THE FORAGING ECOLOGY AND PROVISIONING STRATEGIES OF SYMPATRIC FUR SEALS
Arctocephalus gazella AND *Arctocephalus tropicalis*
AT MACQUARIE ISLAND

by

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This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person except where due acknowledgement is made in the text.

Susan A. Robinson

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Susan A. Robinson   9 November 2001

Antarctic fur seal female 'C33' and pup

For

Laurie Andrina Robinson

ABSTRACT

Antarctic *Arctocephalus gazella* and subantarctic *A. tropicalis* fur seals (Pinnipedia: Otariidae) have very different lactation strategies (ie. duration of pup rearing periods), the former taking four months to rear its pups and the latter, ten months. At Macquarie Island these two species are sympatric, which is unusual for fur seals, and their lactation periods overlap for the first four months. The aim of this study was to examine the importance of phylogenetic constraints and environment on the lactation strategies of these seal species at Macquarie Island. This was undertaken by comparing their provisioning strategies at this location, primarily in terms of maternal energy acquisition at sea (foraging behaviour and diet) and on shore energy transfer to the pup (attendance behaviour, milk composition, milk intake, pup growth and fasting).

The diet, diving behaviour and foraging location of *A. gazella* and *A. tropicalis* females were compared during the austral summer period when pup-rearing of the two species overlapped. The prey of the two fur seal species was very similar, with the myctophid *Electrona subaspera* being the predominant prey item (94 % numerical abundance from identifiable fish remains). There were no major differences in the diving behaviour, with both species diving almost exclusively at night with very short and shallow dives averaging 10 - 15 m and 0.5 - 0.9 min. Both species foraged north of the island with most activity concentrated at two sites: within 30 km, and around 60 km north. Comparing the foraging strategies of *A. gazella* and *A. tropicalis* from different locations showed their behaviour to be flexible. At Macquarie Island, under the same environmental conditions, the two species chose a similar diet, and used similar diving behaviour and foraging locations.

The maximum foraging range, area prospected and foraging trip duration were investigated in lactating *A. gazella* in relation to central place foraging theory. There was substantial overlap in area use between years, between foraging trips of different females and between foraging trips of the same individuals. Distance to foraging areas, total distance travelled, area foraged and pup mass gain increased with increasing foraging trip duration. This agrees with the predictions of central place

foraging theory: that both energy gained from, and time spent in, a foraging patch should increase with the increasing distance of that patch from the central place.

The influence of phylogenetic and environmental factors in shaping pup growth strategies for *A. gazella* and *A. tropicalis* were also examined. For *A. gazella* and *A. tropicalis* respectively, birth mass (6.0 and 5.8 kg), growth rate to 120 days (84 and 83 g/d), and weaning mass (14.8 and 14.8 kg) were similar for both species. Maximum mass (15.4 and 19.0 kg) age at maximum mass (108 and 200 d) growth rates to maximum mass (89 and 70 g/d) and weaning (83 and 42 g/d), and age at weaning (122 and 298 d), for *A. gazella* and *A. tropicalis* respectively, varied significantly between species. Sex-based differences in mass and growth were evident in both species. Growth rates and weaning mass were relatively high compared to similar measurements for these species at other locations. Lactation length (weaning age) did not vary from other populations of these species. The local environment appeared to have a greater influence on birth mass, growth rates and weaning mass. Despite phylogenetic differences and differences between current and ancestral marine environments, the pup growth of the two fur seal species was very similar. Weaning age, being phylogenetically fixed, however, had the strongest influence on pup development and growth.

The provisioning strategies of the two fur seal species were examined with respect to the composition of their milk, the amount of energy transferred and the attendance behaviour of the mothers. Fasting mass loss gave an indication of the energetic cost of body maintenance in the pups of the two species, and was 23 % lower in *A. tropicalis* pups suggesting a lower energy demand. The milk composition of the two species was similar for the period of overlap and milk lipid increased throughout lactation. Milk lipid and protein contents averaged for the four month lactation period of *A. gazella* were 41.8 ± 0.73 % and 10.8 ± 0.16 % (n = 135) respectively, and for the longer lactation of *A. tropicalis*, 49.05 ± 2.03 % and 9.5 ± 0.28 % (n = 26) respectively. Milk and milk energy consumption for the two species was not significantly different. Attendance behaviour of mothers of both species was similar with respect to the duration of overnight (< 24 h) trips, extended (> 24 h) trips and shore attendance, but the proportions used by each species varied significantly. Lactating *A. gazella* spent

less time in overnight trips, more time at sea and, overall, undertook less foraging trips than *A. tropicalis*.

I conclude that the phylogenetically controlled energy demands of the pups drives the provisioning process but the environment dictates how often and how much energy can be supplied. Fur seal mothers respond to pup energy demands and environmental variables through their attendance cycles. The greater energy demands of *A. gazella* pups results in their mothers spending more time at sea and undertaking longer foraging trips. Mothers of *A. tropicalis* pups can meet lower pup demands with mostly short foraging trips. The regular use of overnight foraging trips by both species is possible at Macquarie Island because prey resources are abundant and close to the island, and the fur seal population is small, reducing competition for nearby resources.

Provisioning strategies and pup growth are governed by a combination of evolutionary and environmental factors. Pup growth strategies have evolved with physical and physiological limitations on development which they cannot change, even in a situation of rich prey resources. *A. tropicalis* pups have evolved with energy conserving behaviours and/or physiology and cannot change their rate of development to wean in a shorter time like *A. gazella*. Of the two maternal strategies, it is likely the strategy of *A. gazella* is more expensive during the period of lactation overlap, but overall, with a longer lactation period, it is likely to be more expensive for *A. tropicalis* to raise a pup.

ACKNOWLEDGEMENTS

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Chapter 1

GENERAL INTRODUCTION

1.1   BACKGROUND

The two fundamental components of the life history of pinnipeds (true seals, walruses fur seals and sea lions) are marine feeding and parturition on a solid substrate (Costa 1993). Phocids (true seals), odobenids (the walrus) and otariids (fur seals and sea lions) have evolved different strategies to cope with the temporal and spatial separation of these activities (Bonner 1984, Oftedal *et al.* 1987, Costa 1993, Boness and Bowen 1996). Phocids have the most complete separation of the marine and terrestrial phases. Most species of phocid seals do not enter the sea during the period of pup rearing, with mothers supplying their own and their pup's energy requirements solely from energy stored as blubber during their pre-parturition time at sea. Odobenid females adopt the opposite approach, and take their young with them a few days after parturition and nurse them at sea, on ice floes or on land, and otariids regularly undertake foraging trips to sea during which time pups remain fasting on shore. The provisioning strategies of otariid mothers must therefore balance the time spent acquiring energy at sea with the fasting ability of their pups on land (Boyd 1998). One consequence of the otariid approach is that the period of pup dependence is much longer than for phocids.

Provisioning of young mammals is energetically the most demanding component of reproduction (Oftedal *et al.* 1987, Clutton-Brock 1991, Boness and Bowen 1996). In otariids, provisioning comprises three parts: acquisition of energy at sea, the pattern of delivering energy (in the form of milk) to the young, and the quality and quantity of milk delivered (Gentry and Kooyman 1986, Trillmich 1990). Given that females maximise their reproductive success by rearing young which themselves are likely to reproduce, it might be expected that the components of provisioning these offspring would be under strong selection pressure (Boness and Bowen 1996).

The characteristics of provisioning strategies have been well studied in pinnipeds (Bonner 1984, Kovacs and Lavigne 1992, Costa 1993, Boness and Bowen 1996, Boyd

1998) and particularly in otariids (Gentry and Kooyman 1986, McCann 1987, Bester and Bartlett 1990, Trillmich 1990, Goldsworthy 1992, Georges and Guinet 2000). Both phylogenetic constraints and environmental conditions are thought to influence the characteristics of provisioning strategies in otariids. Some aspects which are rigid within species (such as the fasting ability of pups, weaning age in some species) may be genetically determined, while more flexible attributes (such as attendance behaviour, diving behaviour) may be environmentally mediated (Gentry and Kooyman 1986, Trillmich 1990).

The seminal work by Gentry and Kooyman (1986) and authors therein, proposes that in fur seals, the broad suites of traits related to pup rearing (collectively referred to in this thesis as provisioning or maternal strategies) are correlated with latitude. They proposed that the maternal strategies of fur seals have been shaped primarily by the seasonality and predictability of marine resources. Selection pressure arising from these differing environmental conditions has resulted in the evolution of a range of maternal strategies that will maximise lifetime reproductive success (Gentry *et al.* 1986).

Otariid species of high latitudes, (the northern fur seal *Callorhinus ursinus* and the Antarctic fur seal *Arctocephalus gazella*) exist in highly predictable, but also highly seasonal environments (Gentry and Kooyman 1986b). These species have evolved mechanisms to enable a short lactation period ensuring that pups are brought to weaning during the brief period of high prey availability. Fur seals associated with low latitudes (eg. Galapagos fur seal *A. galapagoensis*) face environments with only slight seasonal variation, but which are subject to episodic reductions in prey availability (ie. El Niño events) (Trillmich 1990). These species require an extended and flexible lactation to cope with environmental uncertainty, and can take up to three years to wean a pup. Most species of otariids occur in temperate environments (eg. the subantarctic fur seal *A. tropicalis*) where breeding strategies typically fall between these two extremes, but can be quite variable. This is believed to reflect their evolving in an environment generally lower in food resources compared to high latitudes, but not subject to strong seasonality or episodic failures in food availability (Gentry and Kooyman 1986b).

More recent work now suggests environmental conditions may be a more accurate index of the variation in maternal strategies than latitude (Trillmich 1990, Boness and Bowen 1996, Francis *et al.* 1998). However, the work of Gentry and Kooyman (1986) still provides a strong base for the characterisation of, and investigation into, provisioning strategies of fur seals.

Fur seals are an ideal group for studying the evolution of maternal strategies, as there are several species within a single genus (*Arctocephalus*) which range from the tropics to sub-polar regions. To investigate the dual constraints of phylogeny and environment on the evolution of fur seal maternal strategies, it would be informative to undertake a study where species that use different maternal strategies occur in the same environment. This would effectively control for the environmental variables when making species comparisons (at least during periods when lactation in both species overlaps) and give insights into aspects of behaviour, physiology, and growth that are constrained by phylogeny (genetic factors), and those which are flexible and most influenced by environmental factors. A limited number of otariid breeding sites include two or more sympatric species that would enable such a comparative study to be undertaken. The Galapagos Islands (Galapagos fur seal *Arctocephalus galapagoensis* and sea lion *Zalophus californianus wollebaecki*) (Trillmich and Lechner 1986) and San Miguel Island (northern fur seals *Callorhinus ursinus* and Californian sea lions *Z. californianus*) (Antonelis *et al.* 1990) are two sites in the north Pacific Ocean, but only provide comparison between fur seals and sea lions which are morphologically different, particularly in body mass. However in the Southern Ocean there are two island groups and a single island where the Antarctic and subantarctic fur seals breed sympatrically, Prince Edward Islands, Îles Crozet and Macquarie Island, respectively (Condy 1978, Jouventin *et al.* 1982, Shaughnessy and Fletcher 1987). The New Zealand fur seal (*A. forsteri*) is also present at Macquarie Island, vagrant males visiting during late summer (Shaughnessy and Fletcher 1987). Comparative studies on these species have occurred most notably at Macquarie Island (Goldsworthy 1992, Goldsworthy *et al.* 1997, Goldsworthy and Crowley 1999, Goldsworthy 1999) and Marion Island (Bester and Wilkinson 1989, Bester and Bartlett 1990). This study expands on previous work at Macquarie Island by using much larger sample sizes and including satellite tracking data, milk intake estimation and pup mass loss data.

1.2   SPECIES AND STUDY SITE

1.2.1   *Antarctic and subantarctic fur seals*

Extant fur seals are represented by two genera: *Arctocephalus* with 8 species, most of which occur in the southern hemisphere, and a single species, *Callorhinus ursinus*, in the northern hemisphere (King 1983), that has been found to be phylogenetically distant to *Arctocephalus* (Wynen *et al.* 2001 and references therein). Fur seals are polygynous and usually breed in dense colonies on beaches and coastal rock platforms (Bonner 1984). Females give birth to a single offspring in the summer and after a week of perinatal attendance, they are mated then depart for sea, beginning a cycle of alternating foraging at sea with suckling the pup on land (Bonner 1984, Gentry and Kooyman 1986a). Lactation lasts between 4 and 12 months but may be prolonged to up to 3 years in some species depending on environmental conditions (Gentry and Kooyman 1986a). Most fur seal species breed in temperate areas with an 11 month lactation. It is possible this is the ancestral maternal strategy and others have derived from this (Georges pers. comm.).

The original fur seal populations of the Southern Ocean were severely depleted by harvesting for furs during the 19th century (Repenning *et al.* 1971). At Macquarie Island (54° 30'S, 158° 55'E), fur seals were exterminated by sealers in the early 1800s (Cumpston 1968) and did not recolonise until the 1950s (Shaughnessy and Shaughnessy 1988). It is still unknown which fur seal species originally inhabited the island.

Antarctic fur seals occur south of the Antarctic Polar Front (APF) at South Georgia, South Sandwhich, South Shetlands, Bouvet, Kerguelen, Heard and McDonald Islands (King 1983), as well as occurring in sympatry with *A. tropicalis* north of the APF at Crozet, Marion and Macquarie Islands (Condy 1978, Jouventin *et al.* 1982, King 1983, Shaughnessy and Fletcher 1987). Bird Island at South Georgia has the largest population, with a pup production reported at around 378,000 in 1991 (Boyd 1993). The global pup production, as far as it has been assessed, is estimated at 400,000 (Hofmeyr *et al.* 1997) giving a population (at that time) of between 1.4 and 1.8 million Antarctic fur seals. By comparison, the Antarctic fur seal population at

Macquarie Island is very small, with an annual pup production of around 135 pups in 2000-01 (S. D. Goldsworthy unpublished).

The more temperate subantarctic fur seal is found on islands north of the APF: the Tristan da Cunha, Prince Edward and Amsterdam Island groups in the Indian and Atlantic Oceans (Tollu 1974, Condy 1978, Bester 1980, King 1983) as well as Macquarie Island (Shaughnessy and Fletcher 1987). Total pup production from information available, was estimated at around 80,000 (Hofmeyr *et al.* 1997), giving a population of between 227,000 and 356,000. At Macquarie Island, around 25 pups are born a year (S. D. Goldsworthy unpublished).

Antarctic fur seals have a lactation length of approximately four months and subantarctic fur seals approximately ten months (Payne 1979, Bester 1981). Both species bear their pups early in the austral summer. Post natal development in *A. gazella* is rapid, with pups beginning to moult to their adult coats at 8 weeks (Payne 1979, Bester and Wilkinson 1989), and at 16 weeks weaning and dispersing from the colony prior to winter (Payne 1977, Bonner 1984). Pups of *A. tropicalis*, over their longer lactation appear to develop more slowly than *A. gazella* and do not begin moulting until 12 weeks of age (Bester and Wilkinson 1989). They do not wean until after winter, in the following spring.

This thesis examines, in the two fur seal species at Macquarie Island, the maternal energy acquisition at sea and the transfer of this energy to young on shore. Previous work in these areas, which provides much of the background information for this thesis, is outlined below.

In fur seals, the acquisition of energy at sea involves locating and capturing suitable prey species. Both Antarctic and subantarctic fur seals have been reported feeding on densely schooling pelagic prey such as myctophids at Macquarie and Marion Islands (Goldsworthy *et al.* 1997, Klages and Bester 1998) and krill at Bird Island (Doidge and Croxall 1985). There is variation in the diets between sites (Klages and Bester 1998), with Antarctic fur seals in the Kerguelen – Heard Island region including more demersal fish species in their diet (Green *et al.* 1991, Cherel *et al.* 1997) and

subantarctic fur seals from Gough Island taking mostly pelagic squid (Bester and Laycock 1985).

Both fur seal species are nocturnal foragers with dives occurring at dawn and dusk generally deeper than those around midnight (Croxall *et al.* 1985, Goldsworthy *et al.* 1997). At Bird Island, South Georgia, the majority of dives by *A. gazella* were very shallow (< 20 m) and short (< 3 min)(Boyd and Croxall 1992). Similar diving behaviour has been reported for the South Shetland Islands (Costa *et al.* 2000). Shallower (median 10 m) and shorter (< 0.8 min) dives were used by both fur seal species at Macquarie Island (Goldsworthy *et al.* 1997), and for *A. tropicalis* at Amsterdam Island, means of 20 m and 1 min have been reported (Georges, Tremblay *et al.* 2000).

Fewer studies have examined foraging range. Antarctic fur seals from South Georgia have been reported to forage within a mean range of 140 km of the shore (Boyd *et al.* 1998), and within a mean range of 100 km at the South Shetlands (Goebel *et al.* 2000). Antarctic fur seals from Îles Kerguelen have been recorded travelling further, out to a mean of 160 km. The only previous study on the foraging range of subantarctic fur seals has reported incomplete trips out to 700 km (Georges, Bonadonna *et al.* 2000).

The on shore components of provisioning strategies in fur seals involve the pattern of attendance by mothers to provide milk for their pups, the quality and quantity of milk delivered and the resultant pup growth (Gentry *et al.* 1986). Fur seals transfer energy to their pups in the form of lipid rich milk (Oftedal *et al.* 1987). Previous studies of milk composition for both *A. gazella* and *A. tropicalis* report average milk lipid contents to be around 40 % (Arnould and Boyd 1995a, Goldsworthy and Crowley 1999, Georges *et al.* 2001). Milk lipid content has also been found to be highly variable between individuals (Arnould and Boyd 1995a, Goldsworthy and Crowley 1999).

For both *A. gazella* and *A. tropicali*s, pup growth has been described as linear for 0 to 120 days of age (Doidge *et al.* 1984, Kerley 1985). From birth to weaning, *A. gazella* grow at a rate of about 80 g.d^{-1}(Payne 1979, Kerley 1985, Doidge and Croxall 1989,

Goldsworthy 1992). For *A. tropicalis*, with the longer lactation, mean growth rate over 300 days is significantly lower, at around 40 g.d^{-1} (Tollu 1974, Kerley 1985, Goldsworthy 1992, Georges and Guinet 2000).

The link between energy acquisition at sea and transferring energy to the pups, is the mothers' patterns of alternating foraging trips with bouts of suckling on shore. At Bird and Marion Islands, Antarctic fur seals forage in a cycle of 4 to 5 days at sea with a mean of 2 days ashore (Doidge *et al.* 1986, Bester and Bartlett 1990). Lactating *A. tropicalis* females, during summer, undertake on average 5 day foraging trips (though OFTs may not have been detected by observations) with 2 days ashore at Marion Island (Bester and Bartlett 1990) and trips of around 10 days with 4 days ashore at Amsterdam Island (Georges and Guinet 2000). Previous work at Macquarie Island has reported mean foraging trip duration to be very short for both species, at around 2 days, and shore bouts of < 2 days. Attendance behaviour at this location included a significant proportion of overnight trips (Goldsworthy 1999).

1.2.2 *Macquarie Island*

The field work for this thesis was conducted at Macquarie Island (54°30'S, 158° 55'E) (Figure 1.1a). It is a long narrow island (35 x 5 km) orientated roughly north-south and is the exposed part of a raised ridge of ocean floor situated north of the Antarctic Polar Front and just south of the Subantarctic Front. Fur seals breed almost solely at the northern tip of the island (North Head) in three locations (Figure 1.1b). The colonies of *A. gazella* occupy gravelly beaches at Secluded Beach and Aerial Cove, and *A. tropicalis* breed on rock platforms in Goat Bay and at the south end of Secluded Beach where they are within tens of metres of *A. gazella* territories.

1.3 AIMS OF THE PROJECT

The aim of this study was to examine the importance of phylogenetic constraints and environment on the provisioning strategies of sympatric fur seals at Macquarie Island. This was undertaken by comparing the provisioning strategies of the fur seals at this location, primarily in terms of maternal energy acquisition at sea (foraging behaviour

and diet) and on shore energy transfer to the pup (attendance behaviour, milk composition, milk intake, pup growth and fasting).

I spent a total of 24 months at the field site, including three summers and one winter period. The fur seal colonies were visited daily during the 6 month periods surrounding summer and twice or more per week in the winter. Data from the two winters I was absent were collected by colleagues. Data from related studies (by S. Goldsworthy) were used to boost sample sizes on two occasions.

A brief synopsis of how the aspects of fur seal provisioning were investigated during this field work, is detailed below.

1.3.1 *Maternal energy acquisition*

- Foraging area was determined using satellite transmitters to provide information on the distance to, and location of, foraging areas.
- The diving behaviour was monitored using Time-Depth Recorders.
- The diet of the seals was assessed from scat analysis, which was a non-invasive method to indicate the major prey groups targetted.

1.3.2 *On shore energy transfer*

- Pup growth was measured to estimate birth mass, growth rates and weaning mass.
- Attendance behaviour was monitored using small flipper mounted VHF transmitters to enable the measurement of the time allocated to foraging at sea and attending the pup on shore.
- Pup mass loss was measured during times of fasting (ie. in the mothers' absence), to provide a relative measurement of field metabolic rate.
- Milk samples were collected and the composition analysed, providing information on the energy density of the milk
- The water turnover of pups was measured by tritium dilution to provide information on milk and energy consumption.

1.4 ORGANISATION OF THESIS

This thesis comprises six chapters: an introductory chapter, four data chapters and a general discussion. Chapters 2 and 4 have been submitted for publication to *Marine and Freshwater Research* and *Australian Journal of Zoology*, respectively. All the data chapters have been written as separate papers for publication, thus there is some repetition of information in the Methods sections of the chapters.

The project was designed to investigate the provisioning strategies of fur seals and to reflect this, the thesis has been divided into two chapters (Chapters 2 and 3) detailing maternal energy acquisition and two chapters (Chapters 4 and 5) examining energy transfer to the pup.

Chapter 2 is a comparison of the foraging ecology of the two fur seal species, covering diet, diving behaviour and foraging areas used. Chapter 3 provides more detail of the foraging areas of Antarctic fur seals, particularly with respect to area use between years, between females and between foraging trips of the same female. A similar data set was not available for subantarctic fur seal females due to their low numbers. Chapter 4 reports on the similarities and differences in pup growth of the two species. Chapter 5 describes the transfer of energy from mothers to pups: milk composition, energy consumption and the link between pup energy demands and the mothers' attendance behaviour. The General Discussion describes and synthesises the main findings.
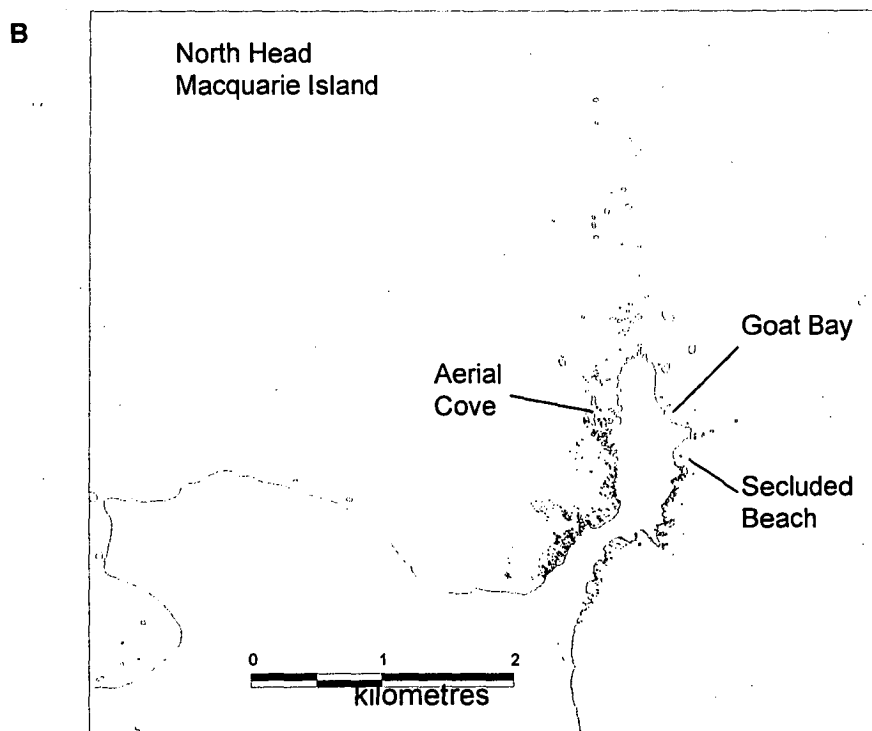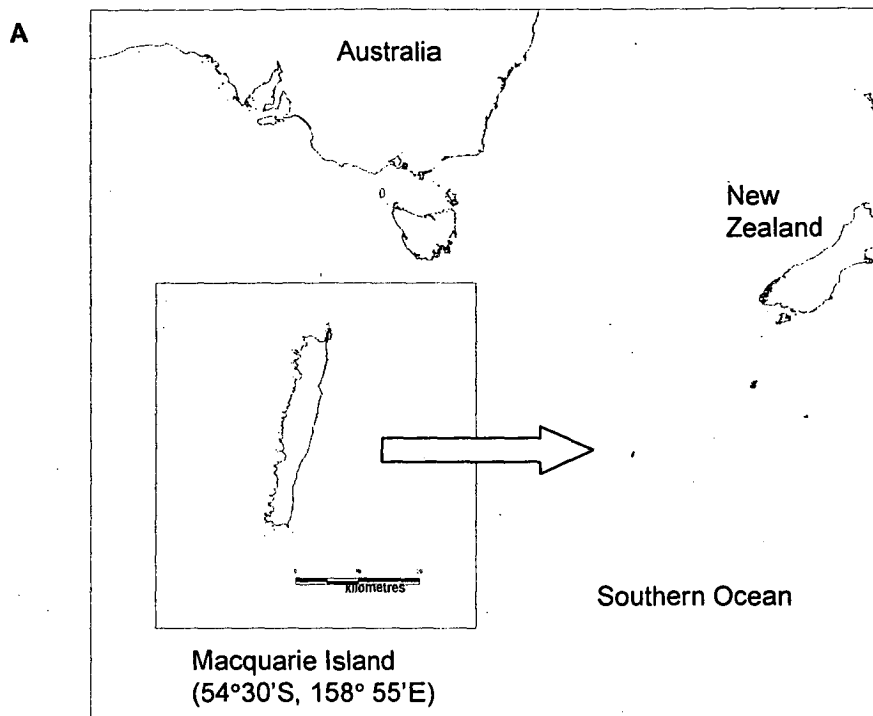
Figure 1.1 a and b
(a) Location of Macquarie Island in the Southern Ocean.
(b) Location of fur seal colonies at North Head.

CHAPTER   2
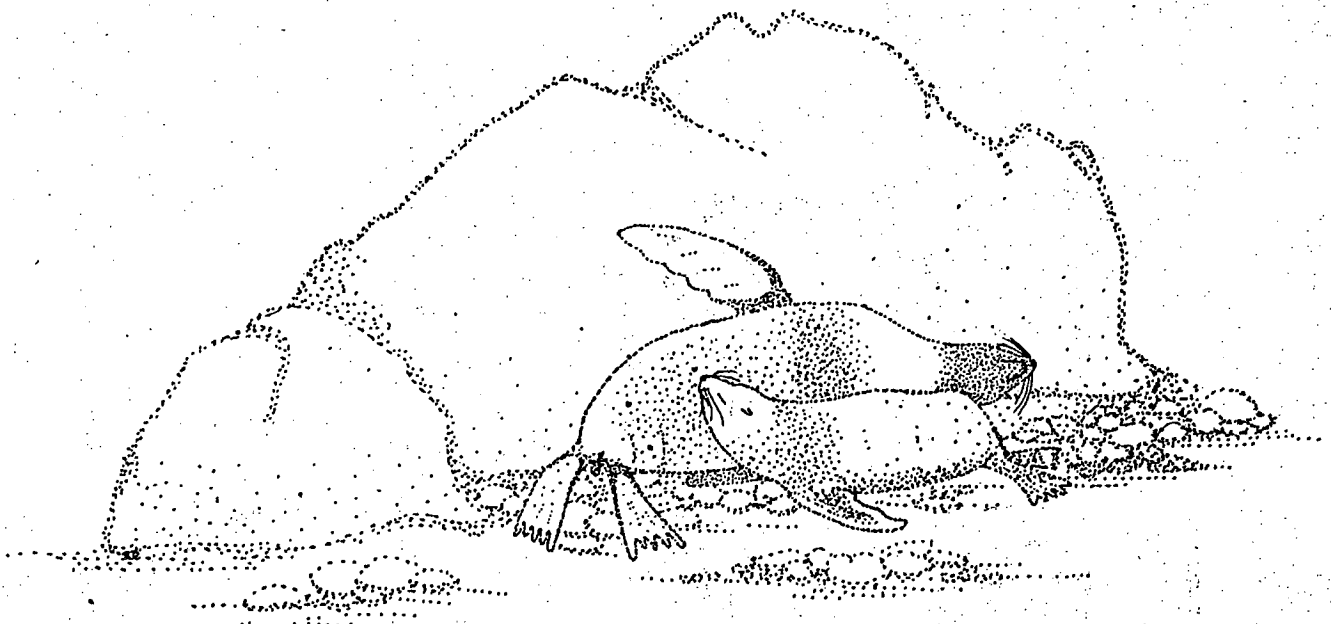
Chapter 2

THE FORAGING ECOLOGY OF TWO SYMPATRIC FUR SEAL SPECIES AT MACQUARIE ISLAND, *ARCTOCEPHALUS GAZELLA* AND *A. TROPICALIS*, DURING THE AUSTRAL SUMMER

2.1   INTRODUCTION

The subfamily Arctocephalinae, the southern fur seals, began diversifying around 5 to 3 million years ago (Repenning 1975). Speciation is likely to have occurred in environments varying in seasonality and predictability of prey resources, which has resulted in the evolution of different breeding strategies in fur seals, each suited to a particular combination of environmental variations (Gentry and Kooyman 1986a). Broadly, Arctocephalines of high latitudes, (eg. Antarctic fur seal *Arctocephalus gazella*) contend with highly predictable seasonal environments (though an exception occurs, Priddle *et al.* 1988, McCafferty *et al.*1998), and have evolved a short lactation period so that pups are brought to weaning within a brief period of high prey availability (Gentry and Kooyman 1986a). Zones of low latitude are often associated with environments of low seasonal variation and subject to unpredictable fluctuations in prey availability (i.e. El Niño events). Fur seal species of these regions (eg. *A. galapagoensis*) have evolved extended and flexible lactation periods. Temperate species (eg. *A. tropicalis*) exhibit a breeding strategy between the two extremes, probably evolving in an environment low in food resources, variable within a certain range, though not subject to massive failure (Gentry and Kooyman 1986a).

