear mixed-effects models using Eigen and S4. R package version 0.99999911-5. <http://lme4.r-forge-project.org/>
- Boersma, P.D.; Davies, E.M. 1987. Sexing monomorphic birds by vent measurements. *Auk* 104: 779-783.
- Bourgeois, K.; Curé, C.; Legrand, J.; Gómez-Díaz, E.; Vidal, E.; Aubin, T.; Mathevon, N. 2007. Morphological versus acoustic analysis: what is the most efficient method for sexing Yelkouan shearwaters *Puffinus yelkouan*? *Journal of Ornithology* 148: 261-269.
- Bretagnolle, V. 1996. Acoustic communication in a group of nonpasserine birds, the petrels. pp 160-178 In: Kroodsma, D.E.; Miller E.H. (eds) *Ecology and evolution of acoustic communication in birds*. Ithaca: Cornell University Press.
- Bretagnolle, V.; Attié, C.; Mougeot, F. 2000. Audubon's shearwaters *Puffinus lherminieri* on Réunion Island, Indian Ocean: behaviour, census, distribution, biometrics and breeding biology. *Ibis* 142: 399-412.
- Brooke, M. de L. 1978. Sexual differences in the voice and individual vocal recognition in the Manx shearwater (*Puffinus puffinus*). *Animal Behaviour* 26: 622-629.
- Brooke, M. de L. 1988. Sexual dimorphism in the voice of the greater [sic] shearwater. *Wilson Bulletin* 100: 319-323.
- Burger, A.E.; Lawrence, A.D. 2001. Census of wedge-tailed shearwaters *Puffinus pacificus* and Audubon's shearwater *P. lherminieri* on Cousin Island, Seychelles using call-playback. *Marine Ornithology* 29: 57-64.
- Burnham, K.P.; Anderson, D.R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd ed. New York: Springer-Verlag.
- Cure, C.; Aubin, T.; Mathevon, N. 2009. Acoustic convergence and divergence in two sympatric burrowing nocturnal seabirds. *Biological Journal of the Linnean Society* 96: 115-134.
- Floyd, R.B.; Swanson, N.M. 1983. Wedge-tailed shearwaters on Muttonbird Island: an estimate of the breeding success and the breeding population. *Emu* 82: 244-250.
- Garkaklis, M.J.; Sims, C.V.; Bradley, J.S.; Wooller, R.D. 1998. Breeding phenology of wedge-tailed shearwaters *Puffinus pacificus* on Rottneest Island, Western Australia. *Emu* 98: 317-319.
- Griffiths, R.; Double, M.C.; Orr, K.; Dawson, R.J. 1998. A DNA test to sex most birds. *Molecular Ecology* 7: 1071-1075.

- Gross, A.O.; Moulton, J.M.; Huntington, C.E. 1963. Notes on the wedge-tailed shearwater at Heron Island, Great Barrier Reef, Australia. *Atoll Research Bulletin* 99. Washington, D.C.: Pacific Science Board.
- Holmes, G. 1975. Black-winged petrel on Mutton Bird Island, New South Wales. *Australian Bird Bander* 13: 53-55.
- James, P.C.; Robertson H.A. 1985. Sexual dimorphism in the voice of the little shearwater *Puffinus assimilis*. *Ibis* 127: 388-390.
- Jouventin, P.; Aubin, T. 2000. Acoustic convergence between two nocturnal burrowing seabirds: experiments with a penguin *Eudyptula minor* and a shearwater *Puffinus tenuirostris*. *Ibis* 142: 645-656.
- Kuroda, N. 1954. *On the classification and phylogeny of the order Tubinares [sic], particularly the shearwaters (Puffinus), with special considerations on their osteology and habit differentiation*. Tokyo: Published by the author.
- Lane, S.G. 1997. Short-tailed shearwater *Puffinus tenuirostris* on Muttonbird Island, Coffs Harbour, New South Wales. *Corella* 21: 98.
- Mackin, W.A. 2005. Neighbor-stranger discrimination in Audubon's shearwater (*Puffinus l. lherminieri*) explained by a "real enemy" effect. *Behavioural Ecology and Sociobiology* 59: 326-332.
- Nakagawa, S.; Cuthill, I.C. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews* 82: 591-605.
- Nakagawa, S.; Schielzeth, H. 2013. A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 133-142.
- Norris-Caneda, K.H.; Elliott, J.D. 1998. Sex identification in raptors using PCR. *Journal of Raptor Research* 32: 278-280.
- O'Dwyer, T.W.; Priddel, D.; Carlile, N.; Bartle, J.A.; Buttemer, W.A. 2006. An evaluation of three field techniques for sexing Gould's Petrels (*Pterodroma leucoptera*) (Procellariidae) *Emu* 106: 245-252.
- Roberts, P.E.; Merritt, F.D.; Floyd, R.B. 1974. Wedge-tailed shearwaters on Muttonbird Island, Coffs Harbour, NSW. *Emu* 75: 19-22.
- R Development Core Team 2013. *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org/> Accessed 30 July 13.
- Serventy, D.L. 1956. A method of sexing petrels in field observations. *Emu* 56: 213-214.
- Shallenberger, R.J. 1973. Breeding biology, homing behaviour, and communication patterns of the wedge-tailed shearwater, *Puffinus pacificus chlororhynchus*. Unpubl. PhD thesis. University of California, Los Angeles, U.S.A.
- Swanson, N.M.; Merritt, F.D. 1974. The breeding cycle of the wedge-tailed shearwater on Mutton Bird Island, NSW. *Australian Bird Bander* 12: 3-9.
- Temeles, E.J. 1994. The role of neighbours in territorial systems: When are they "dear enemies"? *Animal Behaviour* 47: 339-350.
- Thompson, N.S.; LeDoux, K.; Moody, K. 1994. A system for describing bird song units. *Bioacoustics* 5: 267-279.
- Van Gessel, F.W.C. 1978. An estimate of the population density of shearwaters breeding on Broughton Island, New South Wales. *Corella* 2: 52-53.
- Warham, J. 1990. *The petrels - their ecology and breeding systems*. London: Academic Press.
- Warham, J. 1996. *The behaviour, population biology and physiology of the petrels*. London: Academic Press.
- Wickham, H. 2009. *ggplot2: elegant graphics for data analysis*. New York: Springer.
- Wragg, G. M. 1985. The comparative biology of fluttering shearwater and Hutton's shearwater and their relationships to other shearwater species. Unpubl. M.Appl.Sc. thesis, University of Canterbury, New Zealand.
- Zuur, A.F.; Ieno, E.N.; Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1: 3-14.