Factors affecting reproductive success of southern elephant seals, *Mirounga leonina*, at Marion Island

by

Ian Stewart Wilkinson

Submitted in partial fulfilment of the
requirements for the degree of

Ph.D (Zoology)

in the
Faculty of Science
University of Pretoria
Pretoria

February 1992

**For mum, dad and my
family that are so
many miles away**

Factors affecting reproductive success of southern elephant seals, *Mirounga leonina*, at Marion Island

by

Ian Stewart Wilkinson

Supervisor: Professor R J Van Aarde
Mammal Research Institute
Department of Zoology
University of Pretoria
Pretoria

ABSTRACT

Timing and duration of the breeding season at Marion Island is the same as it was in the 1970's, and is the same as other breeding sites at similar latitudes.

Pup production for the whole island declined at 4,8% per annum between 1951 and 1989, while in the main study area it slowed to 1,9% per annum between 1983 and 1989. First year survival was 60%, all cows aged six years and older produced pups (at a ratio of 1,04:1 male:female), and cows pupped for the first time at a mean age of 4,41 years. Mortality among three year old females was high, possibly resulting from increased physiological stresses of gestation and lactation, and a possible change in feeding area. The low net reproductive rate (R_0=0,661) is a consequence of the low numbers of females being recruited to the adult breeding population.

Low density harems provided a favourable environment to rear pups, and maternal age, size and social status did not effect reproductive success. Dominant bulls achieved over 98% of the observed matings, and sexual activity was related to the numbers of oestrous cows. Cows were mated several times but chances of conception were not related to frequency. The long oestrus period (3 to 4 days) may be an adaptation to ensure fertilisation in a high density harem situation. The date a cow was mated during the season had no effect on her chances of conceiving.

Male pups were heavier at birth and weaning than females, and larger cows produced, and reared larger pups than small cows. Growth rates were dependant on birth weight, and not on the sex of the pup. Neither pre or post-natal investment differed between the sexes and thus no observed increased "costs" to the cow of producing one sex or the other were evident. High ranking cows skewed the sex ratio of their offspring in favour of males, the mechanism for which is not understood. Cows produce the sex that has a higher probability of future reproductive success, regardless of the costs involved in its production.

ACKNOWLEDGEMENTS

My special thanks go to Professor Rudi van Aarde for initiating the study and for his supervision and unfailing confidence in my ability to carry it out. Financial and logistic support for the study were provided by the South African Department of Environment Affairs, and the Public Works Department built the observation tank without which this work would have been extremely uncomfortable, if not impossible. I was the recipient of a doctoral bursary from the Foundation for Research Development during part of the study and I thank them for their financial support. The Sea Fisheries Research Institute are thanked for the facilities and time they put at my disposal in the final stages of the preparation of this dissertation. Clairol Inc. (SA) are thanked for hair dye provided to bleach mark the seals.

I would like to thank Charlie Pascoe, Jaco Swart & Rory Heather-Clark for field assistance and friendship through the seemingly endless dawn to dusk observation periods at Trypot Beach.

This study would not have been possible without the background information obtained on this population during the 1970's and 1980's and I thank the biologists and technicians for the work they did. I am especially grateful to Dr Patrick Condy whose organisation and planning at the outset of this programme in 1973 provided such a good foundation on which to build.

I thank the biologists of the 43rd, 44th and 45th Marion teams who provided me with the opportunity to discuss my ideas and problems with this work with them while in the field Namely: Steve Hunter, Steven Chown, Jan Crafford, Jonathan Bloomer & Colin Du Plessis. Other members of Marion 43, 44 and 45 for their assistance with counting, tagging and weighing elephant seals, in particular Johnny Kieser, Ivan Dalglish, Peter Bartlett, Dave Baker, Sampie Ferreira and Deon Muller. Sampie Ferreira, Hendrik Pansegrouw, Francois Roux and André le Cock counted elephant seals and checked flippers for tags for two seasons after my departure from Marion which provided extra data to incorporate into this thesis.

I benefitted from discussions with Drs Neil Fairall, Albert van Jaarsveld, Andrew McKenzie,

Willem Ferguson, Phillip Richardson, Jean-Paul Roux, Professor Anne Rasa, messrs Rob Davies, George Ellison, Chris Willis, Steven Giddings and Mark Anderson. Dr Hector Dott derived the equation used in the estimation of variance around the estimate of age at first pupping in Chapter 4. Dr J Ward Testa helped with the Jolly-Seber population analysis.

Special thanks go to Marthán Bester for his advice, for introducing me to the wonders of Subantarctic Marion, for his friendship and passing on to me his infectious enthusiasm for the "fin footed" ones. Finally, I would like to thank Marion Island itself for showing me how important the simple things in life really are.

LIST OF CONTENTS

LIST OF TABLES PAGE

LIST OF FIGURES PAGE

CHAPTER 1

GENERAL INTRODUCTION

Life history

Southern elephant seals, *Mirounga leonina*, are the largest of the 34 extant species of pinniped (King 1983). Males may reach 5 metres in length and weigh up to 3000 kg, while females rarely exceed 3 metres in length and 500kg in weight (King 1983). Sexual dimorphism is extreme, and in some cases males may reach a weight ten times that of the female (McCann, Fedak & Harwood 1989). Data on longevity are scarce with sightings of branded animals at Macquarie Island suggesting longevity of 23 years in both sexes (Hindell & Little 1988, Hindell 1991). Southern elephant seals spend about 75% of their time at sea, and the remainder on land during two haulout periods. Immature individuals haulout during the summer to moult and then again for a short period during winter, a haulout for which no specific function has been ascribed (Carrick, Csordas, Ingham & Keith 1962a, Condy 1979). Mature animals haulout to breed during the early part of the summer and then again to moult at the end of the summer (Laws 1956a, Carrick *et al.* 1962a, Carrick, Csordas & Ingham 1962b, Condy 1979). The timing of these haulout periods is illustrated in Figure 1.