The original fur seal populations of the Southern Ocean were severely depleted by harvesting for furs (Repenning *et al.* 1971) and at subantarctic Macquarie Island (54° 30'S, 158° 55'E), fur seals were exterminated by sealers in the early 1800s (Cumpston 1968). They did not recolonise until the 1950s (Shaughnessy and Shaughnessy 1988) and it is not known which fur seal species originally inhabited the island. Currently, Antarctic fur seals (*Arctocephalus gazella*) and subantarctic fur seals (*A. tropicalis*) breed at this site. They have very different lactation strategies,

taking four months and ten months, respectively, (Payne 1977, Bester 1981) to raise their pups.

Female fur seals are central-place foragers (Orians and Pearson 1979) alternating between periods of foraging at sea and suckling their pups on land (Bonner 1984). They generally feed on densely schooling, vertically migrating pelagic prey such as krill or myctophids over continetal slopes (Reid 1996, Goldsworthy *et al.* 1997, Klages and Bester 1998). Both *A. gazella* and *A. tropicalis* breed in the austral summer and at Macquarie Island there is overlap in the pup-rearing period for the initial four months (Goldsworthy 1992).

Both species have been studied at their allopatric sites revealing a variety of foraging behaviours. At South Georgia, *A. gazella* females feed on mostly krill at shallow depths (Croxall *et al.* 1985), foraging over the contental slope and beyond up to 350 km from the colony (Boyd *et al.* 1998). Foraging behaviour at Cape Shirreff varies with bathymetry and prey type (Goebel *et al.* 2000) and at Îles Kerguelen and Heard Island, a higher proportion of benthic items are found in *A. gazella* diets (Cherel *et al.* 1997, Green 1997). At Amsterdam Island *A. tropicalis* is less well studied: this species undertakes relatively long foraging trips to consume myctophids (Georges, Bonadonna *et al.* 2000, Georges, Tremblay *et al.* 2000), and at Gough Island pelagic cephalopods are the main prey (Bester 1987).

Does this variety in fur seal foraging behaviour relate more to species differences or to the local environment? Given that the two species behave differently at different locations, will their foraging behaviour be the same at the same breeding site, particularly in view of their divergent lactation strategies?

The sympatric populations at Macquarie Island provide an unusual opportunity to compare the foraging behaviour in two taxonomically similar species with different lactation strategies under identical environmental conditions. The study compares the foraging ecology, in particular the diet, diving behaviour and foraging zones of these sympatric fur seals at Macquarie Island, during the first four months of pup-rearing.

2.2 MATERIALS AND METHODS

2.2.1 *Study site and species*

This study was conducted at North Head, Macquarie Island (54° 30'S, 158° 55'E) during February and March 1991, December 1995 to April 1997, and from December 1997 to April 1998. Antarctic fur seals *Arctocephalus gazella* and subantarctic fur seals *A. tropicalis* have preferred substrate types, beaches and rock platforms respectively, but breed within tens of metres of each other. The populations of each species are low in numbers, *A. gazella* producing around 135 pups per year, and *A. tropicalis* around 25 pups a year (S. D. Goldsworthy unpublished). This places some constraints on sample sizes obtainable at Macquarie Island.

2.2.2 *Diet*

Through the austral summers of 1995-96 and 1996-97 (December to April), fresh fur seal scats were collected opportunistically from territories of *A. gazella* and *A. tropicalis*. To ensure samples were from breeding females, collections were made in areas where they were known to suckle their pups, or opportunistically from animals under restraint for other aspects of the study. Scats were labelled and frozen at -18°C until analysis in the laboratory. Prior to analysis, the scats were thawed in hot water and rinsed through 0.5 mm sieves so that all hard parts larger than this could be collected and dried. Squid beaks and crustacean remains were stored in 70 % ethanol.

Fish otoliths were identified using otolith reference guides by Hecht 1987, Williams and McEldowney 1990 and Reid 1996, were referred to a specialist (R. Williams, Australian Antarctic Division), or were compared to reference collections (M. A. Lea, Y. Cherel, S. Robinson unpublished). Cephalopod beaks were referred to a specialist (K. Evans, University of Tasmania) and identified using a reference collection, as were crustraceans (K. Beaumont, J. Kitchener, Australian Antarctic Division).

Fish otoliths were classified on the basis of erosion: Class 1 - not eroded, Class 2 - minimal erosion (edge relief still sharp), Class 3 - significantly eroded, Class 4 - not

identifiable. Otoliths from classes 1 and 2 were measured along their maximum length using a dissecting microscope fitted with a 0.1 mm eye piece graticule. From these measurements and reference equations from Williams and McEldowney (1990), fish standard length was estimated.

2.2.3 *Devices, capture and attachment*

Diving behaviour was recorded using Mk3, Mk 5 and Mk 6 Time Depth Recorders (TDRs)(Wildlife Computers, Redmond, WA, USA). All TDRs were programmed to sample depth every 5 s and had a depth resolution of ± 1 m, except for one device in March 1996 used for 2 deployments which had ± 2 m resolution. TDR protocol was wet/dry timed so that haul-out periods were recorded.

Four Telonics ST-10 satellite platform transmitter terminals (PTTs) (Telonics, Mesa, AZ, USA) in waterproof epoxy housing (Sirtrack, Private Bag 1404, Havelock North, NZ) were used. Each unit (with glue) measured 130 x 50 mm x 320 g. The PTTs had a continuous repetition rate of 50 seconds and transmitted continuously. A saltwater conductivity switch deactivated the transmitter when below the water surface to save battery power. The ST-10 PTTs transmitted to ARGOS receivers on National Oceanic and Atmospheric Administration (NOAA) polar orbiting satellites.

Those seals equipped with instruments were captured using a hoop net, weighed with 50 ± 1 kg scales (Salter, Melbourne) and restrained on a board with adjustable straps. PTTs had a 50 x 130 mm strip of Velcro™ (hooked section) glued to the underside with Cieba Geigy Araldite™ K268 two part epoxy and secured with two plastic cable ties. This was allowed to set before the package was attached with epoxy to the fur of the seal. The animals' fur was cleaned of oil with acetone, and if wet was first dried with 70 % ethanol. The TDR or PTT was positioned between the scapulae. The epoxy was applied to the fur within a plastic stencil, which was then removed leaving the device embedded in the glue. Devices were removed by cutting the fur underneath with a scalpel blade. The Mk 3 TDRs were secured with two hose clamps looped through a small perspex mount, attached as described above.

2.2.4 *TDR deployments and dive data*

In 1990-91, Mk 3 TDRs and in 1995-96, Mk 5 and Mk 6 TDRs were deployed on
seals for one to eight foraging trips (Table 2.1). These devices were recovered from
seals within 6 hours of them returning from a foraging trip at which time females
were re-weighed. Hexadecimal files from TDRs were converted to decimal files using
the 3M software (Wildlife Computers). Each foraging trip was then corrected for
variation in surface depth using the software 'DiveView' (B. Dumsday, University of
Melbourne) run in 'LabView' (National Instruments, USA). Descriptive parameters
(see below) for each individual dive were then extracted using the software 'DIVE'
(S. Greenhill, Murdoch University). Double the maximum depth resolution was
chosen as the minimum depth to be considered a dive (ie. 4 m). This was likely to
remove most of the travelling dives.

Table 2.1
TDR models deployed, depth transducer resolutions, number of seals instrumented
and range of number of foraging trips per seal, for species and study period, January –
March 1991, December 1995 – March 1996.

Year	Seal species	TDR type	Depth resolution (m)	Seals intrumented	Foraging trips (range)
1991	*A. gazella*	Mk 3	1	9	1-4
	A. tropicalis	Mk 3	1	4	1-2
1995-96	*A. gazella*	Mk 5	1	8	2-6
		Mk 6	2	1	6
	A. tropicalis	Mk 5	1	3	3-8
		Mk 6	2	1	4

In the 1995-96 austral summer, 60 foraging trips were recorded from 13 deployments
(*A. gazella* n = 9, *A. tropicalis*, n = 4) and 22 foraging trips from 13 deployments (*A.
gazella* n = 9, *A. tropicalis*, n = 4) were recorded for the 1991 season (some aspects of
which are published in Goldsworthy *et al.* 1997). These foraging trips were described
by 6 parameters: (1) foraging trip duration (days), (2) number of night dives per hour
of night, (3) dive duration (minutes), (4) maximum dive depth (metres), (5) proportion
of the night spent submerged and (6) total vertical depth per night hour (metres/hour).

Because very little diving activity occurred during daylight hours, parameters 2, 5 and 6 were calculated on the basis of night hours rather than foraging trip hours. The varying duration of night over the study period was calculated from AUSLIG (Australia) sunset and sunrise tables.

In order to avoid lack of independence of data caused by multiple observations per individual animal, in those cases where multiple trips were recorded, the mean value for each parameter was calculated to give single values for each seal.

Each TDR record was divided into separate foraging trips on the basis of the recorded haul-out periods. Only periods of greater than 2 hours at sea were regarded as foraging trips. This excluded short swims off the colony caused by heat or disturbance, but included short overnight trips. Foraging trips were classed as either extended (> 24 h) or overnight trips (< 24 h) for each species (see Goldsworthy 1999) and were analysed separately.

Discriminant Function Analysis (DFA) was used to test for differences in diving parameters between the species and to determine which parameters were important in distinguishing the two species. There were too few data to perform these analyses comparing within species between years. The data from both years were therefore pooled, and the assumption made that intra-species variation would be greater than inter-annual variation.

2.2.5 *Satellite transmitters and data treatment*

The four PTTs were repeatedly deployed during December to March of 1996-97 and 1997-98. A total of 31 deployments were made: 13 in 1996-97 and 18 in 1997-98 resulting in useable data for 77 complete foraging trips.

All data were obtained from the ARGOS system (Toulouse, France). The accuracy of the various location classes given by ARGOS was assessed using hits from a known location (Secluded Beach, Macquarie Island) (Table 2.2). Accuracies stated by ARGOS were within the range of errors found in this study, although the mean location accuracy was at least twice that reported by ARGOS. Several other studies

have compared the accuracy of ARGOS locations with that of a known point with similar results (Stewart *et al.* 1989, Keating *et al.* 1991, McConnell *et al.* 1992, Hull *et al.* 1997, Brothers *et al.* 1998, Bonadonna *et al.* 2000). Filtered Class 0 and Class A hits were included in this study as their mean accuracies were found to be similar to each other and less than 10 km.

Table 2.2

Summary of assessment of the accuracy of ARGOS location classes.

Location Quality	Number of hits assessed	Mean ± SE (km)	Range (km)
3	3	0.48 ± 0.29	0.09 – 1.03
2	11	1.16 ± 0.21	0.19 – 2.58
1	28	2.09 ± 0.28	0.09 – 6.34
0	19	6.07 ± 0.86	1.78 – 15.05
A	7	5.83 ± 1.32	2.43 – 11.83
B	7	45.12 ± 6.54	10.23 – 62.21
Z	0	-	-

The data were filtered with a forward, backward iterative velocity filter based on that of McConnell *et al.* (1992). The maximum travelling speed of fur seals calculated from ARGOS locations of Class 3, 2 or 1, with an accuracy of < 1 km, was 4.82 km/h (1.3 m/s). Locations were thus filtered using an estimated maximum velocity of 6 km/h (1.7 m/s). Foraging trips of duration > 24 hrs (extended foraging trips) with a maximum range greater than 10 km were selected for analysis. Overnight trips were treated separately due their close proximity to the colony.

Filtered locations were assigned to cells of 0.1° latitude by 0.1° longitude identified by a nodal latitude and longitude. The seals' entry and exit times for these cells were calculated using surface velocity information derived from satellite fixes. From this, at-sea night-time locations (time of maximum foraging activity, Goldsworthy *et al* 1997) and movements of animals were isolated for analysis, and their foraging activity expressed as time per cell. For the separate foraging trips of each seal, time spent in each cell was summed and converted to a proportion of total foraging time per cell. Individual seals thus contributed one set of values for their foraging activity. These values were summed for each species and again converted to proportional time

per cell, thus correcting for the different number of individuals per species. The cells in which seals spent the upper 50 % of their proportional foraging time (i.e. the 50th cumulative percentile), were determined and used to indicate the most important foraging areas, ie. those areas where the most night hours were spent. These proportional foraging times per cell were interpolated and plotted using the GIS software MapInfo™ (MapInfo Corporation) and Vertical Mapper™ (Northwood, Geoscience).

Locations of seals undertaking overnight foraging trips close to the colony (often within 10 km) were accepted if the following criteria were met: (1) the seal was observed absent from the beach at the preceding evening observation or subsequent morning observation, (2) a night location of accuracy Class 3, 2 or 1 was recorded, (3) the location was further than 2 km from the colony (mean Class 1 accuracy being 2 km).

Individual fur seals of both species (1996-97 n = 27, 1997-98 n = 37) were concurrently fitted with flipper tag mounted VHF transmitters (Sirtrack, Havelock North, NZ), as per Goldsworthy (1999) so that foraging trip duration could be accurately measured. This was compared to trip durations from seals instrumented with PTTs. Twice daily checks (08:30 and 17:00) were made of the colony for tagged females for further information on movements.

Statistical packages used in the analyses were StatView (SAS Institute, USA) and SYSTAT (SYSTAT Inc., Illinois) for Student's T-tests, Analysis of Variance, Analysis of Co-Variance and Discriminant Function Analysis. Means are given with standard errors, P values are significant at < 0.05.

2.3   RESULTS

2.3.1   *Diet*

Ten scats per month for *A. gazella* and *A. tropicalis* were examined from December through to April for the 1995-96 and 1996-97 breeding seasons. A total of 200 scats

were examined; 100 from *A. gazella* and 100 from *A. tropicalis*.

All scats contained remains of fish (otoliths, bones or scales), 8 % of the samples included squid beaks and 2 % had remnants of crustaceans. Sagittal otoliths were present in all samples, and non-sagittal otoliths present in 95.3 % of samples. The latter were not used in any further analyses, being non-diagnostic, apart from being associated with the Myctophidae. A total of 10,548 sagittal otoliths were counted. Between 1 and 350 sagittal otoliths (mean ± SE of 52.7 ± 4.1) (Table 2.3) were found per sample.

Table 2.3
Numbers of scats analysed and prey remains in fur seal diet in the austral summers of 1995-96 and 1996-97 combined, for *A. gazella* and *A. tropicalis*.

	A. gazella	*A. tropicalis*	All samples
No. of samples	100	100	200
Months sampled in 1995-96	5	5	10
Months sampled in 1996-97	5	5	10
Total otoliths	5321	5227	10548
Mean ± SE otoliths/sample	53.2 ± 5.7	52.3 ± 6.0	52.7 ± 4.1
Range of otoliths/sample	1 - 350	1 - 310	1 - 350
Otoliths identifiable to species	42 %	39 %	40 %
Identifiable fish species	8	7	8
Samples with cephalopods	9	8	17
Samples with crustaceans	1	3	4

All sagittal otoliths showed some signs of erosion from digestion with 23 % unidentifiable to any level of taxa. Eight fish species were identifiable, including a pair of species which, when eroded, were difficult to distinguish positively from each other (*Gymnoscopelis nicholsi* and *G. piabilis*). Of the 200 samples, 193 contained otoliths identifiable to species level. Using these otoliths, numerical abundance (NA) was calculated for individual samples (Table 2.4). *Electrona subaspera* was the most abundant fish species, occurring in 99.5 % (frequency of occurrence, FoO) of samples with a mean NA of 93.9 %. The next most common was the *Gymnoscopelis nicholsi / piabilis* complex, found in 19.7 % (FoO) of samples, and mean NA 3.4 %. Other fish species had less than 7.3 % FoO and numerical abundance less than 1.1 %.

Table 2.4
Percentage frequency of occurrence (FoO %) and percentage numerical abundance (NA %) of identifiable otoliths from individual diet samples for both fur seal species, 1995-96 and 1996-97 combined.

Fish species	*A. gazella* (n = 98)		*A. tropicalis* (n = 95)		All samples (n = 193)	
	% NA	% FoO	% NA	% FoO	% NA	% FoO
Electrona subaspera	93.6 ± 1.5	99.0	94.2 ± 1.4	100	93.9 ± 1.0	99.5
Electrona carlsbergi	1.2 ± 1.0	4.1	0.8 ± 0.6	4.2	1.0 ± 0.6	4.2
Gymnoscopelis sp.	2.9 ± 0.9	22.5	3.8 ± 1.3	16.8	3.4 ± 0.8	19.7
Bathylagus antarcticus	0.1 ± 0.1	2.0	0.3 ± 0.3	2.1	0.2 ± 0.1	2.1
Krefftichthys anderssoni		0.0	0.1 ± 0.1	1.1	< 0.1	0.5
Icichthys australis	0.02 ± 0.02	1.0		0.0	< 0.1	0.5
Magnisudis prionosa	0.8 ± 0.3	9.2	0.2 ± 0.1	4.2	0.5 ± 0.2	6.7
Protomyctophum normani	1.4 ± 0.8	9.2	0.7 ± 0.3	5.3	1.1 ± 0.4	7.3

Of 200 samples, 17 (7.9 %) contained cephalopod remains, 11 of which contained identifiable lower beaks. Of these, 9 samples contained *Morotuethis knipovitchi*, and 1 sample each contained *M. robsoni* and *Kondakovia longimana*. Nine samples came from *A. gazella* (5 with identifiable cephalopods of 3 species) and 8 samples from *A. tropicalis* (4 containing *M. knipovitchi*).

Crustacean remains were present in 4 (2 %) samples. They were highly digested and some could only be identified to family level. Hyperiid and gamariid amphipods were most common, with FoO 100 % and 25 % respectively. Those identifiable to species were all *Themisto gaudichaudii* (FoO 75 %).

2.3.2 *Inter-specific comparison*

A complete Discriminant Function Analysis (DFA) was used to detect differences in the diet between years and between the two seal species. No difference between years or seal species was evident (Wilks' Lambda = 0.806, approx. $F_{30,549}$ = 1.40, P = 0.079. For data pooled across years, the diets were very similar: *E. subaspera* 99 % and 100 % by FoO and *Gymnoscopelis* sp. complex 22 % and 17 % by FoO for *A. gazella* and *A. tropicalis*, respectively. By numerical abundance, all taxonomic groups were very

similar between the two seal species, and *E. subaspera* was the most common prey species.

2.3.3 *Size of prey species*

Electrona subaspera was the only prey species with a large enough sample for size analysis. Using a 3-way ANOVA, variation in estimated standard length of *E. subaspera* was investigated with respect to seal species, year and month. There was no difference in the length of fish taken by the two seal species within a year ($F_{1,379}$ = 2.412, P = 0.121), but there was a significant difference in mean fish length between years: 90.6 ± 0.8 mm for 1995-96, 94.4 ± 0.7 mm for 1996-97 ($F_{1,379}$ = 6.362, P = 0.012). This difference however, is unlikely to be biologically significant for the seals. The mean length of *E. subaspera* also varied across the months ($F_{4,379}$ = 4.9, P = 0.001) (Figure 2.1). There were no interaction effects.

2.3.4 *Diving behaviour*

Both species of seal dived almost exclusively at night, with 96 % of dives occurring after sunset and before sunrise in 1995-96, and 93 % in 1991. Both species undertook short, relatively shallow dives (*A. gazella* n = 11,332 dives, *A. tropicalis* n = 7263 dives) averaging 10 - 15 m and 0.5 - 0.9 min (Table 2.5). Maximum depth was approximately 100 m and the sum of vertical depth (one way) travelled per night hour averaged between 100 and 200 m. Seals were submerged for around 12 % of the available night.

The diving behaviour of the two species were examined with respect to overnight (OFTs) and extended foraging trips (EFTs) using a complete Discriminant Function Analysis (DFA) on the pooled 1991 and 1995-96 TDR data. Foraging trip duration was removed from the analyses. The full DFA found no difference in the diving behaviour of the OFTs and EFTs for either species (*A. gazella*: Wilks' Lambda = 0.776, $F_{5,24}$ = 1.387, P = 0.2645, *A. tropicalis*: Wilks' Lambda = 0.740, $F_{5,7}$ = 0.491, P = 0.775).
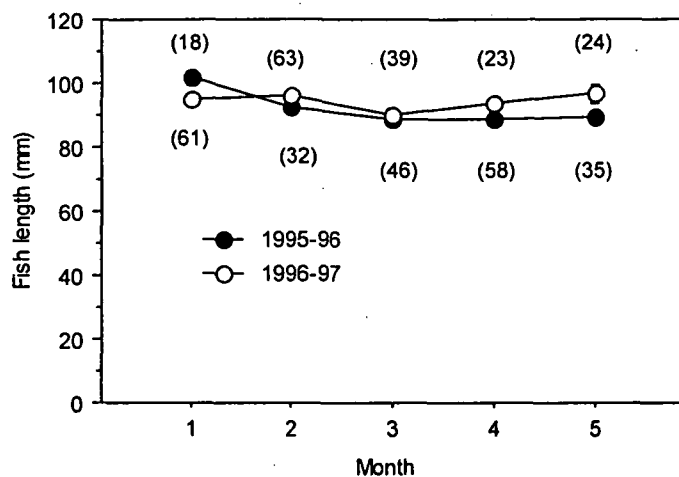
Figure 2.1

Mean standard length (mm) ± SE (n) of *Electrona subspera* calculated from otoliths found in scats of *A. gazella* and *A. tropicalis* combined (n = 399), for the austral summer months of 1995-96 and 1996-97. Months 1 to 5 are December to April, respectively.

Table 2.5

Foraging trip and dive parameters from TDR deployments. *Mean ± SE derived from average values from individual seals. See methods for details of parameters.

	A. gazella		A. tropicalis	
	1995-96	1991	1995-96	1991
Deployments	9	9	4	4
Total foraging trips	39	16	21	5
Overnight trips	24	6	15	1
Foraging trip duration range (d)	0.7 - 7.9	0.3 - 7.8	0.2 - 9.6	0.4 - 8.5
Total dives	5501	5831	4298	2965
Dives per trip - range	4 - 1165	54 - 1053	4 - 1776	176-1286
Maximum dive depth (m)	126	98	95	108
Mean dive depth ± SE (m)	15.8 ± 0.2	13.6 ± 0.2	9.9 ± 0.1	14.2 ± 0.2
Median dive depth (m)	9	9	8	10
Maximum dive duration (min)	4.70	4.17	3.00	3.67
Mean dive duration ± SE (min)	0.87 ± 0.01	0.70 ± 0.01	0.65 ± 0.1	0.69 ± 0.01
Median dive duration (min)	0.59	0.51	0.51	0.51
% night dives/all dives*	94.2 ± 1.8	91.4 ± 2.3	98.9 ± 0.8	94.9 ± 1.5
No. of night dives/night hr*	7.3 ± 2.2	12.2 ± 1.2	11.2 ± 4.8	14.4 ± 2.8
% Night spent submerged*	9.8 ± 2.4	13.0 ± 1.8	13.0 ± 7.1	14.6 ± 3.4
Vertical depth/night hr* (m/h)	103.7 ± 27.4	152.4 ± 22.4	107.2 ± 46.8	195.9 ± 44.0

Extended and overnight foraging trips were separated for the analyses as it was believed they were functionally different (see Goldsworthy 1999). DFA was used on the six parameters calculated, for determining if foraging behaviour during OFTs varied between the two species (pooled 1995-96 and 1991 data, *A. gazella* n = 12, *A. tropicalis* n = 5). None of the variables were found to discriminate the two species (P > 0.05 for all variables) for OFTs.

A DFA also found no significant difference between the two species for parameters calculated for EFTs (Wilks' Lambda = 0.638, $F_{6,19}$ = 1.794, P = 0.154).

2.3.5 *Foraging location using PTTs*

A total of 2560 at-sea location fixes were received over the two summer periods. After filtering and extracting the night time at-sea fixes of Class 3, 2, 1, 0 and A, 1283

(50 %) remained. Overall, extended foraging trips from 31 female fur seals (n = 77 trips) covered a mean maximum distance of 58.2 ± 3.4 km from the colony, resulting in a mean round trip distance of 154.6 ± 9.2 km. The mean duration of all foraging trips analysed was 3.4 ± 0.2 d (Table 2.6).

Table 2.6
Summary of PTT deployments: foraging distances and durations estimated from ARGOS data.

	A. gazella		*A. tropicalis*	
	1996-97	1997-98	1996-97	1997-98
No. of females	10	17	3	1
No. of foraging trips > 24 h	24	39	11	3
Minimum round trip distance (km)	55	35	22	66
Maximum round trip distance (km)	290	319	485	151
Mean foraging range ± SE (km)	58.1 ± 5.3	60.3 ± 3.9	54.0 ± 19.8	46.5 ± 11.2
Maximum foraging range (km)	116	126	227	68
Mean trip duration ± SE (d)	3.9 ± 0.3	3.2 ± 0.2	3.2 ± 0.8	2.0 ± 0.6

Foraging trip durations of seals deployed with PTTs were compared to those carrying small flipper mounted VHF transmitters during the relevant months of 1996-97 and 1997-98. Due to the removal of short foraging trips from the PTT data set, only trip durations > 2 days were compared. Foraging trip durations determined by VHF and PTTs were not significantly different for 1996-97 (T-test: df = 25, P = 0.1721, mean 3.69 ± 0.15) or 1997-98 (T-test: df = 36, P = 0.1804, mean 3.34 ± 0.11).

Using data pooled for the two years and mean values for each female (*A. gazella* n = 27, *A. tropicalis* n = 4), foraging trip duration and maximum range were found to be significantly positively correlated:
A. gazella maximum range = 13.082 * trip duration + 12.028, R^2 = 0.600, (ANOVA $F_{1,25}$ = 37.487, P < 0.0001).
A. tropicalis maximum range = 20.349 * trip duration - 6.309, R^2 = 0.947, (ANOVA $F_{1,2}$ = 36.069, P = 0.027).

Inter-annual differences in maximum distance from the colony and foraging trip duration were investigated for *A. gazella*. Where there were multiple trips per seal, mean values for trip duration and maximum distance were taken. ANCOVA indicated

a significant relationship between maximum distance and trip duration ($F_{1,23}$ = 7409.339, $P < 0.0001$) and that this relationship was significantly different between the years ($F_{1,23}$ = 744.803, $P = 0.016$). There was no difference between the slopes of the two relationships ($P = 0.097$). Given the level of error surrounding PTT locations at sea (up to 10 km), the maximum distance for 1996-97 (mean $\pm$ SE = 58.14 $\pm$ 5.32) and 1997-98 (mean $\pm$ SE = 60.31$\pm$ 3.88), are approximate.

For a descriptive overview, and to improve sample size for *A. tropicalis*, foraging trips from the two seasons were pooled for each species. The interpolated area covered by 100 % and the upper 50 % of the cumulative proportion of foraging time was calculated for *A. gazella* and *A. tropicalis* (Table 2.7).

Table 2.7
Area (km^2) covered by 100 % and the upper 50 % cumulative proportion of night-time activity (presumed foraging), and total hours used in analysis for each species.

	100 % (km^2)	> 50 % (km^2)	Total activity (h)
A. gazella	5512	985	1656
A. tropicalis	6753	802	259

For *A. gazella*, the core foraging activity (upper 50 %) occurred NNE from the island (Figure 2.2 a), covering an area approximately 70 km long and 25 km wide, along the eastern shoulder of Macquarie Ridge. The highest number of foraging hours were spent immediately north of the island. The foraging activity of *A. tropicalis* was also focussed north of the island parallel to and to the east of the ridge (Figure 2.2 b). There was greater dispersion in the interpolation for *A. tropicalis*, with points of core foraging activity at 100 km away to the southwest and east.

There was 25 % overlap of the core areas for the two species. Of the single core area for *A. gazella* along the Macquarie Ridge, 46 % was also used by *A. tropicalis*. The two species overlapped in the area where both had the highest activity: i.e. within 30 km of the island, over the Macquarie Ridge. Core areas for both species also overlapped at approximately 54° 00'S 159°12'E, about 60 km NNE of the island.
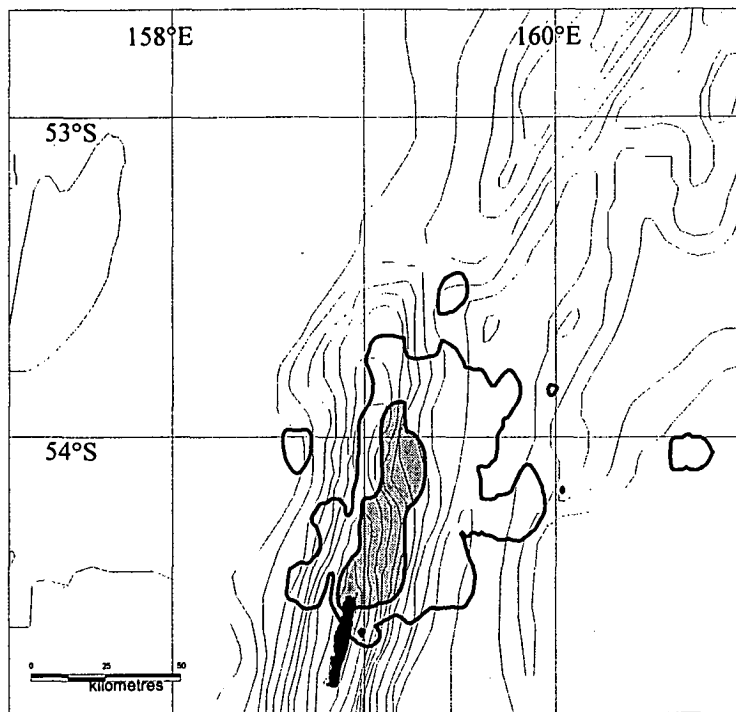
A. *A. gazella*
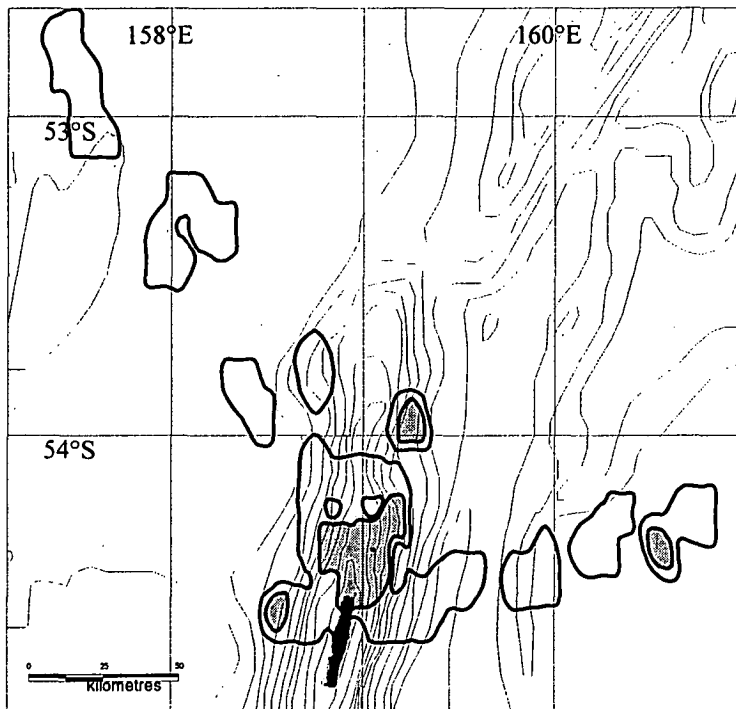
B. *A. tropicalis*

Figure 2.2

Macquarie Island and surrounding bathymetry: interpolated foraging area calculated from foraging time per cells of 0.1° latitude x 0.1° longitude (a) *A. gazella* (n = 27 females and 63 trips) and (b) *A. tropicalis* (n = 4 females and 14 trips) compiled from 1996-97 and 1997-98 PTT data. The areas where seals spend the upper 50 % of their cumulative proportional foraging time are shaded. Outlined areas are all areas visited by seals at night, presumed foraging area. Contour intervals from island, 100, 200, 500, 1000, 2000, etc. to 6000 m.
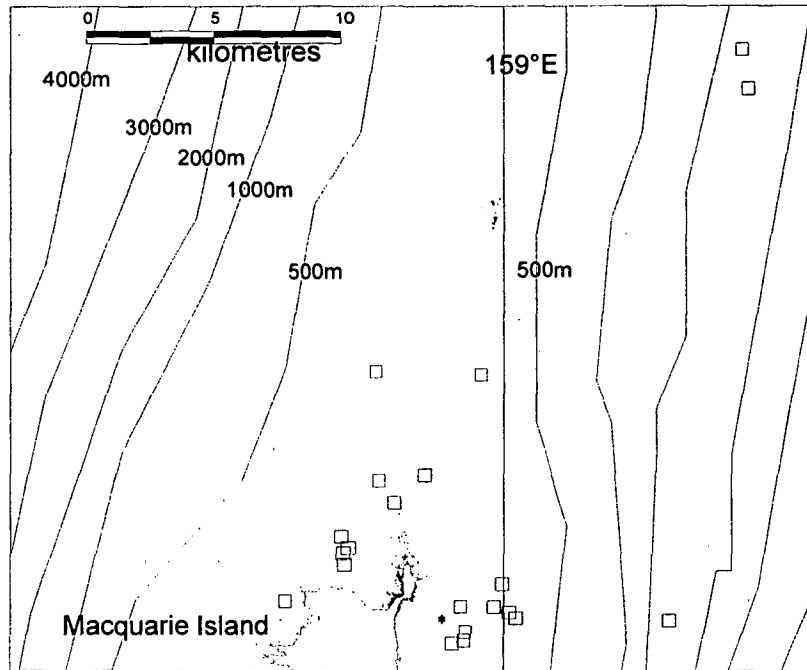
Figure 2.3
Overnight foraging trip locations of *A. gazella*, and a single
A. tropicalis location denoted with *.

