

CHAPTER 2

CHARACTERISATION OF AUSTRALIAN FUR SEAL VOCALISATIONS

Summary

The vocal repertoire, structure and behavioural context of airborne vocalisations produced by Australian fur seals, *Arctocephalus pusillus doriferus*, are described using recordings made of animals at a breeding colony on Kanowna Island, Bass Strait, Australia. This is the first comprehensive study detailing the acoustic characteristics of vocalisations and their associated behaviours for this species, allowing for comparative studies across otariids. The study identified six different call types that were classed as either aggressive or affiliative: three for males (bark, guttural threat and submissive call); five for females (bark, guttural threat, submissive call, growl and Pup Attraction Call); one for pups and yearlings (Female Attraction Call). The vocalisations were compared amongst age and sex classes within the species and with other otariids. Similarities in the overall structure and function of some calls within the species, particularly those produced by females, yearlings and pups (Pup Attraction Call and Female Attraction Call), were evident. Furthermore, investigations on barks produced by male Australian fur seals indicated that the rate of production is altered when the context changes, being slower when males were stationary and advertising their territorial status and faster when males were involved in confrontations with other males or actively herding females.

A version of this chapter is in preparation for submission:

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2.1 Introduction

Social communication is a complex term to define, and is best described from an evolutionary and functional perspective (Poole 1985). A social signal is behaviour which has evolved to convey information to conspecific with the object of modifying its behaviour for the benefit of the signaller (Poole 1985) where one animal's behaviour influences the behaviour of another (Miller 1991). The receiver not only needs to detect the signal itself but should also discriminate significant variations in signals for efficient communication (Richards and Wiley 1980). Several modes of communication exist including tactile, olfactory, visual and acoustic signalling. In pinnipeds, vocal signalling is employed in both short and long range communication however the effectiveness of this signalling varies with environmental conditions (Serrano and Terhune 2001). Signals used in long range communication are less reliant on contextual information and are simple, discrete and repetitive (Miller 1991). Repetitive calls are often highly redundant but may be advantageous in noisy breeding areas, where there are many animals vocalizing simultaneously in close proximity (McElligott and Hayden 1999). Short range signalling is less influenced by environmental degradation, allowing animals to employ multiple sensory channels simultaneously. In graded communication, the properties of signals can change gradually over a series, which allows the recipient to compare and contrast subtle differences in successive repetitions (Miller 1991). Signals can thus provide recipients with information about a sender's current behavioural state and inclinations (Miller 1991). It is proposed that communicatory signals usually evolve to increase the efficiency of information transfer (Wiley and Richards 1982).

In general, the breeding strategies of colonial seals are similar with individuals congregating in large numbers on acoustically complex breeding rookeries. Fur seals and sea lions are highly polygynous, displaying sexual dimorphism with males being up to four times larger than females (Riedman 1990). Typically, males compete aggressively to establish and maintain territories where females will give birth. Unsuccessful males are usually ousted

to the periphery of the colony (Warneke 1979). Subsequently, females arrive at islands, give birth and mate shortly thereafter. They nurse their pups until they depart to forage at sea (Riedman 1990). This nursing-foraging cycle occurs until weaning, which varies between 4-24 months, depending on the species (Bowen 1991). The first departure usually occurs 5-10 days post-partum, depending on the species (Insley *et al.* 2003b). While there are many similarities in the breeding tactics employed among otariids, differences in environmental conditions may lead to variations in breeding strategies and behaviour (Boness 1991).

Vocalisations play an important role for individual recognition of animals and reproductive purposes (Falls 1982; Roux and Jouventin 1987). It has been suggested that while vocalisations of sympatrically occurring seals are generally similar they also have measurable differences that act as isolation mechanisms keeping species discrete (Page *et al.* 2002b; Stirling and Warneke 1971). However, there are a few occurrences where interbreeding of sympatric species has occurred producing hybrids e.g. Antarctic, *Arctocephalus gazelle*, and subantarctic, *A. tropicalis*, fur seals on Macquarie Island (Page *et al.* 2001). Mating between two different species appears to be associated with recognition errors (Insley *et al.* 2003b). The hybrid species produce vocalisations that are distinct from both parents, suggesting that some features may be genetically inherited (Page *et al.* 2001). Australian fur seals occur sympatrically with New Zealand fur seals (Stirling and Warneke 1971), therefore both species should have significant vocal differences between them, permitting species recognition.

Australian fur seals, *A. pusillus doriferus*, are the largest of all fur seal species (Warneke and Shaughnessy 1985), breeding on ten islands located in Bass Strait, south-eastern Australia (Kirkwood *et al.* 2005). The species follows the typical otariid breeding strategy, aggregating in dense social groups during a synchronous annual breeding season. Australian fur seals, like other fur seals are highly vociferous, using calls for territorial maintenance and defence, reproductive purposes and the identification of individuals (Stirling and Warneke 1971). While Australian fur seals are taxonomically classed within the

Arctocephalinae, they display numerous vocal and behavioural traits resembling that of sea lions (Otariinae) (Warneke and Shaughnessy 1985). Stirling and Warneke (1971) provided qualitative descriptions of the vocalisations produced by Australian fur seals. However, there has been no detailed quantitative analysis of these calls and their acoustics properties, which would be advantageous for comparative studies across pinniped species.

In the present study, therefore (1) the vocal repertoire and acoustic structure of vocalisations produced by this species are described both qualitatively and quantitatively; (2) the behavioural context of calls is examined; and (3) the differences in the acoustic structure of the bark call produced by male Australian fur seals are investigated under different behavioural contexts.

2.2 Materials and Methods

Vocal recordings were conducted on the breeding colony on Kanowna Island (39° 10'S, 146° 18' E) Bass Strait, south-eastern Australia. Kanowna Island has an annual production of ca 2300 Australian fur seal pups (Kirkwood *et al.* 2005). This island has two main colonies: East Valley and Main Colony. Recordings were made during two consecutive breeding seasons (10 - 16 December 2000 and 6 - 13 December 2001). Pups during this recording period were aged newborn-1 month of age, while yearlings were aged approximately 12-13 months.

In-air vocalisations of Australian fur seals were recorded using a Sony digital tape recorder (TCD-D8) with a directional K6/ME66 Sennheiser microphone (frequency response 50 – 20,000 Hz \pm 2.5 dB). Recordings were made at a distance of 5-25 m from the vocalizing animal and were usually conducted during 0800-1100 h and 1700- 2000 h of each day. Individuals were recorded at different locations and sampled during a single recording to avoid re-sampling the same focal animal.

Only calls with high signal-to-noise ratios were examined. Vocalisations were analysed using SIGNAL 3.1 software package (Engineering Design,

Massachusetts), at a sampling rate of 25,000 Hz, a Frequency Resolution of 1024-point Fast Fourier Transforms (FFT) and an Analysing Bandwidth of 24.41 Hz (sampling Rate / FFT). Monitor settings produced cursor error rates of ± 5.36 msec in the time domain and ± 30.30 Hz in the frequency domain. Call features analysed are described in Table 2.1. Data of the bark call produced by males and the Pup Attraction Call (PAC) and Female Attraction Call (FAC) produced by females and Australian fur seal pups has been documented in Tripovich *et al.* (2005, 2006) and Chapter 3.

Behavioural observations were recorded to provide a context for each call. Calls were classified according to the sex of caller (adults only), type of call produced, the behavioural posturing of the caller and the intended recipients of the call. The intended recipient of the call was the animal that was in direct line of sight of the caller. Calls that were not obviously directed to a particular animal or group of animals were categorised as unclassified calls. In some instances these calls were directed to the colony and in others, these were an attempt to search for an individual within a group of animals.

The acoustic features of the bark, produced by male Australian fur seals, are described for four different behavioural categories: stationary, walking, confrontation and herding. Stationary involves the focal animal vocalising while remaining in the same position. Walking is when the vocalising seal moves in a forward direction, alternating one flipper with the other. The behavioural category, confrontation, includes the physical and non-physical interactions the focal male makes in association with other male seals. Herding involves the interactions a male makes in association with females e.g. actively chasing females or nuzzling etc.

As the data could not be normalised (using \log_2 , square root and arcsine transformations), non-parametric Kruskal-Wallis tests were used to identify any overall differences of acoustic parameters between the four behavioural contexts. Subsequently, Mann Whitney tests were used to evaluate pair-wise differences between contexts and the physical structure of vocalisations.

Table 2.1. Description of 14 variables measured in Australian fur seal vocalisations.

| Call characteristics | Description |
|--|---|
| Number of Call Parts (NP) | This describes the number of units per call. The study followed the procedure by Phillips and Stirling (2000) for this call feature. |
| Total Call Duration (DUR) | Total duration of the whole call (msec). |
| Number of call parts per call (Parts/Call) | Number of call parts divided by the Total Call Duration in seconds (parts/sec). |
| Peak Frequency start (PEAK F1-start) | This was measured from the start of the call. It describes the location of the energy band or harmonic that has the most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak. |
| Peak Frequency mid (PEAK F1-mid) | This was measured from the centre of the call. It describes the location of the energy band or harmonic that has the most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak. This call feature is also referred to as PEAK F1. |
| Peak Frequency end (PEAK F1-end) | This was measured at the end of the call. It describes the location of the energy band or harmonic that has the most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak. |
| Second Peak Frequency mid (PEAK F2) | This was measured from the centre of the call. It describes the location of the energy band or harmonic that has the second most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak. |
| Third Peak Frequency mid (PEAK F3) | This was measured from the centre of the call. It describes the location of the energy band or harmonic that has the third most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak. |
| Fourth Peak Frequency (PEAK F4) | This was measured from the centre of the call. It describes the location of the energy band or harmonic that has the fourth most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak. |
| Fundamental frequency (F_0) | Lowest visible harmonic in tonal calls (Hz). This was taken from the centre of the band. |
| Percentage of Quavering (Quav) | This is the percentage of the call that contains frequency modulation, known as quavering. |
| Duration of Unit (Dur Unit) | This describes the duration in (msec) of the short duration sound with frequencies that are harmonically related. |
| Duration of Inter-unit (Inter-unit dur) | This is the distance between two bark units (msec). This distance must not exceed 353 msec otherwise it is termed an inter-bout period |

(Tripovich et al 2005).

Minimum frequency (MIN F)

Lowest part of the call (Hz).

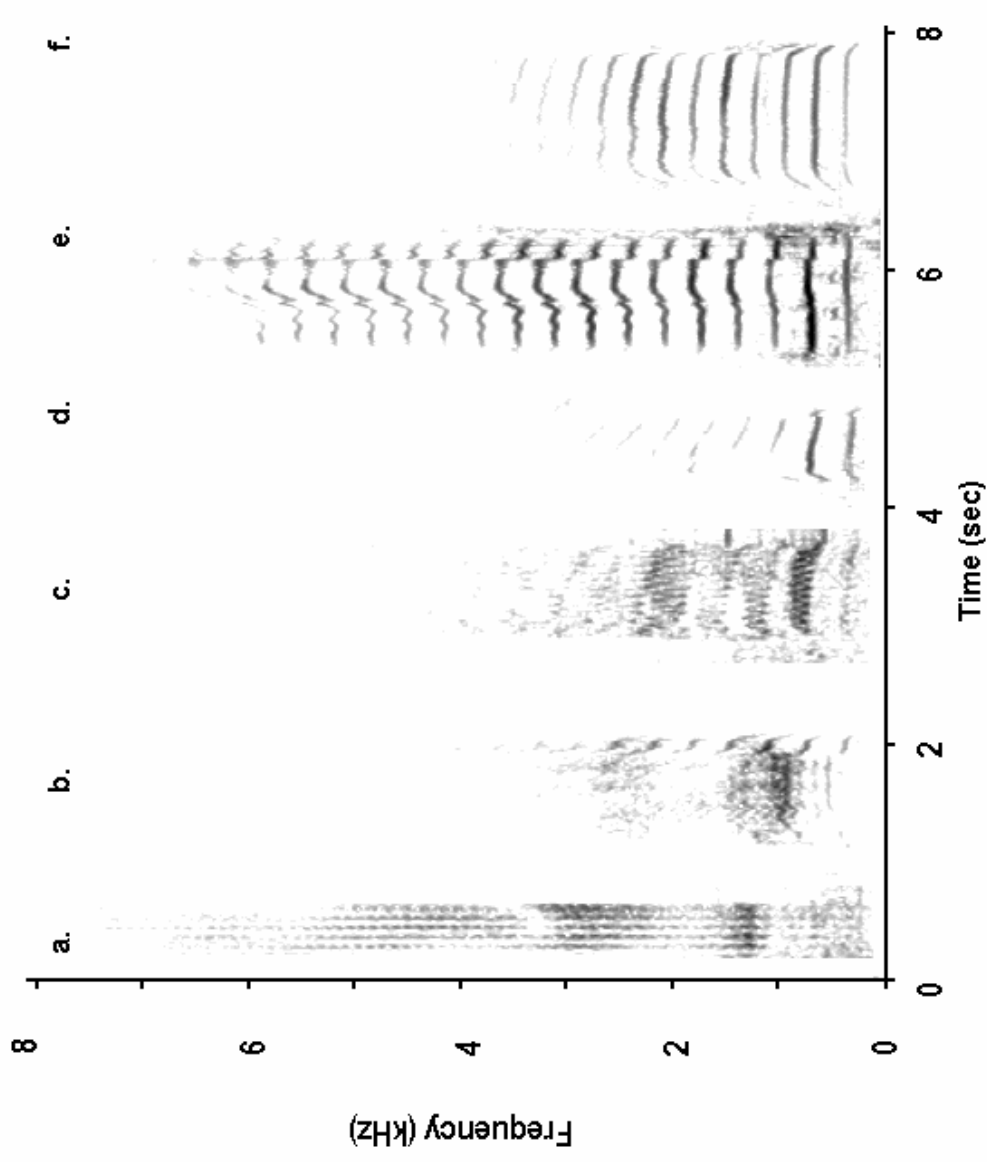


Figure 2.1. Sonogram of various types of Female Attraction Calls produced by pups and yearlings and Pup Attraction Calls produced by female Australian fur seals. From left to right: a. Pulsed Female Attraction Call produced by pup; b. Combination call (Pulsed and tonal) produced by pup; c. Tonal with FM (quavering) produced by pup, d. Tonal Female Attraction Call produced by pup, e. FAC produced by yearling; and f. Pup Attraction Call produced by females.

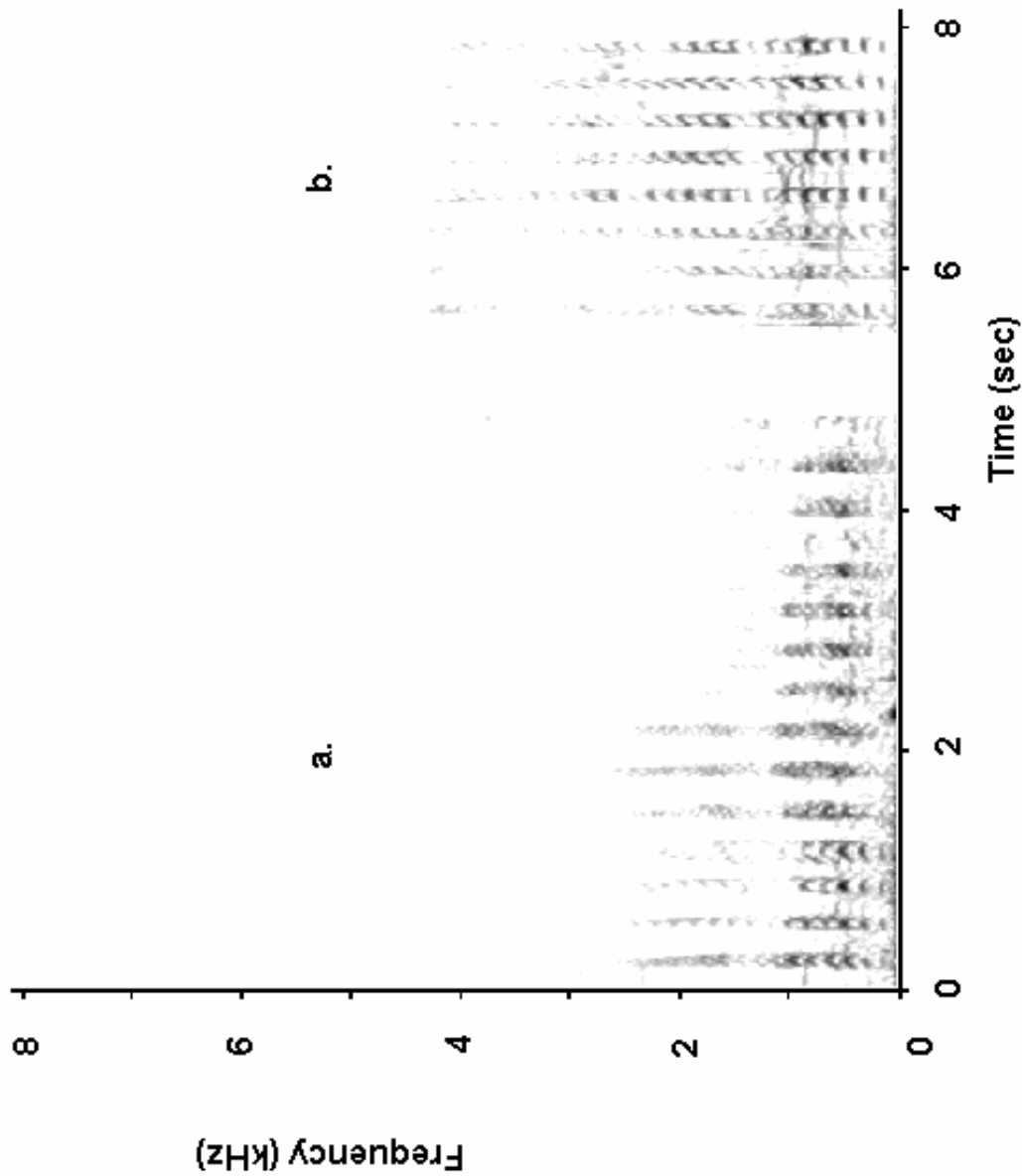


Figure 2.2. Sonogram of the bark call produced by a. female and b. male Australian fur seals.

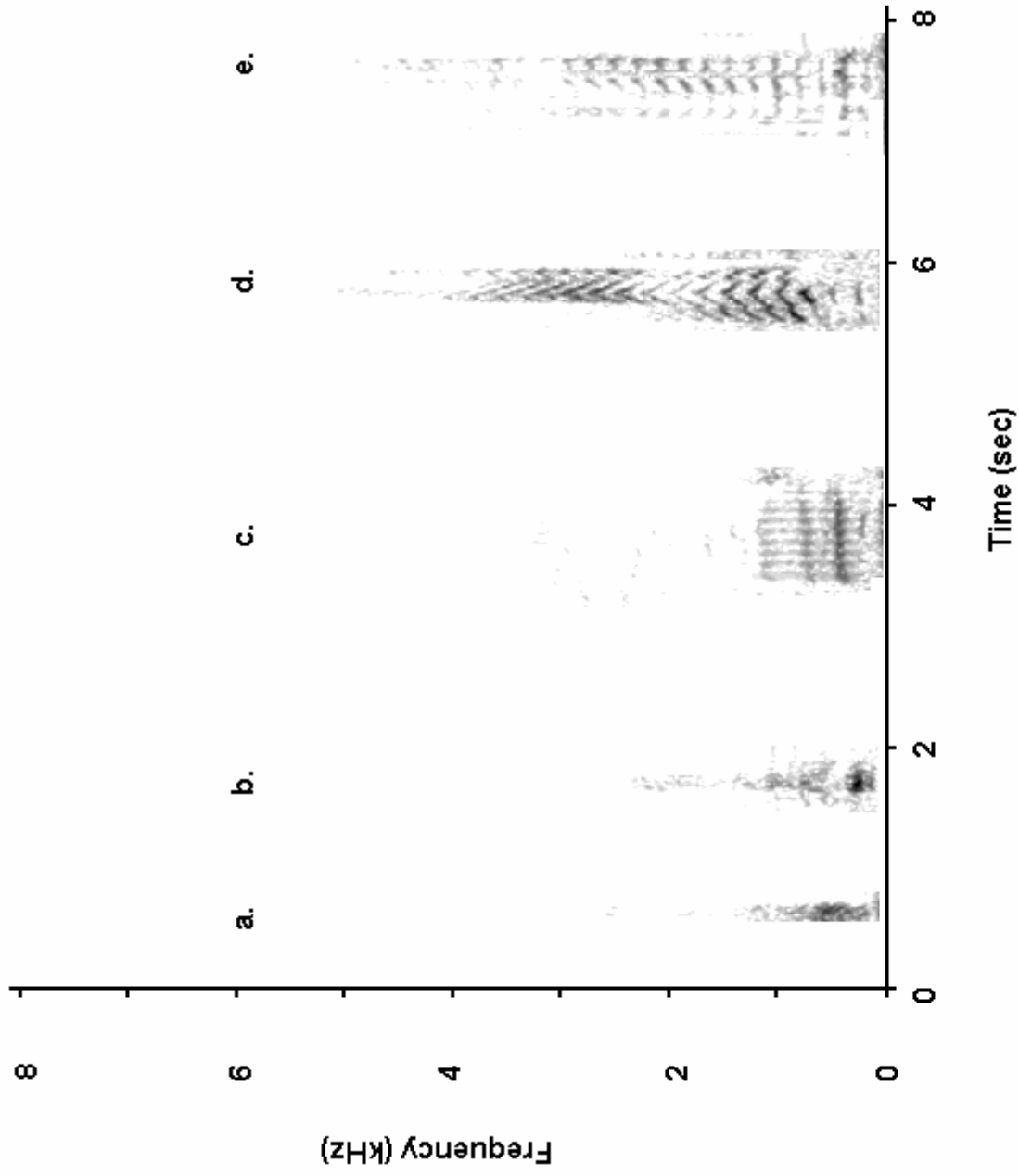


Figure 2.3. Sonogram of various call types produced by female and male Australian fur seals. a. guttural threat produced by females and b. males. c. growl produced by female Australian fur seals. d. submissive call produced by females and e. males.

2.3 Results

2.3.1 Affiliative calls

These include the FAC (pups and yearlings), the PAC (females) and the submissive call (males and females).

FAC-pups and yearlings

Australian fur seal pups and yearlings produce tonal, pulsed or combination (pulsed \pm tonal) FACs (Figure 2.1a-e) (see also Chapter 4) ($n = 90$ from 9 pups and $n = 50$ from 8 yearlings). Pup calls are relatively short (579 ± 150 msec) and composed of several parts (5.0 ± 2.6) (Table 2.2) when compared to yearling calls which are slightly longer (640 ± 193 msec) and contain less call parts (2.6 ± 1.9). A small percentage of quavering (fast frequency modulation) is present in pup calls ($16\% \pm 27$) with a notably larger percentage of quavering in FACs produced by yearlings ($52\% \pm 98$). The maximal energy band is higher in pups being at approximately harmonic three while in yearlings it is usually at harmonic two. The fundamental frequency is similar in both age groups (Table 2.2). This call was recorded when pups or yearlings were stationary, moving around the colony searching for their mothers or when interacting with females and nuzzling them (Table 2.5).

Table 2.2. Characterisation of call variables of the Female Attraction Call produced by Australian fur seals pups and yearlings.

| Female Attraction Call | PUPS | YEARLINGS |
|-------------------------------|---------------------------------|---------------------------------|
| | Mean \pm SD | Mean \pm SD |
| Sample size | n = 90 calls | n = 50 calls |
| Individuals | 9 | 8 |
| NP | 5.0 \pm 2.6 | 2.6 \pm 1.9 |
| Dur | 578.6 \pm 150.1 | 639.7 \pm 192.8 |
| Parts/Call | 9 \pm 4 | 4 \pm 3 |
| PEAK F1-start | 1333.7 \pm 611.0 | 1090.7 \pm 412.9 |
| PEAK F1-mid | 1397.3 \pm 673.6 | 1020.9 \pm 299.4 |
| PEAK F1-end | 1331.1 \pm 648.1 | 979.9 \pm 321.2 |
| PEAK F2 | 1335.8 \pm 830.3 | 1371.2 \pm 704.8 |
| PEAK F3 | 1234.5 \pm 912.6 | 1451.5 \pm 747.2 |
| F₀ | 341.8 \pm 61.9 | 334.1 \pm 61.1 |
| QUAV | 16.1 \pm 27.2 | 52.1 \pm 98.4 |

Pup Attraction Call

Female Australian fur seals produce long, frequency modulated harmonic calls (1030 \pm 279 msec) (n = 156 from 13 females) (Figure 2.1f). The majority of call energy is located in harmonic one and two (Tripovich *et al.* 2006) with a fundamental frequency of 262 \pm 35 Hz (Table 2.3). This call was observed when females were stationary, nuzzling pups, moving around the colony, returning from foraging at sea or awakening from sleep.

Table 2.3. Characterisation of calls produced by female Australian fur seals.

| Female Calls | BARK | GUTTURAL THREAT | SUBMISSIVE CALL | GROWL | PAC |
|----------------|---------------------|-------------------|-------------------|-------------------|--------------------|
| | Mean \pm SD | Mean \pm SD | Mean \pm SD | Mean \pm SD | Mean \pm SD |
| Sample Size | n = 9 calls | n =76 calls | n = 13 calls | n =25 calls | n = 156 calls |
| Individuals | 9 | 33 | 8 | 16 | 13 |
| NP | 10.2 \pm 4.8 | - | - | 10.8 \pm 5.5 | - |
| Dur | 3567.4 \pm 1842.4 | 176.9 \pm 53.0 | 857.8 \pm 597.6 | 756.0 \pm 478.1 | 1030.3 \pm 278.5 |
| Parts/Call | 3.0 \pm 0.4 | - | - | 17.6 \pm 6.0 | - |
| Dur Unit | 155.8 \pm 66.6 | - | - | - | - |
| Inter-unit Dur | 185.8 \pm 66.6 | - | - | - | - |
| F ₀ | 156.8 \pm 73.0 | - | - | - | 262.1 \pm 34.6 |
| PEAK F1 | 689.3 \pm 223.3 | 361.0 \pm 188.5 | 814.8 \pm 327.7 | 298.5 \pm 130.6 | 827.7 \pm 374.5 |
| MIN F | - | 108.5 \pm 41.0 | 209.5 \pm 50.7 | 113.4 \pm 50.9 | 178.8 \pm 44.4 |

Submissive call

The submissive call is produced by both males and females, usually as one animal is attempting to retreat from a confrontation. It is emitted as a tonal or pulsed call or a combination of both (Figure 2.3d and 2.3e). It may also contain frequency modulated regions. The duration of the submissive call is shorter in males (males: 659 ± 371 msec and females: 858 ± 598 msec) and the minimum frequency is higher in frequency (males: 256 ± 153 Hz and females: 210 ± 51 Hz) (Table 2.3 and 2.4).

2.3.2 Aggressive vocalisations

The guttural threat (males and females) and growl (females) were classified as aggressive vocalisations.

Guttural threat

The guttural threat in males and females is a short duration, low frequency call with no tonal regions (Figure 2.3a and 2.b). In males this call is exclusively used in highly aggressive interactions with other males. In females it is also used in aggressive interactions but is directed to other females, pups and yearlings (Table 2.5). This call may be produced as a single call unit or produced in a bout and may be intermixed with bark calls. Usually this call is associated with stereotypical fighting postures and displays, with males producing the guttural threat either in a forward lunge or in an upright position with a forward and rapidly directed motion of the head towards the intended male recipient. The guttural threat has a maximal energy at 214 ± 70 Hz in males and 360 ± 189 Hz in females. The minimum frequency is lower in males (Mean \pm SD = 77 ± 31 Hz) than it is females (Mean \pm SD = 109 ± 41 Hz) and slightly longer in duration in males (Mean \pm SD = 203 ± 106 msec) than females (Mean \pm SD = 177 ± 53 msec) (Table 2.3 and 2.4).

Table 2.4. Characterisation of calls produced by male Australian fur seals.

| Male Calls | BARK | GUTTURAL THREAT | SUBMISSIVE CALL |
|-----------------------|---------------------|----------------------------|----------------------------|
| | Mean ± SD | Mean ± SD | Mean ± SD |
| Sample size | n = 90 calls | n =105 calls | n = 14 calls |
| Individuals | 9 | 28 | 10 |
| NP | 19.7±12.6 | - | - |
| Dur | 5945.7 ±3917.6 | 203.0±105.6 | 658.8 ± 370.6 |
| Parts/Call | 3.3 ± 0.5 | - | - |
| Dur Unit | 136.6 ± 35.4 | - | - |
| Inter-unit Dur | 173.3 ± 50.0 | - | - |
| F₀ | 140.3 ± 24.1 | - | - |
| PEAK F1 | 514.9 ± 173.9 | 214.1± 69.5 | 545.9 ± 242.9 |
| MIN F | - | 77.0 ± 31.0 | 256.2±153.0 |

Growl

The growl is a low frequency, rapidly pulsed call with maximal energy located at 299 ± 131 Hz (Table 2.3; Figure 2.3c). It is produced by females during aggressive interactions with pups, yearlings, other females and males (Table 2.5).