Identification of stocks

Southern elephant seals have a circumpolar distribution with the major breeding colonies situated on islands in latitudinal proximity to the Antarctic Convergence (Laws 1956a, Carrick *et al.* 1962a) (Figure 2). The world population, which numbers around 700,000 (Table 1) is divided into three so called 'stocks' (Laws 1960). These stocks are centred around South Georgia (islands in the South Atlantic and the Valdes peninsula, Argentina), Macquarie Island (islands in the Southern Pacific Ocean) and Iles Kerguelen (islands within the Southern Indian Ocean). These stocks are apparently discrete, with little or no gene flow between them (Gales, Adams & Burton 1989). Differences in skull characteristics (Lydekker 1909 in Gales *et al.* 1989), rate of pups (Bryden 1968a) and adult morphometrics (Bryden 1968b) have been

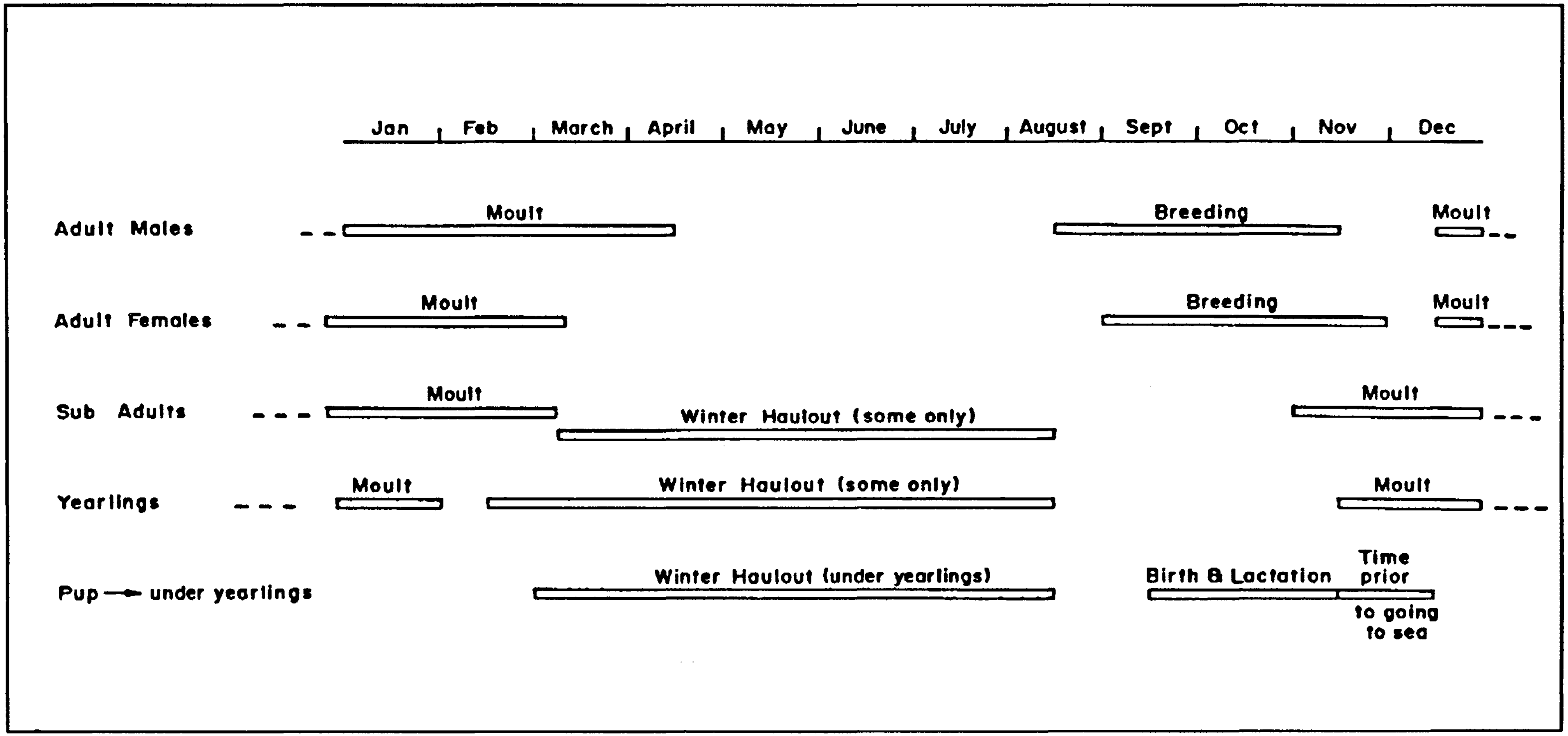

Figure 1. Schematic presentation of the annual cycle of southern elephant seals at Marion Island. Bars represent the period over which specific sex and age classes occur on the island (Data from Condy 1979 and present study).

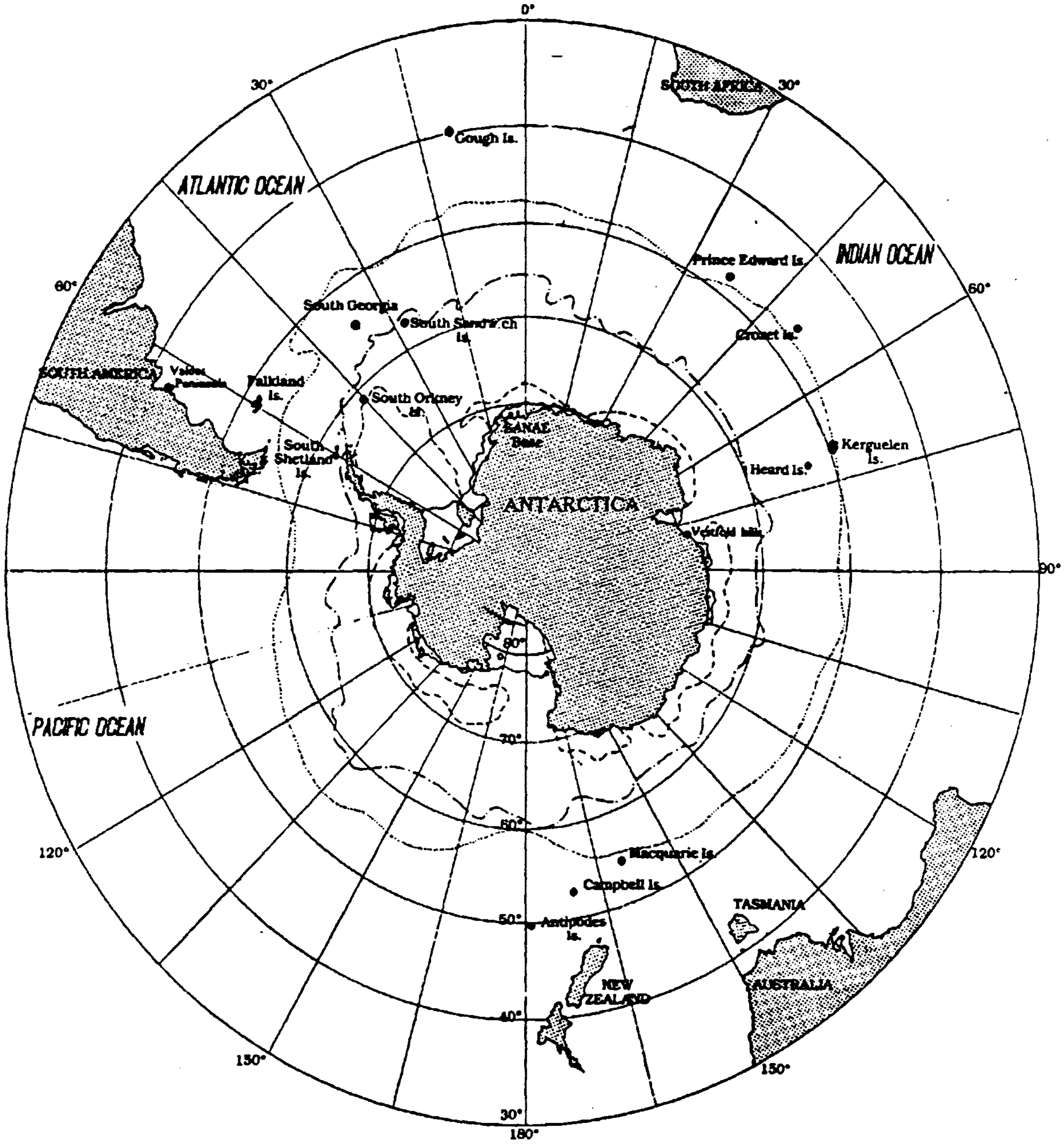

Figure 2. Map of the southern oceans showing the location of islands on which southern elephant seals breed, as well as the position of the Antarctic Convergence (·······), and mean winter (-·-) and summer (- -) pack ice limits (Modified from Smithers 1983).

