

Vocal identity and species recognition in male Australian sea lions, *Neophoca cinerea*

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SUMMARY

The acoustic channel is important for communication in otariids (fur seals and sea lions). Discrimination between species, sex or individuals is essential in communication; therefore insight into the role of vocalisations in recognition is vital to understanding otariid social interactions. We measured vocalisations and their use in discriminating sex and species in male Australian sea lions (*Neophoca cinerea*). Barking calls of mature males were recorded and analysed based on five acoustic parameters. A discriminant function analysis classified calls to the correct individual at a classification rate of 56%, suggesting that male barking calls are individually distinctive with the potential to facilitate individual vocal recognition. Playback experiments were used to assess the role of vocalisations in sex and species recognition both in and out of the breeding season. Males showed significantly stronger reactions to both conspecific and heterospecific males than they did to conspecific females and were most responsive during the breeding season. Australian sea lion males have the most depauperate vocal repertoire of any otariid. This simple repertoire may reflect the ecological circumstances in which these animals breed, with very low colony densities, asynchronous breeding and low levels of polygyny. Yet even in this simple system, males are able to discriminate between males and females of their own species, and distinguish the calls of conspecifics from other species. The barking calls of male Australian sea lions have sufficient information embedded to provide the potential for individual discrimination and this ability will be assessed in future studies.

Key words: vocal communication, species recognition, Australian sea lion, *Neophoca cinerea*

INTRODUCTION

Recognition allows animals to distinguish others and may operate at a number of levels. Recognition has been demonstrated between species, mates, kin, sexes and individuals, and acts to facilitate individuals directing appropriate behaviours toward others (Insley et al., 2003; Tibbetts and Dale, 2007). Stereotypic acoustic signals are used as the mechanism of recognition in a wide range of taxa from anurans (Bee and Gerhardt, 2001) to birds (Aubin and Jouventin, 2002; Falls, 1982) and mammals (McComb et al., 2003; Reby et al., 2001). Vocal recognition may be used at a number of levels ranging from the most intimate, parent–offspring, between mates, during intra- and inter-sexual encounters and in intra- and inter-specific interactions. Consequently, identifying the degree to which the individuals involved recognise each other may help us understand social interactions. A precursor to vocal recognition is that animals produce vocalisations that contain sufficient unique information to be identified to species or sex, whereas individual vocal recognition requires sufficient information to be individually distinctive (Falls, 1982). In the case of pinnipeds (seals, sea lions, fur seals and walrus) mother–pup vocal recognition has been clearly identified as an important component of mother–offspring relations and call structure is complex and individually distinctive (Charrier et al., 2001; Charrier et al., 2002; Charrier et al., 2003; Hanggi, 1992; Insley, 2001; McCulloch and Boness, 2000; Petrionovich, 1974; Renouf, 1985; Trillmich, 1981). Fewer studies have investigated vocal repertoire in males (Roux and Jouventin, 1987), or its role in sex and/or species recognition (Page et al., 2002).

In a number of otariid pinniped species males display a complex repertoire of threat calls, many of which are graded and vary in acoustic structure (for a review, see Insley et al., 2003). In the case of some otariids (fur seals and sea lions), similar male vocalisations have been described in different species [e.g. the ‘bark’ (Fernandez-Juricic et al., 1999; Stirling, 1971; Stirling, 1972; Stirling and Warneke, 1971)]. Unless these calls contain unique traits that enable species to recognise their own kind, confusion may arise and matings that may fail or lead to genetically inferior hybrid offspring may occur (Page et al., 2001). Therefore, by producing species-specific calls and, critically, having the ability to discriminate these call types, inter-specific mating and unnecessary inter-specific male conflict may be avoided in closely related species. For instance in Antarctic (*Arctocephalus gazella*), Subantarctic (*A. tropicalis*) and New Zealand (*A. forsteri*) fur seals breeding sympatrically on Macquarie Island, males produce ‘barks’ with species-specific differences (Page et al., 2002). This suggests that in these three otariid species at least, vocal communication may be important for species recognition (Page et al., 2002; St Clair Hill et al., 2001). However, whether these species can recognise these calls as coming from different species has yet to be experimentally assessed.

Male Australian sea lions *Neophoca cinerea* (Péron, 1816), use vocalisations in a range of social interactions (Marlow, 1975) and their breeding distribution overlaps with that of a closely related species, the New Zealand fur seal (Shaughnessy et al., 2005). If Australian sea lion calls contain species-specific traits then these calls may be used in species recognition, to identify potential mates,

to identify potential rivals for mates, and reduce inter-species conflict.

Male behaviour varies in and out of the breeding season. Male otariids are highly aggressive during the breeding season defending females or territory from rival males (Wartzok, 1991). By contrast, out of the breeding season males may be found lying side by side. While aggressive interactions do still occur, the degree of ferocity is reduced. Vocalisations are still used outside the breeding season, as dominant males vocalise while displacing subordinate males (Marlow, 1975). Although this suggests that vocalisations may be important in male communication both in and out of the breeding season, it is likely that the use of vocalisations by males and motivation to discriminate and react to conspecifics will differ between breeding and non-breeding seasons.