Single locations for overnight trips were established (Figure 2.3). Fourteen animals were recorded during 22 OFTs. A single OFT location for A. tropicalis was recorded. The maximum distance from the island for an OFT location was 25 km, however most (77 %) overnight foraging activity was within 6 km of the island to the east and northwest. Most recorded overnight locations were in waters less than 200 m (68 %) depth though some (14 %) were in waters deeper than 1000 m.

2.4   DISCUSSION

Flexibility in the foraging behaviour of fur seals has been recorded in several studies (McCafferty *et al.* 1998, Boyd 1999, Georges, Tremblay *et al.* 2000, Harcourt *et al.* 2001, Lea *et al.* in press (b)). In this study of sympatric species with different lactation strategies, it was found that both exploited the marine environment in very similar ways. This supports the idea that observed differences in foraging behaviour between species and within species at different locations are environmentally, rather than phylogenetically, mediated.

2.4.1   *Diet*

Inferring diet from faecal samples in pinnipeds is a common technique, but may contain biases. The quality and number of remnant hard parts of prey in faeces can be affected by several factors: (i) seals may vomit, losing part of accumulated remains, (ii) differential digestion of hard parts in the stomach (related to otolith size and density, diet composition, resistance of fish skulls to digestion) may remove items and/or give a false view of dominance of some prey types, (iii) rate of passage of digesta and foraging trip duration may affect what remains in the faeces, and (iv) faecal deposits contain remains of an unknown number of feeding episodes from an unknown period of time (Helm 1984, da Silva and Neilson 1985, Jobling and Breiby 1986, Murie and Lavigne 1986, Dellinger and Trillmich 1988, Croxall 1993). These factors contribute to the inherent variability in determining diet from faecal samples. However, with proper caution, scat analysis can provide qualitative and some quantitative information (North *et al.* 1983, Dellinger and Trillmich 1999). Dellinger and Trillmich (1988) believe that ratios of different teleost fish species in South American fur seal (*A. australis*) and Californian sea lion (*Zalophus californianus*)

diets can be reliably estimated using large sample sizes. The same authors claimed 45 samples per season to be large enough to overcome major biases (Dellinger and Trillmich 1999). Fifty samples per season were used in the current study.

Cephalopod beaks may accumulate in the stomachs of seals (Gales and Cheal 1992, Reid 1995, Klages and Bester 1998), then be ejected by vomiting. For this study, the cephalopod component in the scats was very low, suggesting for adult female fur seals at this site, the consumption of cephalopods was either minimal or under-estimated.

The diets of the two fur seal species studied were extremely uniform, dominated by one fish species, the myctophid *Electrona subaspera*. No interspecific differences were found in the diet, with *E. subaspera* dominating by numerical abundance and frequency of occurrence in both cases. The *Gymnoscopelis nicholsi / piabilis* complex was the next most important taxon but was substantially lower in abundance and frequency. All other fish species recorded were uncommon, as were cephalopods and crustaceans. It was possible that crustaceans were taken incidentally or secondarily, as amphipods have been recorded as myctophid prey items (Hulley 1990).

Inter-annual differences in diet composition were not evident between species and both appeared to be feeding on similarly sized *E. subaspera* in each year. The decrease in the average length of these fish through both summers, also seen in Goldsworthy *et al.* (1997), suggests recruitment into the fish population and an increase in availability of smaller individuals to the seals.

The main prey species *E. subaspera, E. carlsbergi, G. nicholsi and G. piabilis*, are all small (< 16 cm) mesopelagic fish of generally circum-global distribution, found between the Subtropical Convergence and Antarctic Polar Front (Hulley 1990). At night they undergo upwards vertical migration to between 200 m depth and the sea surface (Hulley 1990) and would thus become available to fur seals in the surface waters. The results of our diving behaviour studies (see below) indicate that the fish are within 20 m of the surface. Trawl surveys in the vicinity of Macquarie Island report myctophids dominating the pelagic fish fauna (Williams 1988).

Similar to this study, the results of earlier work at the same site by Goldsworthy *et al.*
(1997) in 1991, found no separation with respect to prey species for *A. gazella* and *A.
tropicalis*. In a study by Klages and Bester (1998) of the same seal species in
sympatry at Marion Island, where the combined populations were much larger
(approx. 40 000), there was also very little difference in diet.

Green *et al.* (1990) compared the diet of *A. forsteri* and *A. gazella / A. tropicalis*
combined at Macquarie Island. There was strong similarity in fish species consumed
but differences in their proportions in the diets. Larger proportions of cephalopods
and penguins were found in *A. forsteri* diet where all samples came from males. Male
A. forsteri are usually larger in size and not constrained by breeding activities.

As recorded in other studies of Antarctic and subantarctic fur seal diet (Table 2.8),
these seals generally favour densely schooling, small pelagic prey which move into
the surface waters at night. The fur seal prey types appear related to the local
bathymetry, as discussed in Klages and Bester (1998). Islands with narrow shelves are
close to oceanic habitat with pelagic species (eg. Marion and Macquarie Islands), and
islands situated on undersea plateaux or wide shelf areas (Heard and Kerguelen
Islands), provide habitat for benthic and demersal species as well as pelagic species
(Table 2.8). It is likely that fur seals target local prey resources, which would help to
reduce their travelling and energetic costs, and enable frequent shore visits to suckle
pups.

Furthermore, females of both species are similar in average body size (between 28
and 40 kg, S. A. Robinson unpublished) thus little separation with respect to prey size
would be expected in the diet. There may be little competition for prey resources at
Macquarie Island at present due to the population being a fraction of it's pre-sealing
size (Goldsworthy *et al.* 1997) (< 200 breeding females, Goldsworthy unpublished).
The two species are feeding on an abundant nearby food resource, at least during the
summer months. The prey availability and location of their winter foraging grounds
are currently unknown.

Table 2.8

Environment types and predominant prey types from other studies of *A. gazella* and *A. tropicalis*.

Environment	Predominant prey group	*A. gazella* Source	*A. tropicalis* Source
Oceanic	myctophids	Klages & Bester 1998, Goldsworthy *et al*. 1997	Klages & Bester 1998, Goldsworthy *et al*. 1997
Oceanic	pelagic squid and myctophids		Bester & Laycock 1985, Bester 1987
Oceanic & shelf	krill	Doidge & Croxall 1985, Reid & Arnould 1996	
Oceanic & shelf	myctophids and channichthids	Green *et al*. 1991, Cherel *et al*. 1997	

2.4.2 *Diving Behaviour*

Boyd *et al*. (1991) found no differences in foraging trip and shore bout duration between instrumented and non-instrumented *A. gazella*, although Walker and Boveng (1995) showed attachment of two devices (TDRs concurrent with VHF transmitters) significantly affected attendance and foraging behaviour. Bonadonna *et al*. (2000) found *A. gazella* to undertake longer than normal foraging trips when TDR Mk6 devices were attached. For this study only single devices (TDRs or PTTs) were attached to lactating females. There was no difference in the foraging trip durations, for trips greater than 2 days, of females fitted with VHF transmitters compared with PTTs. It was believed the impact on the foraging behaviour of females was minimal for both PTTs and TDRs.

Similar to other fur seal populations feeding on pelagic species (Croxall *et al*. 1985, Boyd and Croxall 1992, Green 1997, Lea *et al*. in press(b)), *A. gazella* and *A. tropicalis* at Macquarie Island were nocturnal foragers, employing short, shallow dives through the night with longer, deeper crepuscular dives as they presumably followed vertically migrating prey through their diel activity. At Macquarie Island both species fed very close to the surface (median depth 8.5 m). This diving behaviour

is the shallowest so far reported for either species (Boyd and Croxall 1992, Green 1997, Costa *et al.* 2000, Georges, Tremblay *et al.* 2000). Using a 4 m cut-off for removing 'surface noise' from dive records, was likely to have excluded some of the near-surface foraging activity and thus the average foraging depth may have been even shallower. Kooyman *et al.* (1986) commented that the lack of dive data recorded for *A. gazella* around midnight may indicate shallow diving which was not detected with TDRs. The use of finer depth resolving recorders (± 0.25 m) and stomach temperature transmitters to determine when prey are ingested, may help determine the importance of near-surface waters for foraging at this location.

Flexibility in the diving behaviour of fur seals has been discussed in recent studies with respect to resource availability between years (McCafferty *et al.* 1998, Boyd 1999), seasonal variation within a year (Georges, Tremblay *et al.* 2000, Harcourt *et al.* in press) and between individuals within a season and between years (Lea *et al.* in press (b)). At Îles Kerguelen, there were greater intra-population differences than found at Macquarie Island between species. Lea *et al.* (in press (b)) found female fur seals at this location to vary considerably in number of dives per night, proportion of vertical depth attained at night and proportions of day and night time dives. Given that fur seals are able to vary their diving behaviour at these different scales, the similarities in diving behaviour of the two species at Macquarie Island suggests similar needs in a heterogeneous environment, or possibly a situation where prey distribution and abundance is relatively homogeneous.

The diving behaviour during overnight and extended trips was not significantly different within species studied here. This was in contrast with Boyd *et al.* (1991) who showed that *A. gazella* females making short trips had a higher dive rate than those on longer trips. Whether prey density at Macquarie Island varies between the foraging areas of overnight and extended trips is not known, but the diving behaviour of these seals suggests not if the rate of diving between EFTs and OFTs does not differ.

2.4.3   *Foraging location*

Interpolation of proportional foraging time per 0.1° latitude by 0.1° longitude cell,

gives a more accurate picture of the importance of foraging areas than the plotting of simple PTT locations. Core areas of foraging activity from extended foraging trips were similar for both fur seal species. These areas extended north from the island directly over and east of the Macquarie Ridge. The sites of most concentrated night-time foraging activity were immediately north of the island within 30 km. The ridge is mostly less than 200 m deep in this area (RAN chart AUS 604). There will be some bias towards hits in this area due to animals moving through this region as they travel to or from the colony. However, as only night-time locations were used in the analysis, reflecting the time of maximum foraging, the area is still likely to be a key location for foraging activity.

Locations obtained from seals during overnight foraging trips were mostly within 10 km of the island. This area is the same as the closest region of high activity seen in the extended trips. As seals generally foraged north of the island, they were likely to use the area to the north on the first and last night of any foraging trip as well as during any overnight foraging activity. It may be that this particular area is consistent in prey availability throughout the summer but not as rich or predictable as the area 60 km north. Both *A. gazella* and *A. tropicalis* allocate a substantial amount of foraging time to overnight trips (15 and 25 % respectively, Goldsworthy 1999, 13 % and 38 % respectively, Chapter 5). It appears this area supports a large amount of foraging activity but alone is not sufficient to fulfil energy requirements as the longer foraging trips target the area further north near 54°00'S 159°12'E.

Optimal foraging theory (Orians and Pearson 1979) predicts that the increase in energy expended to reach a more distant prey patch, for central place foragers such as the fur seal species studied here, should be balanced by the energy gain of the patch. The positive correlation between foraging trip duration and maximum range indicated seals were travelling further from the colony the longer they stayed at sea, rather than feeding for longer close to the colony. Fur seal females would benefit most from longer foraging trips if these trips allowed them to forage in areas where they could build up greater energy reserves relative to short trips (Goldsworthy 1999). Also, as both species appeared to target the same general foraging areas, it was likely these were places where prey availability was consistent and predictable.

The few other studies using satellite location for lactating female *A. gazella* and *A. tropicalis* (Table 2.9), showed foraging areas to be of greater distances from colonies compared to Macquarie Island. It is clear these species are flexible in their foraging behaviour so as to take advantage of local prey conditions.

Table 2.9
Foraging range data from other studies for *A. gazella* and *A. tropicalis*.
*Estimated from Boyd *et al.* (1998), ** complete foraging trip records not obtained.

Species	Maximum foraging range km (n)	Location	Source
A. gazella	68 - 574, mean 160 km (11)	Îles Kergulen	Bonadonna *et al.* 2000
	Up to 350, mostly within 140 km* (21)	Bird Island	Boyd *et al.* 1998
	124, mean 98 km (11)	Cape Shirreff	Goebel *et al.* 2000
A. tropicalis	196 – 706 km** (4)	Amsterdam Is.	Georges, Bonadonna *et al.* 2000

2.5   CONCLUSIONS

It is likely that Arctocephaline fur seal species evolved in allopatry, adapting their breeding strategies to the local environmental conditions and periodicity of fluctuation (Gentry and Kooyman 1986b). Recently brought into sympatry, the Antarctic and subantarctic fur seals at Macquarie Island face the same environment with different lactation strategies to provision their young. This study found the two fur seal species were preying on the same species in similar proportions and size, and that they were able to exploit prey resources very close to their colonies. The diving behaviour of the two species was also very similar.

The current fur seal population at Macquarie Island is significantly fewer than in historic times (Shaughnessy and Fletcher 1987). To sustain the original population, estimated at more than 200,000 (Shaughnessy and Fletcher 1987), a large prey biomass would have been available. At low population density, the two species at this site are using the marine environment without obvious niche separation or resource partitioning during the time of breeding overlap. Whether this similarity in foraging behaviour can persist with much larger populations at Macquarie Island is not known.

Gentry *et al.* (1986), defined maternal strategies in fur seals as "the long- and short-term options by which females produce the largest number of independent offspring in their lifetime". Long-term options relate more to total lifetime reproductive output than to rearing a pup in a given year. Some traits may be flexible in one species but fixed in another, eg. weaning age. Short-term options are flexible and under behavioural control, eg. diving and attendance behaviour (Gentry *et al.* 1986, Boness *et al.* 1996). The aspects of foraging ecology examined in this study appeared to be under behavioural control and substantially influenced by local environmental conditions. The different lactation strategies of *A. gazella* and *A. tropicalis* allow for flexibility in foraging behaviour. Patterns of foraging reflect the abundance and distribution of prey, and in the situation of sympatry at Macquarie Island, the local environmental conditions have resulted in similar foraging behaviour in both species during the overlapping months of pup-rearing.

Chapter 3
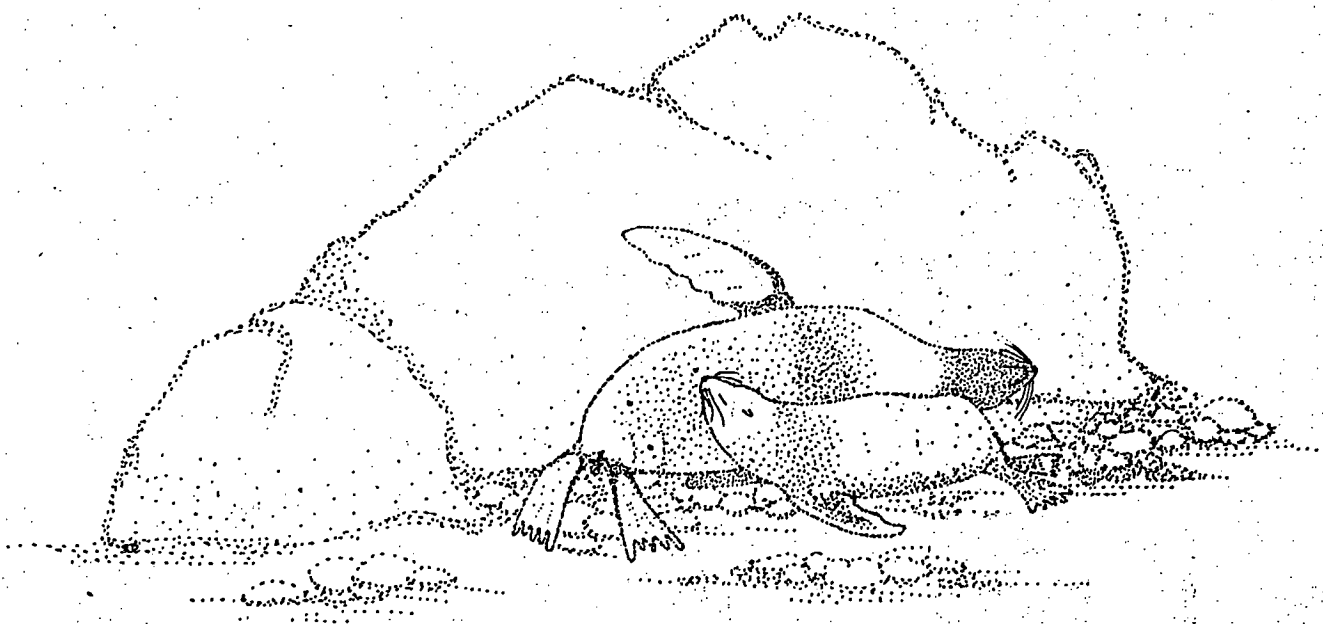
FORAGING AREA USE BY ANTARCTIC FUR SEALS *ARCTOCEPHALUS GAZELLA*: CENTRAL-PLACE FORAGING, INTER-ANNUAL VARIATION AND OVERLAP BETWEEN AND WITHIN INDIVIDUALS.

3.1   INTRODUCTION

Optimal foraging behaviour in its simplest form describes the strategies by which organisms obtain energy for survival and reproduction that will maximise their fitness (Perry and Pianka 1997). Although optimal foraging theory has been heatedly debated over the past thirty years, (see Perry and Pianka (1997) for review), it has been most successful in predicting and explaining simple foraging behaviour, such as the central place foraging of birds feeding young at the nest (Perry and Pianka 1997). In central place foraging, a parent's provisioning cycle should maximise the transfer of energy to offspring (Krebs and Davies 1987) by balancing energetic outlays such as parental travel, foraging costs and fasting of the offspring, with energy intake of the offspring. Central place foraging theory (CPFT) makes two main predictions about the distance at which animals forage from a central place (Orians and Pearson 1979). First, if foraging quality is constant, the optimal energy load returned should increase with increasing distance between the foraging site and the central place, thus making the trip profitable relative to travelling costs. The second is that time in a foraging site should increase with increasing distance to the site; short distance trips are expected to have short feeding site durations and longer distance trips, longer feeding site durations.

The life history of fur seals (Otariidae) involves both a marine phase for energy acquisition and a terrestrial phase for parturition and nursing offspring on land (Bonner 1984, Costa 1993). During lactation, fur seals become central place foragers because of the need to regularly return to a fixed place (the colony) at the end of each foraging trip. This restriction in foraging range has important implications for the provisioning of offspring. Lactating females need to balance their time at sea with the energy consumption of their pups, which are fasting and therefore losing mass in their absence (Boness and Bowen 1996, Boyd 1998, Boyd 1999). Optimal foraging theory

predicts that fur seals should forage in a way to maximise energy gain while at sea to ensure maximum nett energy gain for their pups. This could be achieved by foraging in accordance with the predictions of CPFT, but also by the selection of foraging areas with a high prey concentration. Such areas are often associated with oceanographic and bathymetric features, and their proximity to fur seal colonies may have significant effects on the seals' foraging and provisioning behaviour.

During the past two decades, with the development of remote sensing techniques, there has been much research into the foraging and provisioning behaviour of fur seals. Studies have examined the foraging behaviour and energy acquisition at sea, the transfer of this energy via milk, and the resultant pup growth (Gentry and Kooyman 1986a, Guinet *et al.* 1994, Goldsworthy 1995, Arnould *et al.* 1996, Bester and Van Jaarsveld 1997, McCafferty *et al.* 1998, Boyd 1999, Bonadonna *et al.* 2000, Georges, Bonadonna *et al.* 2000, Georges and Guinet 2000, Goebel *et al.* 2000), but few have specifically tested the predications of central place foraging theory.

Here we examine the variation in foraging site use within and between females over three years, and discuss what these data may indicate about inter-annual variation in patchiness and availability of prey. We examine if the foraging behaviour of lactating Antarctic fur seals fulfills the predictions of central place foraging theory. Specifically, we predict that on longer duration foraging trips fur seals will travel further and forage over a larger area and return more energy to their pups compared to females making shorter foraging trips.

3.2 MATERIALS AND METHODS

3.2.1 *Study site and species*

This study was conducted at North Head, Macquarie Island (54° 30'S, 158° 55'E) Antarctic fur seals *Arctocephalus gazella* breed in low numbers at Macquarie Island, producing around 135 pups per year (S. D. Goldsworthy unpublished). Adult females suckle their pups for about four months over the austral summer period, alternating between short foraging trips to sea (usually 1 to 4 days) and feeding their pups on shore for 1 to 2 days during this time.

3.2.2 *Deployments*

Lactating Antarctic fur seals *Arctocephalus gazella* were studied during the austral summers of 1996-97, 1997-98 and 1998-99. Seals were captured using a hoop net, weighed with 50 ± 1 kg scales (Salter, Melbourne) and restrained on a board with adjustable straps. Telonics ST-10 solid caste satellite transmitters (932 Impala Ave, Mesa, AZ, USA) were deployed. Each was encased in a waterproof epoxy housing (Sirtrack, Private Bag 1404, Havelock North, New Zealand), measured 130 x 60x 25 mm and weighed 320 g. Devices had a repetition rate of 50 seconds and transmitted continously to ARGOS receivers on National Oceanic and Atmospheric Administration (NOAA) polar orbiting satellites when at the sea surface. A saltwater conductivity switch deactivated the transmitter below the surface of the water.

Satellite transmitters had a 50 x 130 mm strip of Velcro™ (hooked section) glued to the underside with Cieba Geigy Araldite™ K268 two part epoxy and secured with two plastic cable ties. The transmitters were positioned on the backs of the animals between the scapulae. The two parts of the Araldite were pre-warmed and mixed, then applied to the fur within a plastic stencil which was then removed leaving the tag embedded in the glue. Four transmitters were repeatedly deployed during December to March of 1996-97, 1997-98 and 1998-99. For *A. gazella*, a total of 42 deployments were made: 10 in 1996-97, 17 in 1997-98 and 15 in 1998-99. Transmitters were removed by cutting the fur under the glue block with a scalpel blade.

3.2.3 *Data Filtering and Plotting*

All data were obtained from the ARGOS system (Toulouse, France) and processed through the Australian Antarctic Division 'ARGOS' program (D. Watts), where locations of Class A and above were selected. These data were filtered with a forward, backward iterative velocity filter (McConnell *et al.* 1992). The maximum travelling speed of fur seals, calculated from ARGOS locations of Class 1, 2 or 3 with an accuracy of < 1 km, was 4.82 km/hr. Locations were therefore filtered using an estimated maximum velocity of 6 km/hr. Filtered locations were then assigned to cells

of 0.1° latitude x 0.1° longitude, identified by a nodal value of latitude and longitude. Using surface velocity information from satellite fixes, the animals'entry and exit times for these cells were calculated. From this, locations and movements of animals at sea at night (the time of maximum foraging activity, Goldsworthy *et al.* 1997) were isolated for analysis. Locations received for each animal were thus converted to time spent per cell. These data were used to investigate the overlap in foraging area use within individuals, and between different animals in the same year.

In order to avoid potential bias from repeated measures within individual seals, a single trip was randomly selected for each of the 42 seals. Foraging time values for each cell were summed for the seals of each year then converted to proportional foraging time per cell. This corrected for the different number of individuals per year. These data were then interpolated and plotted using GIS software MapInfo™ (MapInfo Corporation) and Vertical Mapper™ (Northwood, Geoscience). The upper 50 % of the cumulative proportional foraging time was also calculated and plotted, to indicate the areas of most concentrated foraging activity.

To investigate the relationship between foraging trip duration, area used, maximum range, and total distance travelled, the randomly selected foraging trips per female were used and the above parameters calculated for each trip. Analyses of covariance (SYSTAT 9, SYSTAT Inc., Illinois) with year as the covariate were used to test for significant relationships. Foraging trip duration was taken from the last position at the colony prior to a position being recorded at sea, and the first location at the colony after the last recorded location at sea. These were verified with twice daily observations of the colony (08:30 and 17:00). For this part of the analysis, 'area used' refers to the total interpolated area calculated for each of the selected foraging trips.

3.2.4 *Foraging duration and subsequent pup mass gain*

Between December 1996 to April 1997 and December 1997 to April 1998, the foraging trip durations of 15 and 13, respectively, lactating *A. gazella* females were monitored using small flipper-tag mounted VHF radio transmitters with individual frequencies between 150 and 151 MHz (Sirtrack, NZ). Presence and absence of study animals was recorded with a scanning receiver (2000B, Advanced Telemetry

Systems, USA) connected to a programmable data logger (5040 DCC, Advanced Telemetry Systems, USA). Study animals and their pups were identifiable from uniquely numbered plastic tags (Dalton, Woolgoolga, NSW). Pups belonging to females with VHF transmitters were weighed opportunistically when their mothers were absent and whenever possible just after the mothers' departure. The mass of pups was measured within a day of the mother's arrival, and within a day of her departure. The difference in mass was taken as approximating the mass of milk delivered to the pup, similar to the measurement of 'absolute mass gain' by Guinet *et al.* (2000). These masses were coupled with the durations of the mothers' preceding foraging trips. Where more than one record per VHF mother-pup pair was recorded, one record was randomly selected. Short overnight foraging trips (< 24 h) were not included as it was possible the milk subsequently delivered may have been partially the result of foraging activity prior to that trip.

3.2.5 *Intra-individual foraging area overlap*

Intra-individual spatial overlap was estimated using 0.1° x 0.1° area cells. For each female, the number of cells visited more than once during multiple trips was calculated, then converted to a proportion of the total cells visited for all foraging trips for that female. This was taken as a measurement of the extent to which individual females returned to the same foraging areas on multiple trips. Each cell visited had a foraging time value associated with it, and the proportion of total foraging time spent in repeatedly visited cells was also calculated for each female.

3.2.6 *Inter-individual foraging area overlap*

The overlap of foraging areas used by individuals was calculated using a randomly selected trip for each female. Using a matrix, the foraging area cells visited by each female were compared to the cells visited by each other female of that year. For a selected female, the number of cells common to her and another female were recorded. This was converted to a percentage of the total cells used by the selected female. A column of percentage overlap values (ie. n – 1) thus resulted for each female, and a mean was taken of these. Each female thus had a single value for the extent of her foraging area overlap with all other females.

3.3 RESULTS

3.3.1 *Inter-annual comparison*

Separate years of foraging area used, from one foraging trip per female and plotted from interpolated data, are presented (Figures 3.1 a, b and c, Table 3.1). The areas where female fur seals spent the upper 50 % of their foraging time are shaded. These were the areas of most intense foraging activity. Total (interpolated) area used by seals was larger in 1996-97 and 1997-98, approximately 5000 km², but was less than 4000 km² in 1998-99. In this third study season, the area containing the upper 50 % of foraging activity was also smaller, indicating that seals, probably in response to prey distribution, were concentrating their foraging effort more than in the previous two seasons.

Table 3.1
Interpolated area (MapInfo™) for combined foraging trips (one per *A. gazella* female) for each year of the study. Total area of activity is all area where night hours were spent at sea. Area of > 50 % foraging activity is the area in which seals spent the upper 50 % of their cumulative proportional foraging time.

