ACOUSTIC COMMUNICATION IN AUSTRALIAN FUR SEALS

Joy Sophie Tripovich

A thesis submitted to fulfil the requirements for the degree of Doctor of Philosophy

Faculty of Veterinary Science
University of Sydney
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‘In all things of nature there is something of the marvellous.’

Aristotle

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STATEMENT OF ORGINALITY

All work undertaken in this study was conducted by myself and the responsibility of the co-authors in published chapters was in supervision of the project or to provide editorial advice. This work has not been presented for a degree to any other University or Institution.

Signed……

August 2006

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LIST OF ABBREVIATIONS

PAC	Pup Attraction Call produced by female
FAC	Female Attraction Call produced by pup
PIC	Potential for Individual Coding
DFA	Discriminant Function Analysis
CART	Classification And Regression Tree analysis
CV_b	Coefficient of Variation between individuals
$CV_{i\ grand\ mean}$	Coefficient of Variation calculated for each individual and a grand mean generated
F_0	The distance between each harmonic band
MIN F	Minimum frequency of the first harmonic band
DUR	Duration of the call
MANOVA	Multivariate analysis of variance
ANOVA	Analysis of Variance
msec	millisecond
dB	decibel
Hz	hertz
FFT	Fast Fourier Transforms
Parts/Call	Number of call parts divided by the Total Call Duration
QUAV	The percentage of the call that contains fast frequency modulation, also known as quavering.
PEAK F1	It describes the location of the harmonic that has the most energy distributed in it (Hz).

LIST OF SCIENTIFIC NAMES

African elephant	*Loxodonta africana*
Antarctic fur seal	*Arctocephalus gazella*
Atlantic walruses	*Odobenus rosmarus*
Australian fur seal	*Arctocephalus pusillus doriferus*
barking fox	*Alopex lagopus*
black-headed gull	*Larus ridibundus*
bottlenose dolphin	*Tursiops truncatus*
Californian sea lion	*Zalophus californianus*
field cricket	*Teleogryllus yezoemma*
field cricket	*Teleogryllus emma*
field cricket	*Teleogryllus taiwanemma*
domestic pig	*Sus scrofa domestica*
European green toad	*Bufo viridis*
French Alpine goat	*Capra hircus*
Galapagos fur seal	*Arctocephalus galapagoensis*
Hawaiian monk seal	*Monachus schauinslandi*
king penguin	*Aptenodytes patagonicus*
leopard seal	*Hydrurga leptonyx*
mouse lemur	*Microcebus murinus*
New Zealand	*Arctocephalus forsteri*
northern fur seal	*Callorhinus ursinus*
pika	*Ochotona princeps*
razorbill	*Alca torda*
red deer	*Cervus elaphus*
reindeer	*Rangifer tarandus*
South African fur seal	*Arctocephalus pusillus pusillus*

South American fur seal	*Arctocephalus australis*
South American sea lion	*Otaria flavescens*
southern elephant seal	*Mirounga leonina*
squirrel monkey	*Saimiri sciureus*
subantarctic fur seal	*Arctocephalus tropicalis*
Zebra finch	*Taeniopygia guttata*

GLOSSARY OF TERMS

gregarious	tending to form a group with others of the same species
harem	a mating system where the dominant male will defend and mate with a group of females
oestrus	the periodic state of sexual excitement in the female of most mammals that immediately precedes ovulation
polygyny	the mating of a single male with several females
post-partum	the period following birth
rookery	a breeding or nesting place for some gregarious mammals and birds
sexual dimorphism	the physical differences between male and female individuals that arise as a consequence of sexual maturation, including the secondary sex characteristics
stereotypy	repetitive, performed the same way each time
sympatric	different species or populations that live in the same geographical area
thigmotactic	seeking contact with surfaces

ABSTRACT

Communication is a fundamental process that allows animals to effectively transfer information between groups or individuals. Recognition plays an essential role in permitting animals to distinguish individuals based upon both communicatory and non-communicatory signals allowing animals to direct suitable behaviours towards them. Several modes of recognition exist and in colonial breeding animals which congregate in large numbers, acoustic signalling is thought to be the most effective as it suffers less from environmental degradation. Otariid seals (fur seals and sea lions) are generally colonial breeding species which congregate at high densities on offshore islands. In contrast to the other Arctocephaline species, the Australian fur seal, *Arctocephalus pusillus doriferus*, along with its conspecific, the Cape fur seal, *A. p. pusillus*, display many of the behavioural traits of sea lions. This may have important consequences in terms of its social structure and evolution.