Vocal individuality is a requirement of individual recognition and is influenced by physical characteristics of the individual, context and environment. Vocal individuality has been demonstrated in all species studied to date, however levels of individuality vary between species. Otariids breed in high-density colonies. The in-air territorial vocalisations of the males of four species of fur seal (*Arctocephalus* spp.) and one species of sea lion (*Otaria flavescens*) have all been shown to be both stereotypic and to contain sufficient information to be individually distinctive (Fernandez-Juricic et al., 1999; Phillips and Stirling, 2001; Roux and Jouventin, 1987; Stirling and Warneke, 1971; Tripovich et al., 2005). Call stereotypy in male pinnipeds may function in male–male competition [i.e. neighbour/stranger discrimination (Falls, 1982)]. However, in all other fur seal and sea lion species levels of polygyny are very high and competition among males is intense. The ability to recognize familiar/unfamiliar males and subsequently conserve energy and gauge the risk of combat has selective advantages. Australian sea lions have a unique 18-month breeding cycle, which is asynchronous among breeding colonies. Breeding seasons are prolonged and subsequently levels of polygyny are significantly lower. Hence selection pressures operating on recognition between males and thus vocal individuality in male calls are likely to be lower.

Male Australian sea lions have been observed to use vocalisations during social interactions (Marlow, 1975; Stirling, 1972). The study reported here aimed to explore the degree of individuality in barking calls used by male Australian sea lions in light of their unique breeding system. Given the potential for vocalisations as a means of species recognition, this study also sought to identify whether males could discriminate conspecifics (males and females) based on vocalisations alone and to compare these reactions in and also out of the breeding season, when levels of male aggression are altered and mate selection is no longer operating.

MATERIALS AND METHODS

Study location and animals

This study was carried out on the Australian sea lion, *N. cinerea*, colony at Seal Bay Conservation Park, Kangaroo Island, South Australia (34°41'S, 136°53'E). Data collection took place over two field trips. One trip took place within the breeding season, between the 17th March and 19th April 2006 and the other was conducted during the non-breeding season, between the 3rd and 23rd November 2006.

Vocal repertoire of male Australian sea lions

Preliminary observations of male vocalisations were conducted *ad libitum*. Call types were classified by ear. The barking call was found to be the predominant (almost exclusive) call type used by males. Other vocalizations were recorded opportunistically, but these other

call types were rare and only one recording of each call type was obtained, preventing any further analysis.

Recordings and signal acquisition

Recordings of the barking calls from 13 mature males were performed when they were guarding females during the breeding season. Males were recorded in similar circumstances (when they had been disturbed by another animal or were interacting with the female they were guarding). Males were recorded from a distance of 5–15 m using a Sennheiser MKH 70P 48 shotgun microphone or at a closer distance (3–5 m) using a BeyerDynamic (Heilbronn, Germany) M69 TG microphone mounted on a 3 m boom connected to a Marantz (Eindhoven, The Netherlands) PMD 670 digital recorder. Calls were recorded at a sampling frequency of 22.050 Hz.

Analysis of acoustic parameters

Only calls exhibiting good signal to noise ratio were analyzed. The barking call is always produced in a series. Barks from the same series cannot necessarily be treated as independent and therefore it was important to measure barking calls from more than one series (Insley et al., 2003). Acquiring barking series with good signal to noise ratios was hindered by abiotic noise (wind and sea waves) and hostility of mate guarding males. As a result, it was only possible to measure barking calls from two different series for each male.

In order to measure meaningful bark intervals (see acoustic parameters measured below) it was desirable to measure consecutive barks. For each male, from each of the two series, the 10 consecutive barking calls with the best signal to noise ratios were chosen for analysis. Therefore, two sequences of 10 barking calls from two different series were analyzed for each of the 13 individuals (per individual calls $N=20$, total calls $N=260$).

To characterise the acoustic structure of the barking call, five parameters were measured using Avisoft SASLab Pro (Avisoft Bioacoustics, Berlin, Germany; R. Specht – version 4.36; Fig. 1). Owing to the noisy nature of the male Australian sea lion barking call, the spectral parameters that could be measured were limited. For instance, it was not possible to measure the exact frequency value of the fundamental frequency and its relative harmonics since unlike other male otariids (Fernandez-Juricic et al., 1999; Page et al., 2002; Tripovich et al., 2005) the Australian sea lion barking call did not present a clear harmonic structure. Two temporal features were measured: the total duration of the barking call (Dur; in ms) and the duration between barking calls (Interval Dur; in ms) (Fernandez-Juricic et al., 1999; Page et al., 2002; Tripovich et al., 2005). Three spectral parameters were also measured: frequency value of the first maximum peak in amplitude (Peak 1; in Hz) (Fernandez-Juricic et al., 1999; Page et al., 2002); frequency value of the second maximum peak in amplitude (Peak 2; in Hz) (Fernandez-Juricic et al., 1999; Page et al., 2002) and the ratio of the amplitude values of Peak 1 to Peak 2 (RAMP) (Page et al., 2002).