Year	Foraging trips	Area of >50 % foraging activity (km²)	Total area of activity (km²)
1996-97	10	901	5334
1997-98	17	876	5151
1998-99	15	381	3726

3.3.2 *Inter-individual foraging area overlap*

The spatial overlap of areas between individuals (Table 3.2) was significantly lower in 1996-97 at 22.4 % (± 11.2) compared to 32.2 % (± 15.3) and 35.8 % (± 10.3) for 1997-98 and 1998-99 respectively (ANOVA $F_{2,39}$ = 3.389, P = 0.044).
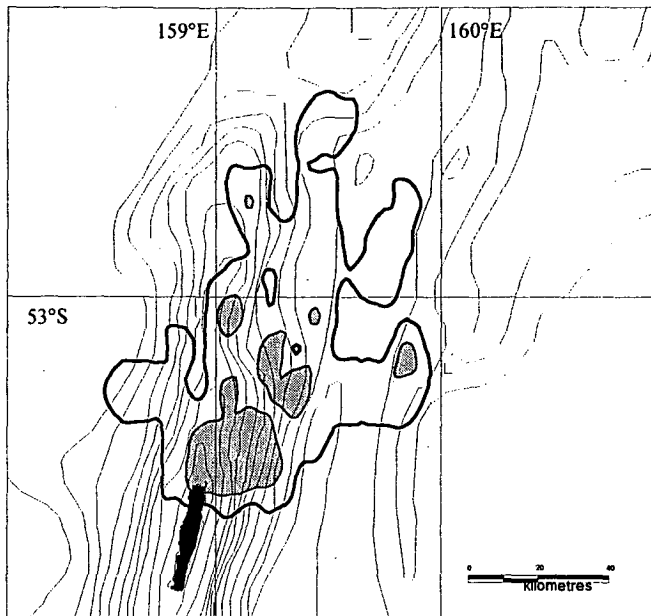
A. 1996-97
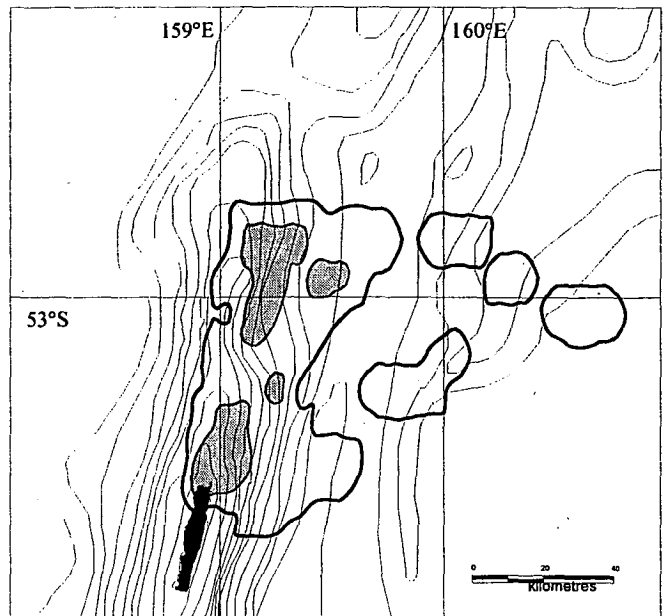
B. 1997-98
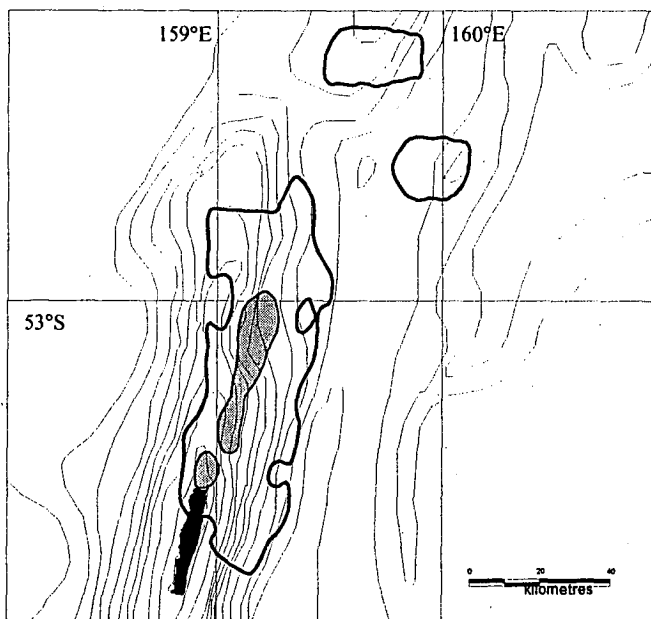
C. 1998-99

Figures 3.1 a, b and c

Macquarie Island and surrounding bathymetry: interpolated foraging area calculated from foraging time per cells of 0.1° latitude x 0.1° longitude. Compiled from single foraging trips per female *A. gazella*, for (a) 1996-97 (n = 10), (b) 1997-98 (n = 17) and (c) 1998-99 (n = 15). The areas where seals spend the upper 50 % of their cumulative proportional foraging time are shaded. Outlined areas are all areas visited by seals at night, presumed foraging. Contour intervals from island, 100, 200, 500, 1000, 2000, etc. to 6000 m.

3.3.3 *Intra-individual foraging area overlap*

Foraging area overlap values (see methods) for individual females were averaged for each year to indicate the relative concentration of foraging effort (Table 3.2). The spatial overlap of areas between foraging trips by the same female was on average 26 %. This level of repeated use was not different between years (ANOVA $F_{2,34} = 0.756$, $P = 0.477$). The proportion of time spent in these repeatedly visited areas was highly variable between individuals (range 0 to 76 %) and not significantly different between years (ANOVA $F_{2,34} = 1.125$, $P = 0.337$).

3.3.4 *Foraging trip duration and distance*

Maximum foraging range, area used and total distance travelled increased significantly with the duration of foraging trips (area: ANCOVA $F_{1,36} = 16.379$, $P < 0.0001$, $R^2 = 0.225$, foraging range: $F_{1,36} = 29.668$, $P < 0.0001$, $R^2 = 0.363$, distance: $F_{1,36} = 84.234$, $P < 0.0001$, $R^2 = 0.626$) (Table 3.3, Figure 3.2). There was no significant difference in the range ($F_{2,36} = 0.942$, $P = 0.399$), area ($F_{2,36} = 0.820$, $P = 0.448$) or total distance travelled by females ($F_{2,36} = 0.050$, $P = 0.608$) between years. Interaction effects between year and trip duration were also non-significant for range ($F_{2,36} = 1.885$, $P = 0.167$), area ($F_{2,36} = 2.478$, $P = 0.098$) and distance ($F_{2,36} = 1.392$, $P = 0.262$).

3.3.5 *Foraging trip duration and pup mass gain*

Foraging durations derived from VHF recordings from Antarctic fur seal mothers in 1996-97 (n = 15) and 1997-98 (n = 13) were combined with subsequent mass gain information from their pups. Pup mass gain was positively correlated with preceding foraging trip duration (Figure 3.3) (ANOVA $F_{1,24} = 6.311$, $P = 0.019$, $R^2 = 0.721$). There was no year effect ($F_{1,24} = 0.005$, $P = 0.943$) or interaction between year and trip duration ($F_{1,24} = 0.004$, $P = 0.949$).

There was no significant relationship between 'rate of pup mass gain' (ie. pup mass gain divided by the number of days in the preceding foraging trip) and the duration of the preceding foraging trip (ANOVA $F_{1,26} = 0.192$, $P = 0.665$, $R^2 = 0.007$).

Table 3.2

Mean ± SE percentage of area cells repeatedly visited by different *A. gazella* females for 1996-97, 1997-98 and 1998-99 during single foraging trips. Mean ± SE of percentage of area cells repeatedly visited on multiple foraging trips by the same females, and the percentage of total foraging time spent in those cells (mean ± SE).

Year Female	Inter-individual overlap % of cells repeatedly visited by individuals	Intra-individual overlap Foraging trips	% of cells repeatedly visited on foraging trips	% of total foraging time spent in cells repeatedly visited
1996-97				
1	20.4	3	40.9	55.2
2	12.8	2	4.2	10.7
3	35.6	4	15.8	37.5
4	11.7	3	19.2	40.8
5	26.7	2	25.0	32.1
6	9.1	1		
7	16.7	2	27.3	33.6
8	36.5	2	16.7	26.2
9	38.9	2	16.7	30.8
10	15.7	4	20.0	43.8
Mean	**22.4 ± 3.5**		**20.6 ± 3.3**	**34.5 ± 4.1**
1997-98				
11	29.9	3	9.1	21.4
12	27.5	3	37.5	66.0
13	48.8	4	41.7	66.7
14	20.0	2	50.0	72.0
15	25.8	3	42.9	58.9
16	27.6	3	38.5	48.3
17	31.8	1		
18	27.8	2	0	0
19	57.8	5	16.7	46.9
20	12.5	4	26.3	49.2
21	42.7	4	37.5	66.3
22	31.3	2	33.3	57.7
23	70.8	2	42.9	74.9
24	23.6	3	9.4	26.6
25	33.0	2	19.1	39.6
26	10.4	2	9.7	30.0
27	26.5	2	10.7	18.5
Mean	**32.2 ± 3.7**		**26.6 ± 3.9**	**46.4 ± 5.5**
1998-99				
28	34.5	2	42.9	72.5
29	34.1	2	35.7	58.1
30	31.4	2	11.8	24.3
31	32.1	2	20.0	63.1
32	17.1	1		
33	46.4	3	45.5	54.4
34	45.0	2	45.5	55.7
35	22.6	2	0	0
36	38.9	2	7.7	18.0
37	50.0	2	33.3	48.4
38	45.2	1		
39	35.7	2	20.0	37.3
40	18.7	1		
41	47.6	2	44.4	67.1
42	37.8	2	33.3	45.2
Mean	**35.8 ± 2.7**		**28.3 ± 4.6**	**45.3 ± 6.3**
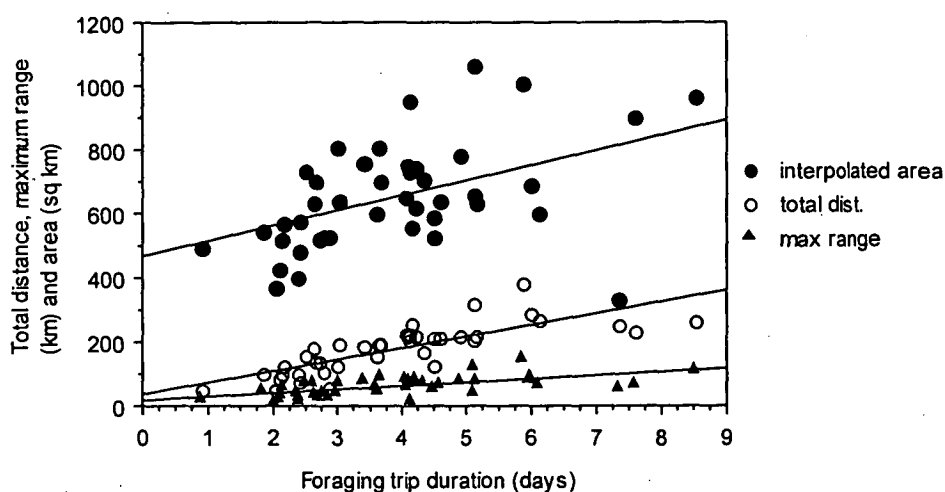
Figure 3.2
Maximum range, total distance and area prospected in
relation to foraging trip duration for *A. gazella* females
(n = 42). FTD = foraging trip duration.
Maximum range = 21.608 + 10.521 * FTD (d); R^2 = 0.363
Interpolated area = 466.236 + 47.848 * FTD (d); R^2 = 0.225
Total distance = 39.197 + 36.001 * FTD (d); R^2 = 0.626
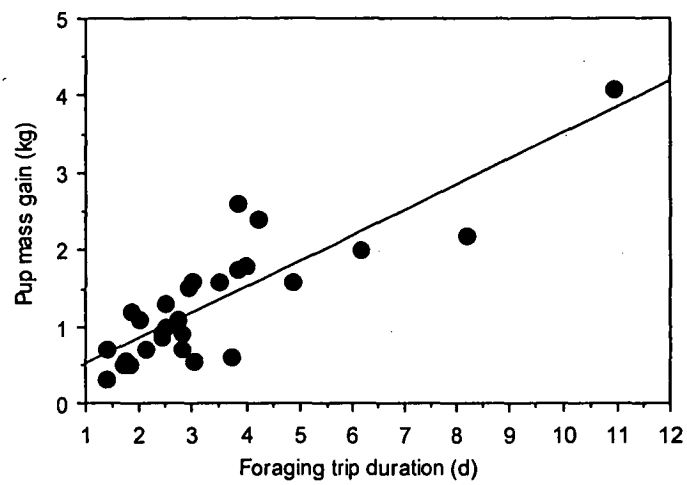
Figure 3.3

Correlation of pup mass gain (kg) to foraging trip duration (days), n = 25.
Mass gain = 0.179 + 0.335 * foraging trip duration (d); R^2 = 0.721.

Table 3.3
Summary of foraging trip parameters for the three summers of study. Foraging trip duration, maximum range and total distance travelled were calculated from ARGOS data, foraging area was calculated in MapInfo™ (see methods).

Parameter	year	Mean ± SE	N	Range
Foraging trip duration (d)	1996-97	4.5 ± 0.7	10	2.4 - 8.5
	1997-98	3.4 ± 0.3	17	0.9 - 5.2
	1998-99	4.0 ± 0.4	15	2.1 - 7.4
Area (km²)	1996-97	684.3 ± 51.3	10	478.4 - 960.5
	1997-98	686.4 ± 40.9	17	369.5 - 1063.2
	1998-99	593.1 ± 41.4	15	332.3 - 1007.5
Maximum range (km)	1996-97	62.2 ± 9.8	10	21.1 - 115.5
	1997-98	65.2 ± 6.8	17	14.2 - 126.3
	1998-99	59.9 ± 7.7	15	19.2 - 147.5
Total distance travelled (km)	1996-97	171.4 ± 27.0	10	58.4 - 289.9
	1997-98	173.1 ± 17.0	17	47.7 - 319.4
	1998-99	191.8 ± 19.9	15	88.6 - 376.8
Foraging trip duration (d)	3 yrs combined	3.8 ± 0.3	42	0.9 - 8.5
Area (km²)	3 yrs combined	652.6 ± 25.7	42	332.3 - 1063.2
Maximum range (km)	3 yrs combined	62.6 ± 4.4	42	14.2 - 147.5
Total distance travelled (km)	3 yrs combined	179.4 ± 11.6	42	47.7 - 379.8

3.4   DISCUSSION

3.4.1   *Foraging area use*

For three austral summers, Antarctic fur seals foraged to the north of the island parallel with, but just to the east of the Macquarie Ridge. Although the seals used the same general area in all three years, the upper 50 % of area used was more dispersed in 1996-97. For the summers of 1997-98 and 1998-99, area used, and therefore probably prey distribution, were strongly associated with the local bathymetry, in particular the Macquarie Ridge. Productivity in the marine environment is typically associated with shelves, shelf slopes and frontal zones (Comiso *et al.* 1993, Moore and Abbott 2000). It is likely the Macquarie Ridge, which is a prominent bathymetric feature of the region, may contribute to enhanced primary production and the

associated concentrations of biomass at higher trophic levels (Abrams 1985). The seals were not foraging randomly from the colony, but rather, restricted their efforts to a particular area. This general area was used consistently by (i) individuals on repeated trips, (ii) different individuals within a year, and (iii) by individuals between years. Local conditions therefore appear important in focussing foraging effort and are likely to influence foraging trip duration. Predictable areas of dense prey can lead to more efficient foraging by reducing search time. The mean foraging trip duration of *A. gazella* at Macquarie Island was one of the shortest for this species (Chapter 5) supporting the idea that prey was available close to the colony and easily accessible.

At Macquarie Island *A. gazella* fed almost exclusively at night taking vertically migrating fish (myctophids) (Goldsworthy *et al.* 1997, Chapter 2). Similar to other locations, they dived repeatedly from dusk to dawn, following the movements of their prey through the water column: crepuscular dives being deepest, and those around local midnight the most shallow (Boyd and Croxall 1992, Goldsworthy *et al.* 1997, Green 1997). The distribution of foraging activity close to Macquarie Island and the regular use of overnight trips (Goldsworthy 1999, Chapter 5) indicated the availability of predictable prey very close to the island. Despite this, the longer trips were to more distant locations. This suggests that the availability of prey was greater at some distance from the island. Spending several days 60 km from the island was apparently more 'profitable' in some way, than spending the same time within 10 km of the island.

3.4.2 *Overlap in foraging areas*

During the summer months, lactating females overlapped substantially in the areas they foraged. This suggests that prey resources in the waters around Macquarie Island were concentrated in specific areas. The significantly lower percentage of area repeatedly visited in 1996-97 suggests prey was more dispersed compared to the following two years. This was also apparent in the plots for the three years (Figure 3.3 a, b and c).

The area used by individual females did not differ between years, but the total area used by these individuals combined, appeared smaller in 1998-99 (Table 3.1). The

mean overlap between individuals was large in 1998-99 (similar to 1997-98) and the area with > 50 % of the foraging activity was the smallest (ie. most concentrated). This suggests females in 1998-99 were not covering less area during their trips, but were overlapping with each other to a greater degree, supporting the idea that prey were more concentrated in that year.

For female *A. gazella*, there was on average a 26 % area overlap between an individual's foraging trips. Average overlap ranged from 0 to 50 %, with only 2 of 37 seals undertaking multiple trips with no common foraging area between trips. This suggests a range of behaviours, from foraging in separate areas on consecutive trips to returning to specific areas. Not repeatedly using a foraging area in the space of two or more trips however, may not mean an area is becoming prey depleted but that other needs are more important. For example, females may need to undertake a long foraging trip to a distant area with greater prey to replenish her body condition, after making repeated short foraging trips.

Time spent in areas common to two or more foraging trips was high (mean 43 %), suggesting that seals were choosing to return to specific areas on consecutive trips in order to concentrate their effort. It also suggests some level of predictability in the distribution of prey resources in the short term (ie. within days). Revisiting areas of known prey availability would increase the rate of energy gain for a foraging trip by reducing costs associated with searching time and travelling time. Females using known and predictable foraging areas would keep their time at sea to a minimum, possibly making more trips per season, and provisioning their pups with more milk than a female spending more time searching during her time at sea. Minimising time at sea would reduce the pups' fasting periods. Other females which spent little time revisiting areas may have moved to other areas due to unsuitable prey availability.

At Îles Kerguelen, *A. gazella* females were found to concentrate their activity in an area characterised by an increase in depth (Bonadonna *et al.* 2000, Guinet *et al.* 2001). Adult female *A. gazella* from South Georgia, in two consecutive years, foraged in the same area which was associated with the edge of the continental shelf (Boyd *et al.* 1998). Similiarly from Livingston Island, in the South Shetland Islands, *A. gazella* targetted the nearby continental shelf break and slope (Goebel *et al.* 2000). It is not

surprising that in a heterogeneous environment that areas likely to be richer in prey
resources are targeted by predators. What is unusual about the Macquarie Island
situation is the concentration of activity so close to the colony. Much of the core
foraging area is within 30 km, with the remainder extending only to 75 km. This may
be related to the unique local oceanographic environment, or to the low population of
fur seals (160 total *A. gazella* and *A. tropicalis* pups, S. D. Goldsworthy unpublished)
and reduced competition for food.

3.4.3 *Central place foraging*

The results of this study indicate that the foraging behaviour of lactating fur seals at
Macquarie Island support the general predictions of CPFT. As predicted, we found
that foraging trips furthest from the colony covered a greater area (using total
interpolated areas for single trips) and round trip distance, and were of significantly
longer duration. In addition, fur seal mothers that returned from longer foraging trips
transferred a greater amount of mass (milk) to their pups than those returning from
shorter trips. Other studies have also demonstrated that milk production over an
attendance period is positively correlated with the duration of the previous foraging
trip in *A. gazella* (Arnould and Boyd 1995), but these have not been able to relate this
to spatial information. Similarly, mass gain in male *A. gazella* pups at Heard Island
(Goldsworthy 1995) and in *A. tropicalis* pups at Amsterdam Island (Georges and
Guinet 2000) was positively correlated with foraging trip duration. Further evidence
of support for CPFT was reported from South Georgia (Boyd 1999) and Îles
Kerguelen (Bonadonna *et al.* 2000), where *A. gazella* showed a positive correlation
between foraging trip duration and distance travelled.

Pup mass gain, when divided by the number of days in the preceding foraging trip,
did not vary for long or short trips. Mothers appeared to transfer the same amount of
energy per day of foraging, irrespective of the duration of the trip. Thus, there
appeared to be little advantage to pups of mothers undertaking either long or short
trips. This finding was consistent with studies by Boyd *et al.* (1991) and Arnould and
Boyd (1995) at South Georgia. Instead, it may be that long foraging trips are an
advantage to mothers by improving their overall body condition (Goldsworthy 1999,
Chapter 2). Pups may gain indirectly from the mothers' improved condition because it

allows them to undertake short trips (including overnight trips) which provide pups with more frequent milk. More frequent feeds may be more beneficial to pups (Goldsworthy 1999, Georges and Guinet 2000), but mothers may not be able to sustain their own maintenance and condition by using short trips alone.

Studies on pelagic seabirds (blue petrels *Halobaena caerulea* and wandering albatross *Diomedea exulans*) have also found long and short foraging trips (Chaurand and Weimerskirch 1994, Weimerskirch *et al.* 1997, Weimerskirch and Lys 2000). Adult body mass was reported to increase with long foraging trips and decrease with short trips. Short foraging trips advantaged the chick with regular provisioning, but there was the energetic requirement for these to be balanced with longer foraging trips which replenished the adults' body reserves (Chaurand and Weimerskirch 1994, Weimerskirch *et al.* 1997). The strategy of alternating short (including overnight) and extended trips by Macquarie Island fur seals may have similar benefits.

3.5   CONCLUSIONS

Antarctic fur seal females at Macquarie Island did not forage randomly from the colony but often returned to areas previously visited. They concentrated their efforts in an area parallel with and east of the Macquarie Ridge where it is likely prey were concentrated and predictable. Local conditions are therefore important in focussing foraging effort and influencing foraging trip duration and frequency, pup growth, and ultimately pup survival. Female fur seals foraged according to the predictions of CPFT: distance travelled, area used and mass gain in pups increased with increasing foraging trip duration. However, even with prey available close to the island, females regularly travelled to areas further away for longer foraging trips, suggesting greater prey availability in those areas. Though longer trips may not advantage pups, they may be important in the maintenance of maternal condition and enable them to subsequently use short trips, which may be more beneficial to the pup. Few mammals are as restricted as fur seals in the time they have available to feed their young (Boyd 1999). It may therefore be particularly important for fur seals to forage economically and ensure overall energy gain from each foraging trip so that offspring growth is maintained and maternal condition does not adversely decline during lactation.

Chapter 4
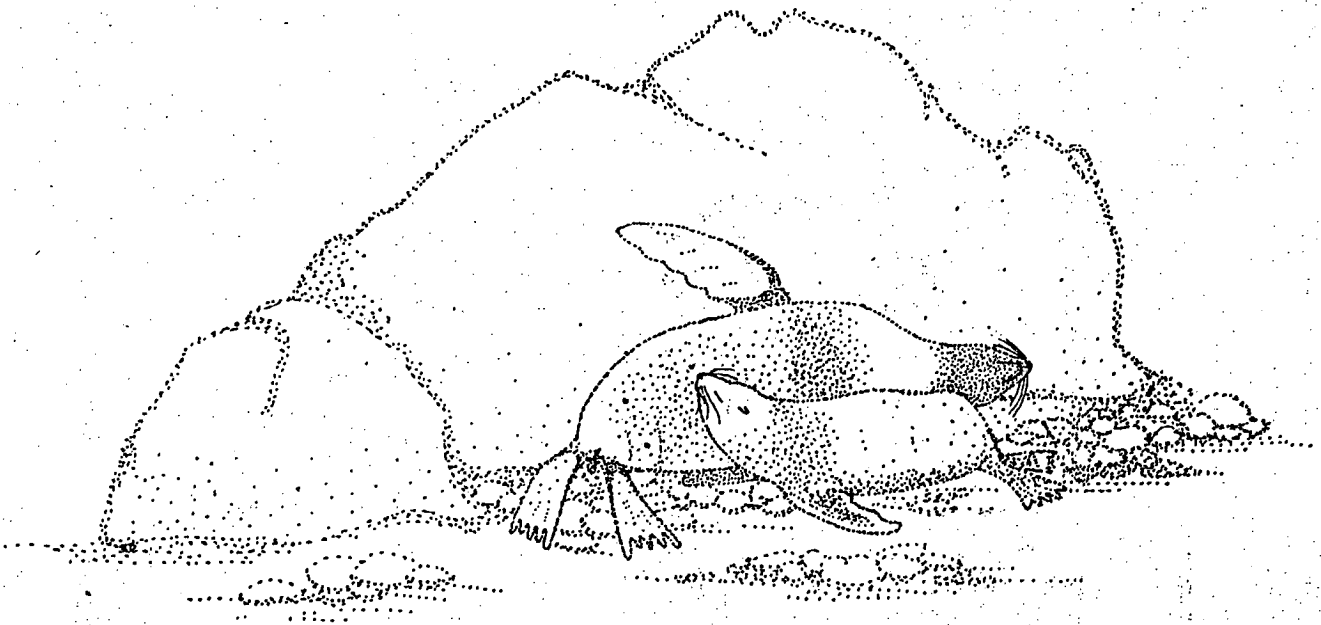
PUP GROWTH IN SYMPATRIC FUR SEAL SPECIES WITH DIFFERENT LACTATION STRATEGIES (*ARCTOCEPHALUS GAZELLA* AND *A. TROPICALIS*) AT MACQUARIE ISLAND.

4.1 INTRODUCTION

In fur seals (Pinnipedia: Otariidae), maternal strategies have been shaped by the seasonality and predictability of ancestral marine environments (Gentry *et al.* 1986). Selection pressure from these environmental conditions has resulted in the evolution of a range of lactation strategies in fur seals in order to maximise lifetime reproductive success (Gentry *et al.* 1986). Fur seals are an ideal group for studying the evolution of maternal strategies as several species in a single genus (*Arctocephalus*) range in habitat from tropical to subpolar. It has been proposed that maternal strategies in fur seals vary with latitude (Gentry and Kooyman 1986a), though recent work suggests environmental conditions may be a more accurate index of the variation (Trillmich 1990, Boness and Bowen 1996, Francis *et al.* 1998). Subpolar fur seal species have a brief lactation period (Kerley 1983, Gentry *et al.* 1986) coinciding with a summer increase in prey availability, while low latitude species have a prolonged and variable lactation lasting up to three years. Temperate fur seals are intermediate, with a lactation length of 8 to 12 months (Condy 1978, Gentry *et al.* 1986).

The end product of these different maternal (or provisioning) strategies is the growth of the young from birth to weaning. Fur seals give birth annually to a single pup on land (with rare exceptions, Bester and Kerley 1983, Doidge 1987), which they periodically suckle between foraging trips to sea. For fur seal pups, the rate of growth to, and mass at weaning and possibly the age at weaning, is the result of the mothers' foraging success at sea, her provisioning pattern and milk composition (Gentry *et al.* 1986, Trillmich 1990, Kovacs and Lavigne 1992, Arnould *et al.* 1996, Georges and Guinet 2000). Some determinants of growth are likely to be under phylogenetic control, whilst others are more likely affected by environmental conditions and their associated variation.

The near extermination of many fur seal colonies from over-harvesting by C19[th] sealers has lead to re-colonisation (Gentry and Kooyman 1986b), in some cases by species possibly not originally present in these areas. The original species of fur seal on Macquarie Island is unknown (Shaughnessy and Shaughnessy 1988), but currently both *A. gazella* and *A. tropicalis* breed there. This sympatry also occurs at Marion Island (Kerley 1983) and Îles Crozet (Jouventin *et al.* 1982). The two species overlap in breeding activities during the austral summer (Shaughnessy and Fletcher 1987, Goldsworthy 1999) with *A. gazella* suckling their pups for four months and *A. tropicalis* continuing through the winter to spring, taking nine to ten months. At Macquarie Island the two species breed within tens of metres of each other, *A. gazella* on beaches and *A. tropicalis* on rock platforms.

Most localities in which fur seals breed are ususally inhabited by only one species, thus when comparing species between sites, the influence of different environmental conditions could have a significant effect. To investigate how growth parameters vary between fur seals with short and long lactation strategies, it would be ideal to view the two species in the same environment. Such an opportunity exists at Macquarie Island with the unusual situation of *A. gazella* and *A. tropicalis* breeding virtually next to each other. This study improves on a previous examination of pup growth at this site (Goldsworthy 1992) by drawing on a much larger sample of pups, and including 3 years of growth data for both species.

This study compares a suite of pup growth parameters resulting from the two provisioning strategies, including birth mass, maximum mass, weaning age and mass, and growth rate. More specifically, the aims were to determine, under the same environmental conditions, (1) whether the different lactation strategies resulted in different patterns of pup growth, and (2) which aspects of pup growth were influenced more by phylogenetic traits and which by environmental factors.

4.2   MATERIALS AND METHODS

The study was conducted at North Head, Macquarie Island (54° 30'S, 158° 55'E) during December 1995 to April 1997, and from December 1997 to April 1998. The populations of each species are low in numbers, *A. gazella* producing around 135 pups

per year, and *A. tropicalis* around 25 pups a year (S. D. Goldsworthy unpublished). This places some constraints on sample sizes obtainable at Macquarie Island.

Pups of *A. gazella* and *A. tropicalis* were weighed at Secluded Beach and Goat Bay during the austral summer seasons of 1995-96, 1996-97 and 1997-98. Data collection for *A. tropicalis* pups continued in each year through winter to spring, until weaning.

Pregnant females were monitored from the time of their arrival on shore. Any untagged females were individually bleach marked (Blonde 3, Clairol Inc., NSW Australia). All pups were individually marked within 14 days of birth with small bleached numbers (Blonde 3, Clairol Inc., NSW Australia). Prior to this, pups were identified by association with their tagged or bleached mothers. When pups reached 7 kg in mass, they were tagged in the trailing edge of both fore flippers with uniquely numbered plastic tags (Dalton, Woolgoolga, NSW). Pups were weighed for the first time after their mothers left on their first post-partum foraging trip (at approximately 7 days of age) and then at weekly intervals for the first six weeks and fortnightly thereafter. Pups of *A. tropicalis* were weighed approximately monthly from May onwards. Pups of both species were weighed opportunistically near weaning in order to incease the temporal resolution of growth data. Mass was measured with a 10 kg x 50 g balance (Salter, Melbourne) until pups weighed close to 10 kg, then a 25 kg x 100 g spring balance (Salter, Melbourne) was used.

Growth rate has been described as linear for 0 to 120 d age for both *A. gazella* (Doidge *et al.* 1984) and *A. tropicalis* (Kerley 1985). Birth mass of pups was estimated by extrapolation from linear regressions of 0 to 120 days of age for both species. Weaning age in both species was estimated at the midpoint between the last observation of a pup and the subsequent observation when it was not present in the colony. Observation frequency around weaning was twice daily for *A. gazella* (March – April) and at least weekly for *A. tropicalis* (September – October). Because a Hooker's sea lion (*Phocarctos hookeri*) was regularly killing pups during the study (Robinson *et al.* 1998), pups not found dead were assumed to have weaned if they survived past 100 d for *A. gazella* and 200 d for *A. tropicalis*.

Weaning mass for *A. gazella* pups was extrapolated from individual linear regression equations for the day of weaning. In this study, because *A. tropicalis* generally lost mass in the weeks prior to weaning, extrapolating weaning mass from linear regression equations would not provide an accurate estimate of weaning mass. For *A. tropicalis*, mass recorded within 10 d of weaning was taken as the weaning mass. For pups weighed more than 10 d prior to weaning, weaning mass was estimated from maximum mass (see Results).

Linear regressions were used to estimate growth rates for the various stages of growth: birth to 120 d of age, birth to maximum mass and birth to weaning. Gompertz growth curves were used to characterise the period of growth from birth to maximum mass. The Gompertz curve was selected as a general growth model as it tended to predict intermediate values for asymptotic values, maximum growth and position of inflection point compared to logistic and von Bertalanffy models (Zullinger *et al.* 1984). A 3-way Analysis of Variance (SYSTAT Inc., Illinois) was used to investigate the effect of species, sex and year on the various growth parameters. Two-way ANOVAs and t-tests (SYSTAT Inc., Illinois) were used where indicated. Means are presented with standard errors, and statistical significance is accepted at $P < 0.05$.

All adult female fur seals were identified from plastic flipper tags (Dalton, Woolgoolga, NSW) and weighed opportunistically through the study program. For both species, females were weighed between November and April, and therefore before blastocyst implantation (Bester 1995). For the analyses, only one mass per female was used. Where more than one mass was available, or a female had more than one pup during the three year study, the first mass was selected.