Table 1. Estimates of the size and status of southern elephant seal populations within the three recognised stocks of the species.

Stock	Locality	Year of pup production estimate	Pup production	Annual rate of change in numbers	Period over which numerical change occurred	Numerical status	Source
South Georgia	South Georgia	1985	102000	0,0	1951-1985	Stable	McCann & Rothery (1985)
	South Orkney Islands	1985	<100	?	1948-1985	Uncertain	McCann (1985)
	Falkland Islands	1960	≈1000	?		Uncertain	Laws (1960)
	Gough Island	1989	28	0,0	1973-1989	Stable	Bester (1990a)
	King George Island	1987	708	-1,9	1980-1987	Declining	Vergani *et al.* (1987)
	Nelson Island	1985	106	?		Uncertain	Vergani *et al.* (1987)
	Valdes Peninsula	1990	9636	+3,2	1982-1990	Increasing	SCAR (1991)
Iles Kerguelen	Marion Island	1989	585	-4,8	1951-1989	Declining	Present study
	Heard Island	1985	13000	-2,4	1949-1985	Declining	Burton (1986)
	Iles Kerguelen	1977	45000	-4,1	1970-1977	Declining	Van Aarde (1980a)
	Iles Crozet	1976	≈3000	-5,7	1966-1976	Declining	Barrat & Mougin (1978)
Macquarie Island	Macquarie Island	1990	22068	-1,6	1959-1990	Declining	Hindell & Burton (1987), SCAR (1991)
	Campbell Island	1986	5	-8,6	1947-1986	Declining	Taylor & Taylor (1989)
	Antipodes Island	1978	113	?		Uncertain	Taylor & Taylor (1989)
World total			≈197000				

ascribed to these stocks.

Both male and female southern elephant seals have been shown to be philopatric (Nicholls 1970), and data from mark-recapture studies show little if any mixing of the populations (Ling & Bryden 1981, Bester 1989). Limited overlap of the Macquarie Island and Iles Kerguelen/Heard Island populations occurs at the Windmill Islands, Antarctica (Gales *et al.* 1989), however, this overlap occurs predominantly during the annual moult of sub-adult males. A small number of cows have given birth at this site (Murray 1981), however, no mature bulls have been recorded in the area during this period and the potential for a flow of genes between the two populations seems minimal.

Population declines and possible causes

The large seasonal concentrations of southern elephant seals on islands, especially during the breeding period, resulted in the development of a large sealing industry at all the sites (McCann 1980, Hindell & Burton 1988a). By the early part of the last century these sealing operations had so depleted the populations that they were reduced to uneconomic levels through most of their range (Busch 1985, Hindell & Burton 1988a). Sealing ceased in the early 1900's, except at South Georgia where a well organised annual catch continued until 1964 (McCann 1980), and numbers at sites other than South Georgia were thought to have recovered to their original levels by the 1950's (Carrick *et al.* 1962a). Since then however, there have been reports of declining populations at islands forming the Kerguelen and Macquarie Island stocks (Barrat & Mougin 1978, Condy 1978, Van Aarde 1980a, Skinner & Van Aarde 1983, Burton 1986, Hindell & Burton 1987, Taylor & Taylor 1989), while those of the South Georgia stock, or more specifically South Georgia itself, have remained stable (McCann & Rothery 1988). Recent reports (SCAR 1991) also suggest a stabilisation of the Kerguelen population between 1984 and 1989.

Numerous factors have been implicated in the declines, but the widespread nature and the similarity in the rates of decline between sub-populations suggests a common cause (Condy 1984). Current hypotheses pertaining to the causes of the declines can be divided into those acting during the terrestrial phase (intrinsic factors) and those acting while the animals are at sea (extrinsic factors).

At Iles Kerguelen the population decline reported by Van Aarde (1980a) has been suggested to be part of a long term fluctuation in breeding population size related to density. Van Aarde (1980a) showed that the degree of long term fluctuation in cow numbers increased with density. Slight increases in cow density on densely inhabited coastlines resulted in large increases in harem size and in decreasing numbers of harems (Van Aarde 1980b). Here a density dependent mechanism has been identified which acts primarily through pup mortality as a function of density of bulls active in and around harems, bull numbers being positively correlated with cow numbers (Bester & Lenglart 1982).

At Marion Island the very low density breeding colonies rule out any intraspecific density dependent effects during their terrestrial phase. Here the decrease in cow numbers and decline of annual pup crop have been ascribed to a possible malfunction of a mechanism ensuring pregnancy due to a scarcity of bulls (Skinner & Van Aarde 1983).

Pelagic phase hypotheses, those involving extrinsic factors, relate to predation and food availability. Killer whales, *Orcinus orca*, are abundant around Marion Island and Ile de la Possession and show regular, annual, visitation patterns which closely parallel those of breeding elephant seals (Condy, Van Aarde & Bester 1978). This may have contributed to the decline of elephant seals at these sites (Barratt & Mougin 1978, Condy 1978), but these predators are infrequent visitors at Iles Kerguelen, Heard Island & Macquarie Islands, and other factors, for example food availability, must be involved there.

The diet of the southern elephant seal is poorly understood, and thus comment on the effects of food availability are speculative at this stage. Laws (1956a, 1977, 1984) concluded that they consume approximately 75% squid and 25% fish, feeding mainly on fish inshore and cephalopods elsewhere.

Food availability can be affected by biological and non-biological factors, such as climatic effects. Sea and air temperatures at Marion Island rose by 0,064°C and 0,048°C per year respectively between 1968 and 1985 and declined at 0,255°C and 0,180°C per year after 1985

(Smith & Steenkamp 1990). Jacka, Christou & Cook (1984) noted an overall warming of the Southern Ocean which will effect productivity (Lamb 1977). An example of this was given by Lamb (1977) who reported that North Atlantic cod and herring grounds changed enormously due to changes in ocean temperatures. Biological factors may operate through competition, and it is possible that food items of prey species of the southern elephant seal are being removed low down the food chain and thus depleting the seal's prey, or that other species are in direct competition with the seal for it's prey.