2.3.3 Dual function call

Bark

The bark was classed both aggressive and affiliative, having dual functionality. In both males and females, it is produced in a series of bark units that form a bout ($n = 90$ from 9 males and $n = 9$ from 9 females) (Figure 2.2a and 2.2b). Each bark unit is rich in harmonic structure having frequency modulated regions in some calls. The fundamental frequency in both sexes is low at $140 \pm$

24 Hz for males and 157 ± 73 Hz in females (Table 2.3 and 2.4). The maximal energy band is lower in males (Mean \pm SD = 515 ± 174 Hz) than in females (Mean \pm SD = 689 ± 223 Hz) (Table 2.3 and 2.4). The bark in males is emitted during a range of both aggressive and affiliative behaviours: during copulation, herding females by chasing or nuzzling them, fighting and/or chasing other males or whilst stationary, lying down and moving around the colony presumably advertising their territorial status (Table 2.5). Barking by females was rare and observed when females were stationary, lying down or when moving around the colony.

Table 2.5. Distribution of calls made by Australian fur seals.

| CALL TYPE | Recipient of call | | | | | | TOTAL |
|--------------------------|-------------------|--------|-----------|------|--------------|--|-------|
| | Males | Female | Yearlings | Pups | Unclassified | | |
| Pups – FAC | | 20 | | 3 | 76 | | 153 |
| Yearlings – FAC | | 76 | | | 24 | | 17 |
| Females – Bark | 8 | 42 | 8 | 25 | 17 | | 12 |
| Females –Guttural threat | | 57 | 4 | 39 | | | 96 |
| Female – Submissive | | 100 | | | | | 15 |
| Females – Growl | 3 | 29 | 32 | 37 | | | 38 |
| Females – PAC | | | 2 | 4 | 93 | | 134 |
| Males – Bark | 9 | 38 | | 1 | 52 | | 185 |
| Males – Guttural threat | 100 | | | | | | 27 |
| Males – Submissive | 85 | 15 | | | | | 13 |

2.3.4 Behavioural context of the bark call

All call features except PEAK F1, F2 and F3 varied with social setting: stationary, walking, confrontation and herding (Kruskal-Wallis test - Table 2.6). Using Mann-Whitney U-tests, each call characteristic that were significant in the Kruskal-Wallis tests, were compared pair-wise, to determine significant differences between two behavioural categories (Table 2.7).

Stationary vs herding: Significant differences in all variables except the F_o were found ($P < 0.052$). The F_o was weakly non-significant ($U = 212.5$; $P = 0.052$) (Table 2.7), suggesting it may alter to a small degree.

Stationary vs walking: PEAK F4 ($U = 188.5$, $P = 0.015$) was the only call variable that differed significantly between animals that were stationary versus walking (Table 2.7).

Stationary vs confrontation: Significant differences were observed in: Parts/Call ($U = 102.5$, $P < 0.001$), Inter-unit Dur ($U = 155.5$, $P = 0.002$) and the F_o ($U = 113.5$, $P < 0.001$, Table 2.7).

Herding vs walking: NP ($U = 133.5$, $P < 0.001$), Dur ($U = 148$, $P = 0.001$), Dur Unit ($U = 164$, $P = 0.003$) and Inter-unit Dur ($U = 159$, $P = 0.002$, Table 2.7).

Herding vs confrontation: Four features varied significantly NP ($U = 163$, $P = 0.003$), Dur ($U = 167$, $P = 0.004$), Dur Unit ($U = 167.5$, $P = 0.004$) and F_o ($U = 109$, $P < 0.001$) (Table 7).

Walking vs confrontation: Only Parts/Call ($U = 170.5$, $P = 0.005$), Inter-unit Dur ($U = 197.5$, $P = 0.025$) and the F_o ($U = 82$, $P < 0.001$, Table 2.7) varied significantly.

Overall, the majority of differences in call variables occurred between males who were stationary and those who were herding females. The call features altered predominately by the different social contexts were those related to the Inter-unit Dur.

Table 2.6. The acoustic features of the bark call produced by male Australian fur seals in association with different behavioural contexts. * indicates significant variation.

| Male Calls | STATIONARY | | WALKING | | HERDING | | CONFRONTATION | | Kruskal-Wallis | | |
|-----------------------|---------------------|---------------------|---------------------|---------------------|---------------|--------------|---------------|--------------|----------------|----|---|
| | Mean \pm SD | n = 25 calls | Mean \pm SD | n = 25 calls | Mean \pm SD | n = 25 calls | Mean \pm SD | n = 25 calls | H | df | P |
| Individuals | 25 | 25 | 25 | 25 | 25 | 25 | 25 | 25 | | | |
| NP | 19.4 \pm 19.4 | 16.2 \pm 16.2 | 29.0 \pm 18.5 | 18.0 \pm 11.4 | 17.10 | 3 | 0.001* | | | | |
| Dur | 6490.3 \pm 5791.4 | 5368.5 \pm 5125.2 | 8966.4 \pm 4881.7 | 5598.5 \pm 3942.0 | 14.29 | 3 | 0.003* | | | | |
| Parts/Call | 2.9 \pm 0.3 | 3.1 \pm 0.4 | 3.2 \pm 0.4 | 3.3 \pm 0.27 | 19.99 | 3 | 0.001* | | | | |
| Dur Unit | 149.4 \pm 36.4 | 143.0 \pm 30.0 | 174.2 \pm 40.0 | 143.6 \pm 24.3 | 10.88 | 3 | 0.012* | | | | |
| Inter-unit Dur | 207.9 \pm 72.1 | 196.7 \pm 68.6 | 145.9 \pm 50.4 | 170.2 \pm 28.3 | 19.84 | 3 | 0.001* | | | | |
| F₀ | 128.1 \pm 35.9 | 126.8 \pm 25.8 | 146.5 \pm 63.0 | 175.2 \pm 46.4 | 28.14 | 3 | 0.001* | | | | |
| PEAK F1 | 731.8 \pm 457.0 | 598.0 \pm 350.1 | 549.1 \pm 264.8 | 725.5 \pm 508.4 | 2.17 | 3 | 0.539 | | | | |
| PEAK F2 | 827.9 \pm 576.7 | 451.5 \pm 187.5 | 656.3 \pm 283.2 | 694.3 \pm 580.6 | 6.31 | 3 | 0.098 | | | | |
| PEAK F3 | 941.7 \pm 632.5 | 817.4 \pm 451.0 | 638.0 \pm 449.1 | 764.6 \pm 598.2 | 3.37 | 3 | 0.338 | | | | |
| PEAK F4 | 1237.7 \pm 622.0 | 819.5 \pm 363.9 | 797.2 \pm 408.9 | 915.6 \pm 636.7 | 8.16 | 3 | 0.043* | | | | |

Table 2.7. Pair-wise comparisons of behavioural contexts using Mann Whitney tests of the bark call produced by male Australian fur seals. * indicates significant variation.

| Mann Whitney | Stationary vs Herding | | Stationary vs Walking | | Stationary vs Confrontation | | Herding vs Walking | | Herding vs Confrontation | | | |
|-----------------------|-----------------------|----------|-----------------------|---------|-----------------------------|----------|--------------------|---------|--------------------------|----------|-------|----------|
| | U | P | U | P | U | P | U | P | U | P | | |
| NP | 150 | 0.001 * | 243 | 0.180 | 308.5 | 0.942 | 133.5 | 0.001 * | 163 | 0.003 * | 239.5 | 0.159 |
| Dur | 168 | 0.005 * | 246.5 | 0.204 | 272 | 0.441 | 148 | 0.001 * | 167 | 0.004 * | 280 | 0.538 |
| Parts/Call | 169 | 0.005 * | 248 | 0.216 | 102.5 | <0.001 * | 223 | 0.084 | 219 | 0.071 | 170.5 | 0.005 * |
| Dur Unit | 193.5 | 0.020 * | 304 | 0.874 | 299.5 | 0.806 | 164 | 0.003 * | 167.5 | 0.004 * | 296.5 | 0.762 |
| Inter-unit Dur | 128 | <0.001 * | 271 | 0.430 | 155.5 | 0.002 * | 159 | 0.002 * | 217 | 0.064 | 197.5 | 0.025 * |
| F₀ | 212.5 | 0.052 | 293 | 0.710 | 113.5 | <0.001 * | 224 | 0.086 | 109 | <0.001 * | 82 | <0.001 * |
| PEAK F4 | 177.5 | 0.008 * | 188.5 | 0.015 * | 215 | 0.059 | 306.5 | 0.912 | 299 | 0.803 | 309 | 0.954 |

2.4 Discussion

Vocalisations produced by Australian fur seals are used in aggressive and affiliative contexts, with the bark call having dual functionality. The calls produced by Australian fur seals are similar in gross form and function to other fur seals but distinct differences in call characteristics and vocal repertoire size are reported. In addition, the physical structure of the bark call produced by male Australian fur seals changes during different behavioural contexts, indicating that some call features are influenced by the emotive state of the caller.

Affiliative calls

The structure of the FAC (pups and yearlings) and the PAC (females), whilst produced by varying age classes, are morphologically similar, particularly in relation to yearlings and females. This finding suggests that the FAC of younger animals may be a precursor of the adult PAC (Phillips and Stirling 2001). Further, the PAC and FAC produced by Australian fur seals are similar in gross formation to other otariid species (Fernández-Juricic *et al.* 1999; Phillips and Stirling 2000). These calls are suggested to be individually unique containing characteristics that permit calls to travel longer distances i.e. long, harmonically rich and frequency modulated (Wiley and Richards 1982) which may help relocate and reunite mothers and offspring during repeated separations (Tripovich *et al.* 2006).

The submissive call of Australian fur seals is produced when an individual is retreating from a confrontation. It is a tonal, high-pitched and frequency modulated call. The submissive call is similar in structure and function to that of South American fur seals (Phillips and Stirling 2001) and is in accordance to Morton's motivational structure theory rules, which states calls that are high-frequency, tonal sounds indicate the sender is appeasing, fearful or approaching in a friendly manner (Morton 1977). Interestingly, this call type is the only vocalisation to have features that are higher in frequency and longer in duration in females than in males. Perhaps this variation may be associated with the

perceived level of threat: the male-male confrontation being a 'high threat' encounter, while female encounters with other females and immature seals constitute a low threat situation.

Aggressive vocalisations

The guttural threat is an explosive, low frequency vocalisation, given by both male and female callers. Its overall structure is similar in males and females of this species, although there are differences in the specific call features, where male calls are slightly longer in duration and lower in frequency. In males, this call type suggests an aggressive willingness and preparedness to fight (Stirling and Warneke 1971). It is employed exclusively during high threat male-male encounters, usually at boundary lines and is suggested to be individually unique (Stirling and Warneke 1971). The seal's posture is fixed and it is assumed that the call's message is unambiguous. In females, this call is also employed during aggressive encounters, but it is directed to a wider range of recipients (i.e. pups, yearlings and other females). In contrast to the male's call, it is usually produced when an individual is in too close a proximity of a female or her pup.

In Australian fur seals, growls are exclusively produced by females in aggressive situations, being rapidly pulsed and low pitched. The calls are directed predominantly towards other females, pups and yearlings and, only on the rare occasions, towards males. In other fur seals, this call is produced by both sexes. Similarly, the full threat call (or 'territorial call'), which is reported in other male fur seals (Roux and Jouventin 1987; Phillips and Stirling 2001), is also absent in Australian fur seal bulls. Roux and Jouventin (1987) proposed that this variation was related to the differences in breeding environments (Roux and Jouventin 1987). Those species breeding on rugged terrain utilise this call, whilst those that breed on more open beaches lack the full threat call and may use other sensory modalities such as sight and smell in the recognition process (Roux and Jouventin 1987). The validity of this hypothesis was later questioned by Phillips and Stirling (2001) as Antarctic fur seals which breed on open beaches, do produce the full threat call (Page *et al.* 2002 a and b).

Dual function call

The bark produced by male Australian fur seals has dual functionality, being used in both aggressive and affiliative interactions. Dual functionality has also been suggested for the Broadcast call produced by male leopard seals, *Hydrurga leptonyx*, where the calls are proposed to function in both mate attraction and territorial defence (Rogers 1996). This is also common in many bird species, where male calls function in guarding and attracting females (Møller 1988).

The bark call is produced by all species of fur seals and sea lions (Phillips and Stirling 2001; Miller 1991) and the call appears to function generally in the same way (Phillips and Stirling 2001; Fernández-Juricic *et al.* 1999; Schusterman 1977). However, the structure of the bark differs between Otariid species. Investigations of South American fur seals, *A. australis*, suggest that their bark does not have any tonal components in the call and each bark unit is relatively short in duration (46 msec; Phillips and Stirling 2001; this study combines both males and females) while in Australian fur seals the bark has tonal regions and is much longer in duration (136.6 ± 35.4 msec in males and 155.8 ± 66.6 msec in females; present study). The bark produced by Australian fur seals has a much lower fundamental frequency, being at least 250 Hz lower than the subantarctic fur seal (Roux 1986). These differences between species may function in keeping species discrete and it is particularly important that there are significant differences between sympatrically occurring species.

Behavioural context – male bark

Barking by fur seals and sea lion males during the breeding season is frequent and has been described as being directional and repetitive, all of which may be an adaptation to the selective pressures imposed by the acoustically complex breeding environments (Peterson and Bartholomew 1969). Structural changes were also evident in the bark call of males within different social settings. The rate of delivery of the bark call altered with behavioural context, being slower when males were stationary, presumably when they were advertising their territorial status and faster when males were involved in confrontations with other males or actively herding females. Varying the acoustic structure of the bark may update recipients on the emotive state of the caller (Schusterman 1977; Miller 1991). Schusterman (1977) suggested by having graded calls reflecting the emotive state of the caller, the vocalising seal could control the movements and behavioural patterns of neighbouring territorial males, non-territorial male intruders and to some degree females (Schusterman 1977). Using a non-physical form of communication to maintain and defend a territory has obvious advantages in relation to energy conservation, particularly as males fast during the breeding season (Schusterman 1977; Fernández-Juricic *et al.* 2001).

Repertoire size

The social structure and the physical environment in which a species lives appear to shape the vocal repertoire and the type of acoustic display that it possesses (Rogers 1996; Rogers 2003). Demonstrating the association between vocal repertoire size and the mating strategy in birds and mammals is a complex issue. Conflicting results are presented in the literature where some research supports the correlation with polygyny and larger repertoire sizes (Evans and Bastian 1969) and others suggest the reverse (Catchpole 1980).

In otariids, differences in the repertoire size of certain species are reported. Australian fur seals and Californian sea lions, while both species are polygynous, are reported to have smaller sized vocal repertoires compared to

other otariids (Stirling and Warneke 1971; Peterson and Bartholomew 1969; Phillips and Stirling 2001; current study). Determination of the factors that influence vocal repertoire size is fraught with difficulty for a number of confounding reasons that include variation in call nomenclature between studies and over-classification of vocal repertoires which has led to over-representation. In addition, the taxonomy of Arctocephalines is still under review, making phylogenetic comparisons with repertoire size difficult. At present, given the information available, it is difficult to ascertain why Australian fur seals have a reduced vocal repertoire, however factors likely to influence its size may be related to breeding environment, social organisation and taxonomic position.

In summary, the vocal repertoire of Australian fur seals has several similarities in the form and function to other otariids, however, there are differences in the acoustic characteristics of calls. These differences may function in species recognition, keeping them isolated. In addition the vocal repertoire size of male Australian fur seals is smaller when compared to other fur seals. The reasons for this remain unclear but may be influenced by the breeding environment, social organisation and taxonomy. In addition, the present study found the acoustic structure of the male bark call is graded and changes with behavioural setting, reflecting parallel changes in the emotive state of the caller which may have important consequences in terms of the animal's ability to maintain and defend his territory and achieve breeding success.

CHAPTER 3

INDIVIDUAL VARIATION IN THE PUP ATTRACTION CALL PRODUCED BY FEMALE AUSTRALIAN FUR SEALS DURING EARLY LACTATION

Summary

Otariid seals (fur seals and sea lions) are colonial breeders with large numbers of females giving birth on land during a synchronous breeding period. Once pups are born, females alternate between feeding their young ashore and foraging at sea. Upon return, both mother and pup must relocate each other and it is thought to be primarily facilitated by vocal recognition. Vocalisations of thirteen female Australian fur seals, *Arctocephalus pusillus doriferus*, were recorded during the breeding seasons of December 2000 and 2001, when pups are aged from newborns to one month. The Pup Attraction Call was examined to determine whether females produce individually distinct calls which could be used by pups as a basis for vocal recognition. Potential for Individual Coding, Discriminant Function Analysis and Classification And Regression Tree analysis were used to determine which call features were important in separating individuals. Using the results from all three analyses: F_0 , MIN F and DUR were considered important in separating individuals. In 76% of cases, the PAC was classified to the correct caller, using Discriminant Function Analysis, suggesting that there is sufficient stereotypy within individual calls, and sufficient variation between them, to enable vocal recognition by pups of this species.

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3.1 Introduction

Recognition between parents and their offspring has been studied extensively in colonial species, e.g. Californian sea lions, *Zalophus californianus*, (Schusterman *et al.* 1992); Mexican free-tailed bats, *Tadarida brasiliensis mexicana*, (Balcombe and McCracken 1992); razorbills, *Alca torda*, (Insley *et al.* 2003b) and king penguins, *Aptenodytes patagonicus*, (Jouventin *et al.* 1999). In some colonial species, offspring are usually mobile at a young age and consequently are able to socialize with similar-aged conspecifics and parents must be able to recognise them when they return from foraging trips (Scherrer and Wilkinson 1993). As parental care promotes the survival of young, thus enhancing the parents' own reproductive success, selection should favor a parent-offspring recognition system (Gubernick 1981).

In pinnipeds, maternal-offspring recognition appears to be widespread, with most exhibiting some degree of recognition. However, there are some exceptions, for example a lack of maternal recognition exhibited by Hawaiian monk seals, *Monachus schauinslandi*, (Job *et al.* 1995). Various sensory modalities such as spatial, vocal and olfactory cues are also considered important in the reunion process between a mother and her pup (Riedman 1990). However, in a crowded breeding colony, acoustic signalling is thought to be more effective for long-range communication (Trillmich 1981).

Breeding and maternal care strategies among the Otariidae (fur seals and sea lions) are generally similar, with mothers giving birth at a natal colony and providing exclusive care to their own young. A few days after birth, females depart on foraging trips offshore and upon their return must relocate their own young within the colony (Riedman 1990). This process continues until weaning. Once pups are born, there is an initial period of bonding where nuzzling and vocalizing occurs between a mother and her newborn (Riedman 1990). Mothers call to pups using the call termed the Pup Attraction Call (PAC) and pups counter call using the Female Attraction Call. This period of intense vocalizing aids imprinting between a mother and her newborn pup (Riedman 1990), and occurs within a few days of birth (Charrier *et al.* 2001a).

For vocalisations to be used in individual recognition they must display stereotypy within individuals and significant variation between them (Falls 1982). Although the presence of individual variation is insufficient evidence that recognition occurs, it is the important initial stage in demonstrating a potential for the recognition process. Individuality of the PAC has been described in several otariid species (Insley *et al.* 2003b) with the overall structure of the PAC showing general similarities, although slight differences were evident between the species (Page *et al.* 2002a; Stirling and Warneke 1971).

Preliminary analysis of the PAC produced by female Australian fur seals suggested it was of a lower frequency than that produced by other *Arctocephalines* (Stirling and Warneke 1971). Detailed information on the structure of the Australian fur seal PAC, however, is lacking so that it is not possible to discern whether it is distinct from, or displays a different degree of individuality than, that of other *Arctocephalines*.

The aims of this study, therefore, were to: (1) establish detailed acoustic parameters that describe the PAC produced by female Australian fur seals; (2) determine the degree of individual variation; and (3) determine the acoustic features that contribute to the individuality of calls.

3.2 Materials and Methods

3.2.1 Study Species

Australian fur seals (*Arctocephalus pusillus doriferus*) come ashore between late October and early December, giving birth 1-2 days later (Warneke and Shaughnessy 1985; Shaughnessy and Warneke 1987). Females then alternate between suckling their young ashore and foraging out at sea, with maternal attendance patterns lasting approximately 1.7 days, and foraging trips increasing in duration as lactation progresses (Arnould and Hindell 2001). Female Australian fur seals suckle pups until they are 10 - 11 months of age (Arnould and Hindell 2001); with lactation generally varying from 9 - 12 months in the Otariidae (see exceptions Bowen 1991).



Figure 3.1. Map of the study site from which vocalisations of female Australian fur seals were recorded. Main and East Colony indicated on map.

3.2.2 Data collection and acoustic analyses

The study was conducted at a breeding colony on Kanowna Island (39° 10'S, 146° 18' E), Bass Strait, Australia (Figure 3.1). This colony has an annual production of ca2300 pups (Kirkwood *et al.* 2005), and the peak pupping date is 1 December (Warneke and Shaughnessy 1985). This island has two main colonies: East and Main Colony (Figure 3.1). Recordings were made over a one week period during two consecutive breeding seasons (10 - 16 December 2000 and 6 - 13 December 2001). Pups during this recording period were aged from newborn to one month of age.

In-air vocalisations of thirteen adult female Australian fur seals were recorded using a Sony digital tape recorder (TCD-D8) with a directional K6/ME66 Sennheiser microphone (frequency response 50 - 20,000 Hz \pm 2.5 dB). Recordings were made at a distance of 5-25 m from the vocalizing animal and were conducted during the early morning or afternoon of each day. Individuals were recorded at different locations and sampled during a single recording to avoid re-recording the same focal animal.

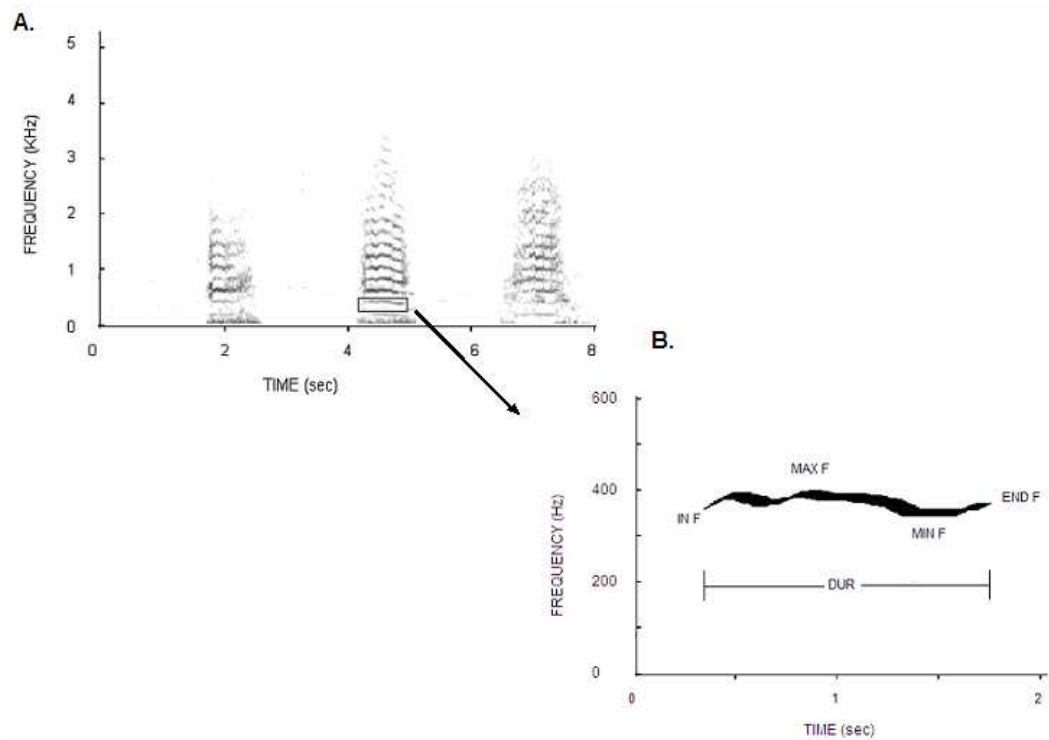


Figure 3.2 A. Sonogram of a Pup Attraction Call (PAC) produced by a female Australian fur seal. B. Harmonic band with associated call features measured from the Pup Attraction Call produced by a female Australian fur seal. Call features measured from sonograms are indicated on diagram.

Thirteen PACs from thirteen females ($n = 156$) with high signal-to-noise ratios were examined, with all calls having rich harmonic structure (Phillips and Stirling 2001). Vocalisations were analyzed using SIGNAL 3.1 software package (Engineering Design, Massachusetts), at a sampling rate of 25,000 Hz, a Frequency Resolution of 1024-point Fast Fourier Transforms (FFT) and an Analyzing Bandwidth of 24.41 Hz (sampling Rate / FFT). Monitor settings produced cursor error rates of ± 5.36 msec in the time domain and ± 25.97 Hz in the frequency domain. Call features analyzed from the PAC are described in Table 3.1 and displayed on sonograms Fig. 3.2a - b and 3.3. Measurements were made on the first harmonic since the fundamental frequency was not always entirely visible on the spectrogram.

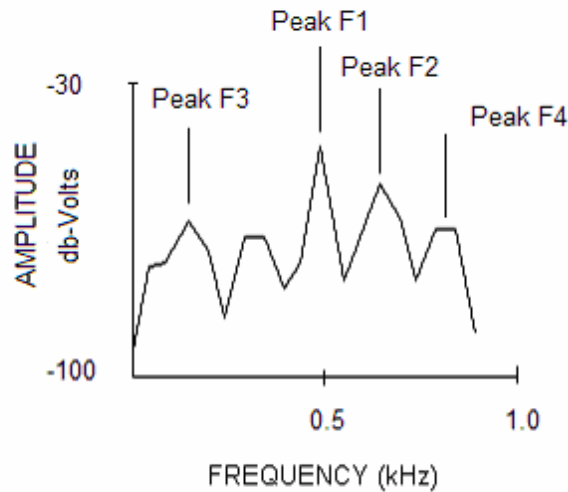


Figure 3.3. Power Spectra of a Pup Attraction Call produced by a female Australian fur seal. Peak frequency indicated on diagram.

3.2.3 Description of the Pup Attraction Call

The description of features and values characterising the PAC are presented in Tables 3.1 and 3.2. As frequency features were measured from the first harmonic band they were divided by two to represent the fundamental frequency. This ensures that results were comparable with other studies as it is more common to represent call features of the fundamental (Caudron *et al.* 1998; Collins *et al.* 2005). The features divided by two were: IN F, END F, MIN F, MAX F and MEAN F.

Table 3.1. Description of 13 variables measured from the Pup Attraction Call produced by female Australian fur seals.

| Pup Attraction Call | Description |
|--|---|
| # Fundamental frequency (F ₀) | As all calls analyzed were harmonically rich, the distance between each harmonic band should be equal. Therefore, the fundamental frequency also equals the distance between two harmonics. To keep measurements uniform, all readings of this feature from the center of the call (Hz). |
| Duration (DUR) | Duration of the first harmonic band (msec). |
| # Initial Frequency (IN F) | Gives the start frequency of the first harmonic band (Hz). |
| # End Frequency (END F) | Explains the frequency of the last point of the harmonic band (Hz). |
| # Minimum Frequency (MIN F) | Minimum frequency of the first harmonic band (Hz). |
| # Maximum Frequency (MAX F) | Maximum frequency of the first harmonic (Hz). |
| * Peak Frequency (PEAK F1) | This was measured from the center of the call. It describes the location of the energy band or harmonic that has the most energy distributed in it (Hz). When there were multiple peaks of equal energy, only the first peak was reported. |
| * Second Peak Frequency (PEAK F2) | This was measured from the center of the call. It describes the location of the energy band or harmonic that has the second most energy distributed in it (Hz). When there were multiple peaks of equal energy only the first peak was reported. |
| Third Peak Frequency (PEAK F3) | This was measured from the center of the call. It describes the location of the energy band or harmonic that has the third most energy distributed in it (Hz). When there were multiple peaks of equal energy only the first peak was reported. |
| Fourth Peak Frequency (PEAK F4) | This was measured from the center of the call. It describes the location of the energy band or harmonic that has the fourth most energy distributed in it (Hz). When there were multiple peaks of equal energy only the first peak was reported. |
| # Mean Frequency (MEAN F) | This was calculated by dividing the call into 15 intervals (i.e. 16 points). The frequency at each of these points was measured and then averaged (Hz). |
| Coefficient of Frequency Modulation (CoFM) | CoFM is as a measure of frequency modulation between consecutive intervals (Harrington 1989). In this study, sixteen data points across H1 were measured and the absolute differences in frequency between these consecutive intervals were summed and then averaged. These averages were then standardized by dividing by the mean fundamental |

frequency of the PAC and then multiplying by 100 (%).