4.2 RESULTS

4.2.1 *General growth parameters*

Available mass and age data for each pup, from birth to maximum mass (*A. gazella,* n = 136 and *A. tropicalis*, n = 32) was fitted with a Gompertz curve. From this, the pups' mass for each day was estimated. These data were then averaged for all pups of a species and fitted with a Gompertz curve (Figure 4.1).
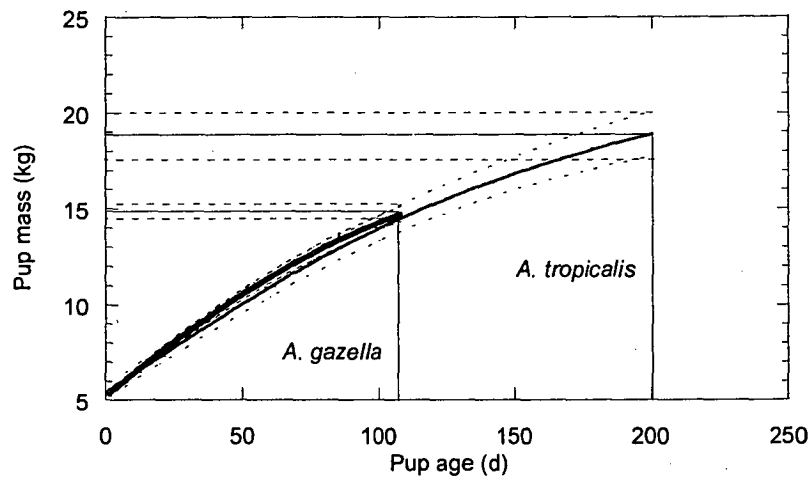
Figure 4.1
Gompertz curves ± 95 % confidence limits (dotted lines), fitted
to averaged mass and age data for *A. gazella*, n = 136, (thick curve)
and *A. tropicalis*, n = 32, (thin curve) from birth to maximum mass.
Vertical lines point to age at maximum mass and horizontal
lines to mean maximum mass for each species.

Mean Gompertz equation for *A. gazella*: $M(t) = 34.9113 * e^{-e^{-0.0181(t-43.3651)}}$ (1)

Mean Gompertz equation for *A. tropicalis*: $M(t) = 24.9030 * e^{-e^{-0.0123(t-39.2088)}}$ (2)

M = mass of pup, t = age of pup (d).

4.3.2 Birth mass

There was no difference in birth mass between the two fur seal species ($F_{1,187} = 0.517$, $P = 0.473$), but birth mass differed significantly between the sexes ($F_{1,187} = 13.626$, $P < 0.0001$) males: 6.3 ± 0.1 kg, n = 100, females: 5.6 ± 0.1 kg, n = 99, and between years ($F_{1,187} = 3.734$, $P = 0.026$). A species * year effect was also present ($F_{2,187} = 6.164$, $P = 0.003$), with birth mass being lower for *A. tropicalis* in the first year (Figure 4.2). Mean birth masses are shown in Table 4.1.

4.3.3 Age at maximum mass

The age at which the heaviest mass prior to weaning was attained, varied significantly between the species ($F_{1,189} = 269.288$, $P < 0.0001$) *A. gazella*: 107.9 ± 1.3 d, n = 161, *A. tropicalis*: 200.3 ± 8.9 d, n = 40, (Table 4.1). There were no year, species or sex interaction effects.

4.3.4 Maximum mass

A significantly greater maximum mass ($F_{1,189} = 61.645$, $P < 0.0001$) was attained by *A. tropicalis* (19.0 ± 0.5 kg, n = 40) than *A. gazella* (15.4 ± 0.2 kg, n = 161). There was also a strong difference between the two sexes ($F_{1,189} = 44.750$, $P < 0.0001$), males: 17.7 ± 0.3 kg (n = 102), females: 14.5 ± 0.3 kg (n = 99) (Figure 4.3), and no interaction effects.

4.3.5 Age at weaning

The age at weaning for the two species was (as expected) significantly different ($F_{1,189} = 4650.161$, $P < 0.0001$) *A. gazella* 122.1 ± 0.9 d (n = 161), *A. tropicalis* 298.3 ± 2.6 d (n = 40) (Table 4.1) while there was no difference in weaning age between sexes

Figure 4.2
Effect of species and year on mean ± SE (n) birth mass for
A. gazella and *A. tropicalis* for three years. Birth mass for
A. tropicalis was significantly lower in 1995-6.

Figure 4.3

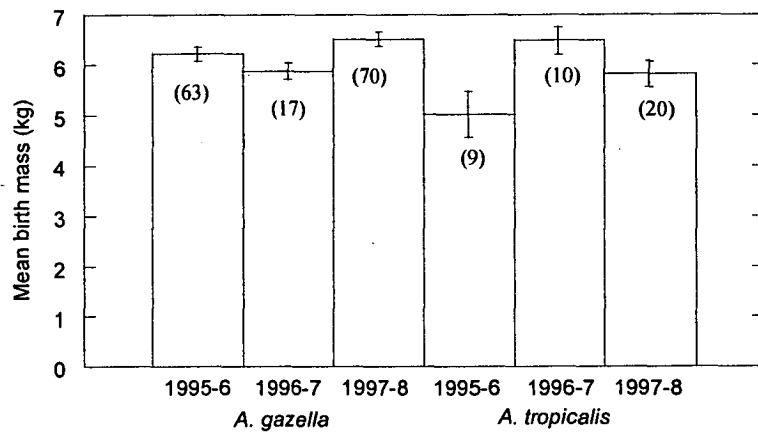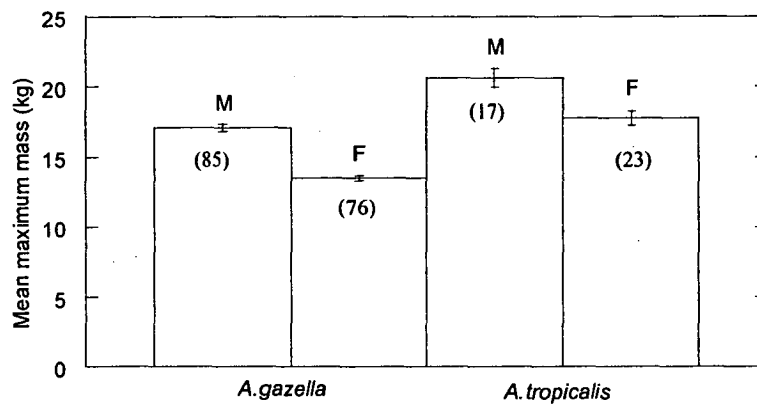Mean ± SE (n) maximum mass attained by both species and sexes of fur seal pups. M = male, F = female. *A. tropicalis* was significantly heavier than *A. gazella*. Males (species combined) were significantly heavier than females.

Table 4.1

Mean pup growth parameters ± SE for *A. gazella* and *A. tropicalis* in relation to species, sex and year. Sample sizes in parentheses. M = Male, F = Female.

Year Species Sex	Birth mass (kg)	Maximum mass (kg)	Weaning mass (kg)	Age at maximum mass (d)	Age at weaning (d)	Linear growth rate 0 to 120 d (g.d^{-1})	Linear growth rate 0 d to maximum mass (g.d^{-1})	Linear growth rate 0 d to weaning (g.d^{-1})
1995-96								
A.gazella M	6.3 ± 0.2 (33)	16.6 ± 0.3 (33)	17.2 ± 0.5 (33)	107.0 ± 2.6 (33)	126.7 ± 8.4 (33)	96.8 ± 3.8 (33)	102.4 ± 3.5 (33)	93.8 ± 3.6 (33)
F	5.9 ± 0.2 (30)	13.5 ± 0.3 (30)	13.2 ± 0.3 (30)	104.3 ± 3.4 (30)	112.9 ± 2.1 (30)	69.8 ± 3.3 (30)	79.1 ± 2.9 (30)	69.8 ± 2.7 (30)
A.tropicalis M	5.4 ± 0.6 (6)	21.7 ± 1.1 (6)	16.1 ± 1.0 (6)	175.2 ± 15.8 (6)	292.8 ± 5.0 (6)	92.18 ± 7.4 (6)	92.7 ± 7.1 (6)	34.7 ± 6.3 (6)
F	4.2 ± 0.6 (3)	17.3 ± 0.8 (3)	13.0 ± 1.4 (3)	200.3 ± 20.6 (3)	292.3 ± 7.1 (3)	71.0 ± 6.0 (3)	68.6 ± 18.0 (3)	43.6 ± 6.8 (3)
1996-97								
A.gazella M	6.2 ± 0.2 (15)	17.3 ± 0.7 (15)	17.1 ± 0.6 (15)	109.9 ± 3.0 (15)	122.4 ± 1.6 (15)	96.7 ± 5.1 (15)	101.9 ± 5.3 (15)	96.1 ± 4.0 (15)
F	5.4 ± 0.2 (12)	13.9 ± 0.5 (12)	13.7 ± 0.4 (12)	99.1 ± 4.2 (12)	118.1 ± 4.3 (12)	77.8 ± 3.8 (12)	81.4 ± 3.6 (12)	75.7 ± 3.7 (12)
A.tropicalis M	7.1 ± 0.5 (2)	18.3 ± 0.3 (2)	16.3 ± 2.0 (2)	218.5 ± 15.5 (2)	292.5 ± 21.5 (2)	77.0 ± 0.0 (2)	59.2 ± 4.5 (2)	38.2 ± 11.5 (2)
F	6.3 ± 0.3 (8)	17.7 ± 0.9 (8)	13.74 ± 1.3 (8)	211.0 ± 22.3 (8)	293.5 ± 10.1 (8)	72.1 ± 4.7 (8)	59.7 ± 4.3 (8)	38.5 ± 3.3 (8)
1997-98								
A.gazella M	6.5 ± 0.2 (36)	17.4 ± 0.4 (37)	16.6 ± 0.5 (37)	113.7 ± 2.8 (37)	124.1 ± 2.3 (37)	93.6 ± 3.5 (37)	95.9 ± 3.2 (37)	91.2 ± 3.5 (37)
F	5.5 ± 0.6 (34)	13.3 ± 0.3 (34)	13.1 ± 0.3 (34)	108.1 ± 2.2 (34)	118.2 ± 1.9 (34)	71.7 ± 2.0 (34)	74.4 ± 2.1 (34)	70.9 ± 2.2 (34)
A.tropicalis M	6.3 ± 0.4 (8)	20.5 ± 1.0 (9)	15.7 ± 0.7 (9)	217.2 ± 20.3 (9)	302.2 ± 3.1 (9)	99.6 ± 4.1 (9)	70.8 ± 8.5 (9)	52.4 ± 7.0 (9)
F	5.5 ± 0.3 (12)	17.9 ± 0.8 (12)	14.5 ± 0.8 (12)	190.0 ± 18.8 (12)	303.8 ± 2.3 (12)	77.7 ± 5.1 (12)	68.5 ± 6.7 (12)	40.7 ± 5.0 (12)
Overall means								
A.gazella M	6.4 ± 0.1 (84)	17.1 ± 0.3 (85)	16.9 ± 0.3 (85)	110.4 ± 1.7 (85)	124.8 ± 1.2 (85)	95.4 ± 2.3 (85)	99.5 ± 2.2 (85)	93.1 ± 2.2 (85)
F	5.6 ± 0.1 (76)	13.5 ± 0.2 (76)	13.3 ± 0.2 (76)	105.1 ± 1.8 (76)	119.1 ± 1.3 (76)	71.9 ± 1.7 (76)	77.4 ± 1.6 (76)	71.2 ± 1.6 (76)
A.tropicalis M	6.1 ± 0.3 (23)	20.6 ± 0.7 (17)	15.9 ± 0.5 (17)	202.5 ± 12.8 (17)	297.8 ± 3.2 (17)	94.3 ± 3.7 (17)	77.2 ± 5.8 (17)	44.5 ± 4.8 (17)
F	5.6 ± 0.3 (16)	17.8 ± 0.5 (23)	14.0 ± 0.6 (23)	198.7 ± 12.5 (23)	298.7 ± 3.9 (23)	74.9 ± 3.2 (23)	65.5 ± 4.3 (23)	40.3 ± 2.9 (23)
Overall means								
A.gazella	6.0 ± 0.1 (160)	15.4 ± 0.2 (161)	14.8 ± 0.2 (161)	107.9 ± 1.3 (161)	122.1 ± 0.9 (161)	84.3 ± 1.7 (161)	89.0 ± 1.6 (161)	82.8 ± 1.6 (161)
A.tropicalis	5.8 ± 0.2 (39)	19.0 ± 0.5 (40)	14.8 ± 0.4 (40)	200.3 ± 8.9 (40)	298.3 ± 2.6 (40)	83.2 ± 2.8 (40)	70.4 ± 3.6 (40)	42.1 ± 2.6 (40)

or years. However, there was a species * year interaction effect ($F_{1,189}$ = 3.145, P = 0.045) with *A. tropicalis* being more variable in age at weaning than *A. gazella*.

4.3.6 *Weaning mass*

For *A. tropicalis*, mass measured within 10 d of weaning was taken as an estimate of weaning mass. From these masses, weaning mass was calculated as a percentage of maximum mass. There was no difference in weaning mass as a percentage of maximum mass between sexes (2-way ANOVA $F_{1,16}$ = 0.142, P = 0.712) or years ($F_{2,16}$ = 0.848, P = 0.446), mean 78.3 % ($\pm$ 2.6), (n = 22). The weaning mass for *A. tropicalis* pups weighed more than 10 d from weaning was estimated as 78.3 % of their maximum mass.

There was no difference in the estimated weaning mass (Table 4.1) of the two species ($F_{1,189}$ = 0.079, P = 0.779), but there was a significant difference between the sexes ($F_{1,189}$ = 32.681, P < 0.0001), males 16.3 $\pm$ 0.2 kg (n = 102), females 13.3 $\pm$ 0.2 kg (n = 99). Weaning mass was not different between years ($F_{1,189}$ = 0.278, P = 0.757) and all interaction effects were non-significant. Weaning mass relative to adult female mass was approximately 40 % for female pups and 47 % for males (Table 4.2).

Table 4.2
Mean $\pm$ SE (n) weaning mass of *A. gazella* and *A. tropicalis* at Macquarie Island and weaning mass as a percentage of adult female mass.

Species	Sex	Weaning mass (kg)	Mass % of adult female
A. gazella	male	16.9 $\pm$ 0.3 (85)	47.5 %
	female	13.3 $\pm$ 0.2 (76)	38.0 %
A. tropicalis	male	15.9 $\pm$ 0.5 (17)	46.7 %
	female	14.0 $\pm$ 0.6 (23)	41.1 %

The difference in mass between maximum mass and weaning mass was significantly greater in *A. tropicalis* (4.2 $\pm$ 0.3 kg, n = 40) than *A. gazella* (0.7 $\pm$ 0.1 kg, n = 161) ($F_{1,189}$ = 183.29, P < 0.0001). This mass difference varied between years ($F_{2,189}$ = 4.769, P = 0.01), but not between sexes ($F_{1,189}$ = 0.579, P = 0.448). There was an interaction effect between species and year ($F_{2,189}$ = 3.993, P = 0.02) with a larger mass difference occurring in 1995-96 for *A. tropicalis*.

4.3.7 *Linear growth rates*

There was no difference in linear growth rate to 120 d for the two species, *A. gazella* 84.3 ± 1.7 g.d⁻¹ (n = 161), *A. tropicalis* 83.2 ± 2.8 g.d⁻¹ (n = 40) (Table 4.1) or with respect to the year of the study. There was however, a significant difference between the two sexes (F $_{1,189}$ = 26.525, P < 0.0001). Mean growth rates (species combined) were 95.2 ± 2.0 g.d⁻¹ (n = 102) for males and 72.6 ± 1.5 g.d⁻¹ (n = 99) for females.

There was a significant difference between the two species in linear growth rate from birth to weaning (F $_{1,189}$ = 131.866, P < 0.0001). Mean growth rate was 82.8 ± 1.6 g.d⁻¹ (n = 161) for *A. gazella*, and 42.1 ± 2.6 g.d⁻¹ (n = 40) for *A. tropicalis*. There was also a significant difference between the two sexes (F $_{1,189}$ = 9.534, P = 0.002). Growth rate in males (85.0 ± 2.7 g.d⁻¹, n = 102) was higher than females (64.1 ± 1.9 g.d⁻¹, n = 99). There was also a significant species * sex effect (F $_{1,189}$ = 6.224, P = 0.002) (Figure 4.4) with *A. gazella* males exhibiting higher growth rates than females, while there was no sex difference for *A. tropicalis*. There was no year effect.

For growth rate from birth to maximum mass there were significant differences between species (F $_{1,189}$ = 25.666, P < 0.0001) and sexes (F $_{1,189}$ = 15.961, P < 0.0001). Mean values were 89.0 ± 1.6 g.d⁻¹ (n = 161) and 70.4 ± 3.6 g.d⁻¹ (n = 40), for *A. gazella* and *A. tropicalis*, respectively. Male and female growth rates were 95.8 ± 2.2 g.d⁻¹ (n = 102) and 74.6 ± 1.7 g.d⁻¹ (n = 99), respectively.

4.3.8 *Mass of adult females*

Mothers of pups were weighed opportunistically through the summer months (November to March). Mean weights of *A.gazella* and *A. tropicalis* mothers were compared using Student's t-test. No difference in mass was found between the two species (t-test: t = 0.275, df = 162, P = 0.392), *A. gazella*: mean 34.5 ± 0.6 kg, n = 122, *A. tropicalis*: mean 34.1 ± 1.1 kg, n = 42.
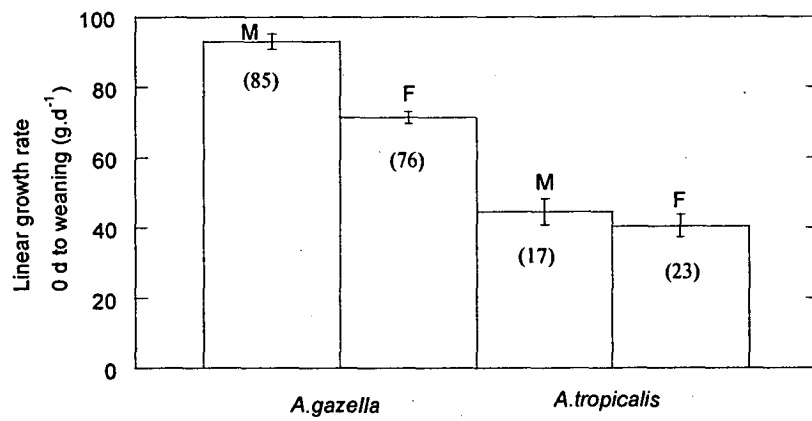
Figure 4.4
Mean ± SE (n) linear growth rate from birth to weaning for male
and female pups of both species. M = male, F = female. Growth rate
was significantly different for the sexes of *A. gazella*, but not
A. tropicalis.

4.4   DISCUSSION

This comparison of pup growth in sympatric fur seals allowed investigation into the importance of phylogenetic and environmental constraints into the shaping of two provisioning strategies with different lactation lengths (approximately 4 months and 10 months). Pups of *A. gazella* grew rapidly to maximum mass and weaned shortly thereafter at around 120 d. The development of *A. tropicalis* was more prolonged, with growth rate slowing after 120 d as they were reared through the winter. Maximum mass was reached at 200 d in *A. tropicalis*, from which point they generally declined in mass to wean at around 300 d. Despite these differences, the two provisioning strategies resulted in pups of similar weaning mass.

4.4.1   *Birth mass*

There was no detectable difference in the extrapolated birth masses of the two species. Similarly, no difference in birth mass of these two species was found in a previous study at the same site (Goldsworthy 1992) or in the sympatric population at Marion Island (Kerley 1985). All three studies however, found significant differences between the sexes in birth mass. Birth mass in otariids has been found to represent a similar proportion of maternal body mass (Kovacs and Lavigne 1992) at about 12 % for smaller fur seal species. Birth masses from this study were higher at approximately 17 % of post-partum female mass for both species.

In the first year of the study, *A. tropicalis* pups were born lighter than *A. gazella* pups, suggesting that resources may have been less available to *A. tropicalis* mothers during gestation prior to the first summer. For species combined, pups of 1996-97 were significantly heavier than the other two years. Prey may have been more available to both species prior to the second summer. Prey availability during gestation has been linked to birth size in *A. gazella* (Boyd and McCann 1989), northern fur seals *Callorhinus ursinus* (Boltnev *et al.* 1998) and Californian sea lions *Zalophus californianus* (DeLong *et al.* 1991).

4.4.2 *Growth rate*

Mass and age data, fitted with a Gompertz curve from birth to maximum mass showed the average growth for pups of the two species was very similar for the time of overlapping development (Dec to Mar-Apr, from 0 - 120 days of age). It appeared that adult females in both species were not only able to provide sufficient energy to their pups when small, but were also able to achieve similar growth rates up to 120 d. Growth rate to 120 d was close to linear for both species. This may be related to consistent prey availability at Macquarie Island during the austral summer. Growth continued for *A. tropicalis* after 120 d, but at a slower rate, with maximum mass achieved at 200 d.

4.4.3 *Age at weaning*

Weaning age and lactation length for both study species was similar to that of conspecifics from other locations (Tollu 1974, Doidge *et al.* 1984, Kerley 1985, Bester and Van Jaarsveld 1997), Guinet and Georges 2000). This supports the hypothesis of weaning age and lactation length being phylogenetically fixed, as has been proposed in other studies (Trillmich 1990, Gentry and Kooyman 1986a). Although presented with the same prey availability and environmental conditions at Macquarie Island, neither species altered its time to weaning from that of conspecifics at other sites.

There was greater variation in the weaning age of *A. tropicalis* compared to *A. gazella*. The study by Gentry and Kooyman (1986a) which compared subpolar, temperate and tropical otariid species, concluded that the extent of variation in weaning age was influenced by environmental factors, the variation decreasing with increasing environmental predictability, seasonality and food resources. They proposed that lower latitude species evolved greater flexibility in some traits to cope with increasing uncertainty in the environment. Pups of *A. gazella* have been recorded as weaning abruptly (Kerley 1983, Doidge *et al.* 1986) and *A. tropicalis* pups over a longer period (> 1 month) (Kerley 1983, Guinet and Georges 2000). For the study population, the range of ages over which *A. gazella* weaned was 52 days, and for *A. tropicalis*, 92 days. Pups of *A. gazella* weaned in autumn, thus dependence was not

prolonged. In contrast, *A. tropicalis* pups ranged from weaning at 230 d at a heavier mass, to continuing their dependence to bring them closer to the onset of the summer at weaning (up to 322 d). Having some flexibility in weaning age acts as a buffer for variation in prey availability while physical development and foraging skills improve (Trillmich 1996).

4.4.4 *Mass at weaning*

In spite of the large difference in weaning age, weaning mass was not different between the two species. This may in part be due to the similarity in size of the mothers. The percentage of adult female mass for pups at weaning has been shown to be roughly similar in most fur seal species, at about 41 % (Gentry *et al.* 1986, Costa 1991). Further, relative weaning mass has been shown to be similar across several mammalian groups including otariids (Lee *et al.* 1991). Intra-specific variation in weaning mass is likely to be related to resource availability, maternal attendance patterns and maternal condition (Doidge and Croxall 1989, Bester and Van Jaarsveld 1997, Georges and Guinet 2000). Thus, in general terms, weaning mass is linked to phylogenetic traits through the size of the mother, but the precise mass at weaning appears more related to environmental conditions which govern how the mothers can provision their pups.

4.4.5 *Maximum mass*

At Macquarie Island maximum mass in *A. gazella* was similar to its weaning mass and on average weaning occurred 1 to 2 weeks after reaching maximum mass. Pups of *A. tropicalis* reached maximum mass at about 200 days of age, then generally declined in mass until weaning at 300 days. Similarly, at Amsterdam Island, *A. tropicalis* pup growth slowed to zero between 165 and 220 days of age before declining to the weaning mass (Guinet and Georges 2000). At both these locations, *A. tropicalis* mothers appeared unable to provide sufficient energy to their pups during the latter part of lactation to maintain their pups' mass. This may in part be due to the increasing costs of gestation. At Amsterdam Island, longer foraging trips and lower milk delivery rates in winter resulted in a negative growth rate, in spite of the pups' ability to reduce their rate of mass loss as winter progressed (Guinet and Georges

2000). It may be that with reduced prey availability in winter, positive growth cannot be maintained by *A. tropicalis* mothers once pups reach a critical mass. This would be the maximum mass, which under favourable conditions might be maintained, but more often declines as weaning approaches.

Why don't pups depart at maximum mass? The risk of mortality may be higher if they departed at around 200 d (approx. July) due to reduced prey resources at this time. They therefore continue dependency, ideally not dropping below a threshold mass prior to weaning. Pups weaning prior to December would allow mothers one to two months of gestation without the added burden of lactation. Also, the recently weaned pups would be entering the local environment as prey resources begin to increase for the coming summer, a more favourable option than weaning in winter.

4.4.6 *Comparison with other studies*

Comparative pup growth data for five fur seal species (Gentry *et al.* 1986) shows that in the first 2 to 3 months of age, relative growth rates are similar across the genus despite differences in lactation strategy. After about the fourth month, the rate of growth declines both in subpolar species, which wean, and in temperate and tropical species which remain dependent for many more months. Results from the current study were consistent with these findings.

Growth rates for various age periods of *A. gazella* and *A. tropicalis* from other locations are presented in Table 4.3. At Macquarie Island, both species' rates of growth over various time periods were similar, or higher, than those from other locations. The growth rate for *A. tropicalis* pups to maximum mass was higher at Macquarie Island than Amsterdam Island. Growth rate to weaning was similar to that of Amsterdam Island pups. Weaning masses were within the range of other studies for both species, and age at which maximum mass was attained in *A. tropicalis* was also comparable between studies (Table 4.3). The particularly high weaning mass for male *A. tropicalis* at Macquarie Island from Goldsworthy (1992), may have been recorded in year of high prey availability. The current study showed this species generally losing mass after about 200 d. Weaning age was similar between conspecifics from different locations, supporting the notion that it is phylogenetically controlled.

Table 4.3

Comparison of pup growth parameters, for different age periods, for *A. gazella* and *A. tropicalis*, from various locations. Mean ± SE (n) (where supplied).

Species Location	Age period	Linear growth rate, male (g.d⁻¹)	Linear growth rate, female (g.d⁻¹)	Weaning mass, male (kg)	Weaning mass, female (kg)	Age at maximum mass (d)	Age at weaning (d) approx.	Reference
A. gazella								
Heard Island	0 – 99 d	79.6 (25)	60.6 (14)					Goldsworthy 1995
Bird Island	0 – weaning	84 (21)	78 (6)	15.4 (21)	14.7 (6)		115 (21) M 112 (6) F	Doidge and Croxall 1989
Bird Island	0 – weaning	98	84	17.0 ± 2.6$^{\alpha}$	13.5 ± 2.1$^{\alpha}$		110-115	Payne 1979
Marion Island	0 – weaning	110.5	74.4	17.8	14.2		111	Kerley 1985
Macquarie Island	0 – weaning (120 d)	85.2 ± 8.0 (13)	69.6 ± 4.1 (15)	16.4 ± 1.3 (13)	13.8 ± 0.6 (16)		*120.1± 2.7 (30) **121.7± 4.3 (21)	Goldsworthy 1992
Macquarie Island	0 – weaning	95.4 ± 2.2 (85)	71.9 ± 1.7 (76)	16.9 ± 0.3 (85)	13.3 ± 0.2 (76)		124 ± 1 (85) M 119 ± 1 (76) F	this study
A. tropicalis								
Macquarie Island	0 – 120 d	94.3 ± 3.7 (17)	74.9 ± 3.2 (23)				298	this study
Macquarie Island	0 – 120 d	78.7 ± 4.9 (6)	49.5 ± 7.5 (5)					Goldsworthy 1992
Marion Island	0 – 120 d	77.8	61.0				287	Kerley 1985
Amsterdam Island	0 – 300 d	45.0	45.0				300	Guinet and Georges 2000
Amsterdam Island	0 – 300 d	44.3	32.3	18.0	14.4	225 d	300	Tollu 1974
Marion Island	0 – 287 d	42.5	32.5	16.4	13.5			Kerley 1985
Gough Island	0 – 320 d			12.9 ± 0.6 (12)	9.5 ± 0.6 (8)		320	Bester 1987
Macquarie Island	0 – weaning	44.5 ± 4.8 (17)	40.3 ± 2.9 (23)	15.9 ± 0.5 (17)	14.0 ± 0.6 (23)		297 ± 3 (17) M 299 ± 4 (23) F	this study
Macquarie Island	0 – weaning	64.5 (6)	31.8 (5)	23.1	13.6		*287.6 ± 10.2 (7) **274.7 ± 13.3 (7)	Goldsworthy 1992
Amsterdam Island	0 – max mass 227 d	37 ± 3 (25)	38 ± 2.2 (29)	11.4 ± 0.4 (29)	11.1± 0.3 (41)	227 d (38)		Georges and Guinet 2000
Marion Island	0 – max mass 203 d	63.1	58.6			203 d		Kerley 1985
Macquarie Island	0 – max mass 204 d	77.2 ± 0.6 (17)	65.5 ± 0.5 (23)			204 d (40)		this study

*1989-90, **1990-91, $^{\alpha}$SD

Pup growth is the result of a mother's foraging behaviour, milk composition and attendance behaviour (Gentry *et al.* 1986). Over a range of marine environments (south and north of the APF, and temperate) it appears these parameters can be varied to produce comparable growth rates and weaning mass among congeners (Table 4.3). Provisioning behaviours (foraging and attendance) are probably less influenced by species phylogeny, and more by particular marine environments (Goldsworthy *et al.* 1997, Goldsworthy 1999). Foraging success affects female condition (Lunn *et al.* 1994) and quality of provisioning, and thus can influence birth mass, pup growth and weaning mass. The similar patterns in growth seen at different locations are likely to be achieved both through the flexibility of maternal foraging and attendance behaviour, and the broad phylogenetic constraints related to the family.

4.4.7 *Sex differences in pup growth*

At Macquarie Island, the mass of male pups exceeded that of females in all stages of growth. Several studies have discussed the possibility of differential maternal expenditure in male and female fur seal pups. Boyd and McCann (1989) found mass was higher in male foetuses than females in *A. gazella*, and differences in male and female post-natal growth rates have been found in previous studies of *A. gazella* (Payne 1979, Doidge *et al.* 1984, Kerley 1985, Goldsworthy 1995). However, studies by Lunn *et al.* (1993) and Lunn and Arnould (1997) on *A. gazella* at Bird Island, and Guinet and Georges (2000) of *A. tropicalis* at Amsterdam Island, found no sex differences in growth rates for serially weighed pups. Lunn and Arnould (1997) suggested that differential resource allocation rather than maternal expenditure may explain the observed differences in other studies. A study by Guinet *et al.* (1999) on a subset of the current study's data, found that the difference in growth rate between male and female *A. gazella* pups was related not to the rate of mass gain, for which there was no difference between the sexes, but to the rate of mass loss in female pups compared to males, with mass specific mass loss being greater in females.