The acoustic communication of Australian fur seals was studied on Kanowna Island, Bass Strait, Australia. Analysing the acoustic structure of vocalisations and their use facilitates our understanding of the social function of calls in animal communication. The vocal repertoires of males, females, pups and yearlings were characterised and their behavioural context examined. Call structural variations in males were evident with changes in behavioural context, indicating parallel changes in the emotive state of sender.

For a call to be used in vocal recognition it must display stereotypy within callers and variation between them. In Australian fur seal females and pups, individuals were found to have unique calls. Mutual mother-pup recognition has been suggested for otariids and this study supports the potential for this process to occur through the use of vocalisations. Call structural changes in pup vocalisations were also investigated over the progression of the year, from birth to weaning. Vocalisations produced by pups increased in duration, lowered in both the number of parts per call and the harmonic band containing the maximum frequency as they became older, suggesting calls are changing constantly as pups grow toward maturity.

It has been suggested through descriptive reports, that the bark call produced by males is important to vocal recognition. The present study quantified this through the analysis of vocalisations produced by male Australian fur seals. Results support descriptive evidence suggesting that male barks can be used to discriminate callers. Traditional playback studies further confirmed that territorial male Australian fur seals respond significantly more to the calls of strangers than to those of neighbours, supporting male vocal recognition. This study modified call features of the bark to determine the importance to vocal recognition. The results indicate that the whole frequency spectrum was important to recognition. There was also an increase in response from males when they heard more bark units, indicating the importance of repetition by a caller. Recognition occurred when males heard between 25-75% of each bark unit, 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 environments, where parts of calls may be degraded by the environment.

The present study examined the life history characteristics of otariids to determine the factors likely to influence and shape its vocal behaviour. Preliminary results indicate that female density, body size and the breeding environment all influence the vocal behaviour of otariids, while duration of lactation and the degree of polygyny do not appear to be influential. Understanding these interactions may help elucidate how vocal recognition and communication have evolved in different pinniped species.

CHAPTER 1

GENERAL INTRODUCTION

1.1 Communication and vocal recognition

Communication involves both a sender and a receiver, where the sender emits a signal conveying information and the receiver interprets the information responding accordingly (Bradbury and Vehrencamp 1998). In general, there are two types of communication signals: discrete and graded. Signals used in long range communication are usually simple, discrete and stereotyped while those used in short range communication are less influenced by environmental degradation and are often graded signals, where animals employ multiple communicatory signals at the same time (Miller 1991). Frequently graded signals are used in aggressive encounters (Phillips and Stirling 2001), where changes in signal structure may reflect the emotive state of the sender.

There are four modes of communication used in both air and water by pinnipeds: visual, olfactory, tactile and vocal. Environmental and biological constraints restrict the use of some modes, particularly over long distances. Visual communication is limited by light and physical obstructions within the environment. Chemical signals that diffuse in air and tactile signals are constrained by distance. Environmentally, vocal signals are the least constrained mode of communication, although the signal degrades with distance (Bradbury and Vehrencamp 1998). Signals used in communication usually evolve to increase the efficiency of information transfer (Wiley and Richards 1982).

Animals have the ability to recognise conspecifics on a variety of levels, e.g. mother-offspring, male-male, mate and species. Each level of recognition may vary in the degree of discrimination required. For example, mother-offspring communication requires a mother to recognise the vocalisation of her offspring amongst the calls of other pups, while species recognition requires an individual to distinguish between the vocalisations of their own species and those of others. The discrimination of vocalisations has major consequences for successful breeding.