Temporal features were measured on the oscillogram (cursor precision=1 ms). Spectral features were measured using the averaged amplitude spectrum (Hamming window, frequency resolution: 10.7 Hz) calculated on the entire length of the call.

Statistical analysis of acoustic parameters

An ideal signal for individual variation will be highly stereotyped within each individual, but will differ noticeably between individuals (Robisson et al., 1993). Inter-individual variation was explored using discriminant function analysis (DFA; STATISTICA version 6, Statsoft Inc., Tulsa, OK, USA; 1984–2002), which compares variation among individuals across several levels

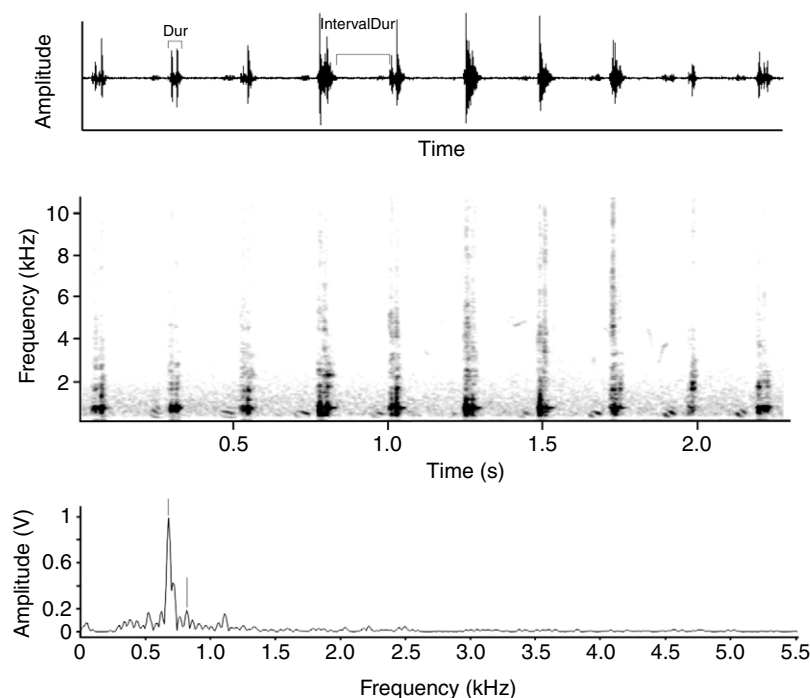


Fig. 1. Barking call of male Australian sea lion displaying parameters measured in acoustical analysis. Top: oscillogram on which duration parameters were measured (Dur and Interval Dur). Middle: spectrogram (FFT: 512 pts; overlap: 100%). Bottom: average energy spectrum on which the first two highest energy peaks, Peak 1 and Peak 2, were measured with their relative amplitude to calculate their ratio (RAMP).

simultaneously. This analysis computes equations or discriminant functions, which combine the characteristics of the calls of an individual in such a way that the call can be assigned to the individual it most strongly resembles (Klecka, 1980). By determining the percentage of calls correctly classified, a measure can be obtained of the ability of the chosen variables to discriminate among individuals. Wilk's lambda was computed to estimate discrimination among individuals and an *F*-test was used to determine its significance at the $\alpha=0.05$ level (Klecka, 1980). No variables were highly correlated and therefore all variables were included in the DFA. A cross-validated DFA was then carried out to test the generality of the function.

To identify if there was any effect of series we constructed a nested GLM with series nested within male.

Species comparison

The barking call of the male Australian sea lion was compared with that of the male subantarctic fur seal to identify the species specificity of this call type. Australian sea lions are highly unlikely to encounter subantarctic fur seals in the wild as their ranges are separated by several thousand kilometres. The subantarctic fur seal was therefore chosen as a control in playback experiments designed to test Australian sea lion vocal recognition. Recordings of male subantarctic fur seals were made on Amsterdam Island (Indian Ocean, 37°55'S, 77°30'E) in 1999–2000. Males were recorded using an omnidirectional Røde M 3500 microphone (frequency bandwidth 150–18 000 Hz \pm 1 dB) mounted on a 2 m boom and connected to a Sony TC-D5M audiotape recorder. Calls were recorded when a male interacted with a neighbouring male. During the recordings, the distance between the animal and microphone was approximately 2 m. Calls were digitised with a 16-bit acquisition card at 22.050 kHz sample rate, using acquisition software (Cool Edit, Syntrillium Software, Phoenix, AZ, USA). Signals were then stored on the hard disk of a PC computer and filtered (0–200 Hz) to remove background noise. Six calls were analyzed from a single series for eight different subantarctic fur seal males (per individual calls $N=6$, total calls $N=48$). The same five parameters measured

for the Australian sea lion were also measured for the subantarctic fur seal calls (Dur, Interval Dur, Peak 1, Peak 2 and RAMP). For each male (eight subantarctic fur seals and 13 Australian sea lions) we took the average value of each acoustic variable. A DFA was then performed to determine the percentage of calls correctly classified to each species.