Further, it has been proposed that sex differences in growth may only manifest when food availability is high (Mattlin 1981, Kerley 1985, Goldsworthy 1992, Bester and Van Jaarsveld 1997, Guinet *et al.* in press). Male pups from several fur seal species

are reported to exhibit higher growth efficiency than female pups when energy delivery rate by mothers is greater (Guinet *et al.* in press). The presence of sex differences in pup growth at Macquarie Island thus suggests there is an abundance of prey resources during the summer. Resources appeared to be reduced during the winter, but the sex differences persisted at maximum mass in *A. tropicalis* and then through to weaning in spite of a loss in mass. Once sex-based differences in mass are established, they appear to be maintained.

4.5   CONCLUSIONS

In spite of the difference in lactation length, the two species can produce pups with similar birth mass, growth rates during the first four months post-partum, and ultimately the same weaning mass. During the initial four months, the foraging behaviour (diving, diet, foraging range) of the two species was very similar (Goldsworthy 1997, Chapter 2). Previous studies have found similarities (but also differences) in attendance behaviour of these species at this location (Goldsworthy 1999, Chapter 5). Milk quality, (further to Goldsworthy and Crowley 1999) and the rate of milk delivery, are the subjects of further investigation (Chapter 5). The ability of pups to extract milk may also have affected attendance patterns (Doidge 1987) and pup growth, but was not examined in this study.

Despite similiarities, significant differences between species were found in maximum mass, age at maximum mass, growth rate from birth to maximum mass, growth rate from birth to weaning, and age at weaning. The longer lactation of *A. tropicalis* not only increased the time component of these parameters, but it was likely the availability of prey decreased during winter and spring, thus reducing the absolute and/or relative energy input to the pups as they grew.

The environment at Macquarie Island did not appear to favour one lactation strategy over the other with respect to the growth parameters measured, but could in fact advantage both species relative to other populations. Macquarie Island is the most southerly of the *A. tropicalis* colonies and the closest to the Antarctic Polar Front. The local marine environment may be more productive relative to environments of colonies further north, thus advantaging this population through the summer, and

possibly the winter months. Both species may be advantaged by low population size, reduced interspecific competition, and possible high prey availability. Growth rates and weaning mass were mid range or higher compared with the same species at other locations.

Sex-based differences were evident in birth mass, maximum mass, weaning mass, and growth rates to 120 d, maximum mass and weaning in both species. As pup mass and growth rate may be related to prey availability, the presence of sex-based differences indicates that food resources may not be limiting for growth in fur seals at Macquarie Island.

This study indicated that lactation length and weaning age were under phylogenetic control and did not vary from other breeding locations when the two species raised pups at the same site. As importantly, weaning age for each species did not vary between different sites despite considerable differences in respective marine environments. The local environment appeared to have a greater influence on parameters such as birth mass, growth rates and weaning mass. Prey availability influences maternal condition which in turn affects pup growth parameters through the transfer of energy. Energy input directly affects mass and mass change. Weaning age, which is linked to rates of physical maturation, would probably have developed over evolutionary time and, as such, would be much less affected by 'short term' external changes such as environmental differences between breeding sites. Despite phylogenetic differences and those between current and ancestral environments, there were aspects of pup growth in the two fur seal species at Macquarie Island that were remarkably similar.

Chapter 5
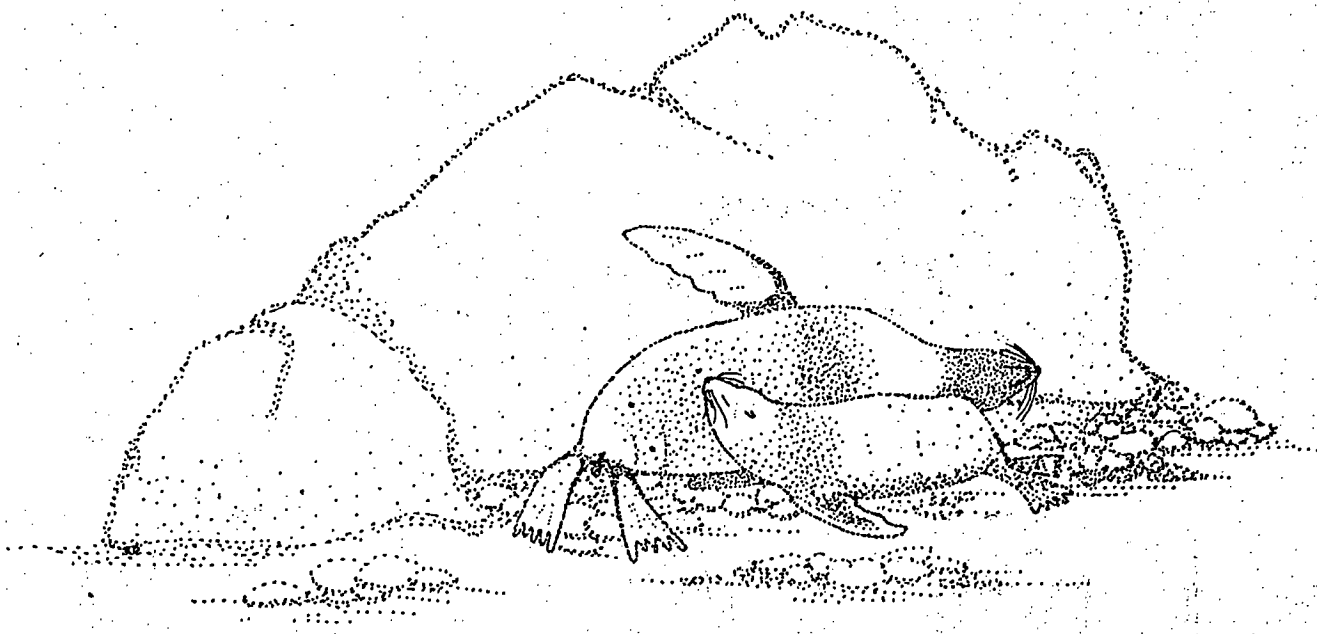
**PROVISIONING OF PUPS IN TWO SYMPATRIC FUR SEALS,
ARCTOCEPHALUS GAZELLA AND *A. TROPICALIS*: PHYLOGENETIC AND
ENVIRONMENTAL DETERMINANTS.**

5.1   INTRODUCTION

Two fundamental components of the life history of pinnipeds are marine feeding and
terrestrial parturition (Costa 1993). Phocids (true seals) and Otariids (fur seals and sea
lions) have evolved different strategies to cope with the temporal and spatial
separation of these activities (Bonner 1984, Oftedal *et al.* 1987, Costa 1993, Boness
and Bowen 1996). Prior to lactation, phocids generally accumulate all their energy
requirements as body reserves to enable them to fast throughout lactation, while
otariids regularly forage at sea to replenish reserves during lactation, leaving the pup
ashore. These have been termed 'fasting' and 'feeding' strategies (Boness and Bowen
1996). The provisioning strategies of otariid mothers must balance the time spent
acquiring energy at sea with the fasting ability of their pup on land.

Lactating fur seals and sea lions nurse their pups for about one week following
parturition, then undertake regular foraging trips. The allocation of time to foraging at
sea can be arranged as a small number of long foraging trips, a large number of short
duration trips or a mixture of both. Foraging trips are generally less than seven days in
duration (Gentry *et al.* 1986) but can be longer than 20 days in winter (Georges and
Guinet 2000, Kirkman *et al.* 2002). These trips are interspersed with shore bouts
which are usually between one and three days duration (Gentry *et al.* 1986). This
pattern of time allocation makes up the attendance cycle and it links the at-sea
components of provisioning with those on shore.

Ideally, fur seals and sea lions must forage in a way that allows for adequate energy
gain to meet milk production and their own maintenance costs while ensuring that
their pup does not fall below a condition threshold in their absence. The rate of mass

loss in pups is related to ambient temperature, activity levels and metabolic rate (Costa and Trillmich 1988, Guinet *et al.* 1999, Arnould *et al.* in press). Pup mass loss influences the overall time a mother can remain at sea, and also the amount of energy the pup will require on her return. A pup that loses a greater amount of mass while fasting on shore will require more food to maintain its mass plus the amount it needs to grow. During the mothers' absence, pups may conserve energy by reducing activity levels but this needs to be balanced with the development of swimming and other physical skills. When on shore, a mother should transfer her energy as quickly as possible to reduce her own fasting costs (Boyd 1998). The duration of time spent ashore is believed to depend on the load of milk delivered (Bester and Bartlett 1990, Boyd 1999), but is also affected by the size of the pup and its related ingestion ability and satiation time (Doidge 1987, Georges and Guinet 2000).

Otariid mothers produce milk from the energy stored as body lipid and protein and may vary in quality and quantity depending on such factors as preceding foraging trip duration, pup age, maternal condition and time ashore (Arnould and Boyd 1995b) (Georges *et al.* 2001). Lipid and protein comprises the energy content of milk (Kleiber 1975, Arnould and Boyd 1995a) thus the energy transferred to a pup is related to the compostion of milk as well as the quantity delivered. After several days, energy transfer efficiency decreases along with both milk production and pup sucking activity (Arnould and Boyd 1995b, Goldsworthy 1999). After this point it may not be economical for the mother to remain ashore.

Otariids have attracted much attention being a behaviourally, morphologically and physiologically similar group occupying a diverse range of environments from tropical to subpolar (Gentry and Kooyman 1986, Trillmich 1990). Much of this work has been improved by a range of telemetric techniques developed for remote monitoring. These include recording foraging activities at sea (satellite transmitters, time-depth recorders) (Harcourt and Davis 1997, Georges *et al.* 2000, Goebel *et al.* 2000), colony attendance (VHF transmitters) (Goldsworthy 1999, Arnould and Hindell 2001), quantification of maternal energy expenditure and energy transfer to the young, using isotope dilution (Arnould *et al.* 1996) .

To investigate the influence of phylogeny and environment on otariid provisioning strategies, it would be advantageous to observe species that employ different strategies in the same environment. A limited number of otariid populations include two or more sympatric species. The Galapagos fur seal (*Arctocephalus galapagoensis*) and sea lion (*Zalophus californianus wollebaeki*) at the Galapagos Islands have provided information on milk composition in relation to foraging trip duration (Trillmich and Lechner 1986). The foraging location, attendance and diet of lactating northern fur seals (*Callorhinus ursinus*) and Californian sea lions (*Z. californianus*) have been investigated at San Miguel Island (Antonelis *et al.* 1990). Studies of provisioning in sympatric fur seals (*Arctocephalus* spp.) include Antarctic (*A. gazella*) and subantarctic (*A. tropicalis*) fur seals at Macquarie Island (Goldsworthy 1992, Goldsworthy *et al.* 1997, Goldsworthy 1999, Goldsworthy and Crowley 1999) and comparative studies into pup growth (Kerley 1985) and female attendance (Bester and Bartlett 1990) of *A. gazella* and *A. tropicalis* at Marion Island. These two fur seal species have very different lactation lengths, *A. gazella* taking about four months to raise a pup and *A. tropicalis*, approximately ten months. Having the environmental variables controlled for in species comparisons helps to clarify which aspects of maternal strategies are phylogenetically, and which are environmentally controlled.

The foraging ecology and pup growth of sympatric *A. gazella* and *A. tropicalis* have been described at Macquarie Island, revealing few inter-specific differences that could account for observed differences in maternal strategies (Goldsworthy 1992, Goldsworthy *et al.* 1997, Chapters 2 and 4). This study quantifies the provisioning strategies and energy transfer of these two fur seals, and investigates: (1) the allocation of time spent foraging at sea and suckling pups ashore, (2) the fasting mass loss of pups and (3) the composition of milk and amount of milk energy transferred in order to assess the importance of phylogenetic and environmental constraints on otariid provisioning strategies.

5.2   MATERIALS AND METHODS

5.2.1   *Study site and species*

Lactating female Antarctic and subantarctic fur seals (*Arctocephalus gazella* and *A. tropicalis*) and their pups were studied at their sympatric colony at North Head, Macquarie Island (54° 30′ S, 158° 55′ E) during December 1995 to April 1997, and from December 1997 to April 1998. The two species overlap in breeding activities during the austral summer (Payne 1977, Goldsworthy 1999) with *A. gazella* suckling for four months (December to March – April) and *A. tropicalis* suckling through the winter to spring, taking 9 to 10 months to raise its pups (Payne 1977, Bester 1981). *Arctocephalus gazella* and *A. tropicalis* have preferred substrate types (beaches and rock platforms respectively), but breed within tens of metres of each other. The median pupping date for *A. gazella* at Macquarie Island is 7 December, and for *A. tropicalis*, 15 December (Goldsworthy 1992). The populations of each species are small in number, *A. gazella* producing around 125 pups per year, and *A. tropicalis* around 25 pups a year (S.D. Goldsworthy unpublished data). This places realistic constraints on the sample size of seals from each species that can be investigated.

5.2.2   *Mass specific mass loss*

To measure the rate of mass loss in fasting pups, pups were opportunistically weighed during periods of their mothers' absence. From these data, records of pup mass meeting the following criteria, were chosen: the 'initial mass' was recorded at least 2 days after the departure of the mother to allow milk in the pup's stomach to be digested, and 'final mass' was measured at least 1 day later (range 1 – 10 d) and prior to the mother's return. The difference between initial and final mass ($M_i - M_f$) was divided by the duration of the fast (Δd), (ie. the time elapsed between mass measurements) to give daily mass loss. This was divided by the initial mass to give mass specific mass loss (MSML) (Guinet et al. 1999).

$$\text{MSML} = [(M_i - M_f) / (\Delta d)] / M_i \qquad (1)$$

Where several mass loss events were recorded for a single pup, one was randomly chosen for the analysis. To confirm the presence or absence of mothers, attendance records from both VHF data and twice daily complete colony observation records (08:30 and 17:00) were used. Mass loss data for *A. gazella* were collected during December to March 1995-96 and 1996-97 and for *A. tropicalis* during December to April 1996-97 and 1997-98.

5.2.3 *Milk composition*

Milk samples were collected from lactating fur seals during the austral summers of 1995-96, 1996-97 and 1997-98, and the austral winter of 1996. Up to 10 ml of milk was manually expressed from one or more nipples from restrained animals, after an intra-muscular injection of 1 ml of 10 I.U. oxytocin (Heriot Agvet, Australia). Some females were caught specifically for the collection of milk samples and others for deployment and retrieval of Time-Depth Recorders and satellite transmitters (Chapter 2) at which time milk samples were also collected. Sampling was thus opportunistic with respect to the time females had spent ashore prior to capture. Milk samples from *A. gazella* (n = 135) were collected from 0 to 120 days postpartum for 1995-96, 1996-97 and 1997-98, and from *A. tropicalis* between 0 and 250 days postpartum in 1995-96, and during the first one hundred days of lactation in 1996-97. Different combinations of samples were used for *A. tropicalis* 0 to 120 d (n = 24) and 0 to 250 d (n = 26) to ensure the independence of data. Females were identified by individual flipper tags and all pupping dates were recorded.

Analysis of milk samples followed the methodology described by Arnould *et al.* (1995) and Arnould and Hindell (1999). Samples were stored in plastic vials at –20° C until analysis. Milk was thawed at room temperature then mixed thoroughly with a high speed stirring rod. All analyses (except ash content) were run in duplicate. Dry mass and water content were determined by drying sub-samples (ca. 1 g ± 1 mg) in

pre-weighed aluminium trays for 24 h at 70° C in a regular oven and then for 24 h at 70° C in a vacuum oven. The dried samples were then cooled in a dessicator before being re-weighed. Ash content was determined by placing single sub-samples of whole milk (ca. 1 - 2 g ± 1 mg) in ceramic crucibles and heating them in an automatic weighing furnace (Leco MAC400 Analyser). Moisture was firstly driven from the samples by heating in air at 120° C until attainment of constant mass. The ash was then determined by further heating in oxygen from 120° C to 550° C for 2 h and then at 550° C until attainment of constant mass.

Protein and lipid contents were then determined using a stoichiometric method (Gnaiger and Bitterlich 1984, Arnould *et al.* 1995). Sub-samples of the dried total solids (100 - 200 mg ± 1 mg) were packaged into pre-weighed tin foils and stored in a dessicator until analysed on an automatic carbon, hydrogen and nitrogen elemental analyser (Leco CHN Analyser) using a certified reference coal (ASCRM 013) as a standard. The measured carbon, hydrogen and nitrogen proportions of dry mass were used to calculate protein and lipid content following the procedures in Gnaiger and Bitterlich (1984), modified to account for the specific characteristics of fur seal milk (Arnould *et al.* 1995). Carbohydrates were not calculated directly, and typically represent less than 0.5 % of the total milk volume (Oftedal *et al.* 1987, Arnould and Boyd 1995a). Goldsworthy and Crowley (1999) analysed milk from *A. gazella* and *A. tropicalis* for carbohydrates and found both to be less than 0.16 %. Gross energy content of milk (kJ.g^{-1}) was calculated by multiplying the derived chemical composition by standard caloric values of energy density for lipid (39.8 kJ.g^{-1}) and protein (23.9 kJ.g^{-1}) (Kleiber 1975).

5.2.4 *Milk consumption*

Milk consumption was determined from the dilution of tritiated water (HTO), following Costa (1988) and Arnould *et al.* (1996). Water turnover in pups was measured from the decrease in HTO in body fluids. Assuming the only exogenous source of water was from milk, consumption could be estimated from milk water content and an estimate of metabolic water production (Lea *et al.* in press (a)).

Two age classes were used in the analysis, age class 1 containing pups at approximately 20 d and age class 2 with pups at around 100 d, (*A. gazella* n = 7 and n = 8, respectively and *A. tropicalis* n = 6 and n = 5, respectively) during December 1995 to January 1996 and March to April 1996. Pups were captured and weighed with a spring balance (25 ± 0.1 kg) at two days after their mothers' departure so that any milk in the stomach was likely to have been digested. An initial 1 to 5 ml blood sample (B_1) was taken from the wrist area of a fore-flipper to determine background levels of HTO, then the pup was injected intramuscularly with a weighed dose (± 0.0001 g) of 1 ml of 5 mCi/ml HTO and placed in an enclosure for 3 h to allow isotopic equilibration (Costa 1987). Pups were reweighed and a second blood sample (E_1) taken for the determination of initial total body water (TBW_i), before being released. Pups were recaptured after about 20 days when the mothers were absent, then reweighed and a blood sample (E_2) taken. From the dilution of the HTO in this sample, the total water turnover for the study period could be determined (Nagy and Costa 1980). Due to the change in body water pool from growth of the pup, a second estimation of total body water (TBW_f) was needed (Nagy and Costa 1980). For this, a second HTO injection (1 ml of 0.5 mCi/ml) was administered and the pup allowed to equilibrate for 3 h before a final blood sample (E_f) was taken. Blood samples were stored whole and frozen at -25°C until analysis.

Water from blood samples was distilled using a technique adapted from Ortiz *et al.* (1978) and Arnould *et al.* (1996), termed 'evaporated-freeze capture'. Blood samples were thawed and a 0.1 ml sub-sample of liquid placed into the upturned lid of a pre-weighed scintillation vial. Upside-down vials were screwed into the lids and placed into racks. These were placed on warming trays set at 50° C with a tray of ice over the top. The water in the sample evaporated with the heat, then condensed inside the vial due to cooling from the ice. Samples and vials were heated for 2 hours until dry, removed from the heat and allowed to cool before reweighing to deduce the mass of the water (± 0.0001 g). Samples were analysed in triplicate.

To each vial containing distilled water, 3.5 ml EcoLite Scintillation Fluid (Research Products Division, Costa Mesa, CA) was added. The specific activity of the samples was then counted in a Beckman LS-6500 Scintillation Counter (Beckman Instruments, Inc. Fullerton, CA) for 10 minutes each sample. Correction for quenching occurred by means of the sample channels ratio and an external standard to set the counting for each sample. Four HTO standards were prepared and counted with each set of samples.

Total body water (TBW) was calculated from the dilution space and corrected using the equation (Arnould *et al.* 1996),

TBW (kg) = 0.11 + 0.97* HTO space (kg).

To account for the change in pup mass over the duration of the experiment, Nagy and Costa's (1980) Equation 5 was used to determine water efflux rates, and Equation 6 for rates of water turnover. Milk consumption was calculated as the difference between total water influx (TWI) and metabolic water production (MWP), divided by the water content of the milk (Ortiz *et al.* 1984, Arnould *et al.* 1996).

Metabolic water production (MWP) was not calculated at this site due the very short fasting periods of pups between sucking bouts. Values for MWP from Îles Kerguelen were used for *A. gazella* (20 ml.kg^{-1}.d^{-1}, Lea *et al.* in press (a)). Îles Kerguelen has a similar subantarctic climate to Macquarie Island, being on the Antarctic Polar Front. For *A. tropicalis* at Macquarie Island, fasting mass specific mass loss (MSML) was 23 % lower than *A. gazella* (see below). Assuming a linear relationship between MSML and MWP, we used a MWP value of 15.4 ml.kg^{-1}.d^{-1} (23 % lower than 20 ml.kg^{-1}.d^{-1}) for *A. tropicalis*.

5.2.5 *Attendance*

Using small flipper tag mounted VHF radio transmitters with individual frequencies between 150 and 151 MHz (Sirtrack, NZ), the attendance behaviour of 10 adult *A. gazella* and 10 *A. tropicalis* females was monitored between December 1995 and September 1996, and 17 *A. gazella* and 2 *A. tropicalis* from December 1996 to April

1997. Presence and absence of study animals was recorded with a scanning receiver (2000B, Advanced Telemetry Systems, USA) connected to a programmable data logger (5040 DCC, Advanced Telemetry Systems, USA). Frequencies were monitored sequentially for 60 s and the number of pulses received was logged continuously over 10 months. Study animals were also visually identifiable from uniquely numbered plastic tags (Dalton, Woolgoolga, NSW).

As the second year of VHF deployments included only two *A. tropicalis* females, there were insufficient samples (females) to analyse for interannual differences between species. We decided to pool the two years of VHF attendance data to enhance the power of analyses to detect inter-specific differences. Data were divided into 20 d blocks from 0 to 120 d pup age for both species and two-way ANOVAs used with species and pup age class as the treatments. To correct for the lack of independence in the data due to the repeated use of individual females, the significance level of P = 0.05 was adjusted for each test using the Bonferoni method (dividing 0.05 by the number of comparisons). The adjusted Bonferoni level of significance is P = 0.004. Foraging trips were separated for some analyses into overnight trips (OFTs) which were less than 24 h and extended trips (EFTs) greater than 24 h (Goldsworthy 1999).

5.3   RESULTS

5.3.1   *Pup metabolism*

Using a General Linear Model with mass specific mass loss (MSML) as the dependent variable, species as the independent variable and pup age as a covariate, log transformed values for MSML in pups were compared between species. There was a significant difference in MSML between species (F $_{1,65}$ = 11.624, P = 0.001) with *A. gazella* (25.5 ± 1.02 g.kg^{-1} day^{-1}, n = 47) losing more mass per unit body mass than *A. tropicalis* (20.1 ± 0.95 g.kg^{-1} day^{-1}, n = 22). There was no relationship with pup age (F $_{1,66}$ = 0.457, P = 0.501). There was also no difference in log transformed MSML between sexes overall (ANOVA F$_{1,67}$ = 0.798, P = 0.375), but when *A. gazella* was

examined separately, there was a tendency towards a sex difference in MSML (ANOVA F $_{1,45}$ = 3.982, P = 0.052).

5.3.2   *Milk composition and pup energy consumption*

Total solids in *A. gazella* milk (0 to 120 d, n = 135) were composed on average, of 41.80 % (± 0.73) lipids (range 20.2 to 61.1 %), 10.79 % (± 0.16) protein (range 6.7 to 16.2 %), and < 1 % ash (carbohydrates were not measured directly). The average water content was 43.49 % (± 0.80) (range 23.1 to 66.5 %). These components accounted for 97 % of the total milk mass. Arnould *et al.* (1995) showed that the unaccounted mass in the stoichiometric method in determining milk composition was due to retained water in oven dried samples but that the estimates of other components and gross energy content were unaffected. The composition of milk of *A. tropicalis*, for the same time period (0 to 120 d, n = 24), was very similar: 40.09 % (± 1.97) lipid (range 20.2 to 59.7 %), 9.95 % (± 0.37) protein (range 6.1 to 13.1 %), < 1 % ash and 46.28 % (± 2.23) water (range 23.7 to 65.0 %). However, over the continued lactation of *A. tropicalis* (0 to 250 d, n = 26) the average lipid content was higher at 49.05 % (± 2.03) (range 25.9 to 67.6 %), and the water content consequently lower at 37.15 % (± 2.29) (range 17.7 to 64.3 %), 9.50 % (± 0.28) protein (range 6.1 to 12.2 %) and < 1 % ash.

The data were pooled for the two years to compare milk composition between species. ANCOVA indicated that the milk composition of the two species between 0 and 120 days post-partum (when they could be compared directly) was not significantly different between species (ANCOVA: lipid $F_{1,157}$ = 0.421 P = 0.517, water $F_{1,157}$ = 0.0.034 P = 0.854, protein $F_{1,157}$ = 2.462 P = 0.119, energy $F_{1,157}$ = 0.137 P = 0.711), However, lipid, water and energy all varied with pup age (ANCOVA: lipid $F_{1,157}$ = 43.758 P < 0.001, water $F_{1,157}$ = 34.010 P < 0.001, energy $F_{1,157}$ = 38.125 P < 0.001). The interactions between species and pup age were non-significant.

Mean lipid levels for *A. gazella*, rose from around 30 % early in lactation to 50 % at the end of lactation. Water exhibited the opposite trend, decreasing from around 50 %

to 30 % (Figure 5.1). Protein was constant throughout lactation in both species (Figures 5.1 and 5.2), while ash content declined. Similar patterns existed throughout the lactation of *A. tropicalis*, measured to 250 d, where mean lipid content increased throughout lactation from 40 % to 60 % (Figure 5.2). For *A. tropicalis*, second order polynomial curves more accurately described the relationships of % lipid and % water to pup age, than linear regressions (Figure 5.2). During the period of lactation overlap, lipid content varied in a similar way for both species (Figure 5.3), however beyond 120 days, lipid content in *A. tropicalis* milk was best described by a second order polynomial curve (Figure 5.3). Although variable over the latter part of lactation, milk lipid remained high, peaking at approximately 197 d, before decreasing.

There were weak but significant positive relationships between milk lipid and energy content, and length of the preceding foraging trip (Figure 5.4). This was calculated using females for which there was accurate information on foraging trip duration using VHF transmitters, Time-Depth Recorders or satellite transmitters, and which were captured within 12 hours of arrival. ANCOVA indicated that lipid content was not different between species: (*A. gazella* n = 25, *A. tropicalis* n = 10, $F_{1,31}$ = 1.172, P = 0.287) but increased with increasing foraging trip duration, ($F_{1,31}$ = 4.555, P = 0.041) such that lipid % = 45.211 + 1.417 * foraging trip duration (d); R^2 = 0.122. The interaction between species and trip duration was non-significant ($F_{1,31}$ = 0.160, P = 0.692. A similar relationship existed for energy content, no species difference (ANCOVA $F_{1,31}$ = 1.288, P = 0.265) but a significant increase with trip duration ($F_{1,31}$ = 4.310, P = 0.046) with gross energy (kJg^{-1}) = 20.524 + 0.553* foraging trip duration (d), R^2 = 0.115. There was no interaction effect ($F_{1,31}$ = 0.203, P = 0.656).

Percentage Total Body Water (% TBW) was estimated for pups of both species. No difference could be detected between species (t-test: t = -0.452, df = 24, P = 0.655) or sexes (t-test: t = 0.889, df = 24, P = 0.383) (Table 5.1).

For both species, average daily milk intake (ml/day) was estimated using HTO dilution over an approximately 20 d period (18 to 27 d) twice during the summer, and compared using 2-way ANOVA for species and age group. No species differences
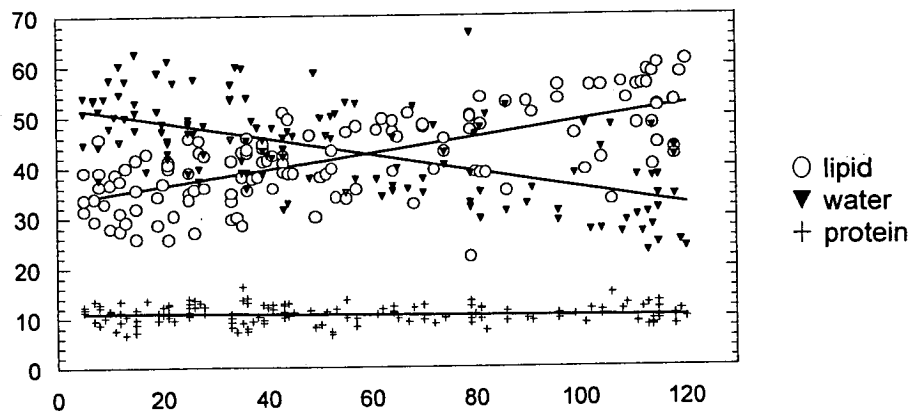
Figure 5.1
Components of *A. gazella* milk. Three years samples
combined, 0 to 120 d (n = 135).

Lipid % = 33.14 + 0.16*pup age; R^2 = 0.461
Water % = 52.37 − 0.17*pup age; R^2 = 0.392
Protein % = 11.15 − 0.007*pup age; R^2 = 0.017
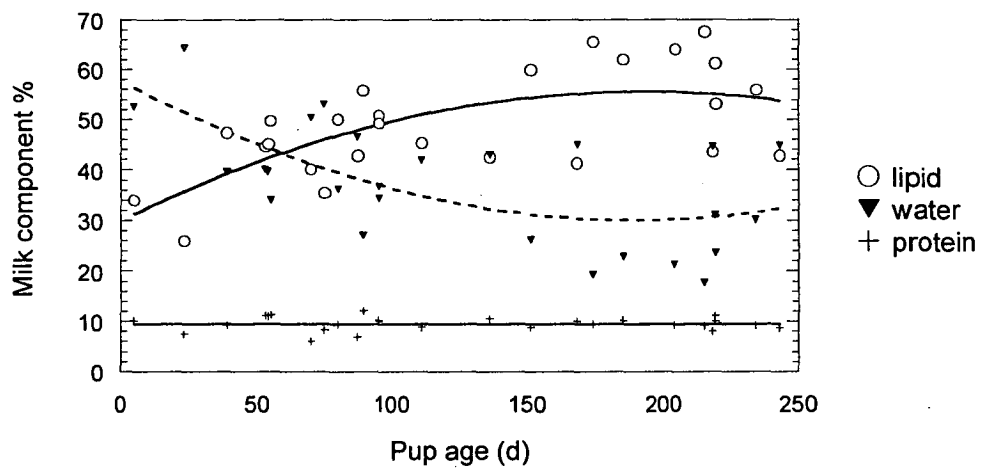
Figure 5.2

Components of *A. tropicalis* milk. Two years samples combined, 0 to 250 d (n = 26). Percentage lipid and water were best described with 2nd order polynomial curves.