+ Peak Energy Band

The energy band number is given to describe the location of the energy band or harmonic that has the most energy distributed in it (Hz). This was measured from the center of the call. When there were multiple peaks of equal energy only the first peak was reported.

Log transformations (log 2) were conducted to normalise variables; * Could not be normalised; + Categorical data.

3.2.4 Statistical analysis of the Pup Attraction Call

Potential for Individual Coding

Potential for Individual Coding (PIC) (Robisson *et al.* 1993; Charrier *et al.* 2002; Charrier *et al.* 2003a) analysis was used to obtain quantitative information about each variable, allowing the comparison of their potential as individuality markers in the recognition system (i.e. if they are likely or unlikely to be used in the individual recognition process) (Charrier *et al.* 2003a). This technique determines a ratio of the between-individual variation relative to the within-individual variation. The analysis first calculates the Coefficient of Variation (CV) for each call feature examined:

$$CV = (SD/Mean) \times 100$$

A corrected CV (CV*) was calculated following Sokal and Rohlf (1985):

$$CV^* = \left(1 + \frac{1}{4n}\right) \times (CV)$$

Where n = number of individuals

Both between-individuals (CV_b) and within-individuals (CV_i) CV values were calculated. The CV_b was calculated for each characteristic for all individuals. While the CV_{i grand mean} was calculated for each individual for each characteristic, and a grand mean was generated. A PIC value was used generated using the following equation:

$$PIC = CV_b / CV_{i grand mean}$$

The higher the PIC value, the greater its contribution is to the individual coding process (Charrier *et al.* 2003a).

Discriminant Function Analysis

In addition to the PIC, Discriminate Function Analysis (DFA) and Classification And Regression Tree (CART) analysis were also used. The DFA compares variation among individuals across several variables at the same time. The analysis is useful as it is likely that combinations of variables are used in the recognition process. The DFA also calculates the percentage of correctly classified calls and therefore determines the ability of the chosen variables to discriminate among individuals (Klecka 1980).

Following normal transformation, DFA was conducted on the variables identified in the PAC, to investigate inter-individual variation (Table 3.1). Peak F1 and PEAK F2 could not be normalised and were excluded from the DFA. In addition, as part of the computations involved in the DFA, the analyses determined whether any of the call parameters were redundant. If there are any redundant variables, the analysis will not proceed until one of them is removed. In the current study there were no variables that were redundant.

To examine the stability of the discriminate function a cross-validation procedure was performed on the results. The data were split into two groups; one group (training data) contained half of the replicates for each individual and was used to determine the discriminate function, while the second group (test data) contained the remaining half of the data and was used to evaluate the stability of the classification. This process was repeated swapping the training and test data, ensuring that each call replicate was used in both the test data-set and training data-set at least once during the cross-validation procedure.

Classification And Regression Tree analysis

There are several assumptions and limitations that are associated with DFA including, normality and homogeneity of variance and it is also sensitive to outliers and missing data. On the other hand, CART analysis is a non-parametric technique that does not assume any specific distribution of data (De'ath and Fabricius 2000) and is therefore more flexible in the variables that can be

incorporated in the analysis. Therefore all variables were considered in CART analysis to determine which were important in separating individual seals.

CART analyses explain differences of a single response variable by repeatedly splitting the data into more homogeneous groups, using combinations of variables (De'ath and Fabricius 2000). Each group is characterised by a value of the response variable, the number of observations and the values of the variables that describe it (De'ath and Fabricius 2000).

Similar to Van Opzeeland and Van Parijs (2004) an initial CART analysis was carried out on the sub sample (12 parameters from 7 individuals) to determine which parameters were important in driving the splits between individuals. In total, 10 variables were found to be important (all except PEAK F4 and CoFM) and these were then used to analyze the complete data-set.

3.2.5 Peak frequency distribution in the Pup Attraction Call

Preliminary analysis indicated the PACs produced by females were rich in harmonic structure but that the energy was not distributed evenly between the harmonic bands. In most individuals, the majority of energy appeared in only one band, with the occasional individual producing the majority of energy in two or three harmonic bands. Consequently, the peak distribution of energy in harmonic bands was examined in females to determine if this call feature could be used as a basis to separate them.

3.3 Results

3.3.1 Description of the Pup Attraction Call

Female Australian fur seals produce loud calls that are frequency modulated and rich in harmonic structure (Figure 3.2a – b and 3.3). Female calls were long, averaging 1030 msec in duration (n = 156 from 13 females, SD= 278.5). The majority of call energy is located in the first and second harmonic band with a fundamental frequency of 262 Hz (Table 3.2).

Table 3.2. Characterisation, Coefficients of Variations and Potential for Individual Coding values of call variables of the Pup Attraction Call produced by 13 female Australian fur seals (n=156). (All frequency variables: Fo, IN F, END F, MAX F, PEAK F1, F2, F3 & F4 are in Hz, Dur is in msec and CoFM is unitless).

| Pup Attraction Call | Mean | SD | CV_b | Mean CV_i | PIC |
|----------------------------|-------------|-----------|-----------------------|----------------------------|------------|
| F _o | 262.1 | 34.6 | 13.5 | 4.6 | 2.9 |
| DUR | 1030.3 | 278.5 | 27.6 | 19.3 | 1.4 |
| IN F | 226.2 | 50.6 | 22.8 | 15.2 | 1.5 |
| END F | 183.9 | 48.1 | 26.7 | 19.4 | 1.4 |
| MIN F | 178.8 | 44.4 | 25.3 | 18.2 | 1.4 |
| MAX F | 290.9 | 44.3 | 15.5 | 6.6 | 2.4 |
| PEAK F1 | 827.7 | 374.5 | 46.1 | 27.1 | 1.7 |
| PEAK F2 | 1055.2 | 546.0 | 52.7 | 43.6 | 1.2 |
| PEAK F3 | 1258.7 | 581.0 | 47.0 | 44.1 | 1.1 |
| PEAK F4 | 1299.5 | 608.8 | 47.8 | 45.3 | 1.1 |
| MEAN F | 251.7 | 34.9 | 14.1 | 5.2 | 2.7 |
| CoFM | 4.4 | 1.6 | 36.7 | 32.4 | 1.1 |

3.3.2 Inter-individual variation

Discriminant Function Analysis

Ten variables from the PAC were used to discriminate amongst thirteen female Australian fur seals using DFA. There were significant differences in individual PAC amongst females (Wilks' lambda = 0.01, F (120, 1054) = 6.35, P < 0.01). Discriminant Function Analysis assigned 76% of the data correctly to individual females, which is greater than would be expected by chance alone (P < 0.0001). Assigning three or more calls correctly per individual was considered significant at the P = 0.05 level. All individuals had six or more calls correctly assigned and therefore all produced individually distinct PACs (Table 3.3).

The training cross-validation procedure resulted in 81% of calls being correctly assigned (P < 0.0001), compared to the test case where 47% of the calls were correctly assigned. The probability of achieving the test percentage by chance is P < 0.01.

Table 3.3. Number of calls correctly assigned by the Discriminant Function Analysis, proportion and position of peak energy bands in the Pup Attraction Call produced by female Australian fur seal.

| Pup Attraction Call | | | |
|----------------------------|--------------------------------------|-------------------|----------------------------|
| Female # | # of calls correctly assigned | Harmonic # | Proportion of calls |
| 1 | 7 | H1 | 12 |
| 2 | 6 | H1 | 7 |
| 3 | 8 | H1 | 12 |
| 4 | 12 | H1 | 9 |
| 5 | 9 | H4 | 11 |
| 6 | 10 | H4 | 5 |
| 7 | 10 | H1 | 9 |
| 8 | 9 | H2, H4 | 10, 9 |
| 9 | 11 | H3, H4 | 7, 6 |
| 10 | 8 | H1 | 9 |
| 11 | 11 | H2 | 10 |
| 12 | 9 | H2 | 11 |
| 13 | 9 | H2 | 9 |

Classification And Regression Tree analysis

Initially a 15-node classification tree was pruned with cross-validation. As suggested by Van Opzeeland and Van Parijs (2004) and De'ath and Fabricius (2000), the 1-SE rule was adopted, this is the smallest tree for which the cross-validated error is within one standard error of the minimum and this produced a 13-node classification tree (Figure 3.4). The analysis classified 74% of the calls to individuals in the training set and 51% in the test set. This result is similar to that from the cross-validation procedure in the DFA. From all calls analyzed from this analysis there was a 26% misclassification rate in the train data-set and a 49% misclassification rate in the test data-set. In this CART the F_0 caused the first major split of the data.

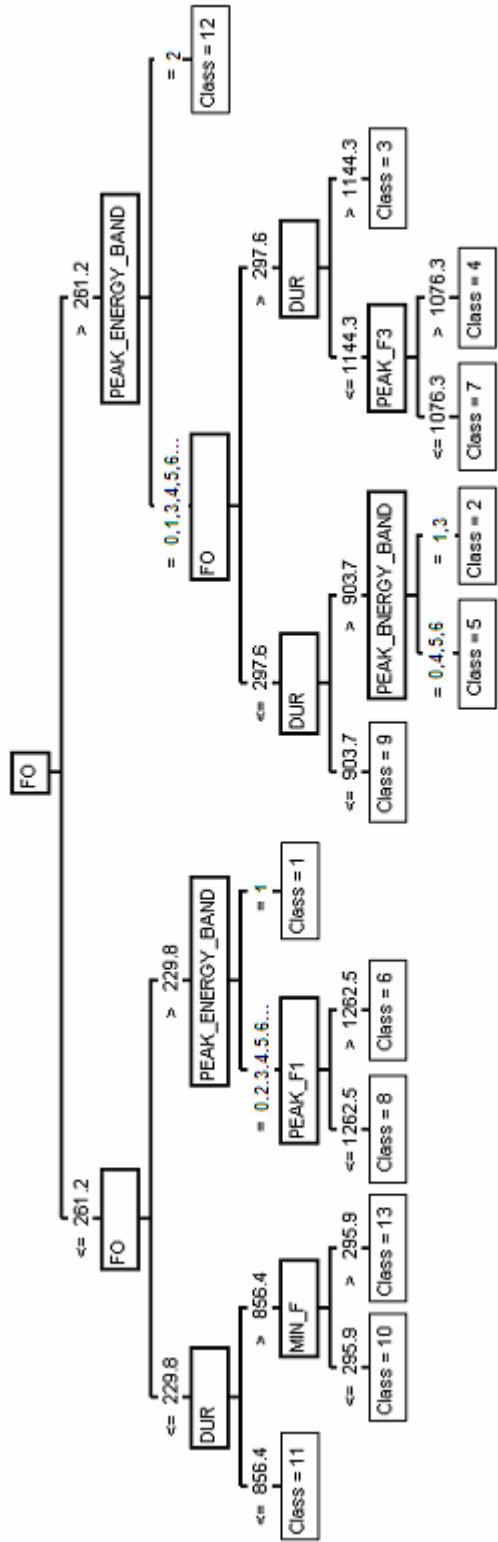


Figure 3.4. A 13-node classification tree showing how vocalisations from 13 individual female Australian fur seals split based on 10 vocal parameters.

Table 3.4. Results of the Canonical Discriminant Analysis comparing the Pup Attraction Calls of female Australian fur seals.

| Pup Attraction Call | | | |
|----------------------------|---------------|---------------|---------------|
| Acoustic Variable | Root 1 | Root 2 | Root 3 |
| F _o | -0.44 | 0.20 | -0.48 |
| DUR | 0.49 | 0.82 | 0.33 |
| IN F | 0.15 | -0.13 | -0.80 |
| END F | -0.44 | 0.49 | 0.03 |
| MIN F | 0.41 | -0.17 | -0.88 |
| MAX F | -0.42 | 0.22 | 0.16 |
| PEAK F3 | 0.07 | 0.32 | -0.61 |
| PEAK F4 | 0.01 | 0.40 | -0.37 |
| MEAN F | -0.49 | -0.42 | 0.99 |
| CoFM | -0.07 | 0.14 | -0.68 |
| Eigenvalue | 8.27 | 0.92 | 0.59 |
| Cumulative proportion | 0.77 | 0.85 | 0.91 |

3.3.3 Classification of variables

Potential for Individual Coding

From the methods of Charrier *et al.* (2003a), the PIC analysis results were used to rank the variables into 3 groups based on the variables' contribution to the coding of individual distinctiveness. The first group represented a high potential for individual coding (2.5-3.0), the second showed medium potential for individual coding (1.4-1.7) and the third group demonstrated a low potential for individual coding (1.1-1.2). F_o, Max F and Mean F (PIC = 2.9, 2.4 and 2.7, respectively) were classified as having a high potential for individual coding. DUR, IN F, END F, MIN F and PEAK F1 (PIC = 1.4, 1.5, 1.4, 1.4 and 1.7, respectively) and PEAK F2, PEAK F3, PEAK F4 and CoFM (PIC = 1.2, 1.1, 1.1 and 1.1, respectively) exhibited a medium and low potential for individual coding, respectively (Table 3.2).

Variables in the first and second groups are likely to be used in the individual recognition process as they were more individualized compared to those of the third group. Variables in the third group were considered unlikely to support any information about the emitter's identity (Charrier *et al.* 2003a).

Discriminant Function Analysis

In the DFA, Roots 1 and 2 were dominated by the following variables: DUR, MIN F, F₀, END F, MAX F and MEAN F. These variables accounted for 85% of the data's variance, indicating that they were the most important in identifying individuals. The other three variables, INF, CoFM and PEAK F3, were included in Root 3 and explained a further 6% of the variance. These variables may be important in separating individual females although to a lesser degree. Once again, PEAK F1 and PEAK F2 were not included in the DFA as they could not be normalised.

Classification And Regression Tree analysis

Important variables considered by primary splitters in this CART were, F₀, PEAK ENERGY BAND, DUR, PEAK F1, PEAK F3 and MIN F. There are differences in the variables found to be important by all three analysis techniques however all agree that the F₀, DUR and MIN F variables are all important in separating individual seals.

3.3.4 Peak frequency distribution in the PAC

Table 3.3 displays the most common peak energy band used by each individual and their frequency of occurrence. The results indicate that most individuals analyzed (Female # 1, 2, 3, 4, 7, and 10) displayed peak frequency in Harmonic One (H1) in most replicate calls. However, some individuals displayed peak energy in Harmonic Two (H2) (Female # 11, 12 and 13) and Four (Female # 5 and 6). There were also individuals (Female # 8 and 9) that equally distributed peak energy in two harmonic bands. As a result this feature alone could only discriminate 2 out of 13 females analyzed in the current study. With the majority of callers using harmonic one (H1), the results suggest that this feature is not a good characteristic to separate individuals.

3.4 Discussion

For an individual seal's call to be unique it must vary from that of other seals and be stable within the caller. This study demonstrates that the PAC produced by female Australian fur seals was correctly classified by the DFA in 76% of cases and is consistent with other previous otariid studies (74% in Antarctic fur seals, *Arctocephalus gazella*, Page *et al.* 2002a; 70% in South American fur seals, *Arctocephalus australis*, Phillips and Stirling 2000; 82% in northern fur seals, *Callorhinus ursinus*, Insley 1992). These values (moderate to high percentage DFA) imply that the vocal recognition system is highly efficient in these species. However a lower percentage DFA would be suggestive of a less efficient vocal recognition system where another mode of identification may be used such as olfaction. Call features found to be important by this study indicate that pups may rely on a combination of frequency, temporal and amplitude-related characteristics to differentiate between the calls of their mother and those of other females. Similar results were found with respect to South American, *A. australis* (Phillips and Stirling 2000) and subantarctic fur seals, *A. tropicalis* (Charrier *et al.* 2003a).

The overall structure of the PAC in Australian fur seals is generally similar to that of other otariid species. However, differences, can be noted between the species, in particular Australian fur seals have a lower fundamental frequency when compared to the other fur seals (Stirling and Warneke 1971). This feature and other call structure variations may allow seals to discriminate among species, and result in reduced inter-breeding. Although the sample size in this study was relatively small, call stereotypy in fur seals appears to be fairly consistent with other studies with similar sample sizes (DFA analysis: South American fur seals = 70%, Phillips and Stirling 2000; Antarctic fur seals = 74%, Page *et al.* 2002a; Australian fur seals = 76%, current study; subantarctic fur seals = 84%, Page *et al.* 2002a; New Zealand fur seals = 88%, Page *et al.* 2002a). Direct comparisons between studies is difficult for a number of reasons, including differences in number of replicate calls per individual, acoustical features measured and the behavioural context of recordings, all of which can affect the degree of individual distinctiveness (Bee *et al.* 2001). Nevertheless, similarities are noted in the degree of call stereotypy of the Arctocephaline species examined to date, with DFA classification rates ranging between 70-88%.

Thirteen acoustic features were analyzed in order to evaluate their importance to call individuality in female Australian fur seals. Six frequency (F_0 , MAX F, MEAN F, IN F, END F and MIN F), one temporal (DUR) and one amplitude related feature (PEAK F1) displayed high to medium PIC values. Five of the preceding features: F_0 , MEAN F, END F, MIN F and DUR and IN F, PEAK F3 and COFM were also important in the DFA. In the CART analysis: F_0 , PEAK F1, PEAK F3, MIN F and DUR were important. Given the results, CoFM, PEAK F2 and PEAK F4, were not considered valuable in discriminating individuals. Although a slightly different range of variables were identified as important for call individuality by all three methods (PIC, DFA and CART), the results from these statistics agree that the F_0 , DUR and MIN F variables were important in separating individual seals. Similar results were reported by Charrier *et al.* (2003a), where in female subantarctic fur seals, the fundamental frequency and the duration of the PAC were identified by PIC analysis, as important.

In the current study, the initial, end and minimum frequencies of the first harmonic were found to be important in separating female callers. Previous studies of

subantarctic fur seals and king penguins indicate that the start of calls may contain more information encoding an individual's identity than the rest of the call (Charrier *et al.* 2003b; Jouventin *et al.* 1999). Although the current study indicates that the features at the start of PACs were important in individual discrimination, it also suggests that the end and minimum frequencies are also important. Playback studies manipulating the PAC would be advantageous to determine whether a pup's ability to recognise its mother is based on these call features.

Previous research on call individuality, have reported duration and peak frequency to be important to an animal's identity. In South American (Phillips and Stirling 2000) and subantarctic fur seals (Charrier *et al.* 2003a) duration is a key feature in distinguishing female callers. On the other hand studies on northern fur seals, *Callorhinus ursinus*, suggested that the duration of a call explained more of an emotive or arousal state of the individual caller rather than providing cues on an individual's identity (Insley 1992). However, in the current study, duration, PEAK F1, and PEAK F3 were found to be important to individuality, while PEAK F2 and PEAK F4 were not considered to be important. This result indicates that PEAK F2 and PEAK F4 are not good individuality markers and may express the emotive state of a caller. Similarly, squirrel monkeys, *Saimiri sciureus*, have been shown to alter the peak frequency of their vocalisations with different behavioural states (Fichtel *et al.* 2001).

Frequency modulation has been shown to be an important characteristic of individual recognition in king penguins (Jouventin *et al.* 1999), and subantarctic (Charrier 2003a) and South American (Phillips and Stirling 2000) fur seals. In contrast, the frequency modulation of calls in the present study was not regarded as important in separating female callers when compared to the other variables examined. Further, it is unknown whether frequency modulation is important in individual recognition in other otariid species, as this feature has only been examined in a few studies to date. There may also be cases where the variables measured may not be totally representative of frequency modulation in calls, as was suggested by Charrier *et al.* (2003a).

In summary, vocal recognition has important consequences to pups who are trying to locate their mothers for nourishment. Based on the parent-offspring conflict theory (Trivers 1974) the burden of reunion is expected to be placed more on pups. Unsuccessful pair reunions may result in a mother's reproductive loss, however, for the pup, pair reunions ultimately mean survival or death. For that reason there are distinct selective pressures for reunion between a mother and her young (Insley 2001). Recent studies have suggested an asymmetry of recognition, however, mutual recognition has been shown in otariids (Trillmich 1981, Insley 2001, Charrier *et al.* 2002, 2003b). In this study, the PAC produced by mothers was correctly assigned in 76% of cases using DFA, which would suggest that pups have the ability to actively find their mothers. The model presented here in this study may have some shortcomings, as is suggested by the low cross validation results in both DFA and CART. This may indicate that pups discriminate female callers by different or additional call variables not included in this study. Other reasons for the low cross-validation results may be related to changes in behavioural contexts which have been shown to alter call features (Schusterman 1977), potentially reducing individual call stereotypy. To further explore this area of vocal recognition, playback studies, where a pup's ability to recognise its mother's voice, should be tested. Additionally this process would determine those features involved in the vocal recognition process.

CHAPTER 4

CHANGES IN CALL STRUCTURE OF AUSTRALIAN FUR SEAL PUPS THROUGHOUT THE MATERNAL DEPENDENCY PERIOD

Summary

Australian fur seals are colonial breeding animals that give birth on crowded rookeries. Females leave their pups unattended for extended periods while they forage at sea. On return to the colony, a mother must relocate her pup amongst the hundreds of other pups. Vocal recognition is thought to play a vital role in maintaining the mother-pup bond. In the present study, vocalisations were recorded from 36 Australian fur seal pups during four different periods, spanning most of the 10-11 month maternal dependence period. The Female Attraction Call was used to determine whether Australian fur seal pups produce individually distinct calls which could be used as a basis for vocal recognition. Potential for Individual Coding, Discriminant Function Analysis and Classification And Regression Tree analyses were used to identify the call features that were important for separating individuals. All three analytical techniques indicated that the fundamental frequency was an important call feature in the individual coding process. Furthermore Parts/Call, DUR, QUAV and features along the maximum frequency (i.e. along PEAK F1) were also considered important to recognition. In 75% of cases, the Female Attraction Call was classified to the correct caller using Discriminant Function Analysis, suggesting that there is sufficient stereotypy within individual calls, and sufficient variation between them, to enable vocal recognition by females. The maximum peak frequency, duration and the number of parts per call changed significantly with pup age, with calls getting longer in duration and lower in frequency and number of parts per call as pups matured.

A version of this chapter is in preparation for submission:

Tripovich, J.S., Canfield, R., Rogers, T.L., and Arnould, J.P.Y. 2006. Changes in call structure of Australian fur seal pups throughout the maternal dependency period. *Marine Mammal Science*, (in preparation).

4.1 Introduction

In a diverse range of taxa the filial bond is primarily based on mother-young recognition (Espmark 1971; Balcombe and McCracken 1992; and Illman *et al.* 2002). In otariid seals (Pinnipedia, Otariidae), mother-offspring recognition is particularly important as females and pups experience repeated separations and reunions that result from females alternating long foraging trips at sea with short suckling periods ashore (Riedman 1990). Therefore misdirection of maternal care is energetically costly and could endanger the survival of pups (Stirling, 1975). The reunion between mother and young may be facilitated through a multi-modal sensory system using a combination of vocal, olfactory and spatial cues (Riedman 1990). However, within a crowded breeding colony, acoustic communication is considered more efficient.

Individually stereotyped calls are a prerequisite for vocal recognition (Falls 1982). Individual variation in mother-pup calls appears present to some degree in all species of otariid seals (Insley *et al.* 2003b). In fact, otariid pup vocalisations display moderate to high levels of individuality across species (60 - 90%), suggesting that mothers can potentially recognise their offspring's calls (Insley 1992; Fernández-Juricic *et al.* 1999; Phillips and Stirling 2000; Page *et al.* 2002a). Current literature suggests that in otariids, acoustic characteristics such as the fundamental and peak frequencies tend to be more dependable markers of identity than other features (Insley *et al.* 2003b).

Australian fur seals are a temperate latitude species with a lactation period lasting 10-11 months (Arnould and Hindell 2001), though a small proportion of females may suckle their pups for a second or third year (Warneke 1982, Hume *et al.* 2001). Pups are born between mid-November and mid-December, with the peak pupping date being December 1st (Warneke and Shaughnessy 1985). As in most other otariid species, Australian fur seals aggregate in high densities during the breeding season, with the annual pup production at most colonies ranging from 1000 to 6000 individuals (Kirkwood *et al.* 2005). An effective recognition system between mother and pup, therefore, is likely to be required throughout the pup-rearing period, especially as pups move around the colony as they grow older and become more mobile.

While individual variation of the Pup Attraction Call (PAC) produced by female Australian fur seals has been reported (Tripovich *et al.* 2006), the level of call stereotypy in pup vocalisations of this species is unknown. Furthermore, while it has been documented that the structure of calls can change with growth and maturation in other vertebrates (Snowdon and Elowson 1992), there is currently little information on how vocalisations change with growth in otariid seals (Charrier *et al.* 2003c). Therefore, the aims of this study were to: 1) describe the Female Attraction Call (FAC) produced by Australian fur seal pups; (2) determine the degree of intra- and inter-individual variability; and 3) assess how these variables change as pups develop throughout the maternal dependency period.

4.2 Materials and methods

4.2.1 Data collection and acoustic analyses

The study was conducted on Kanowna Island (39° 10'S, 146° 18' E), Bass Strait, Australia. The site is a breeding colony of Australian fur seals with an annual pup production of ca 2300 individuals (Kirkwood *et al.* 2005). Data were collected opportunistically during the course of additional studies investigating the vocalisations of adult females and males. The timing of recordings and estimated pup ages were as follows: December 2000 and 2001 (newborn-1 month); January 2005 (1-2 months); April 2001 (4-5 months); and August / September 2005 (9-11 months).

In-air vocalisations of 36 Australian fur seal pups were recorded using a Sony digital tape recorder (TCD-D8) with a directional K6/ME66 Sennheiser microphone (frequency response 50 – 20,000 Hz \pm 2.5dB). Recordings were made at a distance of 5-15 m from the vocalising animal and conducted usually between 0700-1000 h and 1700-2000 h daily, when there were more individuals on the island. Each individual was sampled during a single recording session and at different areas of the colony to avoid re-recording individuals.

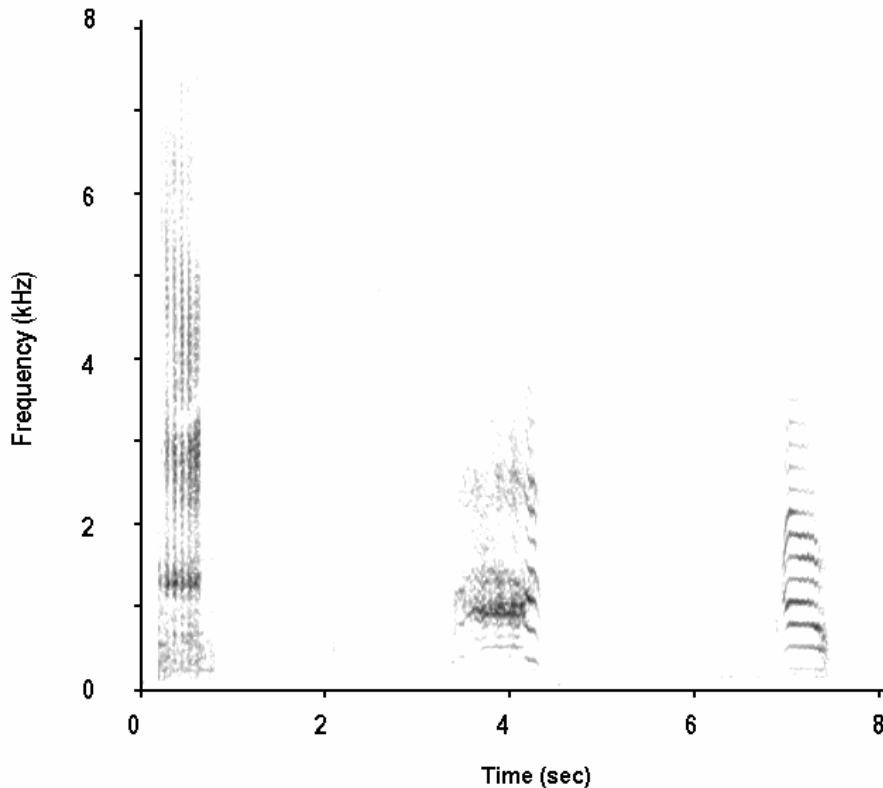


Figure 4.1. Sonogram illustrating the variety of Female Attraction Calls (FACs) produced by Australian fur seal pups. From left to right: pulsed, combination call and tonal call.