Vocal playback experiments

In order to prevent the possibility of pups being harmed by misdirected aggression from males responding to playback tests (Higgins and Tedman, 1990; Marlow, 1975), all playbacks were carried out on non-mate guarding, solitary but fully mature males. Males were tested for their reaction to calls from males and females of their own species, from males of another species (i.e. subantarctic fur seal) and white noise (a control). Using digital audio editing software (Goldwave, St Johns, Newfoundland, Canada; C. Craig 2000 – version 4.19), four types of stimuli were constructed (Fig. 2). The male Australian sea lion stimuli consisted of two series, each of ten barks, with the two series separated by a 3 s interval (average total duration, 7.9 s). The male subantarctic fur seal stimuli consisted of two series of nine barks, with the two series separated by a three-second interval (average total duration, 8.8 s). For the female Australian sea lion, three pup-attraction calls were played, with each call separated by a 3 s interval (i.e. natural rate; average total duration, 9.2 s). For the white noise, two series of 2 s were played and separated by 2 s (total duration, 6 s). To limit pseudo-replication, eight replicates were created for each type of stimulus with each of these eight signals containing calls from a different individual. Signals were broadcast using a Marantz PMD 670 digital recorder connected to an amplified powered portable speaker ANCHOR Explorer Pro (Torrance, CA, USA; 30 W, frequency response: 80 Hz–16 kHz).

Focal males were chosen opportunistically. Fourteen different males were tested during the breeding season and 22 males were tested during the non-breeding season. The presentation order of series was randomly selected for each male. The speaker was placed 10–15 m from the individual being tested and the different types of

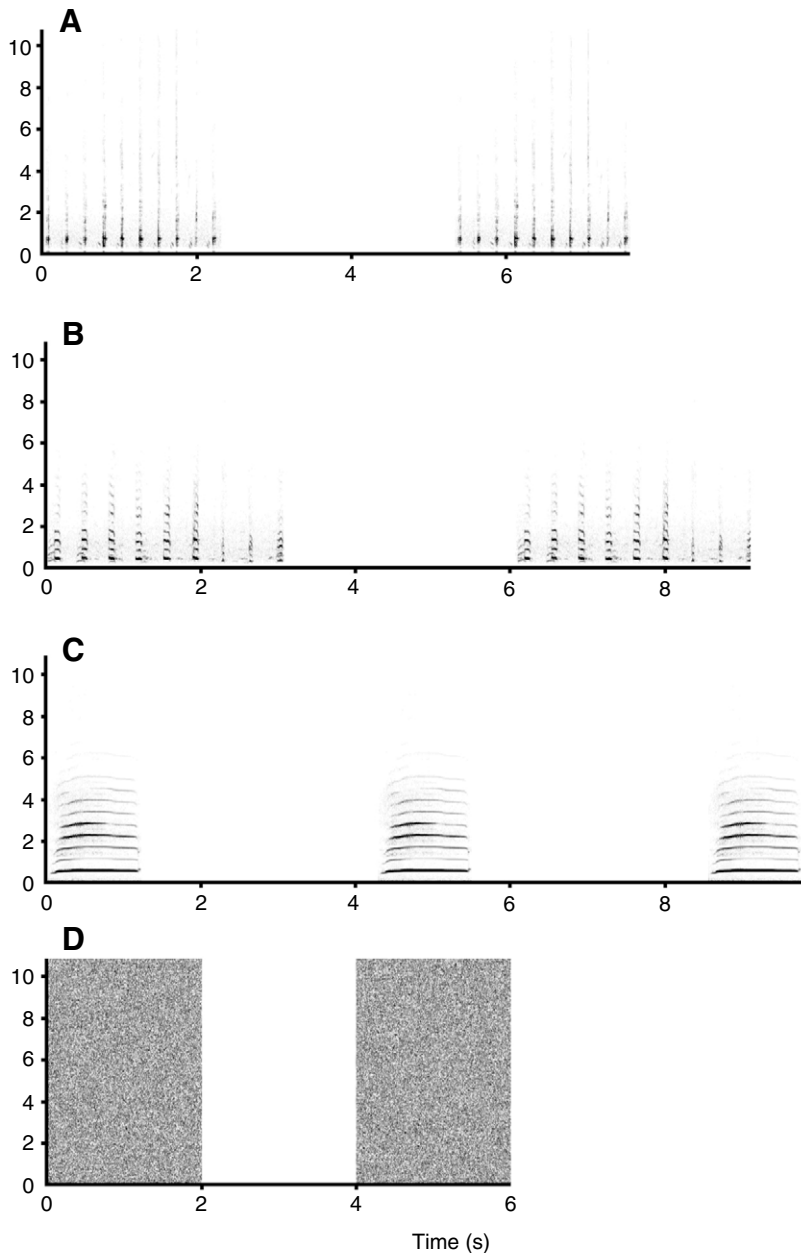


Fig. 2. Spectrograms of the different playback series broadcast to males. (A) Barking calls of male Australian sea lion; (B) barking calls of male subantarctic fur seal; (C) pup-attraction call of female Australian sea lion; (D) white noise.

comparisons to assess differences in male responses to the stimuli within each season. Finally χ^2 tests were used to assess the difference in male responses to conspecific males, conspecific females and subantarctic fur seal males in and out of the breeding season. The alpha level was set at 0.05 throughout. Friedman and Wilcoxon tests were carried out in SYSTAT Version 10 (SPSS Inc., San Jose, CA, USA, 2000). The χ^2 tests were carried out in MINITAB Release 14 (1972–2005 Minitab Inc., State College, PA, USA).