The large, rapidly expanding, Subantarctic fur seal, *Arctocephalus tropicalis*, population at Marion Island (Kerley 1983, Wilkinson & Bester 1990a), which feeds on fish, cephalopods and euphausiids (Rand 1956, Condy 1981) may be competing with the elephant seals, especially the newly-independent underyearlings in the local oceanic zone. At Iles Kerguelen and Heard Island, the Subantarctic fur seal is replaced by the Antarctic fur seal, *A. gazella*, a krill consumer (Doidge & Croxall 1985), which is unlikely to be in competition with elephant seals. However, an important commercial fishery has developed in this area (Everson 1977) which may be competing directly. Van Aarde (1980a) suggested that the decline at Kerguelen between 1970 and 1977 was the result of competition between the elephant seals and the Soviet fishing fleet operating around the archipelago. As mentioned above, the dietary requirements of the elephant seal are poorly known and therefore further speculation is of limited value.

The most recent explanation for the observed declines is that populations are declining to their pre-sealing levels, after having risen to abnormally high levels with the end of commercial sealing at the beginning of the twentieth century (Hindell 1991)

Reproductive success and maternal investment

One aspect of the southern elephant seal's life cycle where a weakness may contribute to the decline is that of reproduction. The hypothesis put forward by Skinner & Van Aarde (1983) suggesting that the numbers of bulls at Marion Island were insufficient to fertilise all the breeding cows, focused attention on the process of pup production in southern elephant seals at Marion Island. The successful production, and rearing, of offspring to independence provides an indication of the evolutionary value of an individual female (Wittenberger 1981). How successful the female is, has been seen in other seals to be influenced by such variables as her age, size and social status (Reiter, Panken & Le Boeuf 1981, McCann 1982, Huber 1987, Ribic 1988).

The contribution of the female to future generations can also be influenced by what sex offspring she produces. Variance in reproductive success among males in polygynous species is usually greater than amongst females (see Clutton-Brock 1988). In both southern elephant seals and the congeneric northern elephant seal, *M. angustirostris,* a male that is successful in mating for just one season can father more offspring than a female can in her entire lifetime (Le Boeuf & Reiter 1988), and thus can produce more grandoffspring for its own mother than a female could. However, few males will ever get the chance to breed, while virtually all females that reach maturity will produce offspring (Le Boeuf & Reiter 1988). Theoretically there is then a conflict in which sex to produce.

Fisher (1930) showed that natural selection favours parents that produce a 1:1 sex ratio where the costs of producing males and females are the same. If one sex is more costly to produce than the other then the sex ratio should be biased toward the cheaper sex by the end of the period of parental investment. Trivers & Willard (1973) modified this theory to show that under certain well defined conditions, natural selection favours deviations from a 1:1 sex ratio at conception, and that these deviations tend to cancel out in the local breeding population.

Where reproductive success varies more widely among the offspring of one sex, and is influenced by parental investment, parents should invest in that sex. Adult females in the best condition should produce the healthiest offspring and be able to provide a greater level of parental investment than females in poor condition. Thus the healthiest females could increase their numbers of grandoffspring by investing in sons (assuming that maternal investment influences the reproductive success of sons more than daughters), as opposed to daughters. Conversely, females in poor condition would do better to produce daughters than sons. Sons born to females in poor condition, that are only able to invest a small amount in their offspring, will be at a competitive disadvantage, while it would have little affect on daughters.

Motivated by the apparent lack of significant departures from the 1:1 sex ratio in mammals, Maynard Smith (1980) offered another model for the evolution of sexual investment in the higher vertebrates. He suggested that the primary sex ratio is fixed at unity, parents can recognize the sex of individual offspring, and the returns (in offspring fitness) are different for the two sexes. In terms of the above it would be evolutionarily stable to invest differently in sons and daughters. In particular:

- if for a given investment the probability of survival is lower for one sex, selection favours greater investment in that sex.

- if one sex has a frequency-dependent component of fitness, such that individuals receiving a greater-than-average investment are fitter, selection favours greater investment in that sex.

- if the sex of an individual can be recognized after an investment *d* it may be evolutionarily stable to invest only in some fraction *r* of the more expensive sex, and to abandon a fraction *(1-r)*. However, such behaviour can evolve only if *d* is a small fraction of the total investment required per offspring.

Objectives of the study

The decline in the southern elephant seal population at Marion Island and the speculation on it's cause(s) was the driving force behind the initiation of this research project. There are three aims which will be considered in this dissertation.

1: To determine the present status of the southern elephant seal population at Marion Island and determine demographic parameters previously unknown for this population.

2: To examine the factors influencing pup production and subsequent reproductive success of female southern elephant seals at Marion Island.

3: To investigate parental investment in this species, and it's applicability to current theories on reproductive investment.

It should be noted that reproductive success here refers to success/failure to raise a pup to the age of weaning.

The following key questions will be asked as a means of addressing the aims above.

Population biology

1. What is the present size of the Marion Island population and how has it changed since research activities on the population began?

2. What are the age specific survival rates of the population?

3. What are the age specific fecundity rates of the population?

4. At what age do cows become sexually mature?

5. What is the net reproductive rate (R_o) of the population?

Reproductive success

1. Is reproductive success related to age, experience, dominance and frequency of copulation?

2. Is reproductive success affected by the time (date) of birth, weaning and oestrus?

3. Is reproductive success affected by a cumulative number of copulations before fertilization will take place?

4. Is reproductive success affected by the sex of the pup?

Parental investment and sex allocation

1. Do levels of parental investment by the cow differ between sexes?

2. Is the sex at birth affected by maternal social status/age?

3. Is the sex at birth affected by previous reproductive experience (i.e. sex of previous pup)?

4. Is sex at birth affected by time (date) of conception?

5. Does the pattern of parental investment seen in southern elephant seals fit with current theories on the subject?

CHAPTER 2

STUDY AREA

Climate

Marion Island (46°54'S,37°45'E) (Figure 3) is situated within the Prince Edward Island group approximately 2300 kilometres south east of Cape Town, South Africa. Systematic meteorological observations have been made since the island was annexed from Britain in 1948 (Marsh 1948). The climate is basically marine with modifications due to the topography of the island itself, and the main features are:

- strong, predominantly westerly winds, with the highest velocities during the day and gales most frequent in the winter.

- relatively low air temperatures, with a mean annual temperature of 5,5°C, with little annual or diurnal variation.

- abundant precipitation in the form of rain, snow or graupel (ice-rain) with a mean annual precipitation of 2576 mm.

- high relative humidity, with little annual or diurnal variation from 80%.

- a high degree of cloudiness, with only 20 - 33% of the possible amount of sunshine reaching the island surface. Daylight duration is 15 h in summer and 9 h in winter (Schulze 1971).