Ten FACs were analysed from each of nine pups during each of the four sampling periods, with recorded calls being tonal, pulsed or a combination of both (Figure 4.1). Only calls with high signal-to-noise ratios were used for analyses. Calls were digitized at a 25 kHz frequency sampling rate and the sonograms representing the variety of FACs are given in Figure 4.1. Call features analysed from pup vocalisations are described in Table 4.1 with characteristics 1-3 and 10-13 measured from sonograms (1024-point FFT window size, precision in frequency: 24.41 Hz). Measurements 4-9 were taken off power spectra. Monitor settings produced cursor error rates of ± 2.86 Hz in the time domain and ± 43.29 msec in the frequency domain.

Table 4.1. Description of variables measured from the Female Attraction Call produced by Australian fur seals pups.

| Female Attraction Call | Description |
|---|--|
| 1) Total Call Duration (DUR) | Total duration of the call (msec). |
| 2) Number of call parts per call (Parts/Call) | Number of call parts (Phillips and Stirling 2000) divided by the Total Call Duration in seconds (parts/sec). |
| 3) Peak Frequency start (PEAK F1-start) | This was measured from the start of the call. It describes the location of the harmonic that has the most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the lower frequency |
| 4) Peak Frequency mid (PEAK F1-mid) | This was measured from the centre of the call. It describes the location of the energy band or harmonic that has the most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak. |
| 5) Peak Frequency end (PEAK F1-end) | This was measured at the end of the call. It describes the location of the energy band or harmonic that has the most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak. |
| 6) Second Peak Frequency mid (PEAK F2) | This was measured from the centre of the call. It describes the location of the energy band or harmonic that has the second most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak. |
| 7) Third Peak Frequency mid (PEAK F3) | This was measured from the centre of the call. It describes the location of the energy band or harmonic that has the third most energy distributed in it (Hz). When there were multiple peaks of equal energy we only reported the frequency of the first peak. |
| 8) Fundamental frequency (F_0) | Lowest visible harmonic in calls containing tonal regions (Hz). This was taken from the centre of the call and measured from the middle of the harmonic band. |
| 9) Percentage of Quavering (Quav) | This is the percentage of the call that contains fast frequency modulation, also known as quavering. |
| 10) Tonal (TON) | Presence or absence of harmonic structure within a call, coded: 0 = not present; and 1 = present. |
| 11) Pulse (PULS) | Presence or absence of pulsing within a call, coded: 0 = not present; and 1 = present. |

4.2.2 Statistical analysis of the Female Attraction Call

Potential for Individual Coding

The between-individual CVs (CV_b) were calculated for characteristic 1-9, for all individuals. While the within-individual CVs (CV_i) were calculated for each individual for each characteristic, and a grand mean was generated. A corrected CV for small samples (CV^*) for each call feature was calculated following Sokal and Rohlf (1985):

$$CV^* = \left(1 + \frac{1}{4n}\right) \times \left[\left(\frac{SD}{Mean}\right) \times 100\right]$$

where n = number of individuals

The Potential for Individual Coding (PIC) (Robisson *et al.* 1993; Charrier *et al.* 2002; Charrier *et al.* 2003a) was calculated by determining a ratio of the between-individual variation relative to the within-individual variation.

A PIC value was obtained using the following equation:

$$PIC = \frac{CV_b}{CV_{igrandmean}}$$

Discriminant Function Analysis

Discriminant Function Analysis (DFA) compares variation among individuals across several variables at the same time. This analysis is useful as it is likely that combinations of variables are involved in the recognition process. DFA also calculates the percentage of correctly classified calls and therefore determines the ability of the chosen variables to discriminate among individuals (Klecka 1980). One of the assumptions of DFA is that all variables must be normally distributed. The call feature QUAV could not be normalised for the 4-5 month data-set and was therefore excluded from all age groups make the analysis consistent. Another restriction of DFA is that only continuous data can be used which eliminated the use of variables

Tonal and Pulsed in the analysis (categorical variables). Furthermore only pups that produced tonal or combination calls were used in the DFA.

To examine the stability of the discriminate function a cross-validation procedure was performed on the data-set. The data were split into two groups: one group (training data) contained half of the replicates for each individual and was used to determine the discriminate function, and the second group (test data) contained the remaining half of the data and was used to evaluate the stability of the classification. This process was repeated, swapping the training and test data-sets to ensure that each call replicate was used in both data-sets at least once during the cross-validation procedure. The results were then averaged to give a mean test and train DFA classification rate.

Classification And Regression Tree Analysis

Classification And Regression Tree (CART) analysis is a non-parametric technique that does not assume any specific distribution of data (De'ath and Fabricius 2000) and is, consequently, more accommodating in the parameters that can be included in the analysis compared with DFA. Consequently, all call types and call characteristics were used in CART analysis, therefore data from all nine pups from each age group were used. Classification trees explain differences in a single response variable by repeatedly splitting the data into more homogenous groups, using combinations of variables (De'ath and Fabricius 2000). Each group is characterised by the value of the response variable, the number of observations, and the values of the variables that describe it (De'ath and Fabricius 2000).

4.2.3 Call structure changes with age

Using multivariate analysis of variance (MANOVA) the combination of variables measured from pup calls were employed to identify any overall significant differences in acoustic characteristics between the sampling periods. A Model I analysis of variance (ANOVA) was used to determine if individual variables changed significantly with age. All variables were normalised by log 2 transformations, except DUR and NP which were normal in their raw form. In addition, least square differences of the

means were used to identify between which age groups significant differences occurred.

4.3 Results

Australian fur seal pups produce tonal, pulsed or combination (pulsed + tonal) FACs. The number parts per call reduced in number from nine parts/sec in December (SD \pm 4.0, n = 90) when pups were newborn-one month of age to two parts/sec in September (SD \pm 1.0, n = 90) when they were nine-11 months old (Table 4.2). Conversely, the duration of the FACs increased from 579 msec when pups were newborn-one month old (SD \pm 150, n = 90) to 784 msec when they were nine-11 months old (SD \pm 273, n = 90). The measurements along the first peak frequency also decreased from harmonic three to harmonic two (Table 4.2), while the second and third peak frequencies showed a high degree of variation among the sampling period, with no clear patterns forming with age. Furthermore, the fundamental frequency appeared to be fairly stable throughout this growth period, with an average fundamental frequency for all four pup ages being 334 Hz.

Table 4.2. Characterisation of the Female Attraction Call produced by Australian fur seal pups from the four recorded months. Nine pups with 10 call replicates for each age group.

| Female Attraction Call | Mean \pm SD | | | |
|-----------------------------|------------------------------|-------------------------|-----------------------------|--------------------------|
| | DEC (newborn – one month) | JAN (one-two months) | APRIL (four-five months) | SEPT (nine-11 months) |
| DUR (ms) | 578.6 \pm 150.1 | 639.7 \pm 192.8 | 569.3 \pm 179.9 | 783.8 \pm 273.1 |
| Parts/call (call parts/sec) | 8.8 \pm 4.0 | 4.2 \pm 2.9 | 4.2 \pm 3.1 | 2.1 \pm 1.0 |
| PEAK F1-start (Hz) | 1333.7 \pm 611.0 | 1090.7 \pm 412.9 | 1012.7 \pm 403.4 | 1028.3 \pm 826.6 |
| PEAK F1-mid (Hz) | 1397.3 \pm 673.6 | 1020.9 \pm 299.4 | 1081.3 \pm 488.7 | 1016.6 \pm 464.2 |
| PEAK F1-end (Hz) | 1331.1 \pm 648.1 | 979.9 \pm 321.2 | 968.2 \pm 393.4 | 923.1 \pm 401.1 |
| PEAK F2 (Hz) | 1335.8 \pm 830.3 | 1371.2 \pm 704.8 | 1251.2 \pm 618.8 | 1415.1 \pm 722.2 |
| PEAK F3 (Hz) | 1234.5 \pm 912.6 | 1451.5 \pm 747.2 | 1418.0 \pm 604.8 | 1482.0 \pm 762.7 |
| F ₀ (Hz) | 341.8 \pm 61.9 | 334.1 \pm 61.1 | 339.1 \pm 81.4 | 319.4 \pm 61.0 |
| QUAV (%) | 16.1 \pm 27.2 | 52.1 \pm 98.4 | 36.9 \pm 40.3 | 25.5 \pm 38.1 |

4.3.1 Potential for Individual Coding

All variables in all age groups examined had a PIC value greater or equal to 1.0, suggesting that all variables, to differing degrees, contribute to the individual coding process. Similar to the study conducted by Charrier *et al.* (2003a), the results from the PIC analysis for this study were used to rank the acoustic variables into three groups based on the variables' potential contribution to the coding of individual distinctiveness (Table 4.3). The first group represents a high potential for individual coding (> 2.0), the second group showed a medium potential (1.5-2.0), and the third group a low potential for individual coding (1.0-1.5). The average PIC values for all call features over the four recording periods were fairly stable with values between 1.3 and 1.6. The most likely call feature used for the individual coding process was the F₀ which had an average PIC value of 1.9 (Table 4.3).

Table 4.3. Potential for Individual Coding values of call variables of the Female Attraction Call produced by nine Australian fur seal pups (replicate calls = 10 each).

| | DEC (newborn – 1 months) | JAN (1-2 months) | APRIL (4-5 months) | SEPT (9-11 months) | Average |
|--------------------------|-----------------------------|---------------------|-----------------------|-----------------------|---------|
| Acoustic Variable | | | | | |
| DUR | 1.3 | 1.4 | 1.5 | 1.4 | 1.4 |
| Parts/call | 1.5 | 1.5 | 1.7 | 1.1 | 1.5 |
| PEAK F1-start | 1.2 | 1.2 | 2.1 | 1.9 | 1.6 |
| PEAK F1-mid | 1.3 | 1.2 | 1.4 | 1.4 | 1.3 |
| PEAK F1-end | 1.0 | 1.1 | 1.1 | 1.1 | 1.1 |
| PEAK F2 | 1.4 | 1.1 | 2.4 | 1.3 | 1.6 |
| PEAK F3 | 1.5 | 1.1 | 2.0 | 1.4 | 1.5 |
| F ₀ | 1.4 | 1.6 | 2.4 | 2.1 | 1.9 |
| QUAV | 1.0 | 1.7 | 1.0 | 1.7 | 1.4 |

4.3.2 Discriminant Function Analysis

Eight variables were used to significantly discriminate amongst the FACs of seven Australian fur seals pups within each of the four sampling periods (Table 4.4). There were significant differences in individual FAC amongst pups with the percent

correct classification ranging from 70-77% of the data (Table 4.5). Roots one, two and three from the four age groups accounted for 86-95% of the data's variance (Table 4.4). The main acoustic features separating individuals from the newborn-one month age group were: Dur, Parts/Call, PEAK F1-start, PEAK F1-mid, PEAK F3 and F_0 while one-two month old pups were best separated using the Parts/Call, and F_0 . The four-five months data-set were distinguished using Dur, Peak F1-mid, PEAK F1-end, and F_0 and the nine-11 month old pups were best separated using the Dur, Parts/Call, PEAK F2 and F_0 (Table 4.4).

Table 4.4. Results from the Discriminant Function Analysis comparing the Female Attraction Call from 28 Australian fur seal pups over the four sampling periods (replicate calls = 10 each).

| Acoustic Variable | DEC (newborn-1 month) | | | JAN (1-2 months) | | | APRIL (4-5 months) | | | SEPT (9-11 months) | | |
|------------------------------|--------------------------|-------|-------|---------------------|-------|-------|-----------------------|-------|-------|-----------------------|-------|------|
| | Root | | | Root | | | Root | | | Root | | |
| | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 |
| DUR | -0.91 | 0.06 | 0.23 | -0.27 | 0.37 | 0.41 | 0.44 | 0.62 | -0.50 | 0.17 | -1.28 | 0.13 |
| Parts/call | -0.42 | -0.96 | -0.07 | -0.87 | -0.49 | 0.10 | -0.08 | -0.29 | -0.07 | -0.01 | -0.54 | 0.32 |
| PEAK F1-start | -0.04 | -0.15 | 0.05 | 0.18 | -0.02 | -0.14 | -0.06 | 0.10 | 0.53 | -0.16 | 0.08 | 0.40 |
| PEAK F1-mid | -0.37 | -0.01 | 0.14 | 0.36 | 0.05 | 0.11 | -0.41 | -0.49 | 0.06 | -0.10 | 0.25 | 0.63 |
| PEAK F1-end | -0.32 | -0.14 | -0.09 | -0.06 | -0.24 | 0.73 | 1.07 | -0.37 | -0.81 | -0.25 | 0.14 | 0.30 |
| PEAK F2 | 0.03 | 0.15 | 0.29 | 0.12 | 0.31 | -0.04 | 0.15 | -0.10 | -0.12 | 0.43 | -0.39 | 0.54 |
| PEAK F3 | 0.28 | -0.14 | 0.53 | -0.01 | -0.03 | -0.45 | -0.11 | 0.20 | -0.10 | 0.02 | -0.44 | 0.40 |
| F₀ | 0.34 | -0.08 | 0.79 | -0.69 | 0.55 | -0.10 | 0.51 | 0.16 | 0.90 | 1.16 | -0.05 | 0.06 |
| Eigenvalue | 1.49 | 1.33 | 0.59 | 2.25 | 1.20 | 0.55 | 5.72 | 1.46 | 1.06 | 5.69 | 2.09 | 0.76 |
| Cumulative proportion | 0.37 | 0.71 | 0.86 | 0.52 | 0.79 | 0.92 | 0.64 | 0.81 | 0.92 | 0.63 | 0.86 | 0.95 |
| Wilks Lambda | 0.065 | | | 0.065 | | | 0.016 | | | 0.018 | | |
| F value (df) | 48, 259 = 4.011 | | | 48, 279 = 4.316 | | | 48, 279 = 7.607 | | | 48, 264 = 6.947 | | |
| Probability | P < 0.001 | | | P < 0.001 | | | P < 0.001 | | | P < 0.001 | | |

Table 4.5. The percentage of Female Attraction Calls correctly classified by the Discriminant Function Analysis and Classification And Regression Tree analysis of Australian fur seal pups (replicate calls = 10 each).

| | DEC (newborn – 1 month) | JAN (1-2 months) | APRIL (4-5 months) | SEPT (9-11 months) | Average |
|------------------------------------|----------------------------|---------------------|-----------------------|-----------------------|---------|
| Correct Classification Rate | | | | | |
| DFA (N = 36 pups) | | | | | |
| Overall data-set | 70% | 76% | 77% | 77% | 75% |
| Cross-validation training data-set | 82% | 79% | 86% | 91% | 85% |
| Cross-validation test data-set | 49% | 39% | 65% | 68% | 55% |
| CART analysis (N = 28 pups) | | | | | |
| Cross-validation training data-set | 60% | 66% | 64% | 71% | 65% |
| Cross-validation test data-set | 40% | 49% | 53% | 52% | 49% |

4.3.3 Classification And Regression Tree analysis

A classification tree was created for each season. Each tree was then pruned using the 1-SE rule to produce the smallest tree for which the cross-validated error was within one standard error of the minimum (Van Opzeeland and Van Parijs 2004, De'ath and Fabricius 2000). This produced an 8-node classification tree for newborn-one month old pups, a 7-node classification tree for the 1-2 month, an 8-node tree for the 4-5 month old pups, and a 9-node tree for the 9-11 month old pups (Figures 4.2-4.5).

Important variables considered by primary splitters in the CART analysis for the newborn-one month old pups were F_o , PEAK F1-mid, Parts/Call, and QUAV; for one-two month olds F_o , QUAV; Parts/Call, PULS, and PEAK F1-end; for four-five month olds F_o , PEAK F1-start, PEAK F1-mid, and QUAV; and for nine-11 month old pups F_o , QUAV, PEAK F1-start, PEAK F1-mid, TON, and DUR (Figures 4.2-4.5).

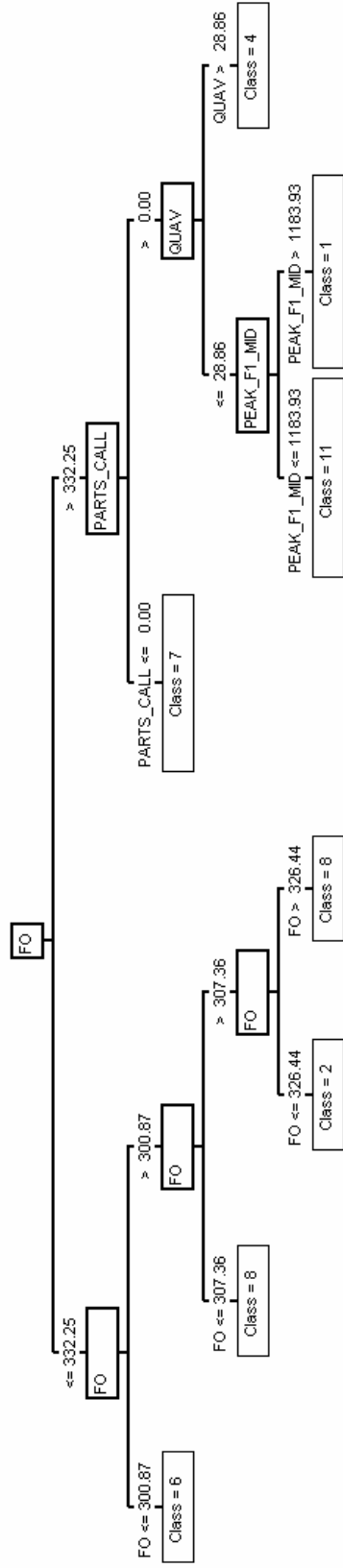


Figure 4.2. An 8-node classification tree showing how vocalisations from nine Australian fur seals sampled during December (pups: newborn - one month old) split based on 11 parameters.

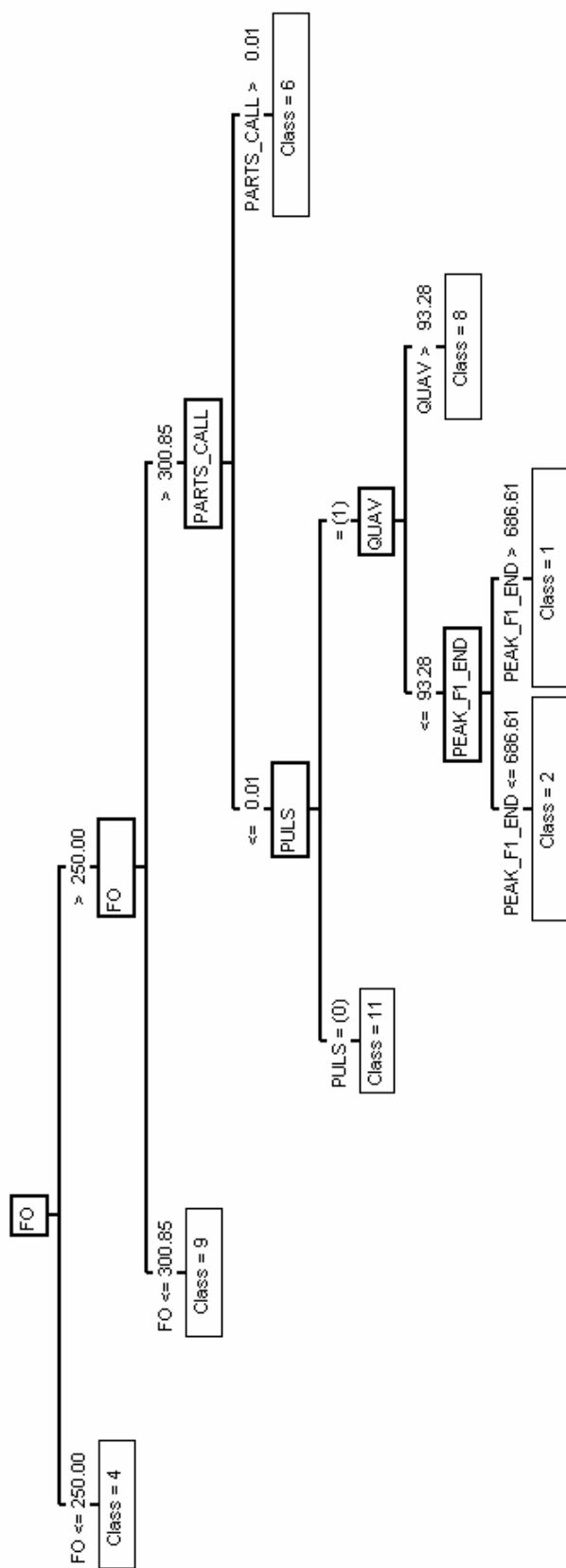


Figure 4.3. A 7-node classification tree showing how vocalisations from nine Australian fur seals sampled from January (pups aged: one-two months), split based on 11 parameters.

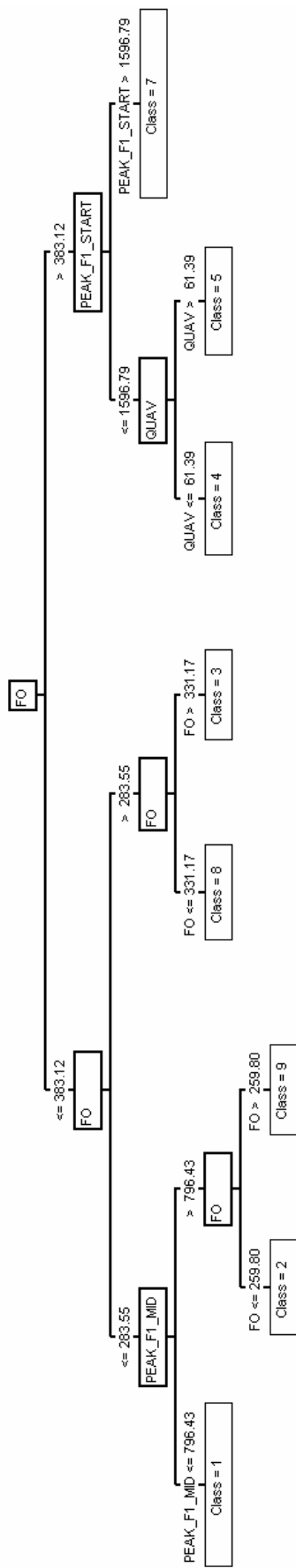


Figure 4.4. An 8-node classification tree showing how vocalisations from nine Australian fur seals sampled during April (pups: four-five months old) split based on 11 parameters.

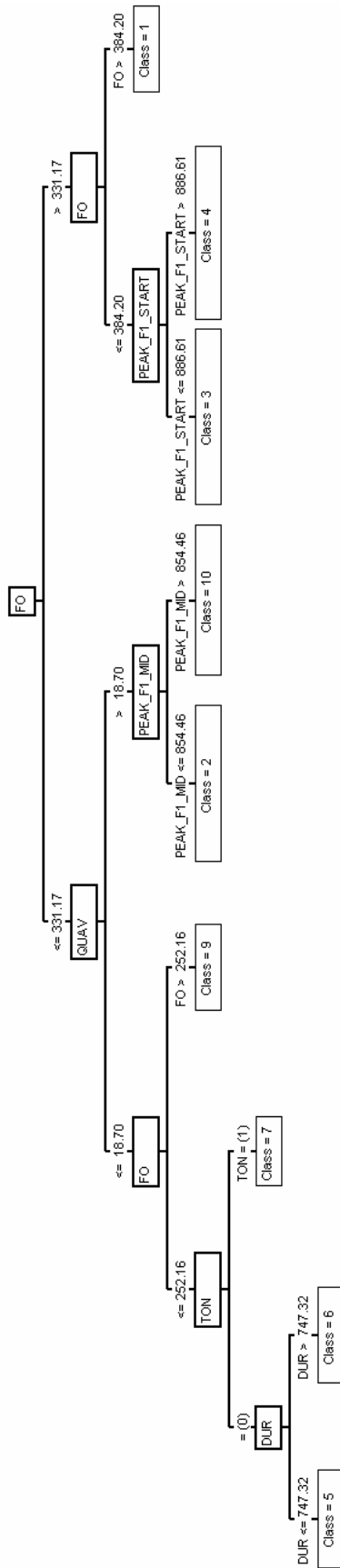


Figure 4.5. A 9-node classification tree showing how vocalisations from nine Australian fur seals sampled during September (pups: nine-11 months) split based on 11 parameters.

4.3.4 Call structure changes with age

MANOVAs revealed significant acoustic differences in vocalisations between age groups (Wilks Lambda = 0.458, $F(24, 879) = 11.33$, $P < 0.001$). ANOVAs further examined individual call variables separately over the four age groups and demonstrated that all call features (except PEAK F2 and F_0) exhibited significant differences between groups (Figure 4.6; Table 4.6).

Table 4.6. Examining the differences in call features for the Female Attraction Call produced by Australian fur seal pups, across the different age groups. Sample sizes for acoustic variables may vary as not all features were present in all calls. *Significant at $P < 0.05$.

| ANOVA | | | |
|-------------------|-------|--------|---------|
| Acoustic Variable | F | df | P |
| DUR | 21.19 | 3,356 | 0.001 * |
| Parts/call | 82.38 | 3, 356 | 0.001 * |
| PEAK F1-start | 8.14 | 3, 356 | 0.001 * |
| PEAK F1-mid | 7.87 | 3, 356 | 0.001 * |
| PEAK F1-end | 11.17 | 3, 356 | 0.001 * |
| PEAK F2 | 0.52 | 3, 356 | 0.522 |
| PEAK F3 | 3.73 | 3, 356 | 0.011 * |
| F_0 | 2.05 | 3, 310 | 0.108 |

Least square differences of the means were used to identify between which age groups significant differences occurred. DUR was stable from newborn to four-five months of age, then calls became significantly longer by nine-11 months of age (Figure 4.6.1). Parts/Call decreased significantly between newborn-one month and one-two month old pups, and then plateaued in pups aged four-five months and again decreased between four-five months and nine-11 months of age (Fig. 4.6.2). Similar trends were noted in PEAK F1 – start, -mid, and -end where there were initial decreases in the values of these call features from newborn-one month to one-two months of age followed by a stabilisation through to nine-11 months of age (Figs. 4.6.3-4.6.7). While in PEAK F3, there was an increase from newborn-one month to one-two month, there was also a stabilisation period after this age through to nine-11 months.

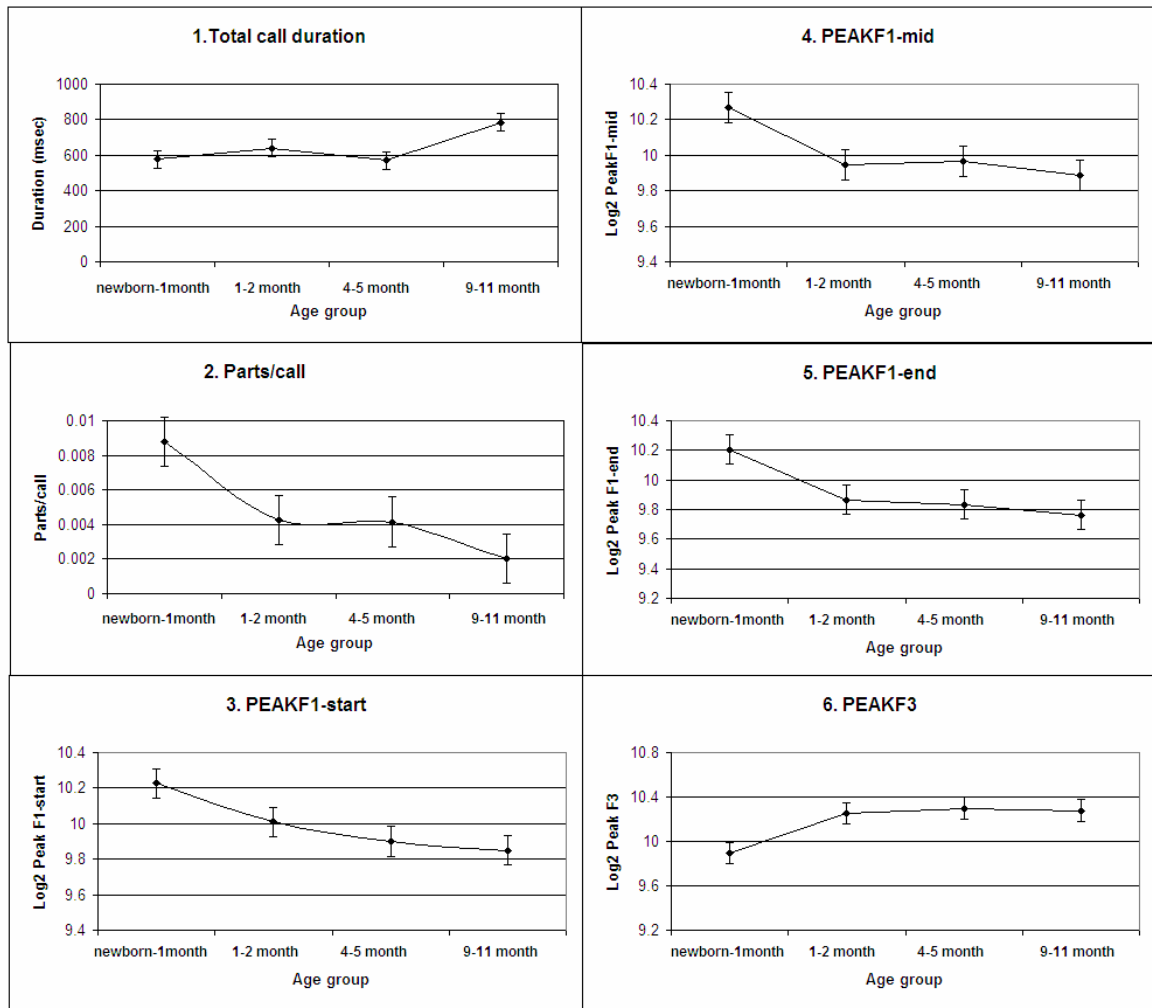


Figure 4.6. Differences in call features in Australian fur seal pups over the four recorded age groups, using ANOVA.