In sympatrically occurring species, differences in vocalisations may act as isolating mechanisms to keep species discrete (Stirling and Warneke 1971), to avoid interbreeding which may lead to hybrid species of lower fitness (Miller 1982). Playback studies on closely related cricket species, *Teleogryllus yezoemma, T. emma and T. taiwanemma*, that have partially overlapping breeding ranges indicate that female crickets could accurately distinguish different species, highlighting the importance of calls in species recognition and maintenance of species isolation (Honda-Sumi 2005). In sympatrically occurring fur seals species, subantarctic, *Arctocephalus* tropicalis, New Zealand, *A. forsteri,* and Antarctic fur seals, *A. gazella,* all display significant variations in their acoustic characteristics. However, while there are differences in the calls of these species, there have been a few cases where interbreeding has occurred producing hybrids e.g. Antarctic, *Arctocephalus gazella*, and subantarctic, *A. tropicalis*, fur seals on Macquarie Island (Page *et al.* 2001). The mating between these two different fur seal species may be associated with recognition errors (Insley *et al.* 2003b). In most cases, however, the differences in acoustic structure of vocalisations should keep species from inter-breeding.

Vocal recognition may play a role in neighbour-stranger interactions, as some territorial species respond more to strangers when compared to neighbouring individuals (Hopp and Morton 1998). This is the 'dear enemy' effect (Fisher 1954). By discriminating neighbours from strangers, animals may lessen the need for ongoing fighting, reducing the associated energy expenditure. Recognition may be based on a group context of familiar versus unfamiliar, as opposed to the recognition of an individual animal. Such discrimination has been demonstrated during playback experiments with a species of pika (*Ochotona princeps*), a small land based mammal of North America (Conner 1985). Similar discrimination has been suggested to occur in some pinniped species (Stirling and Warneke 1971) but has only been tested and reported in one, the subantarctic fur seal (Roux and Jouventin 1987). In general, the role of vocalisations in neighbour-stranger discrimination and the acoustic features involved remains to be investigated in pinnipeds.

Vocal production in many bird and mammal species appears to increase in close association with the breeding season. The trill call of male mouse lemurs, *Microcebus murinus,* is produced mainly during the reproductive period and its function is to advertise the 'quality' of the male. The vocal behaviour of this species is thought to be linked to concurrent hormonal changes during the breeding season (Zimmermann and Lerch 1993). This increase in vocal activity has also been reported in several bird species where, in general, male birds were found to sing more as a mate guarding strategy and as a means of attracting additional females (Møller 1988). Roaring in red deers, *Cervus elaphus*, advances ovulation and regular calling by males can improve their mating success (McComb 1987). In playback experiments on Zebra finches, *Taeniopygia guttata*, male calls induced females to lay eggs earlier or caused synchrony in ovulation, causing females to lay larger clutch sizes (Waas *et al*. 2005). Such experiments highlight the importance of vocalisations in the maintenance of breeding systems. In pinniped species, vocalisations also appear to increase during the breeding season, although these calls have been related to territorial defence but may also function in mate attraction (Insley *et al*. 2003b).

In many circumstances, animals respond differently to kin as opposed to non-familial members (Hopp and Morton 1998). An extensive network of vocal recognition is clearly illustrated in female African elephants, *Loxodonta africana*, where they can distinguish the calls of female family and bond group members from those females outside these groups (McComb *et al.* 2000). Playback studies on mother and offspring pigs, *Sus scrofa domestica*, indicate that piglets produce calls that are litter specific thus allowing mothers to recognise their offspring (Illman *et al.* 2002). In otariid seals, mother-offspring recognition is particularly important as females and pups experience repeated separations and reunions that result from extensive lactation periods (Riedman 1990). Investigations of some otariid species have found a general trend towards an effective recognition system in mothers and offspring (Insley et al 2003a) while such a system has only been suggested in descriptive reports of Australian fur

seals. Detailed studies investigating call individuality and vocal recognition in Australian fur seals are lacking.