Sea surface temperatures measured at the station are low (annual mean = 5,0°C) with little annual variation. Mean sea surface temperatures are higher than the mean air temperatures during the winter months, from May to September (Schulze 1971).

Recent observations show that the sea and air temperatures at Marion Island have risen (Smith

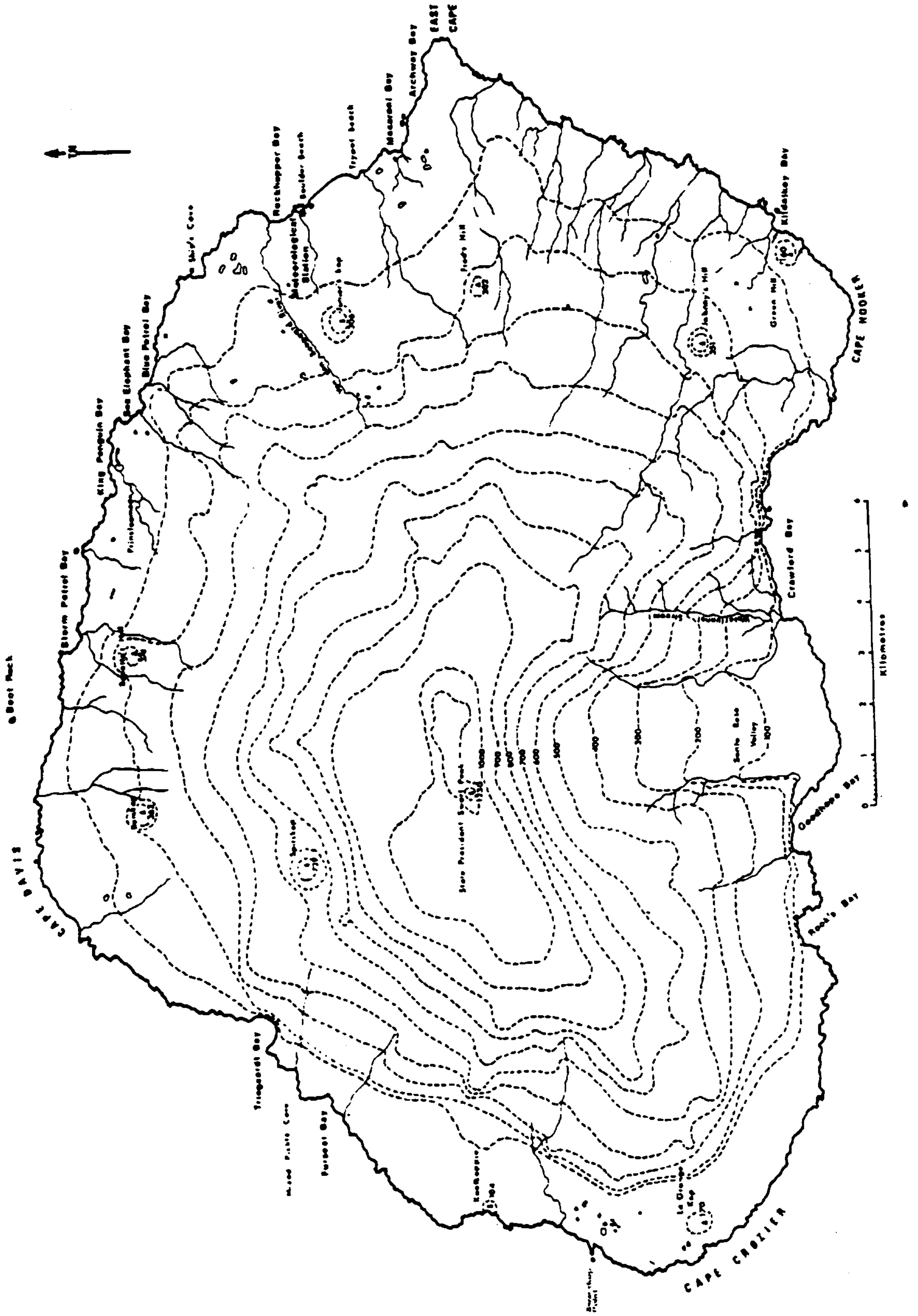

Figure 3. Topographical map of Marion Island, with contour intervals in metres (from Condy 1977).

& Steenkamp 1990) which corroborates data obtained for Heard Island over the period between the 1950's and 1980's (Jacka *et al.* 1984).

An important feature in the same oceanic region as the Prince Edward Islands is the Antarctic Convergence, the boundary between the cold, dense, Antarctic surface water of relatively low salinity and the warmer, less dense Subantarctic water with higher salinity. This boundary where the denser Antarctic water sinks below the warmer Subantarctic water is characterized by a sharp change in surface temperature, aswell as salinity. Schulze (1971) reported it's mean position in this region as 50°S.

Topography

The island is 290 km^2 in area, roughly oval in shape, with a maximum altitude of 1230 metres (State President Swart Peak). It measures 24 km from east to west and 17 km from north to south, and has a circumference of approximately 90 km.

Verwoerd (1971) reports that the island has several distinct physiographic regions; a central highland, an island slope divided into relatively high and relatively low-lying areas and a coastal plane separated in places from the island slope by an escarpment.

Highly irregular coastal configuration is a characteristic of areas formed by the more recent volcanic activity. This coastline is generally composed of sea pounded cliffs up to 15 m high, which comprise the majority of the island's coast. On the stretches of coast where the older substrate meets the sea the topography is different with higher cliffs of around 30 m and escarpments of hundreds of metres. Initial irregularities in these areas have been smoothed over time to produce wide, open bays with stony beaches along the base of the cliffs.

Beach topography

The exposed west coast on Marion Island is characterized by beaches of extremely irregular nature. The constant pounding of the sea has resulted in all but the largest of boulders being removed leaving rough beaches. Where some protection was afforded by the presence of a small cove the beaches have much less rugged surfaces. One such beach, Mixed Pickle Cove, is situated on the exposed west coast but the protection afforded to it by the small cove has resulted in the retention of many smaller boulders and given it a much less rugged appearance than exposed beaches in the area.

On the eastern side of the island, away from the prevailing wind direction, most beaches are made up of small rounded rocks, stones and pebbles. These beaches have a flat, regular appearance but are prone to change during the year as a result of wave action during heavy seas. Many of the beaches on this section of the island occur where streams and rivers enter the sea. At these beaches seals can gain access to inland moulting sites along the drainage lines.

Trypot Beach

Trypot beach (see Figure 3) is situated in the first cove to the south (1,5 km) of the meterological station on the northeast coast of Marion Island. It is a typical drainage line beach (Condy 1977) with a flat and even profile. It is composed predominantly of pebbles and small boulders which contribute to it's flat and even nature. An adjacent vegetated area is an important southern elephant seal moulting site after the breeding season. The beach area is utilised by breeding adults and by immatures during the period of moult and winter resting haulout.