Lipid % = 29.98 + 0.27 * x − (6.92*10^{-4}) *x^2, R^2 = 0.435
Water % = 57.83 − 0.29 * x − (7.69*10^{-4}) * x^2, R^2 = 0.395
Protein % = 9.53 − (2.85*10^{-4})*x, R^2 = 2.17*10^{-4}
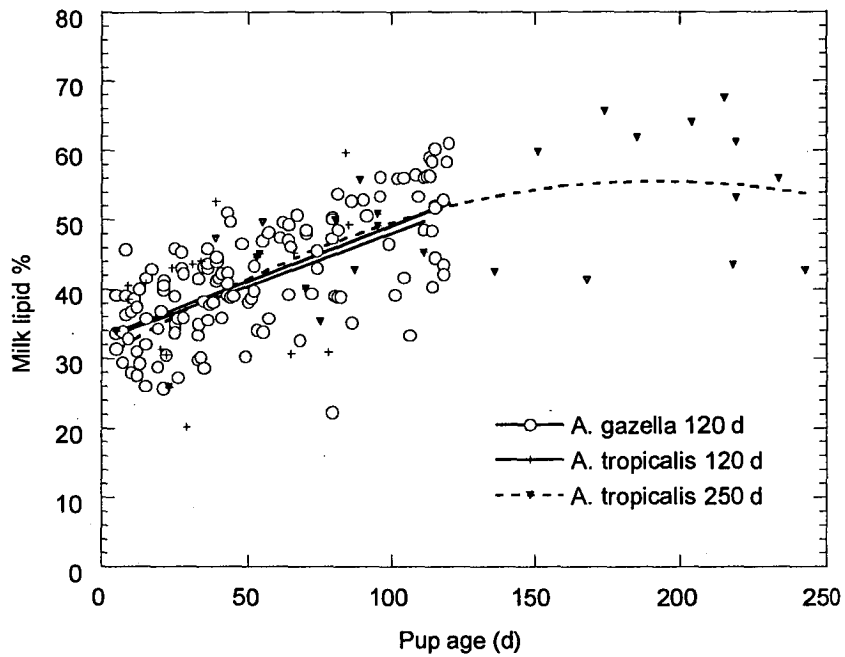
Figure 5.3
Milk lipid % for *A. gazella* 0 to 120 d (1995-96, 1996-97 and
1997-98 combined, n = 135) and *A tropicalis* 0 to 120 d (1995-96
and 1996-97 combined, n = 24) and 0 to 250 d (1995-96, n = 26),
best described with a second order polynomial curve.

A. gazella % milk lipid 0 to 120 d, $y = 33.14 + 0.16x$, $R^2 = 0.461$
A tropicalis % milk lipid 0 to 120 d, $y = 32.78 + 0.15x$, $R^2 = 0.257$
A tropicalis % milk lipid to 0 to 250 d,
$y = 29.98 + 0.27x - 6.92*10^{-4} x^2$, $R^2 = 0.435$
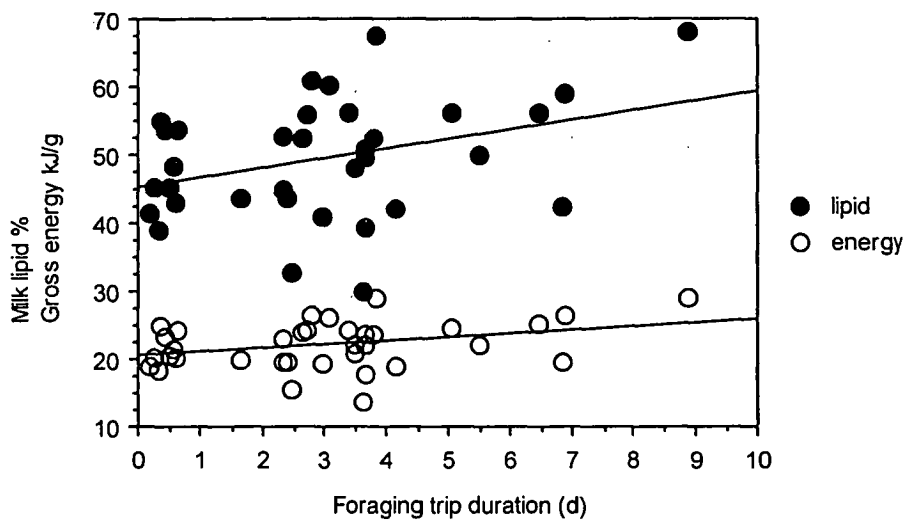
Figure 5.4
Milk lipid % and milk gross energy content with respect to
foraging trip duration (species combined), n = 35.

Lipid % = 45.21 + 1.42 * foraging trip duration; R^2 = 0.122
Gross energy kJ.g^{-1} = 20.52 + 0.55 * foraging trip duration;
R^2 = 0.115

were apparent in daily milk intake (ml.d^{-1}) (F $_{1,22}$ = 1.327, P = 0.262) but there was a significant decrease with increasing pup age (F $_{1,22}$ = 21.462, P < 0.001). There was no interaction between species and pup age. Milk energy (MJ d^{-1}) and mass specific milk energy (MJ kg^{-1} d^{-1}) were compared in the same way. There were no significant differences between species (milk energy: F $_{1,22}$ = 0.301, P = 0.589, mass specific milk energy: F $_{1,22}$ = 0.318, P = 0.578), but significant differences occurred with pup age class (milk energy: F $_{1,22}$ = 10.891, P = 0.003 and mass specific milk energy: F $_{1,22}$ = 6.606, P = 0.017 respectively) (Table 5.2).

Table 5.1
Percentage total body water (TBW %) and total body lipid (TBL %) estimated from HTO dilution for *A. gazella* and *A. tropicalis* pups from 1995-96. Mean ± SE (n).

Species	Sex (n)	TBW %	TBL %
A. gazella	Male (11)	65.2 ± 1.9	11.4 ± 1.6
	Female (4)	61.4 ± 2.7	14.7 ± 2.3
A. tropicalis	Male (4)	64.2 ± 3.6	12.3 ± 3.1
	Female (7)	64.2 ± 2.9	12.3 ± 2.5

Table 5.2
Milk and energy intakes for *A. gazella* and *A. tropicalis* for age class 1 (approx. 20 d age) and age class 2 (approx. 100 d age), estimated from HTO dilution during 1995-96. Mean ± SE (n).

	A. gazella		*A. tropicalis*	
	Age class 1 (n = 7)	Age class 2 (n = 8)	Age class 1 (n = 6)	Age class 2 (n = 5)
Daily milk intake (ml d^{-1})	714.6 ± 115.4	318.5 ± 43.5	598.7 ± 67.5	248.9 ± 69.6
Milk energy (MJ d^{-1})	12.3 ± 2.0	6.9 ± 0.9	11.1 ± 1.3	6.3 ± 1.8
Mass specific milk energy (MJ kg^{-1} kg^{-1} d^{-1})	0.55 ± 0.10	0.35 ± 0.05	0.50 ± 0.07	0.32 ± 0.08

Differences in consumption between the pup sexes in daily milk intake, milk energy per day and mass specific milk energy per day, were investigated. Using data pooled for both species, male pups (n = 15) consumed higher amounts of milk and milk

energy than females (n = 11) in all cases: daily milk intake (t-test: t = 2.463, df = 24, P = 0.022; males mean = 596.5 ± 75.9, females mean = 365.2 ± 55.2 ml d^{-1}); milk energy (t-test: t = 2.378, df = 24, P = 0.026; males mean = 11.3 ± 1.2, females mean = 7.5 ± 0.9 MJ d^{-1}) and mass specific milk energy (t-test: t = 2.170 df = 24, P = 0.040; males: mean = 0.52 ± 0.06, females mean = 0.37 ± 0.04 MJ kg^{-1} d^{-1}).

5.3.3   *Attendance behaviour*

The mean duration of all foraging trips per female, for each 20 d pup age class, was calculated (Table 5.3). Using a two-way ANOVA on log transformed data, *A. gazella* had a significantly longer mean foraging trip duration than *A. tropicalis* (F$_{1,74}$ = 22.502, P < 0.001) during the period of 0 to 120 d pup age. There was also a significant difference between age classes, with mean foraging trip duration increasing over the 120 d period (F$_{5,74}$ = 4.359, P = 0.002). The interaction between species and age class was non-significant, indicating that in both species' foraging trips changed in a similar way with increasing pup age (Figure 5.5). Foraging trip duration for the remainder of lactation (pup age 120-200 d) in *A. tropicalis*, exhibited a general increase to 200 d, with a maximum duration of 28 d at 180 d pup age, after which it declined (Figure 5.6).

Percentage frequency distribution of trip durations for both species presented are in Figure 5.7. Foraging trips were separated into overnight trips (< 1 d, OFTs) and extended trips (> 1 d, EFTs) for several of the subsequent analyses. Overnight trips were frequently used by both species. Of all trips recorded from *A. gazella* (n = 621) and *A. tropicalis* (n = 398) up to 120 d pup age during 1995-96 and 1996-97, 36.6 % of *A. gazella* trips and 70.6 % of *A. tropicalis* trips were OFTs. Foraging trip durations fall into distinct clusters (Figure 5.7) due to females tending to depart in the evenings and returning in the mornings (Goldsworthy 1999).

The mean number of foraging trips per female per pup age class was significantly different between species (F$_{1,74}$ = 9.680, P = 0.003). The mean number of foraging trips per 20 d age class was 6.8 ± 0.3, n = 61 for *A. gazella* and 8.6 ± 0.7, n = 25 for
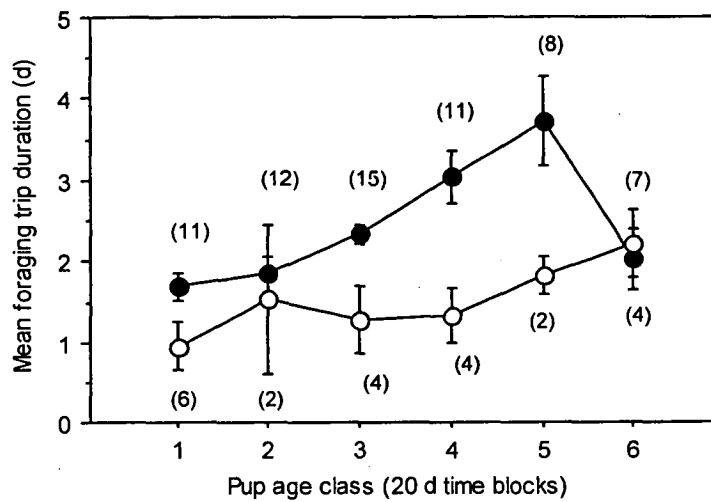
Figure 5.5

Mean ± SE (sample size per age class) foraging trip duration
for *A. gazella* (●) and *A. tropicalis* (○) for pup age class
(20 d intervals from 0 to120 d) for 1995-96 and 1996-97
combined, (total *A. gazella* females = 12, total *A. tropicalis*
females = 27).
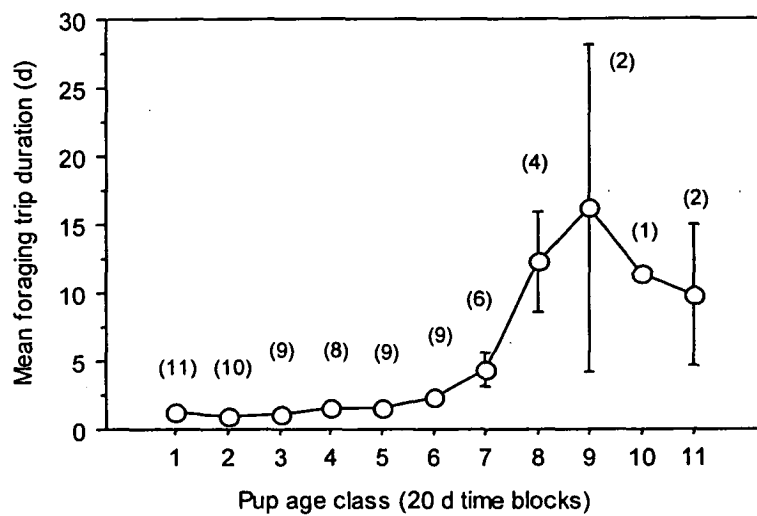
Figure 5.6

Mean ± SE (sample size per age class) foraging trip duration
for *A. tropicalis* for pup age class (20 d intervals from 0 to 220 d)
for 1995-96, (total females = 12).
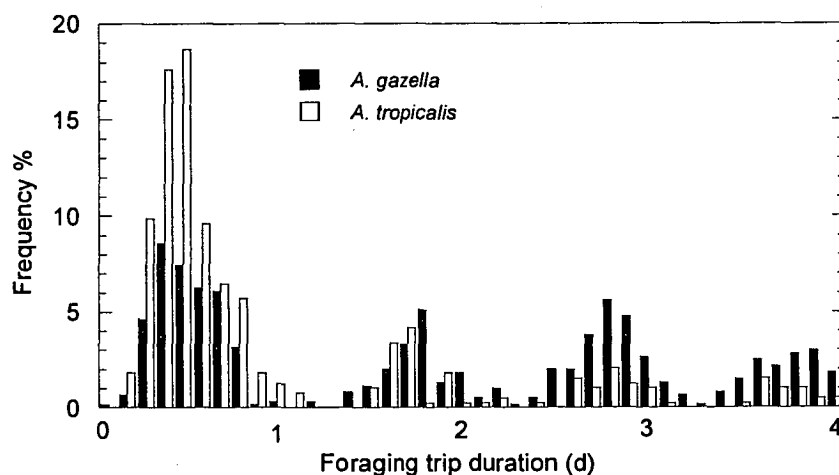
Figure 5.7
Percentage frequency of foraging trip durations up to *four days,
from 27 *A. gazella* adult females, n = 607 trips, and 12 *A. tropicalis*
adult females, n = 386 trips, for 1995-96 and 1996-97 combined.

* For clarity, trips > 4d are not plotted. Full dataset included
A. gazella n = 621 trips, and *A. tropicalis* n = 398 trips,
2.3 % and 2.8 % of trips respectively, were > 4 d.

Foraging trip durations fall into distinct groups due to females
tending depart in the evenings and return in the mornings.

A. tropicalis. There was no significant effect of age class ($F_{5,74} = 2.326$, $P = 0.051$, Bonferoni adjusted level of significance, $P = 0.004$) and no interaction between species and age class (Figure 5.8).

Using a t-test on (arcsine square root transformed) mean proportional sea time in an attendance cycle per female, *A. gazella* was found to spend significantly more time at sea than *A. tropicalis* (t-test: $t = 5.528$, $df = 37$, $P < 0.001$), *A. gazella* mean 75.9 % ($\pm$ 1.4) ($n = 27$), *A. tropicalis* mean 60.6 % ($\pm$ 2.6) ($n = 12$).

Mean proportional values of time spent in OFTs for each female were arcsine square root transformed and compared across the six pup age classes. The species were significantly different ($F_{1,158} = 33.201$, $P < 0.001$). Mean values for % time in OFTs were 12.7 % ($\pm$ 2.0), $n = 114$ and 38.3 % ($\pm$ 4.6), $n = 56$, for *A. gazella* and *A. tropicalis* respectively (Figure 5.9). There was no significant age class effect ($F_{1,158} = 1.868$, $P = 0.103$). The interaction between species and age class was non-significant.

The mean duration of each OFT was calculated for each female, and log transformed values compared across the 20 d pup age classes for the two species using a two-way ANOVA. There was no difference between species ($F_{1,130} = 0.096$, $P = 0.758$) or age class ($F_{5,30} = 0.519$, $P = 0.761$) (Table 5.3).

Mean durations for EFTs (Table 5.3, Figure 5.10) were also calculated and log transformed: there was no difference between species ($F_{1,144} = 1.340$, $P = 0.249$) but there was a significant difference between age classes ($F_{5,144} = 3.634$, $P = 0.004$). The interaction between species and age class was non-significant. Mean proportional values of time spent in EFTs for each female were arcsine square root transformed and compared across the six pup age classes. The species were significantly different ($F_{1,158} = 33.201$, $P < 0.001$). Mean values for % time in EFTs were 87.0 % ($\pm$ 2.0), $n = 114$ and 61.7 % ($\pm$ 4.6), $n = 56$, for *A. gazella* and *A. tropicalis* respectively. The effect of age class, and the interaction between species and age class, was non-significant.

Figure 5.8

Mean ± SE (sample size per age class) number of foraging trips
per adult female per pup age class (20 d intervals from 0 to 120 d)
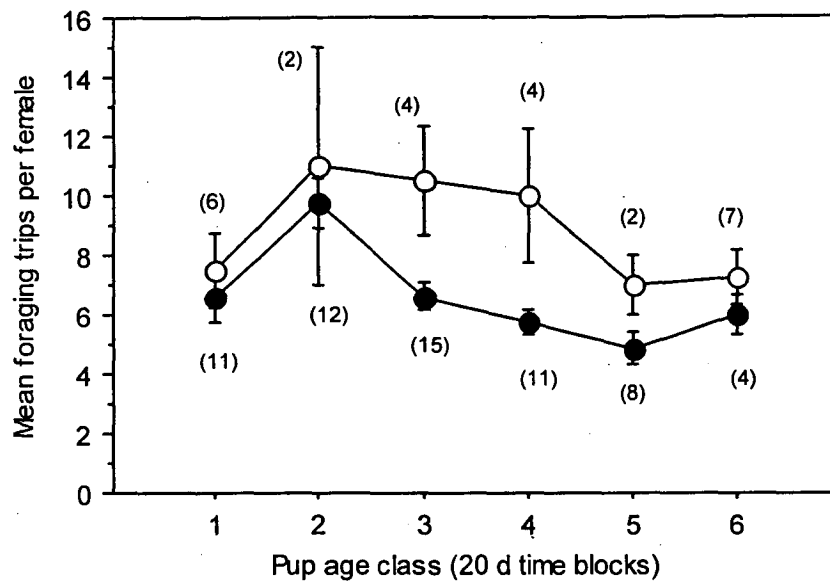for *A. gazella* (total females = 27) (●) and *A. tropicalis* (total
females = 12) (○) for 1995-96 and 1996-97 combined.

Table 5.3

Mean ± SE (n = number of females) of various attendance parameters for six 20 d pup age classes, for the two species. Data is pooled from 1995-96 and 1996-97 VHF deployments. Pup age class: 1 = 0 to 20 d, 2 = 21 to 40 d, 3 = 41 to 60 d, etc.

Species Pup age class	Mean duration of all foraging trips	Mean EFT duration days	Mean OFT duration days	Mean shore duration days	Mean foraging trips per age class	Mean % of sea time spent in OFTs
A. gazella						
1	1.68 ± 0.16 (11)	2.93 ± 0.39 (19)	0.54 ± 0.05 (15)	0.67 ± 0.10 (19)	6.5 ± 0.8 (11)	15.52 ± 3.33 (19)
2	1.84 ± 0.22 (12)	2.86 ± 0.22 (22)	0.45 ± 0.03 (21)	0.45 ± 0.02 (23)	9.8 ± 0.9 (12)	16.34 ± 4.74 (23)
3	2.33 ± 0.12 (15)	3.21 ± 0.15 (22)	0.45 ± 0.03 (19)	0.58 ± 0.07 (21)	6.6 ± 0.4 (15)	7.54 ± 1.23 (22)
4	3.04 ± 0.33 (11)	3.41 ± 0.17 (20)	0.48 ± 0.04 (15)	0.82 ± 0.08 (21)	5.7 ± 0.4 (11)	14.01 ± 6.16 (22)
5	3.72 ± 0.54 (8)	3.72 ± 0.32 (15)	0.42 ± 0.06 (9)	1.08 ± 0.10 (15)	4.9 ± 0.6 (8)	9.34 ± 6.12 (16)
6	2.02 ± 0.38 (4)	3.62 ± 0.63 (11)	0.44 ± 0.04 (9)	0.95 ± 0.18 (12)	6.0 ± 0.7 (4)	15.31 ± 8.10 (12)
A. tropicalis						
1	0.94 ± 0.30 (6)	4.02 ± 1.08 (7)	0.43 ± 0.03 (10)	0.74 ± 0.08 (11)	7.5 ± 1.3 (6)	54.07 ± 13.11 (11)
2	1.53 ± 0.93 (2)	2.23 ± 0.26 (8)	0.44 ± 0.03 (10)	0.56 ± 0.04 (10)	11.0 ± 4.0 (2)	46.86 ± 11.43 (10)
3	1.28 ± 0.41 (4)	2.17 ± 0.21 (7)	0.44 ± 0.03 (9)	0.71 ± 0.05 (9)	10.5 ± 1.8 (4)	46.04 ± 11.59 (9)
4	1.33 ± 0.34 (4)	3.34 ± 0.65 (8)	0.45 ± 0.04 (8)	1.03 ± 0.15 (8)	10.0 ± 2.3 (4)	31.13 ± 9.32 (8)
5	1.83 ± 0.23 (2)	3.32 ± 0.48 (8)	0.45 ± 0.04 (8)	0.75 ± 0.12 (9)	7.0 ± 1.0 (2)	30.62 ± 11.53 (9)
6	2.22 ± 0.43 (7)	4.40 ± 0.64 (9)	0.53 ± 0.03 (9)	0.97 ± 0.15 (9)	7.3 ± 0.9 (7)	15.99 ± 3.83 (9)
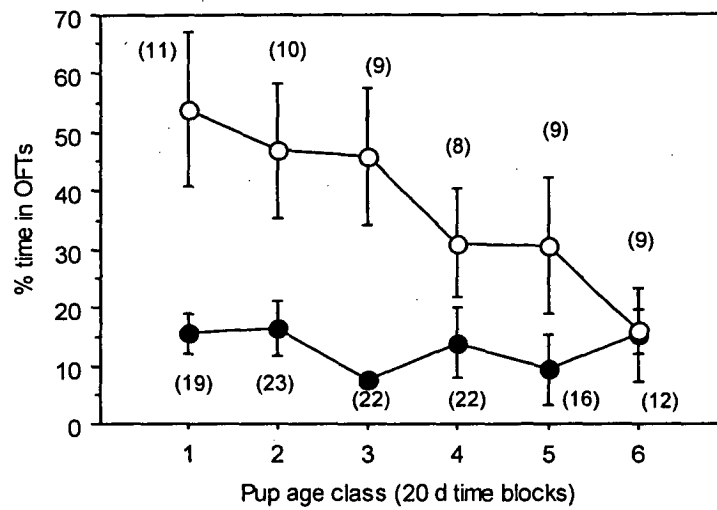
Figure 5.9

Mean ± SE (sample size per age class) percentage of time at
sea spent in OFTs for adult females per pup age class (20 d
intervals from 0 to 120 d) for *A. gazella* (●) (total females = 27)
and *A. tropicalis* (○) (total females = 12) for 1995-96 and
1996-97 combined.
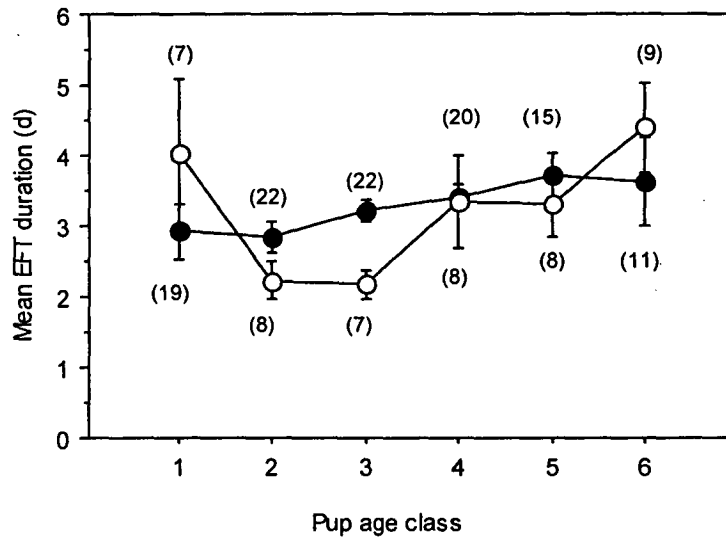
Figure 5.10
Mean ± SE (sample size per age class) EFT duration for
adult females per pup age class (20 d intervals from 0 to
120 d) for *A. gazella* (●) (total females = 27) and *A. tropicalis*
(○) (total females = 12) for 1995-96 and 1996-97 combined.

The mean duration of female shore visits were log transformed and again compared across the six pup age classes. There was no species difference ($F_{5,155} = 2.891$, $P = 0.091$) in shore bout duration, but significant variation in pup age class was evident ($F_{5,155} = 7.193$, $P < 0.001$) (Figure 5.11) with duration generally increasing through the summer. Shore bout duration in *A. tropicalis* continued to increase beyond 120 d to 180 d to a maximum of 3 d, before decreasing.

5.4 DISCUSSION

5.4.1 *Background*

Antarctic fur seals (*A. gazella*) are thought to be adapted to the colder waters south of the Antarctic Polar Front (APF) and subantarctic fur seals (*A. tropicalis*) to warmer waters north of the APF (Gentry *et al.* 1986). Consequently, these two morphologically similar species have been exposed to different selection pressures in each of their preferred habitats, which has resulted in a suite of traits, some fixed, some variable, that enable them to maximise their reproductive success (Gentry *et al.* 1986). The seasonality and predictability of marine resources is thought to be one of the key influences in the selection of traits for fur seal reproductive success (Boness and Bowen 1996). The subpolar environment of *A. gazella* is highly seasonal with prey resources readily available in the summer but sparse in winter. As a consequence, this species has therefore evolved a brief lactation to take advantage of the summer prey abundance (Gentry *et al.* 1986, Trillmich 1990). Pups wean at four months and disperse prior to winter (Bonner 1984). At South Georgia, which may be similar to the ancestral subpolar environment of *A. gazella*, mothers of this species forage in a cycle of 4 to 5 days at sea with a mean of 2 days ashore (Doidge *et al.* 1986). The post natal development is rapid, with pups beginning to moult to their adult coats at 8 weeks (Payne 1979).

It is thought that more temperate species, such as *A. tropicalis*, have evolved in less seasonal environments that are characterised by lower resource availability than subpolar environments, but where sufficient resources extend through the winter

Figure 5.11

Mean ± SE (sample size per age class) shore bout duration for adult females per pup age class (20 d intervals from 0 to 120 d) for *A. gazella* (●) (total females = 27) and *A. tropicalis* (○) (total females = 12) for 1995-96 and 1996-97 combined.
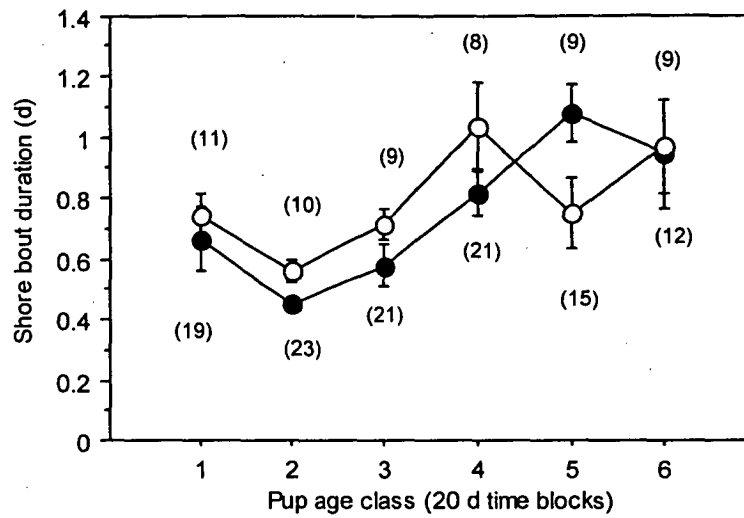
period, enabling longer lactation (Gentry and Kooyman 1986). They occupy the Tristan da Cunha, Prince Edward and Amsterdam Island groups in the Indian and Atlantic Oceans (King 1983), as well as Macquarie Island. At Amsterdam Island, *A. tropicalis* mothers undertake longer foraging trips (11 d) and shore bouts (4 d) during the first 120 days of lactation (Georges and Guinet 2000) than *A. gazella* from South Georgia. The pups fast during these times, then ingest large quantities of milk on the mothers' return (Georges and Guinet 2000). *A. tropicalis* mothers undertake even longer foraging trips during winter (mean 23 d) (Georges and Guinet 2000). It is possible *A. tropicalis* pups have developed methods of conserving energy, such as lowered metabolic rate and lowered activity to enhance the ability to fast for extended periods. *A. tropicalis* females suckle their pups over summer and continue through winter to the spring (10 to 11 months) when weaning occurs (Tollu 1974, Bester 1987). Over the 10 month lactation, *A. tropicalis* pups appear to develop more slowly than *A. gazella,* as they do not begin moulting until 12 weeks of age (Bester and Wilkinson 1989).

Macquarie Island is north of the APF and represents one of the northernmost colonies of *A. gazella* and southernmost of *A. tropicalis*. How do these species rear their pups at this location, and why does *A. tropicalis* persist with a ten month lactation period if food is abundant enough for *A. gazella* to raise pups in four months? For those parts of the provisioning strategy governed by phylogenetic constraints, one would expect to see intra-specific similarities in geographically separated colonies, and differences between the sympatric species. For those aspects influenced more by environmental factors, similarity between species in sympatry, and intra-specific differences between populations would be expected.

5.4.2 *Pup metabolism*

It has been proposed that sex differences in mass specific mass loss (MSML) of otariids may arise from differences in field metabolic rate (FMR) of male and female pups (Guinet *et al.* 1999). Applying this reasoning to the comparison of MSML

between *A. tropicalis* and *A. gazella*, suggests inter-specific differences may exist in the FMRs of pups. This may be due to *A. tropicalis* pups being less active on land or swimming less, equating to lower activity and/or thermal stress. Alternatively, the basal metabolic rate of *A. tropicalis* pups may be absolutely lower than *A. gazella*. Given the possibility that *A. tropicalis* has evolved strategies to conserve energy, related to foraging in a food depauperate environment, a reduced FMR in pups is likely to aid fasting for long periods, as apparent in the Amsterdam Island population (Georges and Guinet 2000). At South Georgia, a study of free-ranging *A. gazella* pups had a mean fasting MWP rate of between 26.5 and 28.4 mL kg d⁻¹. At the same site, a lower value was found when pups were restrained in an enclosure (mean 20.6 mL kg d⁻¹) (Arnould *et al.* in press). This suggests that a reduction in activity can substantially reduce MWP and by inference, FMR and MSML. Reduced energy requirements in comparison to *A. gazella* may be the strategy that *A. tropicalis* brings to Macquarie Island. However in this situation where prey availability appears relatively high, *A. tropicalis* continues to conserve energy. This suggests that fasting strategies, including reduced FMR, MSML and behaviours to reduce activity, are controlled to a large extent by phylogeny rather than environmental factors.