RESULTS

Vocal repertoire of male Australian sea lions

During the course of this study, male Australian sea lions were observed producing three different call types: a barking call, a bleating call and a female-like call (see Fig. 3). The barking call of Australian sea lions was similar in structure to the barking calls described in some other species of otariid in that it was a short sound produced repetitively in a series (Stirling, 1971; Trillmich and Majluf, 1981). However, the call differed from that described for some other species, in that it lacked harmonic structure. Juvenile and sub-adult males also occasionally produced a high-pitched bleating call during agnostic interactions with other individuals. Finally, a few males were observed to use a vocal call, which strongly resembled the calls used by females and pups when searching for each other, albeit very rarely. If produced, this was primarily in response to females' calls, but the call was produced so rarely that its function could not be determined.

Barking call characteristics

The predominant call type produced by males of all ages was the barking call (Fig. 1). The call consisted of a short noisy sound, which resembled a loud click and was produced repetitively in a series. In

Australian sea lions, series of barks may be as short as two to five barks or can last for several minutes. Barking calls and the intervals between barking calls (Dur and Interval Dur) were relatively short with mean durations of 46 ms and 191 ms, respectively (Table 1). The frequency of the first two maximum amplitude peaks (Peak 1 and Peak 2) was interchangeable even within individuals. For each individual, in some calls Peak 1 had a higher frequency, whereas in other calls Peak 2 had a higher frequency. Peak 2 had the highest frequency on average (Peak 1 = 934 ± 480 Hz and Peak 2 = 1362 ± 598 Hz; Table 1). The amplitude ratio between these two peaks was 2.15 on average. Males produced barking series with the mouth fully open, partially open or closed. The vibrissae were always erect. Males produced barking series while lying down and sitting up, while stationary, while moving or even when they appeared to be sleeping. Males were observed directing these calls at intruding males or females, and at the female they were guarding. In some cases, males did not appear to be directing their barks at any particular animal.

calls were broadcast at their respective natural sound pressure level. All males were in a relaxed position prior to a series being played (i.e. they were lying down and appeared to be sleeping). In general, there was a 1–3 min interval between each stimulus type. However, if a male was disturbed by another animal during this interval, we waited for him to return to a relaxed position before playing the next stimulus.

Criteria for response

The response of males was graded on a three-point ethological scale: 0, a weak response (males either made no response or only moved their head in the direction of the speaker); 1, moderate response (males got up in response to the playback, but did not approach the speaker); 2, strong response (males approached the speaker and/or vocalised in response to the playback).

Two Friedman tests were carried out, one for the breeding season and one for the non-breeding season with each test incorporating all four stimuli. Wilcoxon signed ranks were used for pairwise

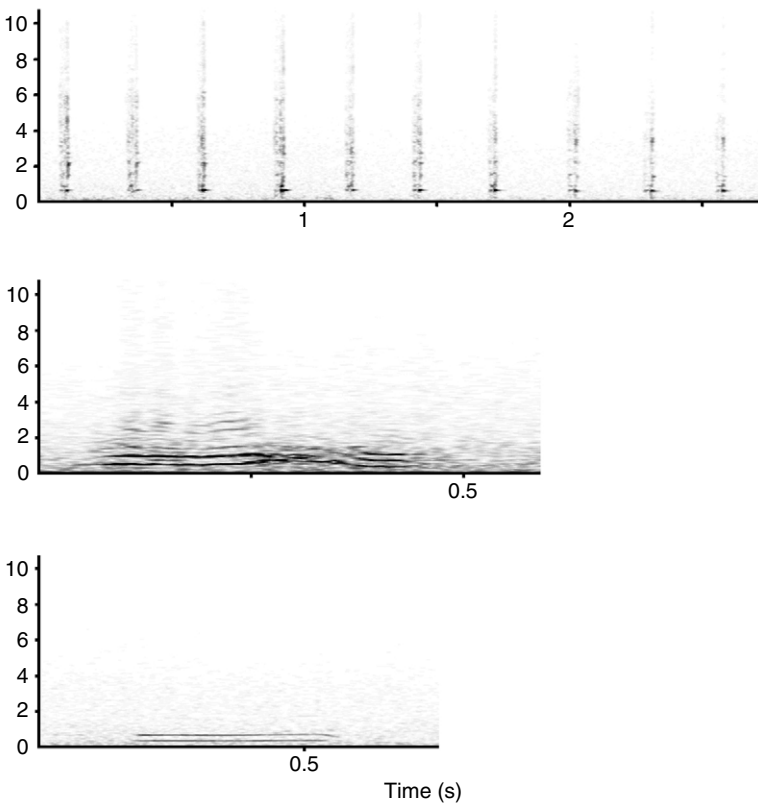


Fig. 3. Vocal repertoire of Australian sea lion males: spectrograms of barking calls (top), bleating call (middle) and female-like call (bottom). (Hamming window, FFT: 512 pts, overlap: 93.75%.)