CHAPTER 3

THE TIMING OF EVENTS WITHIN THE REPRODUCTIVE CYCLE OF SOUTHERN ELEPHANT SEALS AT MARION ISLAND

Introduction

Given that this dissertation is aimed primarily at the events occurring during the breeding component of the annual cycle of the southern elephant seal, it is important to have an understanding of the timing of these events.

Southern elephant seals breed on Subantarctic islands during the summer months (Laws 1956a, Carrick *et al.* 1962b). The first pregnant cows haulout on the breeding beaches between mid-August and mid-September, with the timing being dependant on the latitude of the breeding site (Le Boeuf & Petrinovich 1974, Condy 1979, McCann 1982). Their stay onshore, which lasts from 28 to 31 days (Laws 1956a, Carrick *et al.* 1962b, Condy 1979, Van Aarde 1980a), can be divided into two components, a *pre-partum* and a *post-partum* period. The period prior to the birth of the single black pup averages 5 to 7 days (Laws 1956a, Carrick *et al.* 1962b, Condy 1979, Van Aarde 1980a, McCann 1982). Between 17 and 22 days after parturition the cow comes into oestrus (Laws 1956a, Carrick *et al.* 1962b, Van Aarde 1980a) and is mated, usually, by the bull controlling the harem, often several times (Laws 1956a, Carrick *et al.* 1962b, McCann 1981a). The pup is weaned 19 to 25 days after birth (Laws 1956a, Carrick *et al.* 1962b, Condy 1980, Van Aarde 1980a, McCann 1982) and the cow usually departs immediately, or shortly after weaning the pup.

The timing of the breeding season is known to differ between major island populations, but within a population there is a marked synchrony from year to year (Carrick *et al.* 1962a, Barrat & Mougin 1978, Pascal 1979, Hindell & Burton 1988b). A temporal shift in the season is perhaps best indicated by the date on which the peak number of cows are ashore. On this basis the breeding colonies can be split into three groups. On islands of the Macquarie (Campbell Island and Macquarie Island) and Kerguelen (Heard Island, Iles Kerguelen, Ile de la Possession and Marion Island) stocks, cow numbers peak on the 15th and 16th October

(Sorensen 1950, Angot 1954, Barrat & Mougin 1978, Condy 1979, Van Aarde 1980a, Skinner & Van Aarde 1983, Hindell & Burton 1988b).

On South Georgia, Signy Island and King George Island (South Georgia stock), cow numbers peak between the 22nd and 25th October (Laws 1956a, McCann 1980, McCann 1985), while on Peninsula Valdes in Argentina (South Georgia stock) the peak occurs between the 25th September and 1st October (Le Boeuf & Petrinovich 1974).

The length of the breeding season is best described by the distribution of births, as arrival and departure dates of bull and cow components can vary greatly, with changes in population size and climatic conditions, and may overly extend or shorten the period under consideration (at Signy Island in 1948 the arrival of bulls was delayed by ten days due to the presence of fast ice, Laws 1956a). On both Macquarie Island and South Georgia 80% of births occurred within a three week period (Carrick *et al.* 1962b, McCann 1982), suggesting that the length of the breeding season is similar on both islands.

This chapter aims at 1) comparing the timing and duration of the breeding season at Marion Island with other sites as well as previous values obtained in the 1970's (Condy 1979) at Marion Island. 2) documenting the timing of events within the reproductive cycle of cows at Marion Island, and looking at how variables such as maternal age, size and social status affect the timing of these events.

Methods

Observational procedure

Observations were made at the study colony from the day the first cow arrived until the last cow departed, from dawn to dusk in the austral summers of 1986, 1987 and 1988. Events occurring at night were recorded during the following observation period. All cows were bleach marked to facilitate individual identification (see Chapter 5).

Dates of haulout, birth, oestrus, first copulation, weaning and departure were recorded for each female. The determination of cow size, age and social status have been described elsewhere (see Appendix I).

The first day a cow was observed at the study site, either on the beach or on the surrounding vegetated area, was recorded as her date of haulout, while the cow's date of oestrus was recorded as the first day on which she assumed the lordotic posture when held by a bull. The term lordosis is used following the description of McCann (1981b) in which receptive cows were seen to be *"passive, often quiet and would spread their hind flippers while elevating the perineum in the lordotic posture"*. Copulations were recorded as they occurred, and the first occasion noted for each cow.

The date of weaning was taken as that day on which the cow and her pup became permanently separated. Date of departure was that day on which the cow departed from the breeding beach or from the surrounding vegetated area. If she moved from the beach to the vegetation she was regarded as still present, as she was still accessible to the bulls at the site.

The duration of the period at sea following lactation was calculated for those cows that were seen ashore during the moulting period, provided they had not yet commenced their moult, as the interval between the date the cow departed from the beach and the assumed date on which she returned to moult. At the time of arrival for the moult, beaches were searched on a 7 to 10 day cycle, therefore if a cow was seen during a census she was assumed to have hauled out midway between the date she was resighted at the beach and the date of the previous visit to that beach.

Results

Duration of the breeding season

Daily counts of cows at Trypot Beach for the years 1986, 1987 and 1988 are shown in Figure 4. The dates of first arrival, peak numbers, last departures of cows and pups, along with the period during which 80% of the pups were born and the interval between arrival of the first cow and departure of the last are shown in Table 2. Comparative values for the same site in