4.4 Discussion

Female otariids studied to date have the ability to recognise their own pups through the use of vocalisations (Insley *et al.* 2003b). Results from this study further support this trend in Australian fur seals. The FACs of pups exhibited sufficient stereotypy within callers and significant variation between individuals to support the vocal recognition process by females. This call varies in its structure between individuals, with some pups emitting FACs composed of several call parts and other pups emitting a single part tonal FAC. Similarities in the overall call structure of the FAC are observed between fur seal species, and this call type is suggested to be the precursor to the adult female Pup Attraction Call (PAC) used by mothers to locate their pups (Phillips

and Stirling 2001). In addition, the results of the present study indicate that while calls are stereotyped at a young age, the calls themselves undergo structural modifications as pup's age. These modifications are known to be associated with growth and maturational changes (Snowdon and Elowson 1992).

To investigate vocal individuality in Australian fur seal pups, three analytical techniques were employed: PIC; DFA; and CART analyses. All three techniques were used, based on different reasoning and merit. Both PIC and DFA are more traditional techniques and facilitate the comparison between otariid species. While CART analysis has not been used with significant frequency to date in pinniped vocal studies, it has the advantage of greater flexibility in the parameters that can be included in the analysis, and thus permits the incorporation of more call features. Therefore, to facilitate maximum use of measurable call features and comparison of Australian fur seals with other species, the decision to utilise all three techniques was made. This study found that the F_0 , Parts/Call, DUR, QUAV, and features along the maximum peak frequency of FACs produced by Australian fur seal pups were important to individual call identity in Australian fur seal pups. However, the F_0 was the most likely call feature to be used in separating individuals. This result is consistent with other bird and mammalian studies (Tooze *et al.* 1990, Mathevon 1996, Jouventin *et al.* 1999). The fundamental frequency did not change significantly with age in this study, suggesting that it may be stable during the first year of a seal's life, allowing mothers to identify their young throughout the maternal dependence period, although this theory is speculative given that the study did not follow known individuals over time. It is also suggestive that the vocal apparatus producing the fundamental frequency may not change until seals undergo sexual maturity, this usually occurs when seals are 4 years of age (Warneke and Shaughnessy 1985). Interestingly, this finding is not consistent with Charriers' (*et al.* 2003c) study on subantarctic fur seal pups, where the fundamental frequency of FACs changed with age from newborn to seven months of age. This difference between the two studies may be related to species-specific traits or differing sampling techniques: longitudinal (i.e., following the same individual over time) in subantarctic fur seals and cross-sectional (i.e. sampling different individuals from the specific

age group) in Australian fur seals. Additionally, as stated above, the fundamental frequency does not appear to change from newborn to 9-11 months of age, nor does it appear to change up to the yearling stage (Tripovich unpublished data). However, when examining the PAC of adult females, for which the FAC is believed to be a precursor (Phillips and Stirling 2001), the fundamental frequency is significantly lower at 262 Hz (Tripovich *et al.* 2006) than that calculated for pups (334 Hz). Therefore, a change in the fundamental frequency does occur, but must take place somewhere between yearlings and adult females (which are reproductively active at 4 years) (Warneke and Shaughnessy 1985).

As young animals grow and adopt their adult form, their vocal anatomy changes, causing vocal modifications. Call stereotypy appears established in pups examined in the present study, with changes in vocal structure evident in pups aged between birth and 9-11 months of age. In particular, the duration of calls increased, the number of parts per call decreased, and the maximal energy decreased in frequency over time. During the period between birth and 7-9 months of age, Australian fur seal pups triple in weight (Arnould and Hindell 2002) and undergo substantial growth changes. Changes to body structures associated with vocalisations may occur and impact on vocal production. Snowdown and Elowson (1992) suggest that the lengthening of vocal cords may result in lowering of the frequency of vocalisations while the duration of calls may increase due to increased lung capacity. Such an increase in call duration with age has been found in the 'twitter' calls of squirrel monkeys, *Saimiri sciureus*, and the vocalisations produced by French Alpine goats, *Capra hircus*, (Hammerschimdt *et al.* 2001 and Lenhardt 1977). In the present study, maximal energy was also reported to decrease in frequency with pup age, which is similar to results obtained in subantarctic fur seals (Charrier *et al.* 2003c).

In the present study the number of individuals (and replicate calls per individual) for each sampling period was kept constant in an attempt to reduce the effects of sample size on the percent correct classification score between age groups. Results from previous studies have shown that the percent correct classification scores will increase as the number of individuals decreases and the number of calls per individual increases (Bee *et al.* 2001).

The low cross validation results compared with the overall results from the DFA suggest that there are some weaknesses in the model. There may be other acoustic variables that could be involved in discriminating among individuals (not examined by the present study). Alternatively, intra-individual variation may have been related to differences in the emotive state or sex-related structural differences. Sex-related growth differences have been shown in Australian fur seals (Arnould and Hindell 2002), with male pups being heavier and gaining weight faster than female pups. In the present study, however, pups were not handled so their sex could not be determined. Therefore, the possible effect of sex on the pup vocalisations can not be assessed with the current data. Lastly, given the study was opportunistic in style, the sampling regime may not account for differences that may have occurred across the year.

In summary, the FAC produced by Australian fur seal pups contain enough information to allow mothers to recognise their offspring. Whether this process actually occurs in nature remains unclear, but is likely given that the FAC on average was classified in 75% of cases using DFA. Furthermore, changes in one or more call characteristics were demonstrated in each age group investigated, indicating that pups undergo vocal changes up to 11 months and possibly beyond this age. However, long-term recognition (i.e., over the lactation period) using the FAC may be possible via the fundamental frequency which appears to remain fairly constant during this period. This study also supports the theory put forward in other studies that recognition of offspring by females may be facilitated by mothers learning subsequent versions of their pups' calls as they grow older (Charrier *et al.* 2003c). In addition, increases in duration, decreases in the number of parts per call and the lowering of the frequency of the peak energy band in FACs as Australian fur seal pups age is suggested to be related to growth and maturational changes.

Investigations using playback studies examining how mothers recognise their offspring are recommended. By using artificially modified calls the specific characteristics of vocalisations could be investigated to reveal the importance of each parameter in recognition. It would also be interesting to follow known pups throughout the lactation period to establish if similar changes in call characteristics occur from birth to weaning.

CHAPTER 5

SPECIES-SPECIFIC CHARACTERISTICS AND INDIVIDUAL VARIATION OF THE BARK CALL PRODUCED BY MALE AUSTRALIAN FUR SEALS, *ARCTOCEPHALUS PUSILLUS DORIFERUS*

Summary

Australian fur seals, *Arctocephalus pusillus doriferus*, are colonial breeding animals forming dense social groups during the breeding season. During this time, males establish and defend territories through physical conflicts, stereotyped posturing and vocalisations. While vocalisations are suggested to play an important role in male recognition systems, they have received little attention. Recordings of nine adult male Australian fur seals were made during the 2000 and 2001 breeding seasons at Kanowna Island (39° 10'S, 146° 18' E), Bass Strait, Australia. The in-air bark vocalisations of territory-holding males were used to characterise the bark call and to determine whether males produce individually distinct calls, which could be used as a basis for vocal recognition. Seventeen frequency and temporal variables were measured from a total of 162 barks from nine individual males. The bark series was more reliably classified (83%) to the correct caller compared to the bark unit. This was assigned with less certainty (68%), although the classification was still relatively high. Findings from this study indicate that there is sufficient stereotypy within individual calls, and sufficient variation between them, to enable vocal recognition in male Australian fur seals.

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5.1 Introduction

Vocal recognition has been investigated in numerous bird and mammal species occurring on several different levels; parent-offspring recognition, intra-sexual and inter-specific recognition (Espmark, 1971; Frommolt *et al.* 2003; Jouventin *et al.* 1999; Roux and Jouventin 1987; Stoddard *et al.* 1990). For vocalisations to permit individual recognition between conspecifics, they must display stereotypy within individual calls and significant variation between them (Falls 1982). At the intra-sexual level, neighbour-stranger discrimination has been identified as a recognition process whereby territorial animals are able to discern and respond differently to the vocalisations of intruding stranger males compared to those of neighbours (Bee and Gerhardt 2001a and 2001b; Roux and Jouventin 1987) and is known as the 'dear enemy effect'. The ability of territorial individuals to distinguish between neighbours and strangers has significant advantages by reducing the need for costly fighting and vigilance (Bee and Gerhardt 2001b). Falls (1982) suggests that vocal discrimination occurs through either adaptive learning or habituation, whereas Schusterman *et al.* (2000) suggest that the dear enemy effect is unlikely to be the result of the habituation because the effect spans multiple breeding seasons. It is suggested to be a result of grouping familiar males into a single class whose members are interchangeable.

Otariid seals (fur seals and sea lions) are some of the most sexually dimorphic mammal species, with adult males being up to four times larger than adult females (Riedman 1990). With some minor exceptions (see Boness 1991), the mating system generally involves successful males holding a territory within which females give birth, come into oestrus and mate with the territory-holding male (resource defence polygyny; Riedman 1990). Competition among males for territories can be extreme and large size confers advantages during these conflicts (Warneke and Shaughnessy 1985).

As male otariids fast throughout the breeding season, adopting strategies to conserve energy may be important for successful territory tenure (Arnould and Duck 1997). Previous studies have found that otariid males will fight most rigorously during the period of territory establishment and fighting between neighbouring males is less frequent when boundary areas are

recognised (Roux and Jouventin 1987). Once established, the use of non-physical techniques to maintain boundaries becomes important in conserving energy expenditure and males use ritualised posturing displays and vocalisations to advertise their status (Fernández-Juricic *et al.* 1999; Warneke and Shaughnessy 1985). Therefore, vocal recognition or the ability to distinguish neighbours from intruding challengers (i.e. potential threats) may be of critical importance for conserving energy expenditure and minimising the number of violent conflicts. Indeed, individual variation in male vocalisations, a precursor to neighbour-stranger discrimination, has been statistically demonstrated in the subantarctic fur seal, *Arctocephalus tropicalis*, (Roux and Jouventin 1987) and South American sea lion, *Otaria flavescens*, (Fernández-Juricic *et al.* 1999) (see Insley *et al.* 2003b).

The Australian fur seal, *A. pusillus doriferus*, is the largest fur seal species and differs from other Arctocephalines by displaying numerous sea lion behavioural traits. It has the terrestrial gait of a sea lion and is thigmotactic, tolerating a high degree of bodily contact (Warneke and Shaughnessy 1985). Stirling and Warneke (1971) found the male Australian fur seal to have a reduced repertoire of vocalisations, producing up to three types of calls. This is in comparison with other fur seal species that produce up to seven call types (Phillips and Stirling 2001). In male Australian fur seals, it has been suggested that two call types are used for the maintenance and defence of territories (the bark and adult male guttural threat), and another which is produced in a submissive context (Stirling and Warneke 1971). Barks form the major component of a male's vocal repertoire and can be heard constantly during the breeding season. The bark is suggested to indicate sexual interest, affirmation of territory boundaries and territorial status. The bark call has previously been characterised (Stirling and Warneke 1971), however, only two variables were used to describe a total of ten calls. Furthermore, this study also suggested that Australian fur seals have the ability to discriminate individuals based on their vocalisations. However, individual variation was not documented.

Therefore, the aims of this study were to: 1) establish detailed parameters that describe the bark call produced by male Australian fur seals; 2) determine the degree of individual variability; (3) determine the acoustic variables contributing to individual variation; (4) determine whether call

repetition (i.e. bark series versus bark units) increases caller predictability; and (5) compare call variability and features to other otariid species.

5.2 Materials and Methods

5.2.1 Data Collection

Vocalisations of nine territorial male Australian fur seals of similar size were made on Kanowna Island (39° 10'S, 146° 18' E), Bass Strait, Australia, during the December 2000 (n=8) and 2001 (n=1) breeding seasons.

In-air sound recordings were made using a Sony digital tape recorder (TCD-D8) with a directional K6/ME66 Sennheiser microphone (frequency response 50 – 20,000 Hz \pm 2.5 dB). Recordings were made at a distance of 5-25 m from the vocalising animal and conducted during the early morning or afternoon of each day. Individuals were identified through natural scarring or markings and sampled during a single recording session, with sites varied to avoid re-recording the same focal animal.

5.2.2 Definitions

Calls were termed barks according to the descriptions given by Stirling and Warneke (1971). Barks were further defined into bark units and bark series (Figure 5.1a). A bark unit is a short duration sound with frequencies harmonically related. Bark units occur in repetition forming a 'bout' which is referred to as a bark series (Figure 5.1a). Bark series are separated from one another using the log-survivorship plot (Slater 1974, Slater and Lester 1982). From this plot the Bout Criterion Interval (BCI) is generated, which gives the minimum distance needed to separate bark series. The BCI value was found to be 336msec (Tripovich 1999) with an added 5% buffer to minimise misclassifying inter-unit durations as inter-bout periods, obtaining a BCI of 353 msec. Therefore, each bark unit separated by a shorter duration pause (less than 353 msec) is called an Inter-unit duration (Figure 5.1a). Bark series separated by longer duration pauses (greater than 353 msec) are termed inter-bout periods (Figure 5.1a).

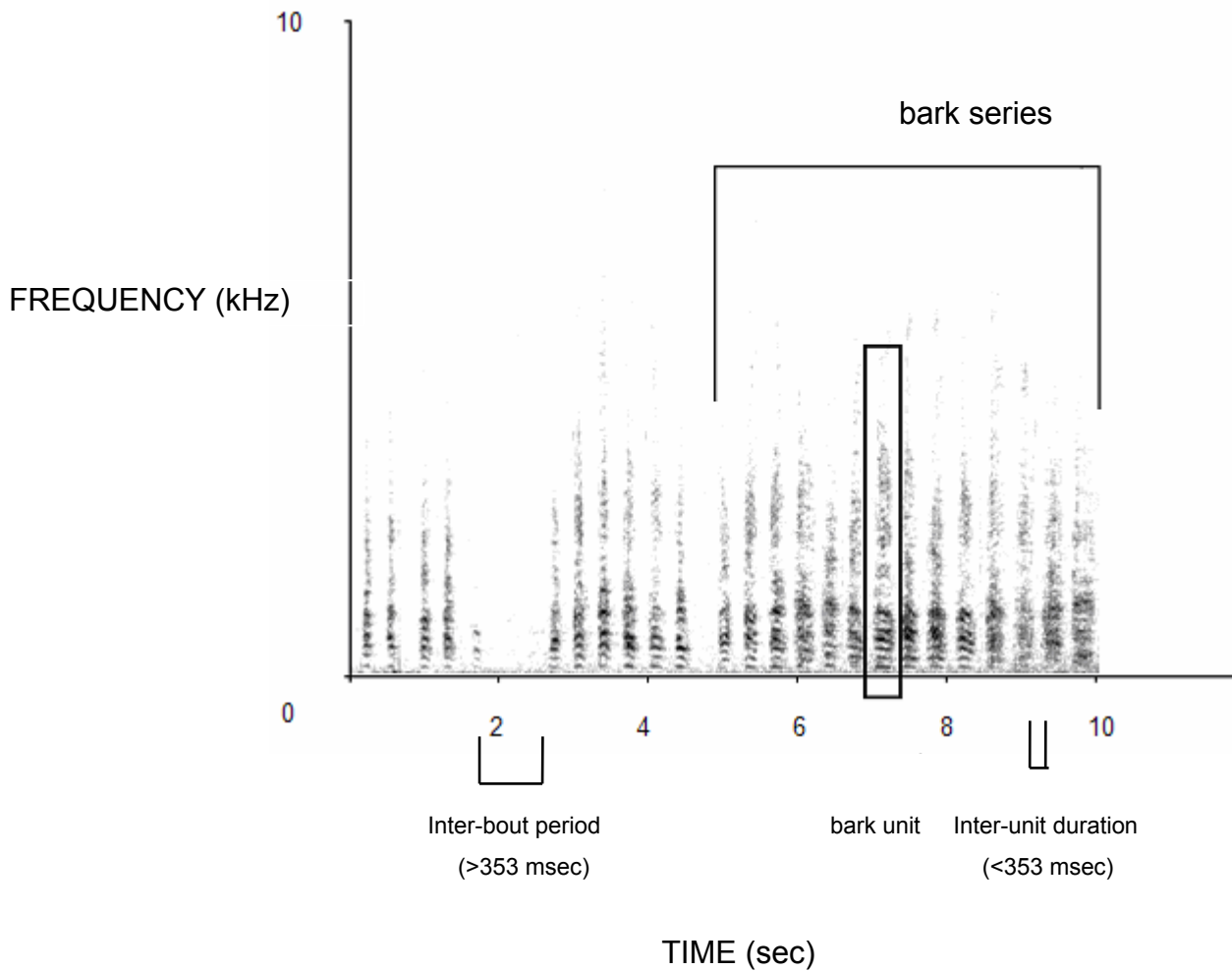


Figure 5.1a. Sonogram of a bark call produced by an adult male Australian fur seal. Call features measured from sonograms are indicated on diagram.

5.2.3 Acoustic Analysis

Only recordings with high signal-to-noise ratios were used for analysis. Characteristics measured from the harmonic band were taken from the first harmonic rather than the fundamental frequency, as it was more clearly represented in sonograms. Call features measured from the harmonic were adopted from Charrier *et al.* (2002 and 2003a) (Table 5.1 and Figure 5.1b).

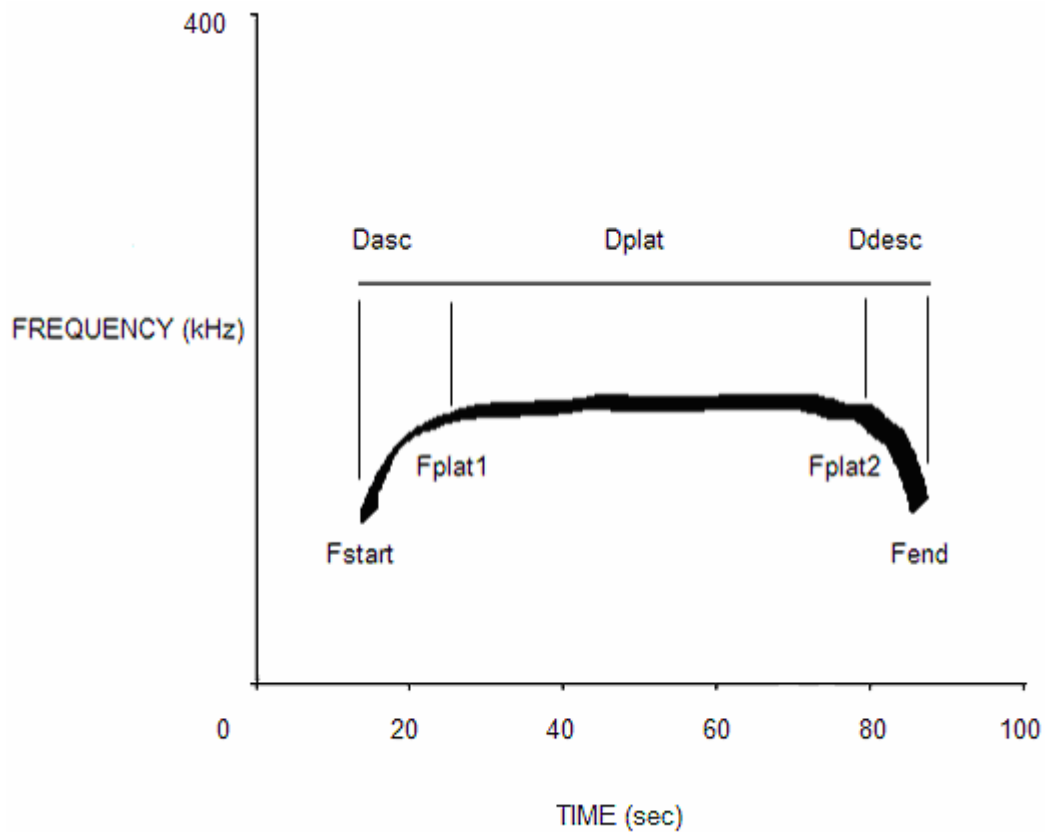


Figure 5.1b. Harmonic band with associated call features measured from a bark unit produced by a male Australian fur seal.

Four frequency variables were measured: start frequency (F_{start}), initial plateau frequency (F_{plat1}), final plateau frequency (F_{plat2}) and end frequency (F_{end}) (Figure 5.1b). The temporal features measured were: the duration of the ascending part (D_{asc}), the duration of the central part (D_{plat}) and the duration of the descending part (D_{desc}). The frequency modulation (FM) characteristics were calculated as follows:

FM_{asc} - slope of the ascending frequency modulation (Hz.msec⁻¹)

$$= \frac{(F_{plat1} - F_{start})}{D_{asc}}$$

FM_{plat} - slope of the central linear part (plateau) of the call (Hz.msec⁻¹)

$$= \frac{(F_{plat2} - F_{plat1})}{D_{plat}}$$

FMdesc - slope of the descending frequency modulation (Hz.msec-1)

$$= (F_{end} - F_{plat2}) / D_{desc}$$

The absolute value of the FM call features: FMasc, FMplat and FMdesc were used for the characterisation of the bark call and for analysis of individual variation on the bark unit and bark series.

Maximum peak frequency (Max peak F), gives the frequency location of the energy band, or harmonic, that has the most energy distributed in it. A power spectra was generated from the centre of the bark unit and used to calculate this feature (Figure 1c).

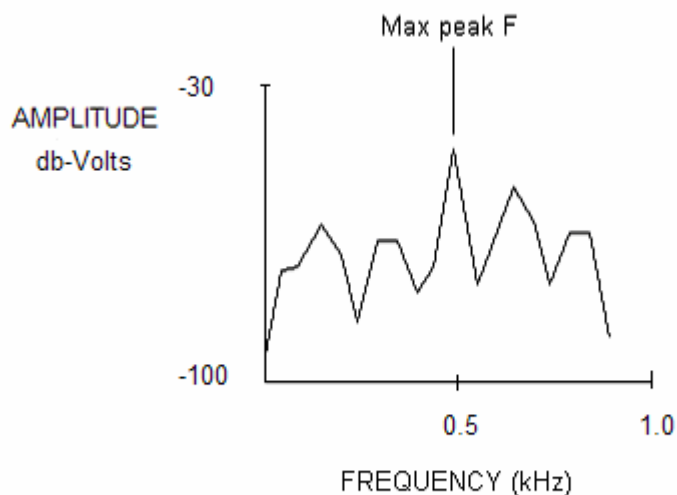


Figure 5.1c. Power Spectra of a bark unit produced by a male Australian fur seal. Max peak frequency indicated on diagram.

Repetition rate (Rep rate) is a mean rate, calculated as the number of call parts (NP) divided by the total duration (Total dur). Linear regression showed that for the majority of bark series analysed there was no significant relationship between the bark unit duration or Inter-unit duration and its temporal position within a bout (62 / 81 and 60 /81 respectively). However, analysis of the bark unit found that 19 out of 81 bouts analysed showed a significant relationship between the bark unit and its temporal position within the bout, with 18 cases showing the bark unit increased throughout the bout

and one case where it decreased. In the Inter-unit duration there was a significant relationship in 21 out of 81 cases, with both an increase (14/81) and decrease (7/81) with the progression of the bout. Therefore, Rep rate was considered static overall in this species.

5.2.4 Characterisation of the bark call

Nine individual males were used to characterise and describe the bark call. Table 5.1 shows the list of features and the number of replicates used for the characterisation process. As frequency features were measured from the first harmonic band, they were divided by two to represent the fundamental frequency. This enables the results to be more easily compared with other studies as it is more conventional to represent call features of the fundamental. The features divided by two are: Fstart, Fplat1, Fplat2 and Fend, these were then used to recalculate FMasc, FMplat and FMdesc. The temporal variables remain unchanged.

Bark unit

Eighteen bark units from nine individuals (n=162) with high signal-to-noise ratios, were used to characterise the bark unit. Up to two bark units randomly chosen from each bark series were used for analysis. Vocalisations for both bark units and series were acquired and analysed using SIGNAL 3.1 (Engineering Design, Massachusetts) at an Analysing Bandwidth of 9.77 Hz (Analysing Bandwidth = Sampling frequency / FFT Window Size) with a Frequency Resolution of 1024-point Fast Fourier Transforms (FFT) and ± 8.93 cursor error rates in the time domain. Call features analysed from the bark unit are described in Table 5.1 and displayed on sonograms and power spectra Figure 5.1 a, b and c.

Bark series

Nine bark series from nine individuals (n=81), with high signal-to-noise ratios were used. Each bark series were characterised using one randomly chosen bark unit in combination with NP, Total dur and Rep rate. All characteristics used to define the bark series are given in Table 5.1 and displayed in Figure 5.1 a, b and c. All temporal features were given in msec, all

frequency parameters were represented in Hz and Rep rate was given in units per msec.

Table 5.1. Call characteristics analysed from bark units and series from male Australian fur seals.

| BARK UNIT | | BARK SERIES | |
|------------------|---|---------------------------------|---|
| * # | Duration of the ascending part (Dasc) | Number of units per series (NP) | |
| * + | Duration of the plateau (Dplat) | # | Total duration (Total dur) |
| * + | Duration of descending part (Ddesc) | | Repetition rate = NP/Total dur (Rep rate) |
| | Duration of Unit (Unit dur) | * | Duration of the ascending part (Dasc) |
| | Duration of Inter-unit (Inter-unit dur) | * | Duration of the plateau (Dplat) |
| * # | Slope of the ascending frequency modulation (FMasc) | * | Duration of descending part (Ddesc) |
| * # | Slope of the central linear part (plateau) of the call (FMplat) | | Duration of Unit (Unit dur) |
| * # | Slope of the descending frequency modulation (FMdesc) | # | Duration of Inter-unit (Inter-unit dur) |
| # | Fundamental frequency (Fo) | * # | Slope of the ascending frequency modulation (FMasc) |
| # | Frequency of Maximum energy (Max peak F) | * # | Slope of the central linear part (plateau) of the call (FMplat) |
| * # | Frequency of start (Fstart) | * # | Slope of the descending frequency modulation (FMdesc) |
| * # | Frequency of plateau 1 (Fplat1) | # | Fundamental frequency (Fo) |
| * # | Frequency of plateau 2 (Fplat2) | # | Frequency of Maximum energy (Max peak F) |
| * # | Frequency of end (Fend) | * # | Frequency of start (Fstart) |
| | | * # | Frequency of plateau 1 (Fplat1) |
| | | * # | Frequency of plateau 2 (Fplat2) |
| | | * # | Frequency of end (Fend) |

* Characteristics adopted from Charrier *et al.* 2002 and 2003a.

Log transformations (log 2) were conducted to normalise variables.

+ Square root transformations were conducted to normalise variables.

5.2.5 Statistical analyses

Intra- versus inter- individual variation

The Potential for Individual Identity Coding (PIC) (Robisson *et al.* 1993; Charrier *et al.* 2002; Charrier *et al.* 2003a) was used to determine which call features would more likely be involved in the individual identity process. This incorporates the Coefficients of Variation (CV):

$$CV = \left(\frac{SD}{Mean} \right) \times 100$$

A corrected CV (CV*) was calculated following Sokal and Rohlf (1985):

$$CV^* = \left(1 + \frac{1}{4n} \right) \times (CV)$$

Where n = population sample (Charrier *et al.* 2002)

The CV was calculated for both CV_b (between-individual) and CV_i (within-individuals). The CV_b was calculated for each characteristic for all individuals, whereas the CV_i was calculated for each individual for each characteristic, and a grand mean was generated. Then a PIC value was used to analyse how great the between-individual variation is relative to the within-individual variation. It was calculated as follows:

$$PIC = \frac{CV_b}{CV_{i\text{grandmean}}}$$

If an acoustic characteristic displayed a PIC value greater than one, then it is considered likely to code for individual distinctiveness (Charrier *et al.* 2002).