1.2 Otariid pinnipeds

The importance of vocal recognition particularly in colonial mammals is widely accepted, with all polygynous pinnipeds being vocal during the breeding season, when large aggregations form on beaches and rocky island foreshores (Evans and Bastian 1969). Pinnipeds are composed of three families: Otariidae (eared seals), Phocidae (true seals) and Odobenidae (Walrus). Otariids are further divided into two subfamilies: fur seals and sea lions. There are nine species of fur seals, eight in the genus *Arctocephalus* and one in the genus *Callorhinus*. Fur seals are distinguished largely on the basis of their geographical distributions, size and behavioural characteristics, yet their taxonomic relationship is still under contention (Brunner 2004; Phillips and Stirling 2001; Stirling and Warneke 1971; Demèrè et al 2003; Wynen *et al.* 2001) (Figure 1.1). The species *Arctocephalus pusillus* has two subspecies: *A. p. pusillus*, the South African (Cape) fur seal and *A. p. dorifeus*, the Australian fur seal (Wickens and York 1997). These two species have been recognised as subspecies on the basis of slight cranial differences (Warneke and Shaughnessy 1985).

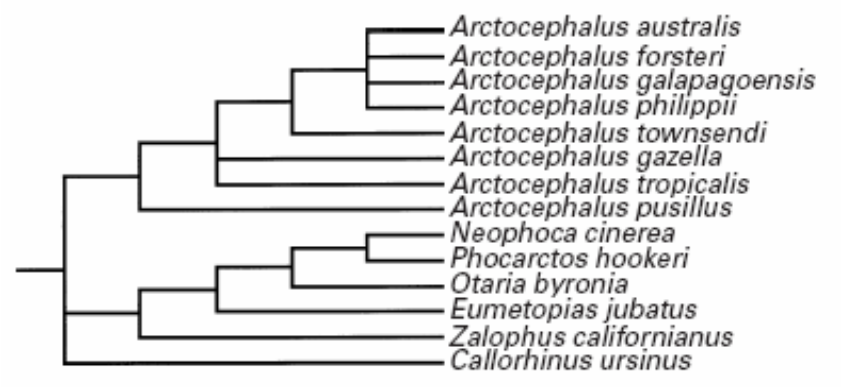

Figure 1.1. The composite phylogeny tree for Otariidae (modified from Bininda-Emonds *et al.* 1999).

Otariids are top order predators having similarities in both their social and reproductive behaviour (Gentry and Kooyman 1986). All otariids are polygynous and gregarious during the breeding season with pronounced sexual dimorphism in all species (Riedman 1990; Bartholomew 1970). Males reach sexual maturity at 3-6 years of age (Atkinson 1997) but do not attain social maturity until 9-14 years. Females are both sexually and socially mature by three years of age, usually producing one young per season until approaching 20 years of age (Gentry and Kooyman 1986). Amongst otariids, the length of lactation varies from 4 months to 24 months (Bowen 1991). A long neonatal dependency period in some otariid species requires the female to adopt a nursing-foraging cycle, where females alternate between foraging at sea and nursing their pups. When returning from sea mothers must relocate their offspring from a large number of other pups on the breeding colony. Therefore, it is imperative that there is some means whereby individuals are able to reunite so that maternal investment is not misplaced (Hangii 1992).

Pinnipeds are amphibious, communicating in both water and on land. Several sensory modes of communication are employed with selection of mode depending on the social relationships of animals, the environment and physiological fluctuations. Olfactory and tactile communication modes employed during the breeding season, are especially important in mother-offspring interactions. Mothers and pups will often reunite with a nose-to-nose touch, which presumably allows confirmation of identity through the use of chemoreceptors (Riedman 1990). Territorial males tend to increase both acoustic and postural displays as they compete with neighbouring bulls to attain territories. Vocalisations used in pinniped communication vary in function, being used in species recognition, territorial defence, mate and kin identification (Insley *et al*. 2003b). Otariids in particular, are excellent mammalian species to study this form of communication, as they use acoustic signals in different social contexts.

1.3 Australian fur seals

Australian fur seals are a temperate latitude species aggregating in high densities during a synchronous annual breeding season. These seals prefer to breed on rocky parts of islands with flat and open parts of islands (Shaughnessy 1999) and are found exclusively on ten islands: Lady Julia Percy Island, Seal Rocks; The Skerries; Judgement Rocks; Kanowna Island; Moriarty Rocks; Reid Rocks; West Moncoeur Island; Tenth Island; and Rag Island (in the Cliffy Group), all islands are located within the Bass Strait waters of south-eastern Australia (Kirkwood *et al.* 2005). The largest colony being at Lady Julia Percy Island with an annual pup population count of 5,899 pups (Kirkwood *et al.* 2005). This species is classified vulnerable in NSW under the Threatened Species Conservation Act as past commercial harvesting has significantly impacted on the original population size and distribution (Warneke and Shaughnessy 1985).