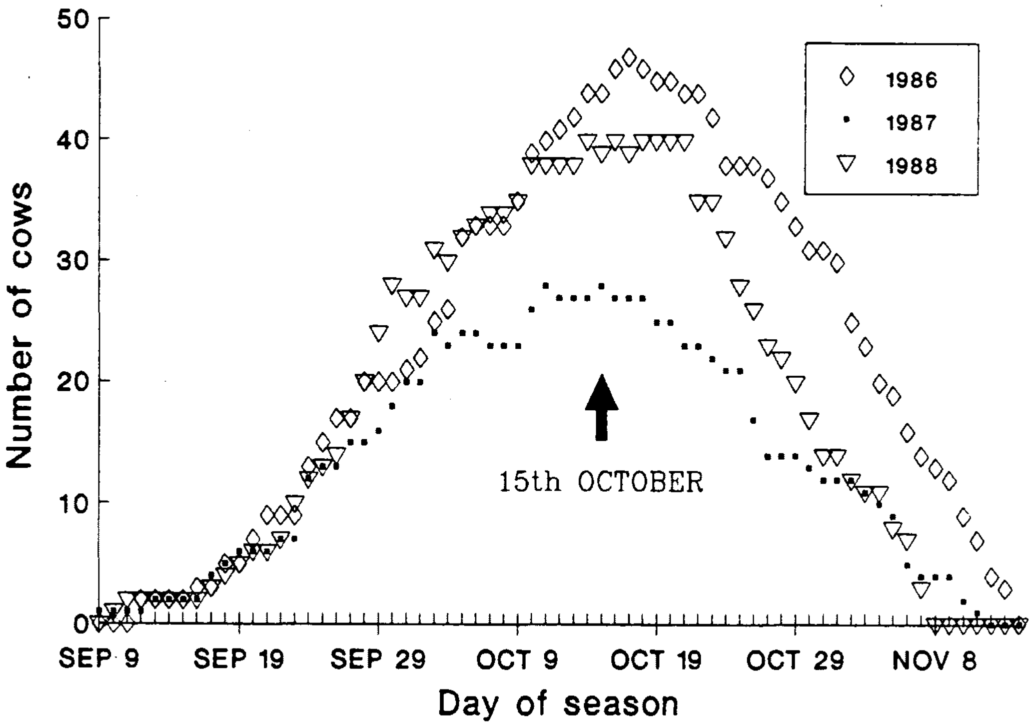

Figure 4. Daily counts of southern elephant seal cows hauled out at Trypot beach, Marion Island during the breeding seasons of 1986, 1987 and 1988. The mean date of peak haulout (15 October) is indicated by a vertical arrow.

Table 2. Breeding chronology of southern elephant seals at Trypot beach, Marion Island from 1986 to 1988. First and last dates of cow arrival, first and last dates of birth, peaks in cow and pup numbers, dates of final departure from the beach by cows and pups, period during which 80% of pups were born (in days), and the number of days from the arival of the first cow until the departure of the last from the study site are shown. Comparative values for the same site from 1973 to 1976 (and 1977*) are also presented. S.D. refers to one standard deviation of the mean.

Parameter	Year					Comparative value (Condy 1979)	
	1986	1987	1988	Mean	S.D.	Mean	S.D.
First cow arrival	12 Sept	9 Sept	10 Sept	10 Sept	1	18 Sept*	5
First birth	15 Sept	16 Sept	17 Sept	16 Sept	1	24 Sept*	5
Last cow arrival	21 Oct	20 Oct	27 Oct	23 Oct	4		
Last birth	25 Oct	24 Oct	27 Oct	25 Oct	2		
Peak in cow numbers	17 Oct	15 Oct	14 Oct	15 Oct	1	17 Oct	5
Peak in pup numbers	25 Oct	24 Oct	21 Oct	23 Oct	2	16 Nov	3
Last cow departure	14 Nov	12 Nov	9 Nov	12 Nov	2	11 Nov	3
Last pup departure	26 Dec	18 Dec	21 Dec	22 Dec	4	23 Dec	3
Number of days in which 80% of pups were born	25	27	21	24,3	3,1		
Number of days from arrival of first arrival to last departure (cows)	63	61	65	63,0	2,0		

the mid 1970's are also provided (Condy 1979).

Timing of events within the reproductive cycle.

The dates on which events occurred, in the present study, as well as the time intervals between events did not differ between seasons (ANOVA) and therefore the results for different seasons were combined. Mean dates of events within the cycle along with mean values for intervals between these events are summarized in Table 3.

Table 3. Means, standard deviations (S.D.) and sample sizes (n) of, (a) dates of events within the reproductive cycle, and (b) intervals between these events, for female southern elephant seals at Trypot beach, Marion Island from 1986 to 1988.

Parameter	Mean	S.D. (days)	n
(a) Timing of events			
Date of haulout	2 Oct	10,2	138
Date of birth	7 Oct	9,5	137
Date of oestrus	25 Oct	9,1	134
Date of first copulation	25 Oct	9,3	134
Date of weaning	28 Oct	9,2	123
Date of departure	29 Oct	9,3	138
(b) Intervals between events			
Haulout & birth	4,7	2,0	137
Birth & oestrus	18,4	1,9	133
Birth & weaning	21,4	1,9	123
Birth & departure	21,8	2,3	137
Haulout & departure	26,5	3,2	138
Departure from rookery and return for moult (pelagic period)	62,1	8,2	50

The length of a cow's haulout period was inversely related to the date on which she hauled out (Figure 5). The length of the *pre-partum* period was also inversely related to the date of haulout (Figure 6), while the *post-partum* interval did not change with a change in date of

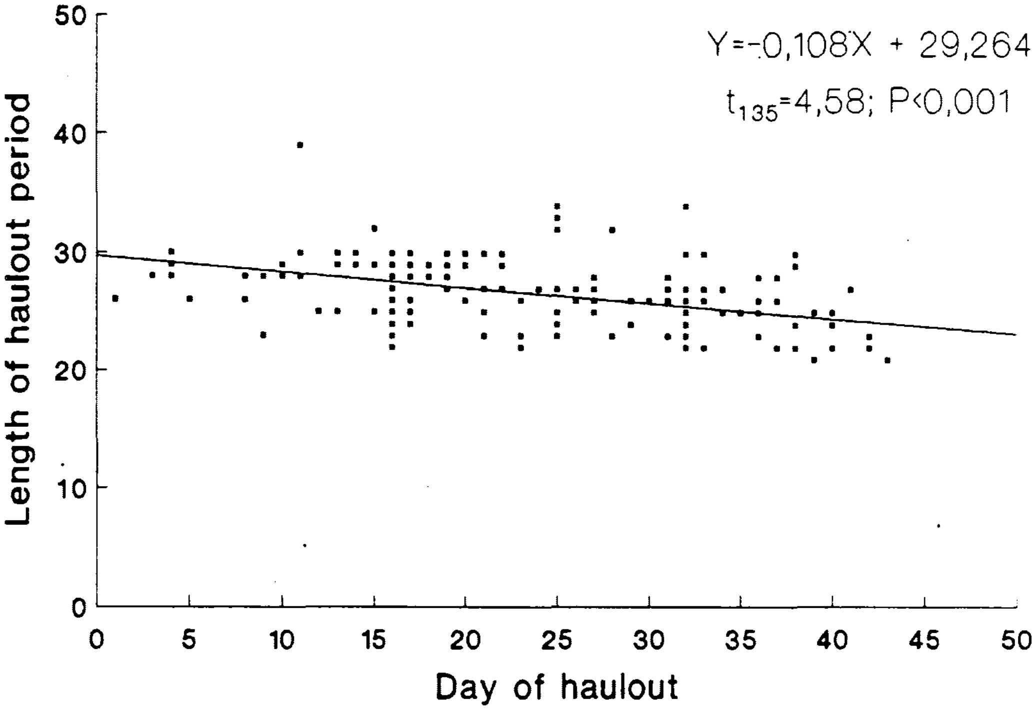

Figure 5. The relationship between date of haulout and the length of haulout period, for breeding purposes, for cows at Trypot beach, Marion Island between 1986 and 1988 (day 1 represents 9 September). The line has been fitted through least squares regression analysis.