Inter-individual variation

Inter-individual variation in bark units and bark series was established using Discriminant Function Analysis (DFA). This analysis determines the variables that are most important in discriminating between individuals. A multiple correlation analysis was performed to determine redundancy of

variables. In the bark units, no variables were highly correlated and as a result, all variables were used in the DFA. In the bark series, NP and Total dur were highly correlated (i.e. greater than 95%) and therefore NP was excluded from further analysis. A binomial distribution was assumed to calculate the probability of achieving the percentage, correctly classified by the DFA, by chance.

To examine the stability of the DFA a cross-validation technique was used. The data were split into two groups; one group (training data) contained two thirds of the data-set and was used to determine the discriminant function, and the other (test data) contained the remaining one third of the data-set and was used to evaluate the stability of the classification. This process was repeated twice (three times in total) varying the groupings so that each call was used in both the test data-set and training data-set. The results of the test data were averaged to evaluate the stability of the discriminant function.

5.3 Results

5.3.1 Characterisation of the bark call

The bark series is a bout of short-duration units (bark units) repeated in a series, each bark unit is harmonically related (Table 5.2). When a bark series is produced, the mouth is slightly open, vibrissae directed forward and the lower jaw is depressed with each bark unit that is produced. This call is given in varying types of postures and may or may not be directed towards the intended recipient.

Table 5.2.Characterisation of the bark call produced by nine male Australian fur seals.

| BARK CALL | Replicates per individual | Mean | SD |
|---|--|-------------|-----------|
| Number of units per series (NP) | 9 | 19.7 | 12.6 |
| Total duration (Total dur) | 9 | 5945.3 | 3917.6 |
| Repetition rate = NP/Total dur (Rep rate) | 9 | 3.3 | 0.5 |
| Duration of the ascending part (Dasc) | 18 | 35.5 | 12.7 |
| Duration of the plateau (Dplat) | 18 | 6.6 | 27.9 |
| Duration of descending part (Ddesc) | 18 | 33.9 | 14.5 |
| Duration of Unit (Unit dur) | 18 | 136.6 | 35.4 |
| Duration of Inter-unit (Inter-unit dur) | 18 | 173.3 | 50.0 |
| Slope of the ascending frequency modulation (FMasc) | 18 | 0.5 | 0.3 |
| Slope of the central linear part (plateau) of the call (FMplat) | 18 | 0.1 | 0.2 |
| Slope of the descending frequency modulation (FMdesc) | 18 | 0.5 | 0.5 |
| Fundamental frequency (Fo) | 18 | 140.3 | 24.1 |
| Frequency of Maximum energy (Max peak F) | 18 | 514.9 | 173.9 |
| Frequency of start (Fstart) | 18 | 138.2 | 27.5 |
| Frequency of plateau 1 (Fplat1) | 18 | 148.2 | 27.9 |
| Frequency of plateau 2 (Fplat2) | 18 | 149.8 | 29.7 |
| Frequency of end (Fend) | 18 | 138.1 | 27.9 |

Table 5.3. Potential for Individual Coding values of call variables in the bark unit and series produced by male Australian fur seals. Significant PIC values given in bold print.

| BARK UNIT | CV_b | CV_i | PIC | BARK SERIES | CV_b | CV_i | PIC |
|------------------|-----------------------|-----------------------|------------|--------------------|-----------------------|-----------------------|------------|
| NP | n/a | n/a | n/a | NP | 66.36 | 63.93 | 1.0 |
| Total dur | n/a | n/a | n/a | Total dur | 68.68 | 64.73 | 1.1 |
| Rep rate | n/a | n/a | n/a | Rep rate | 10.32 | 7.82 | 1.3 |
| Dasc | 36.7 | 34.4 | 1.1 | Dasc | 37.48 | 32.19 | 1.6 |
| Dplat | 43.1 | 31.0 | 1.4 | Dplat | 42.01 | 29.69 | 1.4 |
| Ddesc | 43.9 | 35.9 | 1.2 | Ddesc | 41.87 | 36.37 | 1.2 |
| Unit dur | 26.7 | 18.3 | 1.5 | Unit dur | 25.13 | 16.87 | 1.5 |
| Inter-unit dur | 29.7 | 23.0 | 1.3 | Inter-unit dur | 29.47 | 21.93 | 1.3 |
| FMasc | 76.5 | 71.1 | 1.1 | FMasc | 72.78 | 70.60 | 1.0 |
| FMplat | 139.1 | 126.3 | 1.1 | FMplat | 145.65 | 121.62 | 1.2 |
| FMdesc | 97.6 | 90.7 | 1.1 | FMdesc | 102.93 | 91.55 | 1.1 |
| Fo | 17.7 | 12.4 | 1.4 | Fo | 17.58 | 11.88 | 1.5 |
| Max peak F | 34.7 | 26.3 | 1.3 | Max peak F | 37.31 | 26.66 | 1.4 |
| Fstart | 20.4 | 16.1 | 1.3 | Fstart | 20.42 | 15.59 | 1.3 |
| Fplat1 | 19.4 | 12.9 | 1.5 | Fplat1 | 19.75 | 12.36 | 1.6 |
| Fplat2 | 20.4 | 13.6 | 1.5 | Fplat2 | 21.25 | 14.25 | 1.5 |
| Fend | 20.7 | 14.5 | 1.4 | Fend | 20.70 | 14.27 | 1.5 |

5.3.2 Intra- versus inter- individual variation

Bark units and series

All variables, analysed in this study, have a PIC value greater than one and are therefore likely to contribute to the individual coding process (Table 5.3).

5.3.3 Inter-individual variation

Bark units

There are significant differences in individual bark units between males (Wilks' lambda = 0.0413, F (112, 986) = 5.07, P < 0.0001). Discriminant analysis assigned 68% of the data correctly to individual males; the probability of obtaining this percentage correct by chance is P < 0.0001 (Table 5.4). Assigning four or more calls correctly per individual is considered significant at the 0.05 level. Table 5.5 indicates that all individuals are assigned significantly,

with all having nine or more calls correctly assigned to each individual. Chi square tests indicate that five canonical roots are significant ($P < 0.05$) and account for 96% of the variance of the data. Root 1 is dominated positively by Dplat and negatively by Inter-unit dur and Fplat1 (Table 5.4). Root 2 is dominated positively by Dasc, Dplat and dominated negatively by FMdesc (Table 5.4). The third canonical root (Root 3) is dominated positively by Max peak F and dominated negatively by Ddesc, Unit dur, Inter-unit dur and Fplat2 (Table 5.4). Root 4 is positively dominated by Unit dur, Inter-unit dur, Max peak F, Fplat1 and negatively dominated by Dplat, Ddesc, Fo and Fplat2 (Table 5.4). Root 5 is positively dominated by Dasc, Fplat2 and dominated negatively by Unit dur, Fstart and Fend (Table 5.4).

Table 5.4. Results from Canonical Discriminant Analysis comparing the bark units from male Australian fur seals.

| BARK UNIT | | | | | |
|--------------------------|---------------|---------------|---------------|---------------|---------------|
| Acoustic Variable | Root 1 | Root 2 | Root 3 | Root 4 | Root 5 |
| Dasc | -0.04 | 0.50 | 0.05 | -0.31 | 0.76 |
| Dplat | 0.27 | 0.55 | -0.03 | -0.72 | 0.38 |
| Ddesc | 0.06 | -0.09 | -0.54 | -0.70 | 0.08 |
| Unit dur | -0.06 | 0.33 | -0.49 | 1.46 | -0.67 |
| Inter-unit dur | -0.81 | 0.20 | -1.00 | 0.53 | -0.03 |
| FMasc | 0.10 | 0.25 | 0.03 | 0.39 | 0.05 |
| FMplat | -0.01 | 0.14 | 0.13 | 0.25 | 0.05 |
| FMdesc | -0.07 | -0.21 | 0.31 | 0.10 | -0.29 |
| Fo | -0.07 | 0.20 | 0.01 | -0.69 | -0.11 |
| Max peak F | -0.38 | 0.06 | 0.38 | 0.49 | 0.36 |
| Fstart | 0.17 | 0.23 | 0.29 | 0.30 | -1.00 |
| Fplat1 | -0.51 | 0.24 | -0.12 | 0.94 | 0.39 |
| Fplat2 | -0.21 | 0.16 | -0.56 | -1.16 | 1.10 |
| Fend | -0.42 | -0.12 | 0.33 | 0.42 | -0.93 |
| Eigenvalue | 2.42 | 1.02 | 0.68 | 0.42 | 0.22 |
| Cumulative proportion | 0.49 | 0.69 | 0.83 | 0.92 | 0.96 |

The cross-validation procedure results in 75% of trained calls being correctly assigned compared to the test case where 49% of the calls are

correctly assigned. The result from the test data-set is significantly higher than expected by chance alone $P < 0.0001$.

Table 5.5. Number of calls correctly assigned by the Discriminant Function Analysis for bark unit and series produced by male Australian fur seals.

| Identification | BARK UNIT | BARK SERIES |
|-----------------------|--------------------|--------------------|
| | # of calls correct | # of calls correct |
| Male 1 | 14 | 9 |
| Male 2 | 11 | 8 |
| Male 3 | 10 | 6 |
| Male 4 | 9 | 6 |
| Male 5 | 11 | 7 |
| Male 6 | 16 | 8 |
| Male 7 | 15 | 8 |
| Male 8 | 16 | 8 |
| Male 9 | 9 | 7 |
| Total | 111/162 | 67/81 |

Bark series

There are significant differences in the bark series (Wilks' lambda = 0.0077, $F(128,416) = 3.13$, $P < 0.0001$). Overall, 83% of the data is correctly assigned to individuals, the probability of getting this percentage by chance is $P < 0.0001$ (Table 5.5). Assigning 4 or more calls correctly per individual is considered significant at the 0.05 level. Table 5.5 indicates that all individuals are assigned significantly, with all having six or more calls correctly assigned to each individual. Chi square tests indicate that four canonical roots are significant ($P < 0.05$) and accounts for 88% of the variance of the data. The first canonical root (Root 1) is positively dominated by Dplat, Fstart and negatively dominated by Unit dur, Inter-unit dur, Max peak F and Fplat1 (Table 5.6). The second canonical root (Root 2) is dominated positively by Unit dur, Inter-unit dur, Fo and was negatively dominated by FMdesc (Table 5.6). The third canonical root is positively dominated by FMdesc, Fstart and negatively by Dasc, Dplat, Inter-unit dur, Fo and Fplat2 (Table 5.6). The fourth canonical root

(Root 4) is dominated positively by Rep rate, Ddesc, Fplat2 and negatively by Unit dur and Fplat1 (Table 5.6).

The cross-validation procedure results in 92% of trained calls being assigned correctly compared to the test case where 44% of the calls are assigned correctly. The test percentage result is significantly higher than what you would expect by chance alone $P < 0.0001$.

Table 5.6. Results from Canonical Discriminant Analysis comparing the bark series from male Australian fur seals.

| BARK SERIES | | | | |
|--------------------------|---------------|---------------|---------------|---------------|
| Acoustic Variable | Root 1 | Root 2 | Root 3 | Root 4 |
| Total dur | 0.29 | -0.22 | -0.20 | 0.21 |
| Rep rate | 0.29 | 0.04 | 0.20 | 0.71 |
| Dasc | 0.47 | -0.03 | -0.60 | -0.08 |
| Dplat | 0.82 | 0.30 | -0.60 | 0.27 |
| Ddesc | 0.31 | -0.07 | -0.29 | 0.70 |
| Unit dur | -0.96 | 0.99 | 0.49 | -0.60 |
| Inter-unit dur | -1.05 | 0.60 | -0.54 | -0.01 |
| FMasc | 0.25 | 0.03 | 0.30 | -0.16 |
| FMplat | -0.06 | 0.10 | 0.42 | -0.24 |
| FMdesc | 0.03 | -0.47 | 0.57 | -0.08 |
| Fo | -0.36 | 0.50 | -0.46 | 0.33 |
| Max peak F | -0.53 | -0.03 | 0.52 | -0.40 |
| Fstart | 0.54 | -0.06 | 0.80 | 0.14 |
| Fplat1 | -1.00 | 0.44 | 0.41 | -0.77 |
| Fplat2 | -0.23 | 0.03 | 0.94 | 0.72 |
| Fend | -0.26 | -0.30 | 0.47 | -0.19 |
| Eigenvalue | 4.88 | 1.45 | 1.18 | 0.66 |
| Cumulative proportion | 0.53 | 0.68 | 0.81 | 0.88 |

5.4 Discussion

The bark call produced by male Australian fur seals is structurally comparable to other vocalisations among otariid species such as the Californian, *Zalophus californianus*, (Peterson and Bartholomew 1969) and the South American sea lion, *Otaria flavescens*, (Fernández-Juricic *et al.* 1999), highlighting its similarity with other sea lion species. Comparisons of specific call measurements amongst otariid species was difficult due to the differences in call terminology between studies however, revealed interesting results (Table 5.7). It was apparent that some call measurements such as the fundamental frequency, are different between the species reviewed. It is suggested that the differences in call features are related to species-specific vocal traits (Page *et al.* 2002b).

Male otariid seals are considered to have the potential to recognise their neighbours from strangers through the use of vocalisations (Fernández-Juricic *et al.* 1999; Roux and Jouventin 1987; Stirling and Warneke 1971), with results from this study supporting this suggestion. Barks produced by male Australian fur seals contain a high degree of intra-individual stereotypy and exhibit sufficient inter-individual differences to indicate that vocal recognition may occur. Bark series provided more information on the identity of the caller and, therefore, are potentially more useful in the recognition process. In their natural environment, male Australian fur seals primarily produce barks in series, rarely producing an isolated bark unit. It is more likely that a single bark unit would be lost to the environment as opposed to a bark series where the information is repeated and, therefore, more likely to be received by the intended recipient. Call redundancy has been suggested to allow animals to check the information contained in each unit, several times in succession (Charrier *et al.* 2001b). This repetition is also seen in some otariid species, including the South American sea lion (Fernández-Juricic *et al.* 1999) and the results from the present study may highlight the benefit of a system adapted to suit its breeding environment. It also demonstrates the importance of describing the whole bark series rather than using a single bark unit to represent an individual.

Table 5.7. A comparison of call features for the bark, across five different Otariid species.

| SPECIES | Australian fur | Subantarctic fur | New Zealand | South | Antarctic fur | Californian | Terminology and definitions used by other studies |
|---|-------------------------------------|-------------------------------|-------------------------------|--|-------------------------|---|--|
| | seals, <i>A. pusillus doriferus</i> | seal, <i>A. tropicalis</i> | fur seals, <i>A. forsteri</i> | American sea lions, <i>Otaria flavescens</i> | seal, <i>A. gazella</i> | sea lion, <i>Zalophus Californianus</i> | |
| Author | Tripovich et al. current study | Page et al., 2002b; Roux 1986 | Page et al., 2002b | Fernandez-Juricic et al., 1999 | Page et al., 2002b | Peterson and Bartholomew 1969 | (1) Page et al., 2002b and (2) Fernandez-Juricic et al., 1999 |
| % correct from Discriminant Function Analysis on individual calls | 83% | x | x | 76% | x | X | |
| NP | 19.7 (12.5) | x | x | 3.25 (2.18) | X | 2-19 | |
| Unit dur | 136.6 (35.4) | 100 (0) | 100 (0) | 207 (44) | 300 (0.0) | ~240 ^a | DUR, Duration of call (1) |
| Inter-unit dur | 173.3 (50) | 300 (0) | 300 (0) | x | 200 (0) | ~190 ^a | DURBW, duration between bark calls (1) |
| Fo | 140.3 (24.1) | 391 (55) | x | x | ~ 500 ^a | ~250 ^a | |
| Max peak F | 514.9 (173.9) | X | x | 479 (80) | X | X | Peak 1, peak frequency in order of decreasing amplitude (2) |
| Fstart | 138.2 (27.5) | 254 (5) | 537 (52) | x | 950 (69) | X | INF, Initial frequency of the lowest harmonic at the onset of the call (1) |
| Fend | 138.1 (27.9) | 302 (6) | 696 (91) | x | 1273 (76) | X | ENDF, Frequency of the lowest harmonic at the end of the call (1) |
| Ramp2 | x | 1.12 (0.02) | 0.62 (0.04) | x | 1.30 (0.02) | X | Ratio of amplitudes of the first and third energy peak (1) |

x not measured by study; ^a measured off sonogram

High rates of classification of the DFA on the entire data-set imply that the bark call (both bark unit and series) could be reliably assigned to the correct individual. Studies by Bee *et al.* (2001) indicated that percent correct classification could be affected by the number of replicates and number of individuals used in the analysis. They suggest that an increase in the number of individuals lowered the percent correct classification, and when there was an increase in the replicates per individual it increased the percent correct classification. According to the analysis reported by Bee *et al.* (2001), it may have been expected that the bark unit would have had a higher percentage correct classification as there were twice as many replicates per individual compared to the bark series. However, this was not the case and the results reported in the current study indicate a lower percentage for the bark unit. This emphasizes once again the importance of using the bark series as opposed to the bark unit to describe callers.

This study reported a decrease in the test cross validation results compared with the trained for both bark units and series. This indicated a lack of stability in the model, suggesting that there may be other call features that were not examined by this study that may be important in recognition. Low results may also reflect social context changes that may affect the physical structure of calls (Schusterman 1977), ultimately affecting stereotypy and the ability to correctly classify a call to the correct individual. However, while cross-validation results appear low, they are comparable to other studies (Bee and Gerhardt 2001a, McCulloch *et al.* 1999) and are significantly higher than expected by chance alone.

A combination of both temporal and frequency variables were important in classifying individual callers. This may be attributable to the loud and complex acoustic environment of the breeding colony, where identification may be facilitated by the use of both temporal and frequency parameters for communication. It was also a major finding for other otariid studies where multiple variables were important for the classification of individual callers

(Fernández-Juricic *et al.* 1999; Phillips and Stirling 2000; Charrier *et al.* 2003b). In addition, the variation in the stability of the CVs for most characteristics examined, indicate that not all individuals may be using the same traits in the identification process. This situation was found in bottlenose dolphins, *Tursiops truncatus*, where individuals were discriminated using different acoustic characteristics (McCowan *et al.* 1998).

In relation to bark units, the temporal parameters of Dasc, Dplat and Ddesc as well as unit and inter-unit durations were required to classify individual seals. Peterson and Bartholomew (1969) indicated '...silent intervals between the sounds function as signals themselves...' Therefore, both bark unit and inter-unit are important in discriminating individual male callers. In the bark series, similar temporal features were evident in classifying individuals with the addition of the Rep rate. Thus, varying the rate of delivery of the call may affect an animal's identity. Rep rate is also important in discriminating between individual male Atlantic walruses, *Odobenus rosmarus*, (Stirling *et al.* 1987) where males exhibited significant inter-individual differences in repetition rate.

Frequency parameters fundamental in the classification of individuals for the bark unit and series were: FMdesc, Fo, Max peak F, Fstart, Fplat1 and Fplat2. Therefore, these features may provide vital information on the identity of the caller. While differences in frequency parameters have been related to body size in the southern elephant seal, *Mirounga leonina*, (Sanvito and Galimberti 2000) and European green toad, *Bufo viridis* (Castellano and Giacoma 1998) information on this relationship in Australian fur seals is lacking. However, a study quantifying the differences of vocalisations versus body size would be useful to establish its effect on acoustic parameters.

In summary, the present study has established that Australian fur seals have the potential, through call individuality, to recognise one another through vocalisations. Whether this recognition involves identification of all individuals in the breeding colony or the discernment of a familial individual from a non-familial individual, i.e. neighbours from strangers, is unknown. Further investigations, using playback studies, are needed to demonstrate that vocal recognition

amongst adult male Australian fur seals occurs. While vocalisations may be involved in recognition, it is also clear that other factors such as behavioural posturing and the location of the caller may also play a role in the recognition process.

CHAPTER 6

WHO GOES THERE? THE DEAR-ENEMY EFFECT IN MALE AUSTRALIAN FUR SEALS (*ARCTOCEPHALUS PUSILLUS DORIFERUS*)

Summary

Many species have the ability to recognise other individuals or group members based on unique vocal traits and, thus, direct suitable behaviours towards them. The dear-enemy effect is the response to one type of recognition observed in territorial species where individuals compete to defend a resource area. Territorial individuals respond more to strangers (i.e. unfamiliar animals) than to the neighbouring individuals. If neighbouring males are assumed to pose less of a threat, the territorial individual responds less and avoids unnecessary confrontations with familiar individuals at established boundaries, thus avoiding the costly energy expenditure associated with fighting. The Australian fur seal is a sexually dimorphic species with a polygynous mating system in which males compete to defend an area where females give birth and mate. The present study found that territorial males responded more (vocalising and moving their head and body in the direction of the sound source) to stranger vocalisations than those of neighbours, evidence of the dear-enemy effect in this species. Acoustic features of the bark call were also modified to assess their importance to vocal recognition. There was an increase in response from males when they heard more bark units from strangers, indicating the importance of repetition by a caller. The lower part of the call and the dominant harmonic are important for recognition in Australian fur seal males. The results further indicate that recognition is improved when seals heard the upper part of calls and harmonics surrounding the dominant band, implying the whole spectrum is important. Furthermore, recognition occurs when males hear between 25- 75% of each bark unit from seals. The study demonstrates that male Australian fur seals have the ability to distinguish their neighbours as distinct from strangers, which may have

important consequences in terms of territory defence and, ultimately, reproductive success.

A version of this chapter is in review:

Tripovich, J.S., Charrier, I., Rogers, T.L., Canfield, R., Arnould, J.P.Y. 2006
Who goes there? The dear-enemy effect in male Australian fur seals (*Arctocephalus pusillus doriferus*). *Behavioural Ecology and Sociobiology* (in review)

6.1 Introduction

Animals in a wide variety of taxa have the ability to recognise other conspecifics based on unique vocal traits (e.g. Mexican free-tailed bats, *Tadarida brasiliensis mexicana*, Balcombe and McCracken 1992; razorbill, *Alca torda*, Insley *et al.* 2003b; king penguins, *Aptenodytes patagonicus*, Jouventin *et al.* 1999; reindeer, *Rangifer tarandus*, Espmark 1971; barking foxes, *Alopex lagopus*, Frommolt *et al.* 2003). Vocal recognition occurs on a variety of levels such as: parent-offspring, intra-sexual and inter-specific recognition (Espmark, 1971; Frommolt *et al.* 2003; Jouventin *et al.* 1999; Roux and Jouventin 1987; Stoddard *et al.* 1990), and it plays an important role in allowing animals to distinguish between individuals and direct suitable behaviours towards them during recurring social exchanges (Bee 2003).

In the dear-enemy effect (Fisher 1954), territorial individuals which compete to defend a resource area typically respond more to strangers (i.e. unfamiliar individuals) than to neighbouring animals (Bee 2003, Bee and Gerhardt 2001a). A stranger is either a territorial male from another colony or may be a non-territorial challenging male. This variation in response may be based on the relative threat posed by the different individuals (Temeles 1994). For example, a male that holds a territory during breeding may face the potential loss of both female mates and the territory to a stranger whereas he may lose only mates to a neighbouring male who already has an established territory. This difference in potential loss may explain the reduced fighting intensity observed

between territorial males and their neighbours when compared with that observed between territorial males and strangers (Temeles 1994). Such recognition would avoid unnecessary confrontations with familiar individuals at established boundaries, consequently conserving energy expenditure (Lovell and Lein 2005).

Otariid seals (fur seals and sea lions) are colonial land breeding animals usually congregating on small off-shore islands. They display pronounced sexual dimorphism and have a polygynous mating system (Riedman 1990). Most male fur seals and sea lions are territorial during the breeding season, defending an area in which females give birth and subsequently mate (Riedman 1990). Territories are established through physical conflict, with males typically fighting most aggressively during the period of territory establishment (Roux and Jouventin 1987). Once boundary areas are recognised, combats between neighbouring males are less frequent (Roux and Jouventin 1987) and stereotypical postures and vocalisations are used to maintain boundary areas (Fernández-Juricic *et al.* 1999; Warneke and Shaughnessy 1985). Territorial male otariids fast throughout the breeding season and, therefore, adopting territory maintenance techniques that are energetically conservative may be important for extending territorial tenure (Arnould and Duck 1997). For this reason, vocal recognition or the ability to distinguish neighbours from intruding challengers (i.e. strangers) may be of significant importance for conserving energy expenditure and reducing the number of physical conflicts.

For vocalisations to be used in individual recognition, calls must contain unique features. In the Otariidae, individual stereotypy in male vocalisations has been identified in: Australian fur seals, *Arctocephalus pusillus doriferus* (Tripovich *et al.* 2005) and South American sea lions, *Otaria flavescens* (Fernández-Juricic *et al.* 1999). Traditionally, experimental vocal playback studies have been used to demonstrate the existence of vocal recognition and to investigate the acoustic parameters involved in the recognition process. However, in the Otariidae, preliminary evidence of male vocal recognition has been documented for only

one species, the subantarctic fur seal, (Roux and Jouventin 1987) and little is known of the important acoustic features used in individual recognition of otariids in general (e.g. Charrier *et al.* 2002).

Australian fur seals usually breed on rocky, boulder stack islands and pebble-boulder beaches (Warneke and Shaughnessy 1985). As with other otariids, these territory areas are maintained through the use of vocalisations, stereotypical postures and physical conflicts. In this species, the bark call forms the major component of the male's vocal repertoire. It is thought to indicate sexual interest as well as affirming territorial tenure and boundaries (Stirling and Warneke 1971). Tripovich *et al.* (2005) documented individual call variation and suggested it provided a basis for vocal recognition. However, while individual variation of the bark call may exist, vocal recognition has not been documented, nor have the acoustic parameters that are involved been investigated.

The aims of this study, therefore, were to: 1) determine whether territorial male Australian fur seals are able to discriminate their neighbours' calls from that of strangers; and 2) investigate the call features that may be important in this process. In particular, features identified by Tripovich *et al.* (2005) and Charrier *et al.* (2002 and 2001) were investigated: a) duration of the bark unit b) the frequency of the spectrum; c) the dominant frequency; d) call rhythmicity; and e) the number of bark units.

6.2 Materials and Methods

6.2.1 Study site and recording methods

Vocal playback experiments were conducted on male Australian fur seals on Kanowna Island (39° 10'S, 146° 18' E), Bass Strait, Australia, during the December 2004 breeding season. The island has two main colonies (East Valley and Main Colony) and during the study period these colonies contained a mean number of 44 ± 4.13 territorial males and 169 ± 6.77 territorial males respectively. The densities of female seals from both colonies were similar, with 8.1 cows per bull (East Valley) and 8.3 cows per bull (Main Colony) (J. Gibbens, University of

Melbourne, unpublished data). Territorial males were recorded at both colonies and were identified through natural markings (e.g. scarring) and confirmed to be defending a territory throughout the study period.

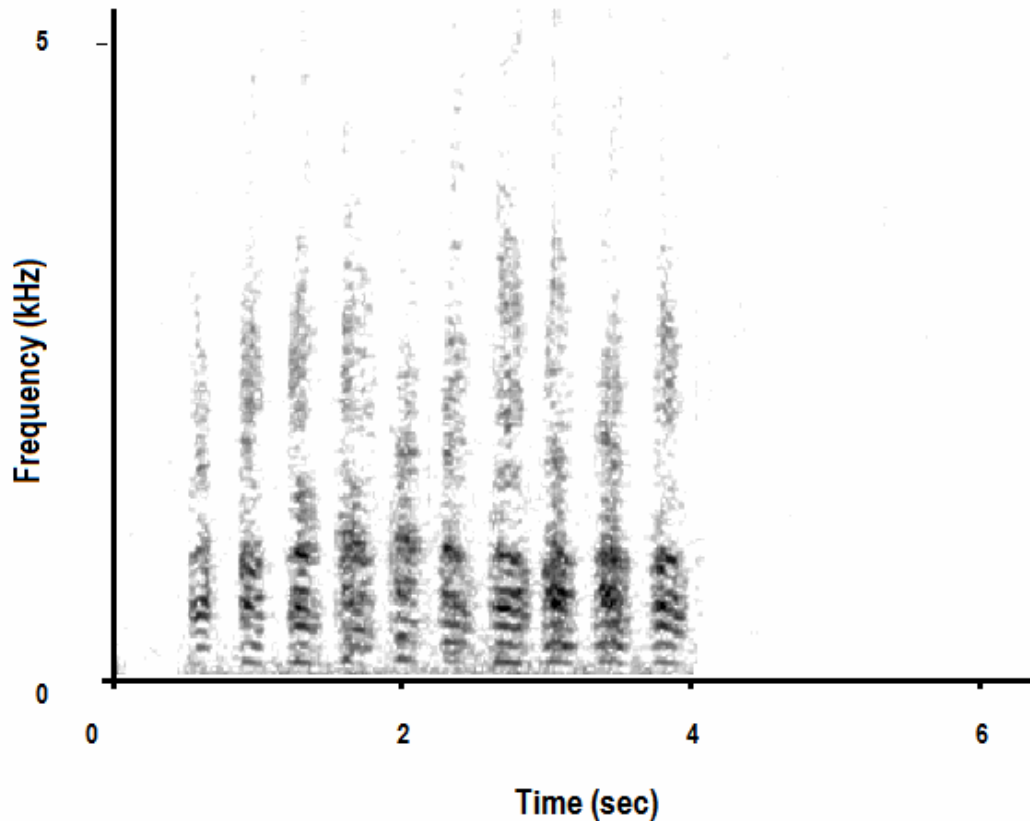


Figure 6. 1. Sonogram of a bark call produced by a male Australian fur seal, *Arctocephalus pusillus doriferus*.