Australian fur seals are positively thigmotactic, tolerating a high degree of bodily contact, a trait that sets it apart from all other *Arctocephalus* species (Warneke and Shaughnessy 1985). Their breeding season is initiated in late October when territorial males begin to arrive onto breeding islands. These males use vocalisations, behavioural posturing and physical contact in an aggressive manner in order to acquire, establish and protect a territory frequented by females in oestrus (Stirling and Warneke 1971; Warneke and Shaughnessy 1985). Territory size and location depends on an animals fighting ability with the size of a males territory averaging 62 m^2 (Warneke and Shaughnessy 1985). From late October to late December, females will come onto rookeries, where they will give birth (median pupping date of 1 December Warneke and Shaugnessy 1985) and later mate. Females are sexually receptive for 5-6 days post-partum (Shaughnessy 1999). They will then alternate between nursing their young and foraging out at sea, continuing this nursing-feeding cycle until pups are about 10-11 months old (Arnould and Hindell 2001). A small proportion of females suckle their pups for a second or even third year (Warneke 1982, Hume *et al.* 2001).

Australian fur seals are highly vocal marine mammals. They are unique as they are taxonomically classed a fur seal but possess many behavioural and vocal traits resembling those of sea lions. Given the distinctive characteristics of Australian fur seals, investigations into the vocal communication of this species may help elucidate the influences shaping the vocal behaviour of pinnipeds.

1.4 Overall aims and structure of the study

The aims of this study were:

(1) To describe both qualitatively and quantitatively the vocal repertoire and acoustic structure of vocalisations produced by Australian fur seals in order to compare this species with other otariids;

(2) To examine the behavioural context of calls to associate its likely function;

(3) To investigate whether differences in behavioural contexts affect the acoustic structure of the bark call produced by male Australian fur seals;

(4) To determine if the bark produced by male Australian fur seals contains sufficient individual variation to be used for vocal recognition;

(5) To determine, using playback studies, whether territorial male Australian fur seals are able to discriminate their neighbours' calls from those of strangers and to investigate the call features that are important in this process;

(6) To determine if the PAC produced by female Australian fur seals contains sufficient individual variation to be used for vocal recognition;

(7) To determine the degree of intra- and inter-individual variability in the FAC produced by pups over four age groups and assess how these variables change as pups develop throughout the maternal dependency period.

This study was conducted over a 5 year period commencing December 2000 until December 2004. In Chapter 2 the acoustic and behaviour recordings collected from December 2000 and 2001 from the breeding colony at Kanowna Island were used to describe the vocal repertoire of Australian fur seals. It forms the first comprehensive description of the acoustic properties of the calls produced by this species. In addition, the acoustic structure of the male bark call

under different behavioural contexts is examined in order to determine if call structure, changes in parallel with emotive state.

The following two chapters focus on Australian fur seal female and pup vocalisations and determine whether their calls contain unique traits that can be used for individual recognition and therefore support the reunion process between mother and offspring. These studies further investigate the call parameters that would most likely contribute to the individual coding process.

The differential response of territorial males to the vocalisations of strangers and neighbours, suggests a recognition process. For this to occur, vocalisations produced by males must display significantly more variation between callers than within an individual. Consequently, Chapter 5 examines the individual variation of male calls and the acoustic properties that may be important in the vocal recognition process. Chapter 6 analyses the results from playback trials, where the ability of males to recognise their neighbours from strangers is tested. This chapter also investigates the call parameters that are important in the recognition of neighbours and strangers.

Chapter 7 summarises the results of the previous chapters, making some preliminary comparisons of vocalisations with life history characteristics, to determine the likely influences shaping vocal behaviour. This chapter also suggests future directions for investigations into the vocal behaviour of Australian fur seals.

This study makes a significant contribution to knowledge of Australian fur seals, a species that has received little attention in the literature. The work provides baseline, acoustic behaviour information on which future studies can expand and describes the vocal recognition abilities, which may have important consequences in terms of breeding success.