Statistical analysis of barking call characteristics
Males differed significantly at the individual level across all measured characteristics. Within the nested GLM, series differed significantly for three parameters, Dur ($P=0.0000$), Interval Dur ($P=0.0000$) and Peak 1 ($P=0.0017$). However, series was non-significant for Peak 2 ($P=0.6411$) and RAMP ($P=0.1518$).

The discriminant function analysis (DFA) performed on the five acoustic parameters revealed a significant difference among males (Wilk’s $\lambda=0.05818$, $F_{60,1141}=15.900$, $P<0.0000$). The overall DFA extracted all parameters and two discrimination roots (eigenvalues: 4.426 and 1.394, respectively; Table 2) that contributed to 95.1% of the total variance (72.4% and 22.7%, respectively; Table 2). Variables such as Dur and Peak 1 were most strongly correlated with the first root, while Interval Dur, Peak 2 and RAMP were more strongly correlated with the second root. The parameters allowing us to distinguish between individuals are mainly represented by Dur and Interval Dur. In addition, the classification matrix revealed that calls were correctly assigned to individuals with an average classification rate of 56% (range: 25%–100%, Table 3). Three males

had low classification rates (25%), but these rates were still significantly greater than that expected by chance ($1/13=7.6\%$; Table 3). The results of the cross-validated DFA were slightly lower, giving a mean classification rate of 45%, however this is still greater than by chance.

Species comparison

For the subantarctic fur seal, Dur and Interval Dur of the barking call unit were found on average to be longer than that of the Australian sea lion (Table 1). The frequencies of the first two maximum amplitude peaks were found to be lower on average in the subantarctic fur seal, however, the ratio between the amplitudes of these two peaks remained very similar (Table 1). The DFA performed on the five acoustic parameters showed a significant difference between species (Wilk’s $\lambda=0.06$, $F_{5,15}=46.628$, $P<0.0000$). The classification matrix revealed that calls were assigned to the correct species at a classification rate of 100%.

Vocal playback experiments

Males exhibited more ‘strong’ reactions during the breeding season (Fig. 4). Males’ reactions during the breeding season were found to differ significantly between stimuli (Friedman: $\chi^2=14.850$, d.f.=3, $N=14$, $P=0.002$). Following the removal of white noise, male response to the three remaining stimuli still differed significantly (Friedman: $\chi^2=6.143$, d.f.=2, $N=14$, $P=0.046$). *Post-hoc* testing revealed that there was a significant difference in male responses to subantarctic fur seal and Australian sea lion male barking calls (Wilcoxon: $z=2.008$, $N=14$, $P=0.045$). There was also a significant difference in male response to the male and female Australian sea lion calls (Wilcoxon: $z=2.683$, $N=14$, $P=0.007$). However, there was no significant difference in male responses to the calls of the female Australian sea lion and the male subantarctic fur seal (Wilcoxon: $z=1.200$, $N=14$, $P=0.230$).

Out of the breeding season male reactions did not differ significantly between stimuli (Friedman: $\chi^2=7.295$, d.f.=3, $N=22$, $P=0.063$). However, given that these results were close to significance, *post-hoc* testing was carried out. *Post-hoc* tests revealed that the only significant difference lay between male reactions to male Australian sea lions and male subantarctic fur seals (Wilcoxon: $z=2.460$, $N=22$, $P=0.014$).

Male reactions to conspecific male calls and subantarctic fur seal male calls differed significantly between breeding and non-breeding seasons ($\chi^2=12.915$, d.f.=2, $P=0.002$ and $\chi^2=11.530$, d.f.=2, $P=0.003$ respectively). Male reactions to conspecific female calls did not differ significantly between seasons ($\chi^2=1.688$, d.f.=2, $P=0.430$).

DISCUSSION

In this study we investigated the potential for individual recognition by assessing the vocal repertoire and measuring vocal individuality in male Australian sea lions. We also tested

Table 1. Number of calls analysed, mean and standard deviation of variables measured in the barking calls of male Australian sea lions and male subantarctic fur seals

Variable	Male Australian sea lion		Male subantarctic fur seal	
	Mean \pm s.d.	N (calls; indiv)	Mean \pm s.d.	N (calls; indiv)
Dur (ms)	46 \pm 16	260; 13	90 \pm 19	48; 6
Interval Dur (ms)	191 \pm 36	260; 13	301 \pm 53	48; 6
Peak 1 (Hz)	934 \pm 480	260; 13	489 \pm 203	48; 6
Peak 2 (Hz)	1362 \pm 598	260; 13	911 \pm 285	48; 6
RAMP	2.15 \pm 1.81	260; 13	2.21 \pm 1.21	48; 6

Dur, total duration of the barking call; Interval Dur, duration between barking calls; Peak 1 and 2, frequency value of the first and second maximum peak in amplitude, respectively; RAMP, ratio of the amplitude values of Peak 1 to Peak 2.