6.2.2 Design of playback experiments

The bark call, which is produced in a bout of short-duration units, (Tripovich *et al.* 2005) (Table 6.1, Figure 6.1) was recorded from vocalising males and used in playback experiments. A neighbour was an individual with a territory bordering that of the subject, while a stranger had a territory from another colony. Vocal recordings were made using a Sony digital tape recorder (TCD-D8) with a directional K6/ME66 Sennheiser microphone (frequency response 50 – 20,000 Hz \pm 2.5dB) and only high quality recordings were used in playbacks. Calls were digitised at 44,100 Hz using Adobe Audition 1.0 (Adobe

Audition Incorporated, California, U.S.A.) and had a noise filter applied to reduce any potential hiss caused by the broadcast of calls through the speaker.

Table 6.1. Characteristics of the bark call produced by nine male Australian fur seals, *Arctocephalus pusillus doriferus* (modified from Tripovich *et al.* 2005).

| <i>Call characteristics – bark call</i> | <i>Replicates per individual</i> | <i>Mean ± SD</i> |
|---|--------------------------------------|-------------------|
| Duration of Unit | 18 | 136.6 + 35.4 msec |
| Duration of Inter-unit | 18 | 173.3 + 50.0 msec |
| Fundamental frequency | 18 | 140.3 + 24.1 Hz |
| Dominant harmonic | 18 | 514.9 + 173.9 Hz |

Trials were conducted from 0700 -1200 h and 1400 -1800 h. The trials contained control and manipulated experiments that were conducted on the same day (see Figure 6.2a and 6.2b for details). As the vocal stimuli in Experiment 1 were not manipulated, it acted as the control experiment. This experiment demonstrated the natural response of territorial males to hearing both neighbour and stranger calls in the wild. The remaining experiments in each trial involved some form of manipulation. Therefore, as Experiment 1 was the natural response of males, it was used to compare it to the other manipulated experiments (i.e. Experiments 2-6), to determine whether these manipulations differed significantly from Experiment 1, illustrating features that may be important to recognition. Each trial lasted approximately 30 min and each treatment was approximately 3 - 4 seconds in duration (10 bark units with inter-unit silences lasting 3 ± 1 sec). Playbacks were broadcast using a MIPRO 707 speaker (frequency response 60 Hz - 20,000 kHz \pm 3 dB). The speaker was connected to a notebook computer and placed 15 m away from the subject, near the boundary of the male's territory. Playback volume of calls were matched to that of naturally-calling seals (68 ± 3 dB SPL at 15 m from the speaker and the calling males, measured with a Radio Shack Model 33-2050 sound level meter set at "C" weighting and fast response). Before a playback session, the sound pressure levels of the different signals were checked to ensure that all signals

matched this sound pressure. To avoid habituation to playbacks, a minimum of five hours separated playback trials at any one site and subjects were never tested more than once on the same day.

Vocal playbacks studies were conducted in two separate trials, with different individuals used in each trial. A summary of this playback design is given in Figure 6.2a and 6.2b with sonograms illustrating the type of manipulation in each treatment. In both trials, all experiments and treatments that were broadcast were randomized, to control for any effect due to order of presentation. Playback trials commenced a minimum of 5 minutes after the speaker was placed into position and only when both the subject and its neighbour were not fighting. Each experiment and treatment was separated by a period of 1-3 minutes of silence; the duration of silence was once again randomised to avoid habituation. During the broadcast of playbacks, the behaviours of subjects were recorded using both hand-written notes by the researcher and recorded by an assistant with a video camera (Sony CCDTR511). The video camera was set to zoom into focal males, generally from a frontal position, which facilitated the detailed examination of responses. All responses were examined by the same researcher (JST). No trials proceeded when there was heavy rain or winds greater than 20 km/h.

6.2.3 Criteria of Response

The response to the playbacks were graded on an ordinal scale from 0 to 3: where 0 was no response; 1 was eye movements towards the speaker (with no head and body movements); 2 was head and/or body movements towards the speaker; and 3 was a vocal response, with or without head and/or body movements. As the results were of an ordinal nature, the responses were analysed using ordinal logistic regression analysis MINITAB Version 14 (MINITAB INC, USA.). This analysis established the significance of any differences between the treatments and determined a probability of each response for each treatment (see Dobson 2001). Results were considered significant at $P < 0.05$.

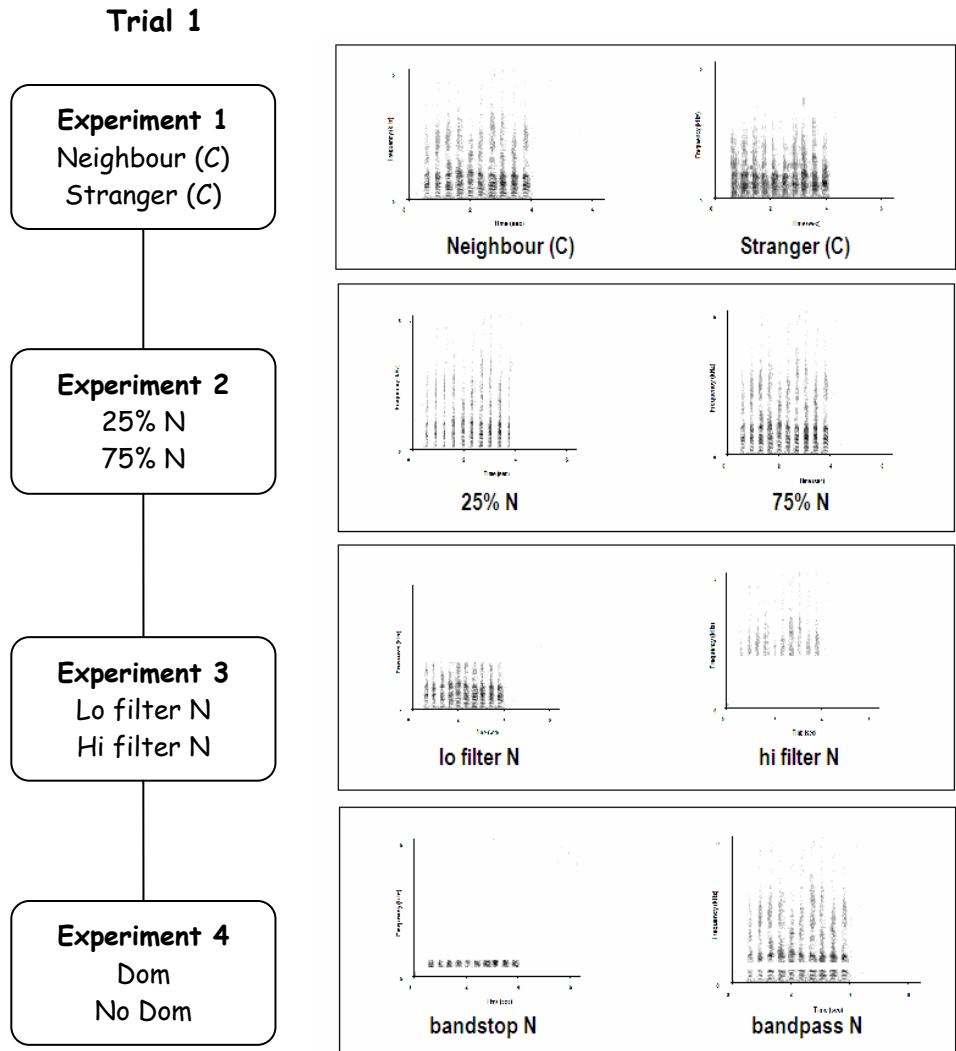


Figure 6.2a. Flowchart of the experimental playback trial 1 with associated sonograms. Abbreviations: *Neighbour (C)* = neighbours call from control experiment; *Stranger (C)* = strangers call from control experiment; *25% N* = first 25% of each bark unit from neighbours; *75% N* = first 75% of each bark unit from neighbours; *lo filter N* = lower spectrum of neighbours call; *hi filter N* = upper spectrum of neighbours call; *Dom N* = dominant harmonic missing from neighbours' call; *No Dom N* = only dominant and surrounding harmonics from neighbours' call.

Trial 1

The first trial consisted of *Experiment 1* (control) and *Experiments 2, 3 and 4* (manipulated vocal stimuli) (Figure 6.2a).

Experiment 1 (Control): Are males able to discriminate neighbours' calls from strangers' calls?

The response of male subjects was examined to investigate whether they recognise and respond differently to the calls of neighbours compared to those of strangers. This experiment contained 3 treatments: treatment 1 - contained ten bark units from the neighbouring male; treatment 2 - had ten bark units from the stranger seal; and treatment 3 - one minute of recorded silence. This was conducted to determine if there are any responses from the emission of sound through the speaker. The response from both neighbour and stranger treatments were compared to determine if they were significantly different. If the responses were significantly different, then the dear-enemy effect was considered present. Once neighbour-stranger recognition was ascertained, investigations were carried out to determine which call features were important in the vocal recognition process.

Experiment 2: Does the whole duration of the bark unit play an important role for neighbour recognition?

In this experiment, the response of subjects was examined to determine if the first quarter, first three-quarters or whole duration of bark units is necessary to recognise neighbours. This experiment involved: treatment 1 - playing the first 25% of each of the ten bark units from neighbours; and treatment 2 - the first 75% of each of the ten bark units from neighbours. The responses from these treatments were then compared to the responses given by subjects that heard the whole duration of bark units from neighbours and strangers from the control experiment (Trial 1, Experiment 1). A response to a manipulated treatment was

considered important to recognition if it was significantly different to the response seen for the control (stranger) but not significantly different to that seen for the control (neighbour), i.e. inducing a neighbour-stranger response. If this did not occur then this treatment would not be considered to contribute information to the identity of callers.

Experiment 3: Is the whole frequency spectrum important for neighbour-stranger discrimination?

The frequency spectrum was investigated to determine if the lower, upper or whole spectrum of calls was important in neighbour-stranger discrimination. Two filter types; low and high pass, were used in this experiment. Low pass filters maintain the lower frequencies while removing the higher frequencies of the call. High pass filters do the reverse, removing the low frequencies and maintain the upper frequencies. Digital filtering were performed using Adobe Audition 1.0, the low-pass and high-pass filters were set to 1000 Hz (FFT window size = 4096 pts, frequency precision = 10.77 Hz) which roughly cut the call in half. This experiment was composed of two treatments: treatment 1 - had the low-passed call containing the fundamental frequency and approximately six harmonic bands ($F_0 + H1 + H2 + H3 + H4 + H5 + H6$) of the ten bark units from neighbouring males; and treatment 2 - contained the high-passed bark units with all harmonic bands above harmonic 6 ($>H6$; the amount of harmonics varied slightly between individuals) from neighbouring males. The responses from these treatments were then compared to the responses given for neighbour and stranger vocalisations, from Experiment 1 (Trial 1). Comparisons to the calls from the control experiment represented a males' reaction to hearing the whole spectrum of calls. A response to a manipulated treatment was considered important to recognition if it was significantly different to the response seen for the control (stranger) but not significantly different to that seen for the control (neighbour), i.e. inducing a neighbour-stranger response. If this did not occur then this treatment would not be considered to contribute information on the identity of callers.

Experiment 4: Is the dominant frequency essential for neighbour-stranger discrimination?

This experiment explored whether the dominant harmonic, i.e., the harmonic band with the highest energy, is important in the vocal recognition process between male Australian fur seals. It was constructed using two types of filters; band-pass and band-stop filters. The digital band-pass filter preserves the specified band while removing all other frequencies and the digital band-stop filter does the opposite, removing the specified band while maintaining all other frequencies. The location of the dominant frequency was determined by visually examining sonograms of calls using Adobe Audition 1.0. As the dominant frequency varied between males, the cut off filters were set to individual male calls (FFT window size = 4096 pts, frequency precision = 10.77 Hz). In this experiment: treatment 1 –the band-stop filter was used to construct calls containing all harmonics except the dominant and surrounding four harmonics; and in treatment 2 - the band-pass filter was used to construct calls containing only the dominant and its four surrounding harmonics. The responses from these treatments were then compared to the responses given for neighbour and stranger vocalisations (whose harmonics were unaffected) from Experiment 1 (Trial 1). A response to a manipulated treatment was considered important to recognition if it was significantly different to the response seen for the control (stranger) but not significantly different to that seen for the control (neighbour), i.e. inducing a neighbour-stranger response. If this did not occur then this treatment would not be considered to contribute information on the identity of callers.

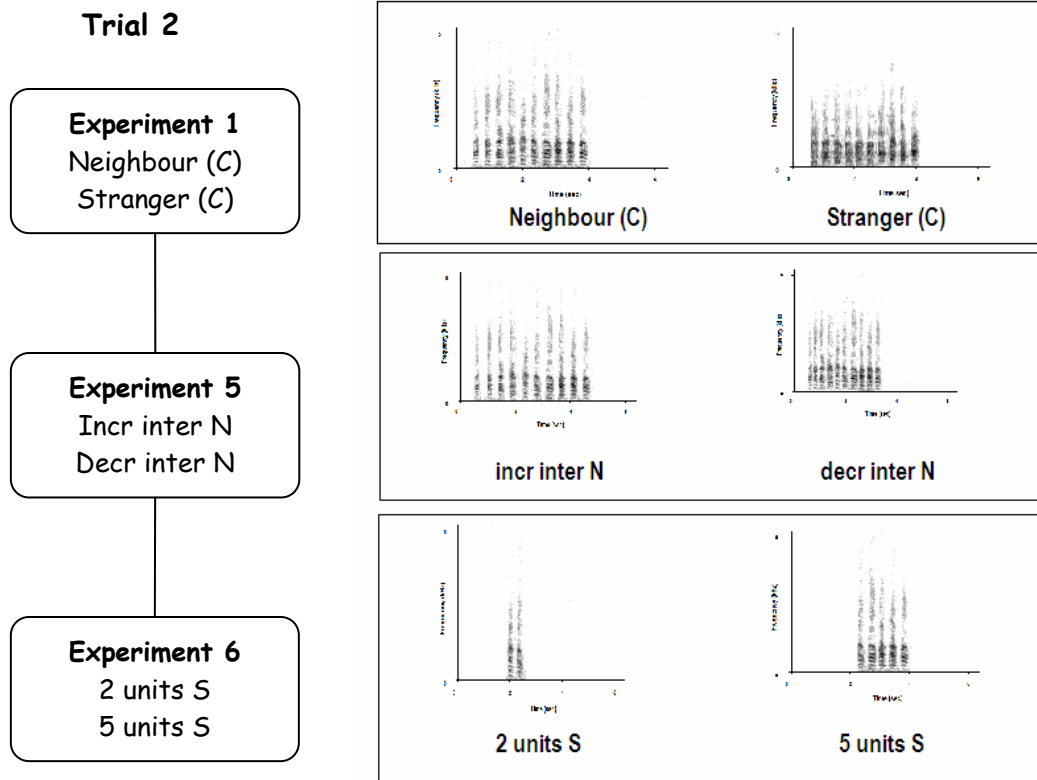


Figure 6.2b. Flowchart of the experimental playback trial 2 with associated sonograms. Abbreviations: *Neighbour (C)* = neighbours call from control experiment; *Stranger (C)* = strangers call from control experiment; *incr inter N* = inter-unit spaces of neighbours' call was lengthened by 25%; *decr inter N* = inter-unit spaces of neighbours' call was shortened by 25%; *2 units S* = two bark units from strangers' calls; and *5 units S* = five bark units from strangers' calls.

Trial 2

The second trial consisted of *Experiment 1* (control) and *Experiments 5* and *6* (manipulated vocal stimuli) (Figure 6.2b).

Experiment 1 (Control): Are males able to discriminate neighbours' calls from strangers' calls?

For details on methodology please see Trial 1, Experiment 1, as they are identical in procedure.

Experiment 5: Is the call rhythmicity important for neighbour-stranger discrimination?

This experiment will determine if the length of the inter-unit spaces between bark units affects the subject's recognition of its neighbour. Two treatments were constructed: treatment 1 - contained a call sequence where the inter-unit spaces of the neighbours call were lengthened by 25%; and treatment 2 - had a call sequence where the inter-unit spaces of the neighbours call were shortened by 25%. The responses from these treatments were then compared to the reactions given by male subjects to both neighbour and stranger calls (from Trial 2, Experiment 1) to investigate the differences between the controls and the manipulated stimuli. In this experiment investigations examined whether recognition is affected by altering the length of the inter-unit spaces. Therefore, if the response to a manipulated treatment affected the neighbour-stranger response, then it would be considered important to recognition. Otherwise, if it did not affect the neighbour-stranger response it would not be deemed to have affected recognition.

Experiment 6: How many bark units are necessary from strangers to elicit a reaction from male subjects?

Male subjects were played a number of different bark units from stranger seals in order to determine how many bark units were necessary to elicit a response.

This experiment contained two treatments: treatment 1 - had two bark units from the stranger seal; and treatment 2 - had five bark units from the stranger seal. The responses from these treatments were then compared to responses given for both neighbour and stranger vocalisations (which had 10 bark units each) from Experiment 1 (Trial 2), in order to investigate the number of units necessary to evoke a response from male subjects. This experiment is fundamentally different from Experiments 2-4, where the manipulated treatments were constructed using neighbouring male calls. In this experiment, the treatments were constructed using stranger seal vocalisations as it would, a priori, be expected to induce a response from focal males. Therefore, when comparing the responses to the control experiment, a response to a manipulated treatment was considered important to recognition if it was significantly different to the response seen for the control (neighbour) but not significantly different to that seen for the control (stranger), i.e. still inducing a neighbour-stranger response (only reversed). If this did not occur, then this treatment would not be considered to contribute information on the identity of callers.

6.3 Results

The observed responses of focal males to the playback experiments are summarised in Table 6.2. Some treatments in some trials had less replicates, as a small number of individuals moved away during the playback or were distracted due to conflict. In this study, three focal males did not respond to any of the treatments in a playback trial. These individuals were classed unresponsive and were then removed from the ordinal logistic regression analysis.

Using the ordinal logistic regression analysis, time of day and colony effect were tested and found to not significantly effect the results ($P = 0.788$ and $P = 0.659$ respectively). Therefore data from different times of the day and from both colonies were combined.

As Experiment 1 was identical in procedure in both trial 1 and 2, the results were pooled for comparison. For Experiments 2-6, *post hoc* comparisons were made between the treatment and the control experiment using ordinal

logistic regression analysis and are presented in Table 6.3 and Figure 6.3. In Figure 6.3., the responses 0 are represented in black, 1 in dark grey and these dark colours illustrate minimal or no responses. In contrast, the lighter colours i.e., the responses 2 are in light grey and 3 in white and these represent positive responses (i.e. vocal and/or head or body movements).

Experiment 1 (Control): Are males able to discriminate neighbours' calls from strangers' calls?

Males responded significantly more to the calls of stranger seals than to the calls of neighbours ($P = 0.001$; Table 6.3). Figure 6.3.1 illustrates that there was an 80% probability that a seal reacted to a stranger's vocalisation by either vocalising or moving its head or body in the direction of the caller whereas there was a 40% probability that focal males will respond to their neighbours' vocalisations in the same manner (Figure 6.3.1). Furthermore, there were no males that responded to the period of emitted silence indicating that there were no effects resulting solely from the broadcast of sound through the speaker, i.e. artificial effect (Table 6.2).

Experiment 2: Does the whole duration of the bark unit play an important role for neighbour recognition?

There were no significant differences between males hearing 25% of neighbour barks when compared with both control neighbour and stranger ($P > 0.1$ in both cases), which may indicate that the duration of the stimuli may not contain enough information to elicit neighbour-stranger discrimination from test subjects. In contrast, the stimuli containing 75% of bark units were long enough to elicit a reaction since it induced neighbour-stranger discrimination, i.e. no difference with control neighbour ($P > 0.1$) but significantly different to control stranger ($P < 0.01$) (Table 6.3). Therefore, it would be suggestive that recognition occurs when males hear between 25-75% of bark units.

Table 6.2. Responses of focal male Australian fur seal, to playback trials conducted in December 2004

| <i>Treatments</i> | <i>Ethological scale</i> | | | | <i>n</i> |
|---|--------------------------|---|----|---|----------|
| | 0 | 1 | 2 | 3 | |
| <i>Experiment 1 – Trial 1 and 2</i> | | | | | |
| Treatment 1: Neighbour | 13 | 5 | 7 | 2 | 27 |
| Treatment 2: Stranger | 5 | 3 | 13 | 6 | 27 |
| Treatment 3: One minute silence | 27 | 0 | 0 | 0 | 27 |
| <i>Experiment 1 - Trial 1</i> | | | | | |
| Treatment 1: Neighbour | 6 | 4 | 5 | 0 | 15 |
| Treatment 2: Stranger | 2 | 3 | 9 | 1 | 15 |
| <i>Experiment 2</i> | | | | | |
| Treatment 1: 1 st 25% of bark unit | 3 | 3 | 7 | 0 | 13 |
| Treatment 2: 1 st 75% of bark unit | 6 | 3 | 4 | 0 | 13 |
| <i>Compare to Neighbour (C) (Trial 1)</i> | 6 | 4 | 5 | 0 | 15 |
| <i>Compare to Stranger (C) (Trial 1)</i> | 2 | 3 | 9 | 1 | 15 |
| <i>Experiment 3</i> | | | | | |
| Treatment 1: Spectrum – lower harmonics | 8 | 4 | 2 | 0 | 14 |
| Treatment 2: Spectrum – higher harmonics | 10 | 2 | 2 | 0 | 14 |
| <i>Compare to Neighbour (C) (Trial 1)</i> | 6 | 4 | 5 | 0 | 15 |
| <i>Compare to Stranger (C) (Trial 1)</i> | 2 | 3 | 9 | 1 | 15 |
| <i>Experiment 4</i> | | | | | |
| Treatment 1: Dominant frequency only | 8 | 4 | 1 | 0 | 13 |
| Treatment 2: Dominant frequency missing | 10 | 2 | 1 | 0 | 13 |
| <i>Compare to Neighbour (C) (Trial 1)</i> | 6 | 4 | 5 | 0 | 15 |
| <i>Compare to Stranger (C) (Trial 1)</i> | 2 | 3 | 9 | 1 | 15 |
| <i>Experiment 1 - Trial 2</i> | | | | | |
| Treatment 1: Neighbour | 7 | 1 | 2 | 2 | 12 |
| Treatment 2: Stranger | 3 | 0 | 4 | 5 | 12 |
| <i>Experiment 5</i> | | | | | |
| Treatment 1: Inter-unit duration – increase | 5 | 3 | 3 | 1 | 12 |
| Treatment 2: Inter-unit duration – decrease | 6 | 0 | 3 | 3 | 12 |
| <i>Compare to Neighbour (C) (Trial 2)</i> | 7 | 1 | 2 | 2 | 12 |
| <i>Compare to Stranger (C) (Trial 2)</i> | 3 | 0 | 4 | 5 | 12 |
| <i>Experiment 6</i> | | | | | |
| Treatment 1: 2 bark units stranger | 5 | 2 | 3 | 1 | 11 |
| Treatment 2: 5 bark units stranger | 3 | 0 | 2 | 5 | 10 |
| <i>Compare to Neighbour (C) (Trial 2)</i> | 7 | 1 | 2 | 2 | 12 |
| <i>Compare to Stranger (C) (Trial 2)</i> | 3 | 0 | 4 | 5 | 12 |

Table 6.3. Results from comparisons with both neighbour and stranger for each treatment using ordinal logistic regression analysis. * indicates statistical significance $P < 0.05$

| <i>Comparison</i> | <i>z</i> | <i>P</i> |
|---|----------|----------------|
| <i>Experiment 1</i> | | |
| Neighbour vs Stranger | -3.59 | 0.001 * |
| <i>Experiment 2</i> | | |
| 25% of bark unit vs Neighbour (C) | -1.59 | 0.111 |
| 25% of bark unit vs Stranger (C) | 1.40 | 0.161 |
| 75% of bark unit vs Neighbour (C) | 0.49 | 0.621 |
| 75% of bark unit vs Stranger (C) | 3.04 | 0.002 * |
| <i>Experiment 3</i> | | |
| Spectrum – lower harmonics vs Neighbour (C) | 1.90 | 0.058 |
| Spectrum – lower harmonics vs Stranger (C) | 3.77 | 0.001 * |
| Spectrum – higher harmonics vs Neighbour (C) | 2.50 | 0.013 * |
| Spectrum – higher harmonics vs Stranger (C) | 4.13 | 0.001 * |
| <i>Experiment 4</i> | | |
| Dominant frequency only vs Neighbour (C) | 1.86 | 0.063 |
| Dominant frequency only vs Stranger (C) | 3.72 | 0.001 * |
| Dominant frequency missing vs Neighbour (C) | 2.39 | 0.017 * |
| Dominant frequency missing vs Stranger (C) | 4.04 | 0.001 * |
| <i>Experiment 5</i> | | |
| Inter-unit duration – increase vs Neighbour (C) | -0.04 | 0.986 |
| Inter-unit duration – increase vs Stranger (C) | 2.69 | 0.007 * |
| Inter-unit duration – decrease vs Neighbour (C) | -0.95 | 0.342 |
| Inter-unit duration – decrease vs Stranger (C) | 2.31 | 0.021 * |
| <i>Experiment 6</i> | | |
| 2 bark units stranger vs Neighbour (C) | -0.37 | 0.713 |
| 2 bark units stranger vs Stranger (C) | 2.72 | 0.007 * |
| 5 bark units stranger vs Neighbour (C) | -2.33 | 0.020 * |
| 5 bark units stranger vs Stranger (C) | 0.38 | 0.703 |

Experiment 3: Is the whole frequency spectrum important for neighbour-stranger discrimination?

The lower part of neighbour calls elicited a significant response to the control stranger ($P < 0.01$) and a lack of significance with the control neighbour ($P > 0.05$) (although weakly non-significant). The upper part of calls evoked a significantly different response to both control neighbour and stranger ($P < 0.05$ in both cases) suggesting that these signals do not allow neighbour-stranger discrimination (Table 6.3). Given the weakly non-significant result elicited by the lower part of the spectrum compared to the control neighbour ($P=0.058$) and the lack of recognition when seals only heard the upper part of calls, it is suggestive that the whole frequency spectrum is important to recognition.

Experiment 4: Is the dominant frequency essential for neighbour-stranger discrimination?

The results of this experiment, where males heard signals missing the dominant harmonic, are consistent with experiment 3 in which responses obtained with the higher part of the call were significantly different to both controls ($P < 0.05$ and $P < 0.001$, respectively). Responses obtained with the lower part of the calls (containing the dominant frequency) were not significantly different from responses obtained with the control neighbour (although weak) ($P = 0.063$). Overall the whole spectrum of calls would be considered important.

Experiment 5: Is the call rhythmicity important for neighbour-stranger discrimination?

Male subjects reacted similarly when hearing the control neighbours' call and the modified neighbours' call, in which the inter-unit duration was increased (rhythmicity slowed) and decreased (rhythmicity accelerated) ($P > 0.1$ in both cases; Table 6.3). However, the subjects' reaction to the modified calls was significantly different to the control strangers' call ($P < 0.05$ in both), suggesting that modifying the call rhythmicity by 25% does not significantly affect a subject's response.