5.4.3 *Milk composition*

Fur seals, like other pinnipeds, produce milk that is high in lipid (and therefore energy) content, compared with milk of most terrestrial mammals. This is believed to be an adaptation to ensure that pups have adequate energy stores for fasting and somatic growth whilst mothers are foraging at sea (Trillmich and Lechner 1986). For *A. gazella* and *A. tropicalis*, over their 4 and 10 month lactation periods, average milk lipid and protein contents were similar to those found in other studies of these fur seal species (Arnould and Boyd 1995a, Goldsworthy and Crowley 1999, Georges *et al.* 2001). Milk lipid and milk water were strongly and inversely related, and changed throughout lactation, whereas protein content remained constant. Carbohydrates and ash are typically low in pinniped milk, usually less than 1% (Oftedal 1984, Oftedal *et al.* 1987 and references therein) as was found in this study.

Milk lipid content of both species was found to be highly variable, both between and within individuals, and this has been reported in other studies of pinniped milk (Kretzmann *et al.* 1991, Arnould and Boyd 1995, Gales *et al.* 1996, Goldsworthy and Crowley 1999, Georges *et al.* 2001). This variation may be related to a number of factors: age of pup, season, foraging trip duration, time ashore (female fasting), amount of mammary evacuation at the time of sampling, body mass and diet (Oftedal 1984, Oftedal *et al.* 1987, Georges *et al.* 2001). Milk composition has been shown to change throughout an attendance bout (usually 1-2 days), with decreasing concentration of lipids and sometimes protein (Costa and Gentry 1986, Arnould and Boyd 1995a, Arnould and Boyd 1995b, Goldsworthy and Crowley 1999). The average milk composition for the two species of fur seal was not significantly different over the first 120 days of lactation. This may relate to using similar foraging areas and having a very similar diet (Goldsworthy *et al.* 1997, Chapter 2) or it may be that fine scale differences could not be detected due to the inherent variability in milk composition. Milk lipid content increased with increasing pup age in a similar fashion for both species which agreed with a previous study at this site (Goldsworthy and Crowley 1999).

The main feature of milk from *A. tropicalis* was that the lipid content increased through lactation to about 200 d before declining, which was similar to *A. tropicalis* from Amsterdam Island (Georges *et al.* 2001) where milk lipid peaked at 180 d. This is interesting, given the differences in environments and foraging trip durations, and suggests a degree of phylogenetic influence, although milk lipid and energy content in *A. tropicalis* averaged for 250 d lactation was higher at Macquarie Island than Amsterdam Island (Table 5.4). For *A. gazella* at Macquarie Island, mean lipid and gross energy content were slightly higher than milk from South Georgia (Arnould and Boyd 1995a) (Table 5.4). It is likely that milk composition is affected by both environmental and phylogenetic influences.

Milk lipid was positively related to the duration of the preceding foraging trip. Other studies of milk composition in different seal species have also reported a positive relationship between foraging trip duration and lipid content (Costa and Gentry 1986,

Trillmich and Lechner 1986, Oftedal *et al.* 1987, Arnould and Hindell 1999) though

Georges *et al* (2001) found for *A. tropicalis* in summer (but not in autumn or winter),

that milk lipid increased as pups aged rather than as a function of foraging trip

duration. Arnould and Boyd (1995b) proposed that energy delivery to the pup was

likely to be limited by the fat storage capacity of the female and could be maximised

by adjusting the lipid content of the milk in response to foraging trip duration.

Table 5.4
Milk lipid and energy contents for *A. gazella* and *A. tropicalis* from different locations. Mean ± SE (n).

Location	Species	Pup age period (d)	Mean lipid (%)	Mean gross energy (kJ.g^{-1})	Reference
Macquarie Is.	*A. gazella*	0 – 120	41.8 ± 0.7 (135)	19.2 ± 0.3 (135)	this study
	A. tropicalis	0 – 120	40.1 ± 2.0 (24)	18.4 ± 0.8 (24)	this study
	A. tropicalis	0 – 250	49.1 ± 2.0 (26)	21.8 ± 0.8 (26)	this study
	A. gazella	0 to c. 120	39.8 ± 1.1 (36)	19.9 ± 0.5 (36)	Goldsworthy and Crowley (1999)
	A. tropicalis	0 to c. 120	38.6 ± 2.5 (17)	18.9 ± 0.8 (17)	
Amsterdam Is.	*A. tropicalis*	0 to c. 250	42.8 ± 0.6 (98)	20.4 ± 0.3 (83)	Georges *et al.* (2001)
		summer	45.0 ± 0.5 (49)	21.0 ± 0.2 (49)	
South Georgia	*A. gazella*	0 – 120	40.5 ± 0.5 (192)	15.7 to 17.3 (192)	Arnould and Boyd (1995a)

The positive relationship found between pup age and milk lipid content has also been

found in other otariid species: Antarctic fur seals at South Georgia (Arnould and Boyd

1995b), northern fur seals *Callorhinus ursinus* (Costa and Gentry 1986), South

American fur seals *A. australis* (Vaz-Ferreira and Ponce de Leon 1987), Australian

sea lions *Neophoca cinerea* (Gales *et al.* 1996), Californian sea lions *Zalophus*

californianus (Oftedal *et al.* 1987), Australian fur seals *A. pusillus doriferus* (Arnould

and Hindell 1999) and *A. tropicalis* at Amsterdam Island (Georges *et al.* 2001). It is

possible that this increase in milk lipid through lactation is due to the increasing of

foraging trip length with pup age.

5.4.4 *Milk and energy intake*

In this study, milk and milk energy consumption were similar between species. Given the likely lower energy demand of *A. tropicalis* pups, it was possible they consumed less milk energy per day than *A. gazella*, although this was probably not detectable due to the large inter-individual variation in milk composition (lipid content could vary by up to 35 % at a given point in lactation and mean values were used). *A. tropicalis* did show lower values for milk and energy intakes than *A. gazella* at all comparisons, though these did not reach significance. Larger samples than were possible from the small population of *A. tropicalis* would be needed to discern significant differences. A power analysis revealed that to detect a 10 % difference in milk lipid content, 113 individuals of each species would need to be sampled, which is higher than the number of breeding *A. tropicalis* females at this site.

Milk and milk energy intake per day, during the period of lactation overlap, declined significantly for both species between age classes 1 and 2. Similar low daily energy intakes near weaning age have been found in *A. gazella* at South Georgia and have been suggested to be part of the weaning process (Arnould *et al.* 1996). Daily energy intakes at South Georgia were approximately 8 MJ.d^{-1} at 20 d (equivalent to age class 1) and 7 MJ.d^{-1} at 100 d (age class 2) (from Arnould *et al.* 1996, fig.4), both similar to *A. gazella* at Macquarie Island. Pup growth in *A. gazella* at Macquarie Island was also comparable to South Georgia (Doidge *et al.* 1984, Doidge and Croxall 1989, Goldsworthy 1992, Chapter 4). It is unclear why *A. tropicalis* would also decrease in milk and milk energy intake at age class 2. That both species show the same decrease suggests it may be related to prey availability.

Unfortunately milk intake could not be directly compared between *A. tropicalis* at Macquarie and Amsterdam Islands due to being measured at different time intervals (daily and per shore bout, respectively). The main differences between these sites was that intake declined from age class 1 to age class 2 at Macquarie, whereas it was similar for the equivalent times at Amsterdam Island (Georges and Guinet 2000). The milk gross energy was higher overall at Amsterdam Island: 21.0 kJg^{-1} summer (age

class 1), 24.3 kJg^{-1} autumn (age class 2) (Georges *et al.* 2001), where *A. tropicalis* has a long foraging cycle. This is in contrast to Macquarie Island where this species has a short cycle: 17.8 kJg^{-1} (age class 1), 20.7 kJg^{-1} (age class 2).

5.4.5 *Attendance*

The foraging trips of fur seals at Macquarie Island have previously been divided into extended foraging trips (EFTs) and overnight (OFTs) by Goldsworthy (1999) who suggested that the two types of trips were functionally different, EFTs building up maternal energy reserves and OFTs optimising energy transfer to the pup. An important difference between the two species in the current study was the percentage of foraging time spent in overnight trips, with *A. tropicalis* spending 3 times more time than *A. gazella* in OFTs. This value was higher than for a previous study (1.6 times) by Goldsworthy (1999). The use of these short trips contributed to the significantly greater number of trips (and consequently more shore visits) by *A. tropicalis* during the 120 d period. Overall, *A. tropicalis* spent 15 % less time at sea than *A. gazella* during the four month period of lactation overlap. If their maternal strategy evolved in a less productive environment (such as Amsterdam Is.) *A. tropicalis* pups may make lower demands on their mothers' energy reserves than *A. gazella* pups, as supported by their lower MSML. This would require *A. tropicalis* mothers to spend less time at sea foraging. Because of the close proximity of prey, *A. tropicalis* can use mostly short foraging trips to provide sufficient energy for their pups. *A. gazella* mothers undertake more EFTs and less OFTs suggesting that *A. gazella* pups are extracting more resources more quickly, requiring their mothers to spend more time at sea to gain energy for milk production and self maintenance and spend less time ashore.

In *A. gazella*, mean foraging trip duration (OFTs and EFTs combined) increased over 0 to 100 d pup age then declined around weaning. Mean foraging trip duration for *A. tropicalis* continued to increase during the period up to 200 d pup age, before declining. This general increase in trip duration has also been observed in northern (Gentry and Holt 1986), Antarctic (Boyd *et al.* 1991, Goldsworthy 1995) and

subantarctic fur seals (Georges and Guinet 2000). Previous work at Macquarie Island (Goldsworthy 1999) showed the duration of EFTs to increase during the period to 60 d pup age then decrease to 120 d pup age for both species. After this point, EFT duration for *A. tropicalis* increased to about 7 d at 160 d pup age before declining (Goldsworthy1999). Short trips early in lactation are likely to be related the small size of pups and their limited capacity for milk ingestion (Costa and Gentry 1986, Georges and Guinet 2000). Both Goldsworthy (1995) and Georges and Guinet (2000) suggested that the greater the pup mass, and therefore its energy demands, the longer the foraging trips need to be. This may be the case for the two species at Macquarie Island. Further, the decrease in foraging trip duration towards the end of lactation in both species may be part of the weaning process and/or related to changes in prey availability.

Most milk (90 %) is transferred to *A. gazella* pups in the first 24 hours of a shore bout (Arnould and Boyd 1995). If this holds for *A. tropicalis* as well, then mothers of both species can take advantage of the lowered consumption rate after this time by leaving the pup to digest whilst undertaking a brief OFT. The benefit of energy gained during an OFT may be greater than remaining ashore fasting and delivering milk at a low rate (Goldsworthy 1999). Adult female *A. gazella* use OFTs but these occur between regular EFTs. Female *A. tropicalis* however, seem able to meet the demands of lactation (during summer) with mostly OFTs. It is likely that pup rearing is more expensive for *A. gazella* than *A. tropicalis* during the time when their pup rearing overlaps.

It is interesting that the duration of shore bouts of the two species were not different. It is possible *A. tropicalis* could also respond to the lower demand of their pups by increasing the shore time (delivering the same amount of milk but over a longer time) and making longer foraging trips to compensate. However, because of the close proximity of prey at Macquarie Island, frequent OFTs are possible and their use with short attendance bouts is likely to be the most economical option for meeting lactation demands. At Amsterdam Island, Georges and Guinet (2000) found that mass transfer to *A. tropicalis* pups was more efficient with short shore bouts due to the mothers'

reduced fasting maintenance metabolism. At that site it was advantageous for pups to consume milk as quickly as possible so that mothers could return to sea. The longer foraging trips at Amsterdam Island suggests that foraging conditions were less favourable than at Macquarie Island.

Table 5.5

Foraging trip durations (FTD) and shore bout durations (SBD) for *A. gazella* and *A. tropicalis* at various locations. Mean ± SE, n = number of foraging trips.

	A. gazella		A. tropicalis		Reference
	Mean FTD	Mean SBD	Mean FTD	Mean SBD	
Marion Is.	5.2 ± 0.3 d	1.7 ± 0.1 d	4.9 ± 0.4 d	2.5 ± 0.2 d	Bester and
(January – March)	(86)	(83)	(62)	(55)	Bartlett (1990)*
Amsterdam Is.			10.8 ± 0.3 d	3.8 ± 0.1 d	Georges and
(summer)			(85)	(85)	Guinet (2000)
South Georgia Is.	4.3 ± 0.2 d	2.1 ± 0.1 d			Doidge *et al*
(0 to weaning)	(139)	(131)			(1986)
Macquarie Is.	2.1 ± 0.1 d	0.6 ± <0.1 d	1.2 ± 0.1 d	0.7 ± <0.1 d	this study
(0 to 120 d)	(620)	(601)	(397)	(390)	

*methods procluded OFTs being detected

Mean foraging trip durations for *A. gazella* and *A. tropicalis* for the 0 – 120 d period for various other sites are compared in Table 5.5. Single studies however, do not show the seasonal or annual variation which can occur in foraging trip duration. The shorter foraging trip durations at Macquarie Island are likely to be due to prey resources being much closer than for the other two sites. Satellite location data indicate OFT areas were within 10 km and EFT areas within 50 km of Macquarie Island (Chapter 2). At Marion Island, where the same species are sympatric, both foraged for a similar duration but *A. tropicalis* had significantly longer shore bouts (Bester and Bartlett 1990). The lower demands of lactation in *A. tropicalis* over *A. gazella* at Marion Island may have been manifested in this way because there was little option for reducing foraging trip duration like there is at Macquarie Island (Bester and Bartlett 1990). Also, methods used at Marion Island procluded the observation of OFTs. Amsterdam Island the attendance strategy of *A. tropicalis* was different again, with females undertaking very long trips and consequently spending longer ashore transferring the energy. The attendance cycles used by lactating fur seals appear to

result from a combination of pup fasting ability and energy demands (Bester and Bartlett 1990, Georges and Guinet 2000), prey availability (Costa *et al.* 1989) and foraging location (Boyd 1998, Francis *et al.* 1998). It is possible other factors like maternal experience and condition may also influence attendance cycles. Pups of *A. gazella* and *A. tropicalis* have different energy demands, to which their mothers respond with different attendance cycles and provisioning patterns.

5.5   CONCLUSIONS

Provisioning strategies are governed by a combination of evolutionary and environmental factors. In fur seals, these strategies have evolved with physical and physiological limitations on pup development, which now remain, even in a situation where prey resources are abundant as is the case at Macquarie Island. *Arctocephalus tropicalis* have evolved with more energy conserving behaviours and/or physiology and cannot wean in a shorter time like *A. gazella*. The phylogenetically controlled demands of the pup drives the provisioning process and the environment dictates how the energy can be supplied. The mothers respond to pup energy demands and environmental variables through their attendance cycles. The low energy demands of *A. tropicalis* pups result in mothers needing to use mostly short foraging trips with occasional long trips to meet maternal energy deficits. This is possible at Macquarie Island because prey resources are relatively abundant and close to the island.
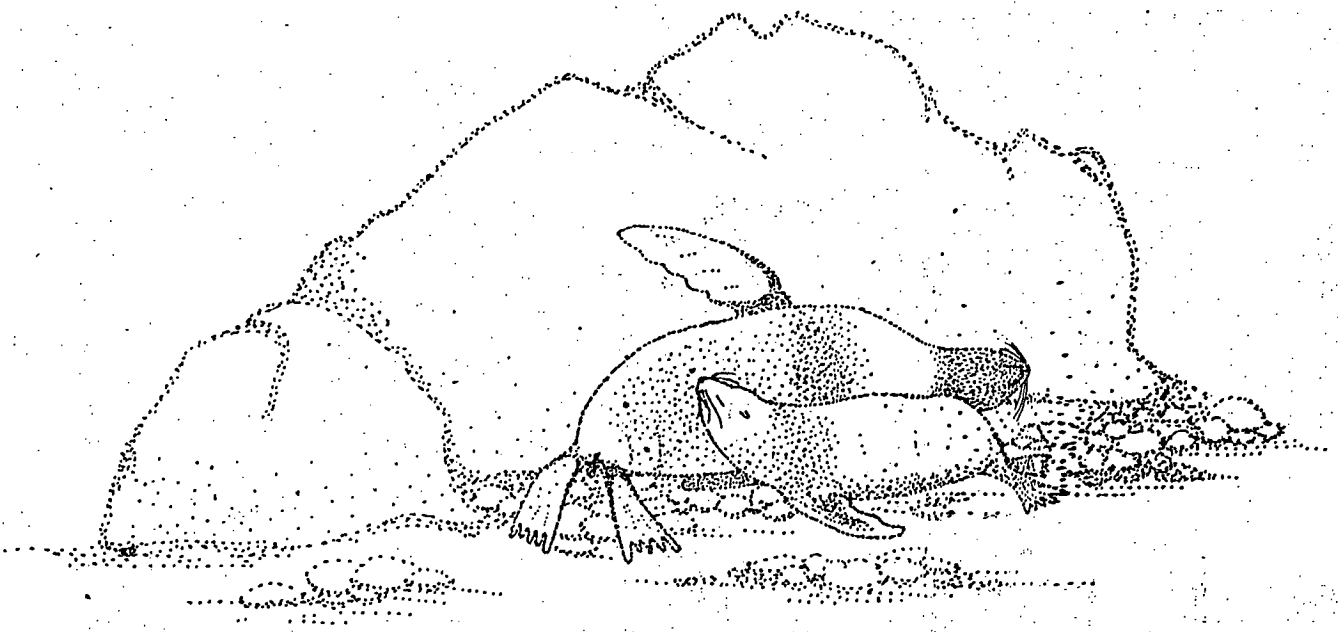
Chapter 6

GENERAL DISCUSSION

6.1   THE STUDY

In this study, the provisioning strategies of *Arctocephalus gazella* and *A. tropicalis*
(Pinnipedia: Otariidae) were investigated over a four year period at Macquarie Island,
where they breed sympatrically. The lactation periods of these species differed in
duration at this site, the former taking on average 122 days to rear its pups and the
latter, 298 days. Their lactation periods overlap for approximately four months
between December and March. At Macquarie Island both species breed on the same
beaches generally within tens of metres of each other, and sometimes occurring in
mixed species breeding territories. It is unusual for fur seals to breed in sympatry, and
the situation at Macquarie Island provides a natural experiment that may contribute to
the understanding of evolutionary processes. The two species are morphologically
very similar and possess similar physiological capacities (Gentry *et al.* 1986,
Trillmich 1990) but differ markedly in the duration of their lactation. This study aims
to compare the provisioning strategies of these sympatric fur seals under the same
environmental conditions, in order to gain insights into the extent to which aspects of
provisioning are constrained phylogenetically or are flexible to environmental
changes.

6.2   SUMMARY

The diets of *A. gazella* and *A. tropicalis* were similar, with both being dominated by
one fish species, the myctophid *Electrona subaspera* (Chapter 2). The *Gymnoscopelis
nicholsi / piabilis* complex was the next most important taxon but was substantially
lower in abundance and frequency. The main prey species are small mesopelagic fish
which feed on amphipods and other crustaceans (Hulley 1990) and are likely to be
associated with areas of high primary productivity such as upwellings and fronts. All
other fish species recorded were uncommon in the diet, as were cephalopods and
crustaceans. Both fur seal species then, seemed to be feeding on open water, pelagic
prey. The pre-dominance in the diet of a single species, both within and between

years, suggests that *E. subaspera* is very common in the waters around Macquarie Island. Trawl surveys in the vicinity of Macquarie Island have reported myctophids dominating the pelagic fish fauna (Williams 1988).

At Macquarie Island, *A. gazella* and *A. tropicalis* foraged at night, using short, shallow dives with deeper and longer dives at dusk and dawn as they presumably followed their vertically migrating prey through their diel activity. For both seal species most of the dives were very shallow, (median depth 8.5 m, Chapter 1). The diving behaviour of *A. gazella* has been investigated at South Georgia, Livingston Island, Heard Island and Iles Kerguelen (Boyd and Croxall 1992, Costa *et al.* 2000, Green 1997, Lea *et al.* in press), and in *A. tropicalis* at Amsterdam Island (Georges, Tremblay *et al.* 2000). The diving behaviour of fur seals at Macquarie Island differed most from seals at other locations being the shallowest so far reported for either species.

The core areas of foraging activity used during extended foraging trips were similar for both fur seal species, though activity for *A. tropicalis* tended to be more dispersed. These areas extended north from the island directly over and to the east of the Macquarie Ridge. Foraging activity was concentrated in two sites: within 30 km north of the island and at 60 km north (Chapter 2). Most locations for overnight foraging trips were within 10 km of the colony. It appeared that *E. subaspera* were also regularly available in the surface waters close to the island as diving behaviour was not different between short overnight and extended foraging trips.

Antarctic fur seal females did not use the seas around Macquarie Island randomly, but rather repeatedly returned to areas previously visited. They concentrated their efforts in an area parallel to and east of the Macquarie Ridge where it is likely prey were concentrated and spatially predictable. Within these areas, seals foraged according to the predictions of central place foraging theory (Chapter 3). Distance travelled, area used and mass gained by pups was found to increase with increasing foraging trip duration. Even with prey available close to the island, mothers regularly travelled to areas further away to forage for longer periods, suggesting that there was greater prey abundance in those areas.

One of the key differences between fur seals at Macquarie Island and other locations, is that adult females undertake overnight (< 24 h, OFT), as well as extended (> 24 h, EFT), foraging trips (Goldsworthy 1999, Chapter 5). At Marion Island, OFTs may occur, but methods procluded their detection (Bester and Bartlett 1990). It is possible that fur seal females regain body condition on longer foraging trips, allowing them to subsequently use shorter trips that may be more beneficial to the pup. The shorter OFTs are also beneficial to the lactating females in that they are likely to reduce the maintenance costs of fasting on shore when energy transfer efficiency falls. A reduction in the costs of energy transfer enables females to shorten the duration of the subsequent foraging trip. It appears the proximity of prey to Macquarie Island allows for the regular use of OFTs. This influence of the local environmental conditions on foraging trip duration and frequency, is likely to have an important effect on pup growth and possibly pup survival.

In spite of the difference in lactation length, the two species produced pups with similar birth mass, growth rates during the first four months post-partum, and ultimately with the same weaning mass (Chapter 4). The species did however differ in several important growth parameters. These were maximum mass, age at maximum mass, growth rate from birth to maximum mass, growth rate from birth to weaning, and age at weaning (Chapter 4). Lactating through the winter months may mean *A. tropicalis* females need to forage during a time of reduced food availability, which would lower the absolute and/or relative energy input to the pups as they grow.

The ecological conditions at Macquarie Island did not appear to favour one lactation strategy over the other with respect to the pup growth parameters measured. In fact the circumstances at Macquarie may even provide an advantage to both species relative to other populations due to the abundant and predictable availability of food, at least during the summer and autumn months. Macquarie Island is the most southerly of the *A. tropicalis* colonies and the closest to the Antarctic Polar Front. The local marine environment appears more productive in summer relative to the environments of *A. tropicalis* colonies further north. It is unknown how seasonal the prey resources are at Macquarie Island, however, the presence of over-wintering *A. gazella* females (Goldsworthy 1999) indicates some level of prey availability in the adjacent area during the mid and late lactation of *A. tropicalis*.

Both species may further be advantaged by low population size and reduced inter-specific competition at Macquarie Island. Growth rates and weaning masses were within the range of, or even higher than those reported for the same species at other locations, indicating they have access to greater prey resources, or prey of greater energy content. Sex-based differences were evident in birth mass, maximum mass, weaning mass, and in growth rates to 120 d and maximum mass, for species combined. Linear growth rates from birth to weaning were different for the two sexes of *A. gazella* but not *A. tropicalis*. These sex-based differences may also support the notion of food resources being abundant at Macquarie Island. Guinet *et al.* (in press) suggested that when food availability is high, male *A. gazella* pups have higher growth efficiency than female pups, but not when environmental conditions are less favourable.

Mass specific mass loss (MSML) in *A. tropicalis* pups was found to be 23 % lower than in *A. gazella* pups of the same age, suggesting inter-specific differences in field metabolic rates (Chapter 5). This may have been due to *A. tropicalis* pups being less active on land or swimming less, equating to lower activity and/or thermal stress. Alternatively, the basal metabolic rate of *A. tropicalis* pups may be absolutely lower than *A. gazella*. Given that it is possible that *A. tropicalis* evolved strategies to conserve energy, related to foraging in a food depauperate environment, a reduced field metabolic rate in pups may aid fasting for long periods, as is seen in the Amsterdam Island population (Georges and Guinet 2000). The difference in MSML may conversely be viewed as elevated in *A. gazella*. In order to develop and grow rapidly to wean in 122 days, a high field metabolic rate may be necessary.

Milk composition was similar for the period of lactation overlap and lipid content increased throughout lactation for both species, averaging 42 % for *A. gazella* to 120 d and averaging 49 % for *A. tropicalis* to 250 d in winter (Chapter 5). Lipid % peaked at around 55 % for *A. tropicalis* at 200 d. Milk water and protein contents were comparable and varied in a similar way for both species through lactation.

Milk and milk energy consumption were not significantly different between the two species' pups. However in both species milk lipid and milk energy levels were

characterised by high levels of inter-individual variation (Chapter 5). The lipid and protein contents of milk need to be accurately known to estimate milk and energy intakes, and a power analysis indicated that a sample size greater than the number of *A. tropicalis* females breeding at Macquarie Island would be required to detect a difference in milk composition between species. However, the observation that mass specific fasting mass loss was significantly lower in *A. tropicalis* pups suggests this species had lower energy demands and may also have been consuming less milk and milk energy.

The durations of OFTs, EFTs and shore attendance bouts were similar between species, however, *A. gazella* spent less of their overall time budget on overnight trips, more time at sea and undertook less foraging trips than *A. tropicalis* (Chapter 5). Of all foraging trips (to 120 d pup age) undertaken by *A. gazella*, 37 % were OFTs, whereas for *A. tropicalis*, 70 % were OFTs. The lower energy demand of *A. tropicalis* pups may have been the proximate reason for their mothers using mostly short foraging trips and spending less time at sea than *A. gazella*. Conversely, the greater energy demands of *A. gazella* pups, require their mothers to spend more time foraging and using longer trips.

6.3 PHYLOGENETIC AND ENVIRONMENTAL DETERMINANTS OF PROVISIONING STRATEGIES IN FUR SEALS

The aspects of foraging ecology examined in this study did not differ between fur seal species despite differences in lactation length, and instead, appeared to be substantially influenced by local environmental conditions. Patterns of foraging by fur seals from other locations also appear to reflect the abundance and distribution of prey in their local areas (Klages and Bester 1998, Lea *et al.* in press). The local environment also appeared to influence parameters such as birth mass, growth rates, weaning mass, and overall foraging trip duration. Maternal energy acquisition comprises the amount of prey consumed and the duration of foraging trips, and is therefore strongly influenced by prey availability. This in turn affects pup growth parameters through the transfer of maternal energy. The close proximity of prey to Macquarie Island allows the use of OFTs by both species and results in seals at this location having the shortest mean foraging trip durations for these species. This study

highlighted that it is these flexible traits, which vary with environmental influence, that are similar between fur seal species in a sympatric situation.

The durations of lactation and weaning age for the sympatric fur seals were similar to those reported for conspecifics from other breeding locations. These are the more rigid traits of fur seal provisioning strategies and believed to be under phylogenetic control. The MSML of pups, and its relationship to pup energy use and demands, appeared to be a critical factor in determining these provisioning strategies. It is probable that for *A. gazella* pups, the greater MSML (denoting higher FMR) aids rapid physical development, which results in earlier weaning age. Greater MSML is also likely to result in higher energy demands by *A. gazella* pups compared to *A. tropicalis*. For *A. tropicalis*, lower MSML (and FMR) is likely to result in lower energy intake and a longer time of development to weaning. It appears the energy demands of the pups, and their subsequent growth strategies, determine the duration of lactation. The growth strategies of the pups, comprising their energy demands and rates of development, appear to be phylogenetically controlled and responsible for the main differences between the two seal species.

The energy demands of pups drive the energy acquisition of females, ie. mothers respond to the needs of their pups, when they have this option. At Macquarie Island, adult female *A. tropicalis* need only to spend a small amount of time at sea to meet their pups' and their own energy demands. They undertake short and frequent foraging trips with only occasional EFTs. Pups of *A. gazella* however, require a larger amount of energy which results in mothers spending more time at sea and using a greater number of EFTs. Attendance patterns are therefore the product of the pups' energy demands (on shore) and the availability of prey (at sea). At Macquarie Island seals take advantage of the close proximity of prey by regularly using OFTs between EFTs. However, for *A. gazella*, with higher pup energy requirements, using predominantly OFTs is not a viable option.

The provisioning strategies of the fur seals at Macquarie Island were composed of both flexible and rigid traits. The flexible traits were those which were similar between species and influenced by environmental conditions, such as diet, diving behaviour, foraging areas used, foraging trip duration, growth rate to 120 days and

pup mass at birth and weaning. The traits which remained different in both species despite living in the same environment, like weaning age, lactation duration, MSML and rate of development in pups, were believed to be under phylogenetic control. It appears for fur seals at Macquarie Island, that the major species differences (weaning age and lactation length) result from phylogenetic differences in pup energy demand and subsequent growth strategies.

6.4   FUTURE RESEARCH

This project has endeavoured to determine the importance of phylogenetic constraints and environment in shaping the provisioning strategies of fur seals. Although much more is now understood about the phylogenetic and environmental influences acting on the foraging ecology and provisioning strategies of these two fur seal species, several important questions have arisen as a result of this work. (i) The metabolic requirements of the pups has been identified as an important proximate determinant of both pup growth and maternal foraging strategies. Therefore, it would be helpful to have a direct measurement of field metabolic rate for pups of both species at this location. These data would both improve our understanding of their energy requirements and provide comparative information with other sites, to further examine the role of the environment in fur seal breeding behaviour. (ii) Quantifying the physical and behavioural development of the pups would help clarify exactly where the developmental differences are for these two species. (iii) For *A. tropicalis* females, obtaining overnight foraging locations with greater accuracy (now available) would provide more precise data on their foraging area use, plus provide information on whether this regular use of very short trips agrees with the predictions of central place foraging theory. (iv) Locating the winter foraging areas of both species (particularly *A. tropicalis*) would fill a large and important gap in the knowledge of their foraging ecology. (v) As the populations of the two species expand, monitoring of reproductive and recruitment rates would help answer the question of which (if either) species is better advantaged by the environmental conditions available at Macquarie Island.

With the current population of fur seals being artificially low due to the sealing in the 19th century, the use of foraging areas very close to the island is currently a viable

option. Recent studies of royal (Hull *et al.* 1997) and king penguins (B. Wienecke pers. comm.), both consumers of myctophids, show foraging areas up to hundreds of kilometres from the island, however further investigations are needed to cover the whole chick rearing periods for these species. Patagonian toothfish also prey on myctophids (Goldsworthy *et al.* 2001), but would be likely separated in foraging depths from fur seals. If fur seal numbers increase at rates similar to other populations (Bester 1980, Hes and Roux 1983, Boyd *et al.* 1990, Hofmeyr *et al.* 1997), this may result in depletion of the prey resources nearer the island. Such depletion may enhance interspecific competition and eventual resource partitioning, resulting in some animals foraging further from the island.

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