Table 2. Results from the discriminant function analysis comparing the barking calls from male Australian sea lions

Acoustic variable	Root 1	Root 2
Dur	-0.730	0.704
Interval Dur	0.627	0.822
Peak 1	-0.238	-0.068
Peak 2	-0.065	0.090
RAMP	0.064	0.122
Eigenvalue	4.426	1.394
Cumulative proportion	0.724	0.951

Dur, total duration of the barking call; Interval Dur, duration between barking calls; Peak 1 and 2, frequency value of the first and second maximum peak in amplitude, respectively; RAMP, ratio of the amplitude values of Peak 1 to Peak 2.

Table 3. Percentage of calls correctly assigned by the discriminant function analysis for the male Australian sea lion barking call

Identification	% correct	No. correct calls
Male 1	80	16
Male 2	55	11
Male 3	60	12
Male 4	25	5
Male 5	55	11
Male 6	55	11
Male 7	100	20
Male 8	75	15
Male 9	45	9
Male 10	25	5
Male 11	25	5
Male 12	40	8
Male 13	85	17
Average	55.77	—
Total	—	145/260

the ability of male Australian sea lions to discriminate between males and females of their own species and to distinguish an unfamiliar species based on responses to vocalisations.

Mature Australian sea lion males were found to emit the barking call in almost all social interactions, despite the existence of at least three call types in their vocal repertoire, plus a guttural threat and growl reported by Stirling (Stirling, 1972), which was never heard in this study. Their vocal repertoire is thus depauperate in comparison with male Southern sea lions, and the majority of fur seal bulls (*Arctocephalus* species), which produce four or more distinguishable vocalisations in different situations (Fernandez-Juricic et al., 1999; Phillips and Stirling, 2001; Stirling, 1972; Stirling and Warneke, 1971; Tripovich et al., 2005).

The barking call of male Australian sea lions was found to be individually distinctive based on five acoustic parameters. We measured acoustic variables from 20 barks for each individual, albeit from only two series. Series was found to have an effect on three of the five parameters that we measured. In an ideal design we would have taken one to two calls from a number of different series for each male, however this would necessitate acquiring good recordings of the same male five to ten times. This was not feasible during the current study as we were unable to mark males because of their short tenure on the breeding beaches and the aggressive nature of breeding bulls and difficulties in obtaining good ambient conditions with prevailing sea and wind noise. Furthermore, we may have found the same results between recording sessions since bark structure (pitch=Peak 1) and bark rhythmicity (Dur and Interval Dur) varies with the context (motivational state and aggressiveness level

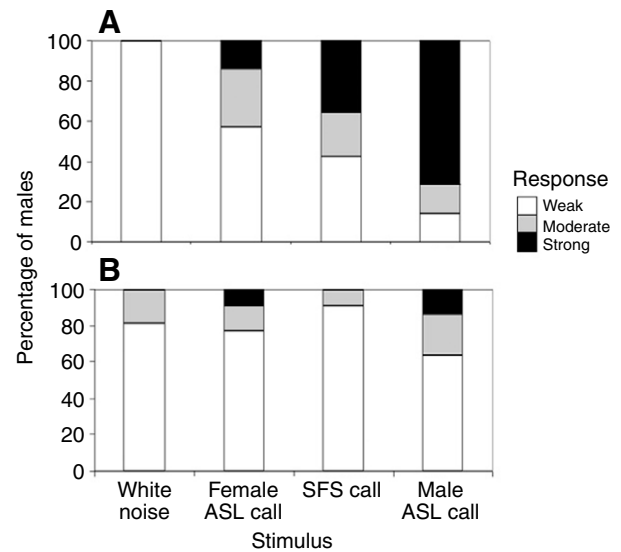


Fig. 4. Male responses to each playback stimulus [white noise, female Australian sea lion (ASL), male subantarctic fur seal (SFS) and male Australian sea lion (ASL)], (A) during the breeding season and (B) out of the breeding season.

fluctuate if there are males around the recorded males, or females moving, or juveniles around). We suggest that this is an extremely interesting result since the results show that some information about motivational state can be encoded in the bark series such as rhythmicity, duration; and some other features are used to encode individual identity. Hence even a simple vocalisation such as a bark series can convey lots of information.

Most studies of individual variability in the vocal calls of male otariids have focused on threat calls, although two previous studies have investigated individual variation in barking calls. For Southern sea lions, discriminant function analysis classified 76% of barking calls to the correct individual (Fernandez-Juricic et al., 1999), and for Australian fur seals, 68% of barking calls were correctly classified (Tripovich et al., 2005). As the acoustic parameters and sample sizes were different for each study, care must be taken in making direct comparisons between species. Nevertheless, individual variation does appear to be lower in the barking calls of Australian sea lions, with only 56% of calls classified to the correct individual.