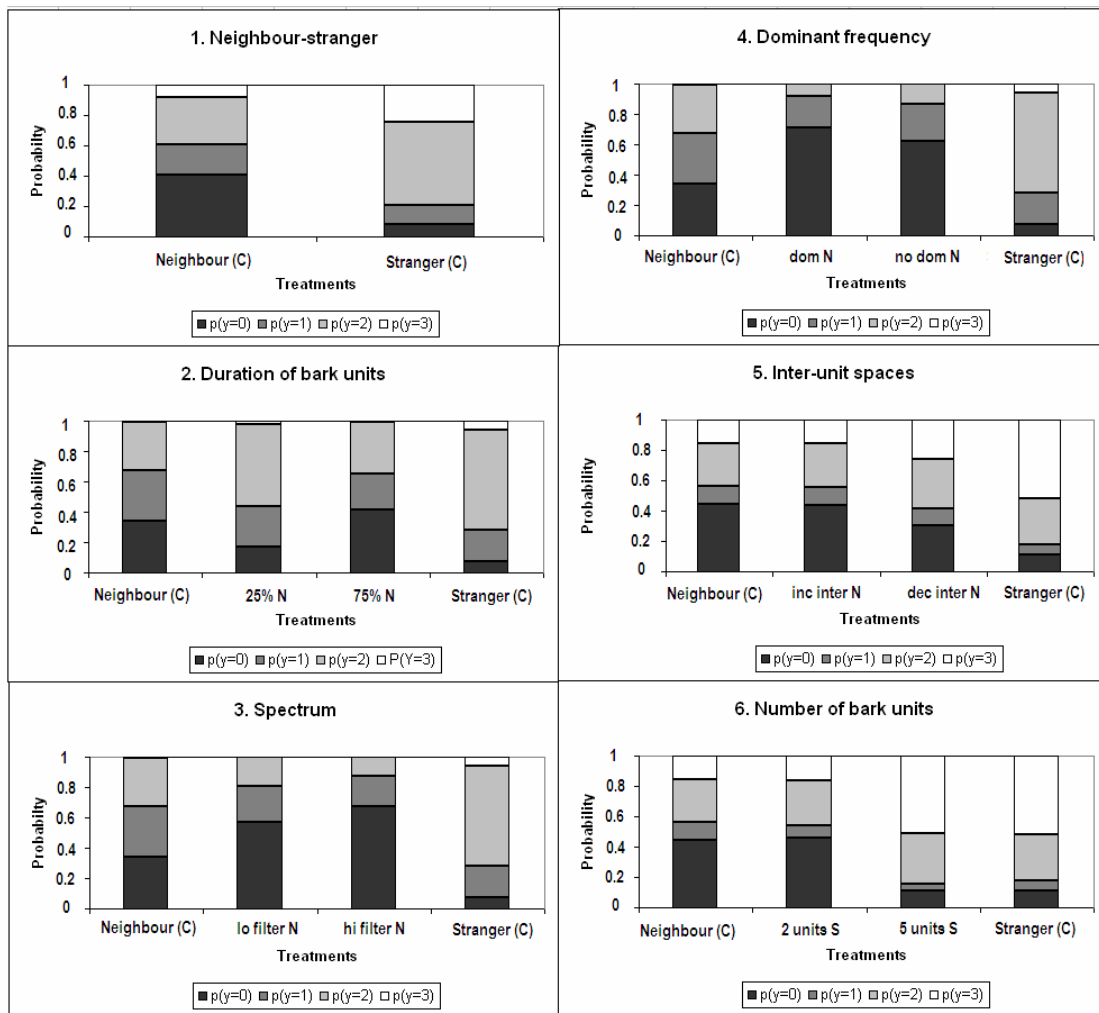


Figure 6.3. Fitted multinomial probabilities from the maximum likelihood fit of the proportional odds model. Where 0 = no response, 1 = eye movements towards the speaker (with no head and body movement), 2 = head and/or body movements towards the speaker; and 3 = a vocal response, with or without head and/or body movements. For each response, the four shaded areas of the stacked bar chart represent the fitted probabilities of the four responses for each treatment.

Experiment 6: How many bark units are necessary from strangers to elicit a reaction from male subjects?

Responses increased when the number of bark units increased (Table 6.2). The signal with only 2 barks elicited positive responses (Table 6.2); however, this was significantly different from those obtained with the control stranger ($P < 0.05$), therefore 2 bark units did not induce a neighbour-stranger response (Table 6.3). Also, there was over a 40% probability that males responded by either vocalising or moving their body/head towards stranger seals when they heard 2 bark units from strangers or ten bark units from neighbours (control neighbour). There was an over 80% probability that males responded in the same way when they heard strangers producing five or ten bark units (control stranger) (Figure 6.3). This indicates that two bark units from strangers evoked similar responses to those observed for the control neighbours' call while five bark units elicited comparable responses to those of the control stranger with ten bark units.

6.4 Discussion

Neighbour-Stranger Vocal Recognition

Temeles (1990) argued that the level of response from territorial individuals depends on the degree of threat posed by neighbour or stranger to the territory holder in terms of fighting ability and potential losses from intrusions. In the present study, the degree of responses by territorial males suggest, strangers present more of a threat than familiar neighbours. Neighbours' fighting abilities are presumed already learnt and, therefore, they represent less of a threat in terms of extending their territory area or stealing a small number of females. In contrast, a stranger may pose a greater threat as their fighting abilities are unknown and may present a greater threat to the territorial male by potentially stealing his whole territory and consequently, all of his females (Temeles 1994). Therefore, neighbour-stranger recognition may help territorial male Australian fur seals avoid unnecessary conflict with familiar individuals, thus conserving energy during territory tenure when males are fasting.

Neighbour-Stranger Vocal Signature

Male seals do not need to hear the whole duration of a bark call to recognise their neighbours. Interestingly, it seems that male seals may recognise seals when they hear between 25-75% of each bark unit of a neighbours' call. This result is similar to the playback studies conducted on subantarctic fur seal pups, where incomplete calls still contained enough information to support recognition. However, the study on subantarctic fur seal pups suggested that the first quarter of calls contained sufficient information for recognition to occur (Charrier *et al.* 2003b) whilst in the present study it is suggested that one quarter to three quarters of the call from males would be needed for recognition to occur.

Individual identity is likely to be encoded in the spectral and frequency acoustic features (Charrier *et al.* 2002). In subantarctic fur seal pups, the fundamental frequency and the lower part of the spectrum of calls appear to encode for an individual's identity (Charrier *et al.* 2002). Studies on South American sea lions (Fernández-Juricic *et al.* 1999), South American fur seals (Phillips and Stirling 2000) and northern fur seals (Insley 1992) have also found these call features to be highly individualised. The results from the present study suggest that the lower part of the call and the dominant harmonic are important for recognition in Australian fur seal males. The results further indicate that recognition is improved when seals heard the upper part of calls and harmonics surrounding the dominant band, implying the whole spectrum is important. Therefore, while both lower and upper harmonics may be important for recognition, they may differ in their importance due to variations in their propagation qualities (Wiley and Richards 1978). The lower harmonic bands may be exposed less to environmental degradation or masking by other environmental noise, while the higher-pitched frequencies of calls are more susceptible to degradation during propagation throughout the environment (Wiley and Richards 1978). Additional playback studies investigating the importance of call harmonics in the vocal discrimination process are needed to clarify this issue.

Tripovich *et al.* (2005) suggested that inter-unit spaces (i.e. silences) between bark units may be important to recognition and context. Changes in call rates have been shown to differ in varying social contexts (Schusterman 1977) and it would seem logical that increasing one's call rate might indicate a more aggressive state and perhaps a willingness to fight. In male Californian sea lions, the bark rate of seals has been found to vary under different behavioural contexts, with the highest call rates being reported during chasing or confrontational situations, implying that changes in call rates reflect the motivational state of the caller (Schusterman 1977). Surprisingly, however, in the current study the results indicated that lengthening and shortening the inter-unit spaces (i.e. making call rhythmicity slower and faster) did not appear to significantly affect an animal's response. This may imply that the inter-unit spaces and changes to call rates do not affect the recognition and response of males, or that a 25% change of the inter-unit duration was not significant enough to elicit a reaction.

Tripovich *et al.* (2005) documented that when a bark series (i.e. calling bout or series of bark units) was examined compared to a single bark unit, the percentage correct classification for an individual was higher in the analysis of the bark series than in the single bark unit. The present study found that when males heard more bark units from strangers that there was an increase in response. These results suggest an increase in the number of bark units may help to improve an animal's ability to recognise individuals. Comparable results have been found in studies on the black-headed gulls, *Larus ridibundus*, where signal redundancy was tested for its importance in parental recognition by chicks (Charrier *et al.* 2001b). Charrier *et al.* (2001b) found that a minimum of four syllables in the parental call was needed to evoke a response from all chicks, further highlighting the importance of signal repetition in colonial breeding environments. The importance of signal redundancy may allow animals to check the information contained in each unit several times in succession. This review process may be important in acoustically complex areas such as those in colonial environments (Charrier *et al.* 2001b). Alternatively, the results may suggest that

animals may perceive fewer bark units as being less aggressive. The current study's results demonstrated that when males heard only two bark units, there was only a weak response from focal males, whereas males that heard more bark units responded more strongly. This may indicate that two units were insufficient to recognise the stranger, or to elicit an aggressive response. Perhaps males need lots of barks before engaging in aggressive behaviour, or that more bark units improve recognition.

In summary, this study supports the occurrence of a neighbour-stranger vocal discrimination in male Australian fur seals. It also demonstrated that there was an increase in response from males when they heard more bark units from stranger seals, indicating that the number of units was important for eliciting a response from males. Furthermore, altering the inter-unit spaces of neighbouring male calls did not affect the response of male subjects, which was surprising as this result is not consistent with other studies and further experimental playbacks are suggested to examine this further. Playback experiments also indicated that the whole frequency spectrums of calls are important to recognition. Finally, investigations reveal that males may only need to hear between 25 - 75% of each bark unit for recognition to occur. Further research examining the importance of behavioural posturing to the recognition process and examining the location of callers on territories would provide useful insights into the importance of these factors to vocal recognition in male Australian fur seals.

CHAPTER 7

GENERAL DISCUSSION

The Australian fur seal is a highly vocal marine mammal, breeding in dense social groups on only ten islands in the Bass Strait. As with other pinnipeds, vocalisations in this species are pivotal to reproductive exchanges and are important on a number of different levels in social organisation, including mother-offspring interactions and male territorial defence. However, while the importance of understanding the acoustic behaviour of pinnipeds is clear, this behaviour in Australian fur seals has received very little attention in the literature, with only one previous study providing descriptive evidence of vocalisations (Stirling and Warneke 1971).

The present study investigated the acoustic behaviour of Australian fur seals by examining wild seals at the remote breeding colony on Kanowna Island, with the aim of describing the physical structure and behavioural context of the animals' calls. The study examined the individuality of vocalisations and the acoustic characteristics that are important in separating callers. These identified characteristics may be used in vocal recognition. It also examined the call structure of pup vocalisations and how these change through the maternal dependency period, then tested vocal recognition in territorial males thus the present study expands the understanding of the acoustic behaviour and vocal recognition abilities of this species and provides information of broader relevance to other colonial breeding species.

7.1 Functionality of vocalisations

Species recognition is important as it allows individuals to recognise other animals as conspecifics, thereby deterring them from interbreeding. By conducting baseline studies on the vocalisations produced by Australian fur seals, the study was able to compare acoustic characteristics between species. Results indicate the PAC, FAC and bark that are produced by Australian fur seal

females, pups and males, respectively, are structurally similar in their gross morphology and function to the vocalisations of other otariid species (Fernández-Juricic *et al.* 1999; Phillips and Stirling 2000; Page *et al.* 2002 a and b). However, the species are clearly distinguishable in their acoustic characteristics. In particular, the PAC (females), FAC (pups) and bark (males) produced by Australian fur seals, have a lower fundamental frequency (Phillips and Stirling 2000; Page *et al.* 2002a; Roux 1986). In male Australian fur seals, the fundamental frequency is much lower than in other fur seals, being at least 250 Hz lower than the barks of the subantarctic fur seals (Roux 1986). In general, a direct relationship exists between the size of an animal and the frequency it can produce, with larger animals capable of producing lower frequency calls (Morton 1977). These species differences may function in keeping species discrete, this aspect being particularly important with respect to sympatrically occurring species, such as Australian and New Zealand fur seals.

A number of vocalisations are employed by both males and females in territorial defence. These are aggressive vocalisations that are structurally low in frequency and pulsed. In male Australian fur seals, the calls used in the defence of territories include the bark and the guttural threat, whereas the full threat call and growl that are reported in other fur seals is missing in this species. In female Australian fur seals, the aggressive vocalisations include the bark, guttural threat and growl. Aggressive vocalisations in females have received little attention in the literature, with the main focus being on mother-offspring vocalisations. However, in resource defence polygyny, evidence suggests that females defend resources within the male's territory, and this in turn may limit the number of mates available to the territorial male and reduce his mating success (Carey 1992).

On the basis of descriptive evidence it has been suggested that the bark produced by male Australian fur seals is important to vocal recognition (Stirling and Warneke 1971). In the dear-enemy effect, territorial individuals which compete to defend a resource area typically respond more to strangers (i.e. unfamiliar individuals) than to neighbouring animals (Fisher 1954). This variation

in response may be based on the perceived level of threat posed by the different individuals (Temeles 1994). In the present study, the call structure of the male bark was analysed to determine if the vocalisations of Australian fur seals fit this theory. Using traditional analytical techniques only, evidence was sought to establish that bark calls were individually distinct. The more novel technique (i.e. CART) was not deemed necessary as most call features could be incorporated into the traditional techniques (i.e. PIC and DFA). Both frequency and temporal parameters were reported as necessary in separating individual callers. The neighbour-stranger recognition system in males was tested in Australian fur seals using playback experiments and the results indicate that territorial males respond more to the calls of strangers than to the calls of their neighbours, supporting neighbour-stranger recognition in this species.

Acoustic modifications of the bark call parameters were used to assess their importance to vocal recognition. The whole frequency spectrum was found to be important to recognition. Furthermore, recognition occurred when males heard between 25- 75% of each bark unit from seals indicating that the whole duration of each bark unit is not necessary for recognition to occur. This may have particular advantages for communication in acoustically complex breeding areas, where calls may be degraded by the environment. Other acoustic manipulations where the inter-unit spaces were increased and decreased by 25%, did not elicit changes in the response of males. This result was surprising as the outcome from the individual variation study indicated that the inter-unit duration would be important.

A substantial proportion of male barks, including those associated with nuzzling and mating, were directed to females during the breeding season. This suggests that these calls are important in inter-sexual relations and mate attraction. In South American sea lions, there is a high degree of association between male vocal behaviour and the factors that influence male mating success, with vocal rates increasing as males monopolize larger numbers of females (Fernández-Juricic *et al.* 2001).

Vocalisations in infant animals are typically high frequency and tonal, vocal characteristics that are adapted for eliciting parental care (Morton 1977). To date, descriptive and qualitative evidence in otariids suggests that calls used by mothers and pups during the reunion process contain unique properties that enable vocal recognition (Insley *et al.* 2003b). In Australian fur seals, similar to other otariids, mothers and pups experience repeated separations and reunions over an extended lactation period. A mechanism for mutual recognition is vital for both mother and pup as both benefit from a successful reunion. This reunion process may be facilitated through a multi-modal sensory system using a combination of vocal, olfactory and spatial cues. In a crowded breeding colony acoustic communication is considered more efficient, as it is less constrained by environmental factors. The present study investigated call individuality in Australian fur seal mother-pup vocalisations. Results indicated that the PAC (females) and FAC (pups) contain enough information to permit the discrimination of individual mothers and offspring. Using a combination of traditional and non-traditional techniques, several acoustic parameters were suggested to be important for recognition.

Investigations into the call structure changes of newborn pups to 11 months of age indicate that calls increase in duration, lower in both the number of parts per call and the harmonic band containing the maximum frequency. These call modifications may be related to the growth and weight changes (Arnould and Hindell 2002), as well as lengthening of the vocal cords and increases in lung capacity, as reported in other vertebrate species (Snowdown and Elowson 1992). This study, together with others, support the hypothesis that long term maternal recognition of offspring may be facilitated through mothers learning new versions of pup vocalisations as these modify throughout postnatal development and maturation (Charrier *et al.* 2003c).

In general the individuality studies of males, females and pups produced some parallels in the call parameters that were important in separating callers. The fundamental frequency and duration were valuable in separating callers in all categories (i.e. females, pups and males). In addition, the maximum peak

frequency was essential in separating pup and male callers, and the inter-unit duration was important in separating male callers only. The PAC (females), FAC (pups) and bark (males) of Australian fur seals are all moderately stereotyped, when compared to other fur seal studies. This may imply that other sensory signals such as vision and olfaction may be used in the recognition process by this species.

7.2 Factors influencing the vocal behaviour of Otariids

The present study examined characteristics that relate to the breeding biology of otariids that are likely to influence their acoustic behaviour. There are large gaps in the literature in these areas amongst the otariid species and this lack of knowledge needs to be addressed before the results of the present study can be analysed in detail. There are also differences in sample size, and differences in the replicates per individual which may account for some of the variances in results between species. Nevertheless, comparisons were made using results from the literature and some preliminary trends are reported.

Species breeding at low densities have more calls in their repertoire as opposed to species breeding in higher female densities, which have in general, lower repertoire sizes (Table 7.1). This pattern is also known to occur in birds, where smaller repertoire sizes are used by males that have access to more females (Catchpole 1980). Vocalisations of polygynous species have evolved primarily through intra-sexual selection where calls are simpler, shorter and stereotyped in structure used in male-male interactions, while vocalisations used in monogamous species, have evolved for use in sexual attraction, where songs are more elaborate, long and complex (Catchpole 1980). Although all otariids are polygynous, this argument may be applied in part to these seals. The selective pressures on species where female congregations on breeding areas are dense may be different to those breeding on areas where there are fewer females. Where females are more densely spaced, calls in males may function primarily in male-male interactions and may need to be simple and repetitive. On the other hand males holding territories in which females are more widely

dispersed may need to defend their territories, but may also attract females to some degree. The requirement to attract females may account for the larger repertoire sizes for these species.

There is a general trend toward greater vocal repertoire in those species breeding on boulder and jumbled rock areas as opposed to those breeding on more open areas (some exceptions e.g., Antarctic fur seal). Roux and Jouventin (1987) suggested that species inhabiting boulder type areas may need to use more call types for communication as other sensory modes, such as vision in relation to behavioural displays, may be constrained by the physical environment. In contrast, species such as Australian fur seals that breed in more open areas, might be able to utilise both calls in combination with other sensory modalities for communication, thereby reducing the need for larger call repertoires. It is suggested that this feature, in association with others, may influence the vocal behaviour of otariids.

The degree of call stereotypy is fairly high in all species investigated, implying vocal recognition can be used by all species. In females the greatest difference in call stereotypy was between South American fur seals (70%) and South American sea lions (90%). This may be related to female density where the need to be more stereotyped, (i.e. more recognisable) to pups may be greater in more crowded areas, such as those in South American sea lions. Similarly, in pup vocalisations, the call stereotypy is lowest in Antarctic and South American fur seals and highest in South American sea lions. This may be a reflection of similar selective pressures for this behaviour which has led to more stereotyped calls, where the acoustic features in South American sea lion pup calls are more distinctive, allowing mothers to recognise their offspring.

There is also a notable difference in the fundamental frequency amongst otariid species in all categories compared (i.e. males, females and pups), being lower in Australian fur seals compared with other fur seal species (Table 7.1). This difference may be related to body size where larger body size of Australian fur seals enables them to produce lower frequency vocalisations (Morton 1977). This aspect was also reported as an influential factor in shaping the acoustic

behaviour of male phocids (Rogers 2003). The degree of polygyny and length of lactation (Rogers *et al.* 2003) did not appear to be influence the acoustic behaviour of both otariids and phocids.

In summary female density, body size and breeding environment all appear to influence the vocal behaviour of otariids, while duration of lactation and degree of polygyny do not appear to be influential.

Table 7.1 Life history characteristics and call features of Otariids.

| SPECIES | Duration of lactation (months) ^{1,2} | Degree of polygyny ³ | Female density (f/m ²) ⁴ | Social organization ³ | Habitat ^{4,5,6} | Male weight (kg) ⁷ | Female weight (kg) ⁷ |
|--|---|---------------------------------|---|--|---|-------------------------------|---------------------------------|
| Northern fur seals, <i>Callorhinus Ursinus</i> | 3-4 | Extreme polygyny | 0.2-0.6 | Extremely large groups; females densely spaced | Island, broken basalt; boulder beaches | 227.0 | 44.8 |
| Subantarctic fur seals, <i>A. tropicalis</i> | 10-11 | Moderate to extreme polygyny | 0.1 | Small to large groups; females well spaced | Island; jumbled rocky coastline | 152.5 | 50.0 |
| New Zealand fur seals, <i>A. forsteri</i> | 9-12 | Polygyny | 0.1 | Small to large groups; females well spaced | Island; jumbled rocky coastline | 164.4 | 55.0 |
| Antarctic fur seal, <i>A. gazelle</i> | 4 | Moderate to extreme polygyny | 0.4-1.1 | Small to large groups; female spacing variable | Island, and open beaches | 155.0 | 38.2 |
| South American fur seals, <i>A. Australis</i> | 7-36 | Polygyny | 0.5-1.0 | Small groups; females well spaced | Island and coastal; rock shelves | 159.0 | 48.5 |
| Galapagos fur seal, <i>A. Galapagoensis</i> | 24 | Polygyny | 0.04 | Small groups; females well spaced | Island; rock shelves; boulder beaches | 64.5 | 27.4 |
| South African fur seal, <i>A. pusillus. pusillus</i> | 6-12 | Moderate to extreme polygyny | 1.4-1.9 | Moderate-sized to extremely large groups; females densely spaced | Island and coastal, rock shelves | 278.0 | 71.0 |
| Australian fur seals, <i>A. p. Doriferus</i> | 11-12 | Moderate to extreme polygyny | 0.2 | Small to large groups; females densely spaced | Island and coastal, rock shelves, open terrain | 307.00 | 84.0 |
| Californian sea lion, <i>Zalophus californianus</i> | 4-8 (up to 12) | Moderate to extreme polygyny | 0.1-0.2 | Moderate-sized to large groups; females densely spaced | Island; sand beaches, rock shelves | 289.0 | 86.0 |
| South American sea lions, <i>Otaria flavescens</i> | 5-12 | Moderate polygyny | - | Moderate-sized to large groups; females densely spaced | Island and coastal; rock shelves, shingle beaches | 300.0 | 144.0 |

| SPECIES | No of calls in repertoire | 8, 9, 10, 11, 12 | in male bark | % correct DFA male | 10, 11, 13 | Male F ₀ | 10, 13 | % correct DFA female PAC | 6, 8, 11, 14, 15 | % correct DFA pup FAC | 6, 8, 11, 15, 16 | Pup F ₀ | 6, 8, 16 |
|--|---------------------------|------------------|--------------|--------------------|------------|---------------------|--------|--------------------------|------------------|-----------------------|------------------|--------------------|----------|
| Northern fur seals, <i>Callorhinus Ursinus</i> | ? | | - | | | - | | 82 | | 79 | | x | |
| Subantarctic fur seals, <i>A. tropicalis</i> | 3-7 | | x | | | 391 (55) | | 84 | | 83 | | 520 (19) | |
| New Zealand fur seals, <i>A. forsteri</i> | 5-7 | | x | | | x | | 88 | | 79 | | 729 (63) | |
| Antarctic fur seal, <i>A. gazelle</i> | 5 | | x | | | X | | 74 | | 52 | | 666 (12) | |
| South American fur seals, <i>A. Australis</i> | 7 | | x | | | x | | 70 | | 60 | | 1030 (18.5) | |
| Galapagos fur seal, <i>A. Galapagoensis</i> | 7 | | x | | | x | | x | | x | | x | |
| South African fur seal, <i>A. pusillus. pusillus</i> | 3-7 | | x | | | x | | x | | x | | x | |
| Australian fur seals, <i>A. p. Doriferus</i> | 3 | | 83 | | | 140.3 (24.1) | | 76 | | 75 | | 342 (62) | |
| Californian sea lion, <i>Zalophus californianus</i> | 2 | | x | | | x | | x | | x | | x | |
| South American sea lions, <i>Otaria flavescens</i> | 4 | | 76 | | | x | | 90 | | 90 | | x | |

1 = Atkinson 1997; 2 = Bowen 1991; 3 = Riedman 1990; 4 = Boness = 1991; 5 = Goldsworthy et al. 1999; 6 = Page et al. 2002(a); 7 = Lindenfors et al 2002; 8 = Phillips and Stirling 2001; 9 = Stirling and Warneke 1971; 10 = Tripovich et al. 2005; 11 = Fernandez-Juricic et al., 1999; 12 = Peterson and Bartholomew 1969; 13 = Roux 1986; 14 = Tripovich et al. 2006, 15 = Insley 1992; 16 = current study.

7.3 Are Australian fur seals vocalisations more like sea lions?

Previously, it has been suggested that the behaviour and vocalisations of Australian fur seals resemble more of sea lions rather than those of fur seals (Warneke and Shaughnessy 1985). Throughout the study it was apparent that differences existed in the vocal characteristics between Australian fur seals and other fur seal species but due to the lack of sufficient data, detailed comparisons were not possible. However what was evident was that the fundamental frequency characteristic of Australian fur seal vocalisations was more similar to sea lions than to those of fur seals. The opinion of the author is that both the larger body size and breeding environment may influence and shape the vocalisations of seals. Firstly, Australian fur seals are the largest of all fur seals (Table 7.1) and are comparative in size to other sea lions, and in general, larger animals are capable of producing lower frequency calls (Morton 1977) which may account for the lower frequency (particularly in barks produced by males) reported for Australian fur seals and sea lions compared with other fur seals. And secondly, the differences in the vocalisations may be related to the variation in breeding environments. In general, Australian fur seals and sea lions (from available data to date) produce lower frequency bark calls and breed in more open areas, while fur seals produce higher frequency barks and breed on more jumbled rocky areas (Table 7.1). The potential for scattering of vocalisations is greater in jumbled rocky areas and so having higher frequency calls that are more directional would be advantageous in those environments, which may explain for the differences in frequencies between the Australian fur seals and sea lions compared with all other fur seals (Wiley and Richards 1978).

7.4 Future research

Acoustic signals play a very important role in the breeding success of a wide variety of species. The current study described the calls produced by males, females, yearlings and pups throughout the breeding season, providing valuable information on the vocal behaviour of a species that has not been studied in great detail. This information provided by this study allows the opportunity for researchers to compare this species with other pinnipeds and the results may elucidate general evolutionary patterns.

Future research could extend the playback studies to investigate the recognition abilities of mothers and offspring. Artificial modification of the calls would be advised in order to determine the call features that are required for the individual identification process. The choice of variables for modification could be based on the results of the individual call variability studies, which highlight the call parameters most likely to be important to the recognition process.

Behavioural development studies involve examination of the changes that occur as the young grows and matures (Martin and Bateson 1993). The present study investigated changes in pup vocalisations utilising a cross-sectional sampling approach. An alternative method of analysis known as longitudinal analysis, involves sampling the same individuals through time. It would be ideal if seal pups could be sampled using longitudinal in addition to cross-sectional techniques and results compared.

In the present study the recognition abilities of male Australian fur seals was investigated. Future experiments testing a male's ability to recognise individual neighbours would prove interesting as it can reveal whether male vocal recognition is based on males recognising individuals or recognising a group of animals as either familiar or unfamiliar. Furthermore while the present study reports valuable information on a colonial male seal species, it would be interesting to conduct playback studies on male seals that utilise other breeding strategies such as those that of solitary species (e.g., leopard seals, *Hydrurga leptonyx*) or those having harems (e.g., southern elephant seals, *Mirounga leonina*). This may provide further insights into the evolutionary patterns or environmental constraints affecting social communication in pinnipeds.

Vocal communication and recognition between mothers and offspring and between males may involve other features (e.g. amplitude modulation, sound pressure levels, and others) not measured in the present study. These call features may improve the percent correct classification scores. Other features such vision, spatial orientation and smell may also play a role in the recognition process and investigations on these factors could help reveal

important information on the recognition process in seals and in understanding the reproductive success in fur seals.

Lastly, vocalisations emitted by Australian fur seals are not produced in isolation. It appears that different call types are used in combination during certain behavioural contexts. Other studies on primates have indicated that these call combinations are not produced randomly and that the order of the combinations may have meaning (Crockford and Boesch 2005). This study has provided the necessary baseline descriptions of single call units, which can then be utilised to investigate the importance of call combinations in the communicative process.

Sexual reproduction creates a social environment of conflict and competition among individuals as each attempt to maximise its genetic contribution to subsequent generations (Alcock 1993). Vocalisations are a major component in the breeding communication of Australian fur seals. Consequently, investigations made by this study broaden our understanding on the acoustic behaviour of Australian fur seals and the influences shaping vocalisations, all of which may ultimately impact the breeding success of an individual.

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