Comparisons among species suggest that colonial life and different breeding systems affect levels of individual recognition (McCulloch and Boness, 2000). The mating system of Australian sea lions is one of female defence polygyny (Boness, 1991). Australian fur seals show resource defence polygyny in large, crowded colonies and successful males may mate with many females over a short period (Tripovich et al., 2005), while Southern sea lions exhibit resource defence and female defence mating strategies at different colonies depending upon colony density and topography (Boness, 1991; Compagna and Le Boeuf, 1988). Different levels of vocal individuality may reflect the different selection pressures imposed on individual vocal recognition by each of these breeding strategies. For instance, in resource defence systems where males may fast and maintain a single territory in a crowded colony for the entire breeding season, males who recognise their neighbours have a significant advantage since they can conserve energy through the reduction of conflict with neighbours. For Australian sea lions breeding in low density colonies with mate

guarding, few rivals and very low levels of polygyny, the ability to recognise a neighbouring male may not be such a significant advantage. Alternatively, the low densities themselves may have eased selection pressures driving individual distinctiveness in calls in the Australian sea lion compared to other more gregarious species, as there are so few other males to distinguish between.

The identification of stereotypy based on acoustic analysis enables the isolation of acoustic cues likely to encode individual identity. However, it does not prove that these individualised parameters are used effectively in a recognition context. Whether Australian sea lion males do use vocalisations to distinguish familiar/unfamiliar males as in subantarctic fur seals (Roux and Jouventin, 1987) or whether lower levels of vocal individuality relate to a lack of recognition will require testing with playback experiments.

This study is the first to investigate sex and species recognition in otariids based on vocalisations and employing playback experiments. Male vocal recognition was compared in and out of the breeding season when male aggressiveness and motivation to distinguish conspecifics is likely to differ. Males clearly discriminated between males and females of their own species, as well as being able to discriminate these from calls of another species, the subantarctic fur seal.

The breeding distribution of Australian sea lions overlaps with that of the New Zealand fur seal although the two species do not breed in sympatric colonies. Nevertheless Australian sea lions are likely to encounter New Zealand fur seals at sea or when hauled out and may therefore have previous experience with their call which could bias their response. Our experiments were designed to test the reaction of Australian sea lion males to calls of their own species and to calls of a related, but completely unfamiliar species. The subantarctic fur seal was chosen for playback experiments since its call has temporal similarities to the Australian sea lion call, but is very unlikely to ever have been previously encountered.

The responses of Australian sea lion males to our stimuli clearly show that they are able to use vocalisations to discriminate calls of their own species from those of an unfamiliar species. It also appears that male reactions to each type of stimulus (Australian sea lion male, Australian sea lion female and unfamiliar species male) may reflect the level of threat posed by the emitter of each respective call.

Male reactions to the call of the female Australian sea lion were very similar in and out of the breeding season albeit reactions to female calls were slightly stronger during the breeding season. Responses were relatively muted compared to their responses to other males of either species. While males are expected to be more sensitive to calling females during the breeding season because males may use these calls to locate females close to oestrus (Marlow, 1975), the low densities of Australian sea lion colonies combined with prolonged breeding season reduce the likelihood of encountering an oestrous female even during the breeding season. Investigation of every calling female would be energetically exhausting and time intensive, hence males should primarily assess the potential threat of a caller and the responses seen reflect this.

Searcy and Brenowitz (Searcy and Brenowitz, 1988) suggested that in species recognition two types of errors can be made. In 'type 1' errors an individual rejects the stimulus of its own species, while in a 'type 2' error a stimulus of another species is accepted. For territorial male birds a type 1 error is more detrimental than a type 2 error since the failure to react accordingly to a conspecific may mean the loss of territory or mates while an aggressive reaction to a heterospecific involves only the cost of approaching and displaying

to the incorrect target (Searcy and Brenowitz, 1988). This concept also has relevance for male otariids.

Male reactions to subantarctic fur seal and Australian sea lion males were significantly different both in and out of the breeding season with males reacting more strongly to their own species' barking call during both seasons. This suggests that males discriminated between their own and unfamiliar species during both periods. During the breeding season male reactions to both its own species and unfamiliar species barking calls were much stronger than they were out of the breeding season. During the breeding season the cost of making a 'type 1' error is greater since it could result in the loss of potential mates, so males are likely to react more aggressively to both call types. The increase in strength of reaction to unfamiliar species calls during the breeding season may also reflect the hormonal state of breeding bulls. In other species of otariids, such as South American fur seals and Southern sea lions, breeding bulls will attack heterospecific males (Harcourt, 1992).

Australian sea lion males have the most depauperate vocal repertoire of any sea lion. This simple repertoire may reflect the ecological circumstances in which these animals breed, with very low colony densities, asynchronous breeding and low levels of polygyny. Yet even in this simple system, males are able to discriminate between males and females of their own species, and distinguish the calls of conspecifics from other species. The barking calls of the male Australian sea lion have sufficient information embedded to provide the potential for individual discrimination and this ability will be assessed in future studies.

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