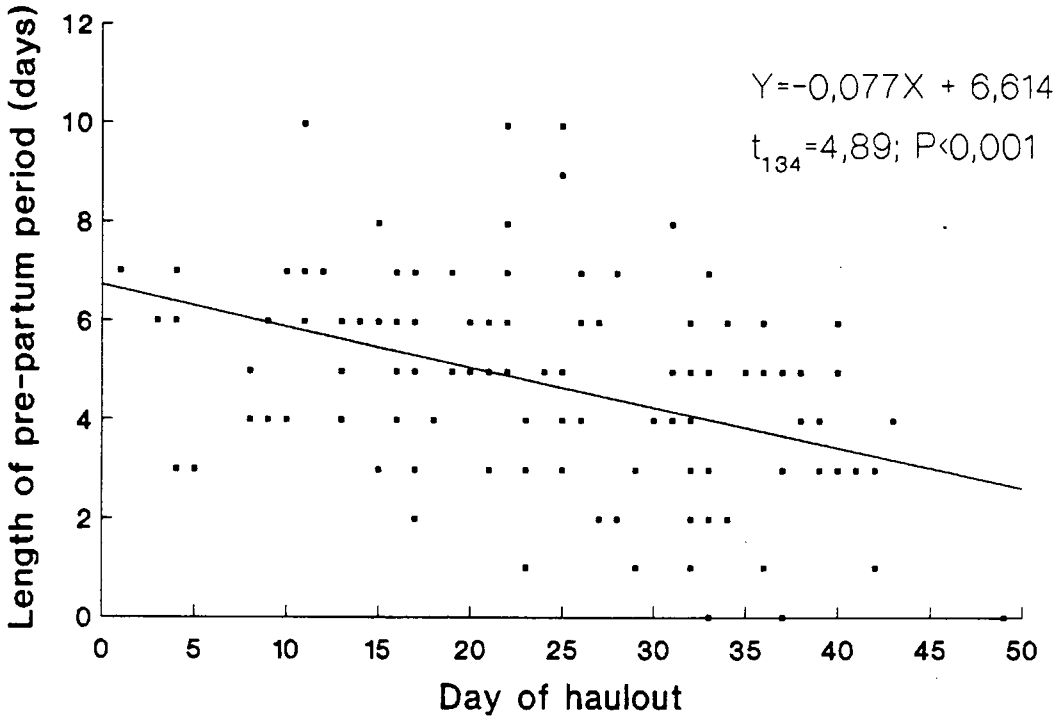

Figure 6. The relationship between date of haulout and the length of the pre-partum (arrival to birth interval) component of the breeding haulout period for cows at Trypot beach, Marion Island between 1986 and 1988 (day 1 represents 9 September). The line has been fitted through least squares regression analysis.

haulout.

The distribution of pelagic periods of cows in the present study are shown in Figure 7. The mean (±1 S.D.) interval spent at sea by the 50 cows was 62,1 ± 8,2 days, mean values for all years were combined as there were no differences between years. The length of time spent at sea was negatively correlated with the duration of breeding haulout (r_{49}=-0,29; $P<0,05$), but not with maternal age, size or social status, or whether a cow successfully reared her pup (Table 4).

Table 4. The duration of the post lactation pelagic period of female southern elephant seals at Marion Island. Comparisons are given for cows of different age, social rank and size, as well as those which reared their pups and those not doing so. Comparisons between age groups were made using ANOVA (Zar 1984), while the other comparisons used Mann-Whitney tests (Zar 1984). S.D. and n refer to standard deviation and sample size respectively.

	Duration of post lactation pelagic phase			Statistical test results	
	Mean	S.D.	n	Test result	P value
Age class 1	64,5	2,6	8	$F_{2,47}$= 0,535	>0,05
Age class 2	61,0	8,9	21		
Age class 3	62,2	8,9	24		
Small	62,8	5,1	12	z=1,91	>0,05
Large	59,2	10,5	12		
Low rank	63,9	8,7	22	z=1,28	>0,05
High rank	60,3	7,7	27		
Weaned pup	61,9	8,1	47	z=0,45	>0,05
Did not wean pup	63,3	11,6	3		

The effect of maternal variables on timing of events

The length of time that a cow spent ashore during the breeding haulout period did not differ for cows that weaned their pups and those whose pups died before weaning (t_{135}=0,237; $P>0,05$). Mean dates of occurrence of the six events within the reproductive cycle, as well

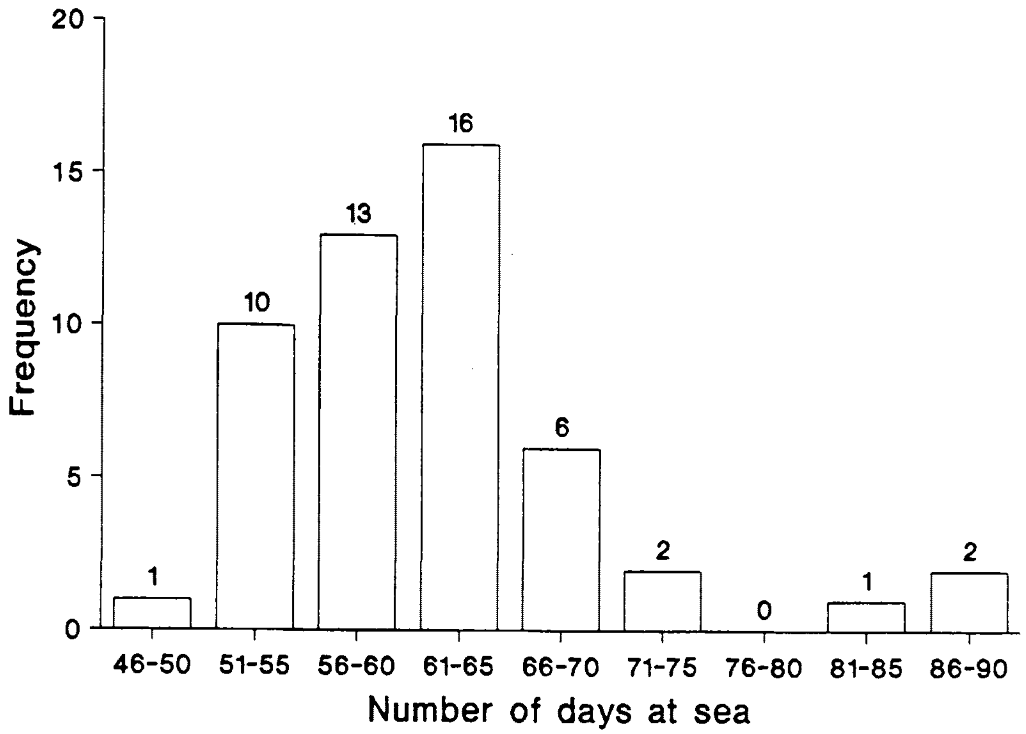

Figure 7. The number of days spent at sea between the day of departure at the end of the breeding season, and the arrival for the annual moult of 50 southern elephant seal females at Trypot beach, Marion Island between 1986 and 1988.

as mean values for *pre-* and *post-partum* periods did not differ between cows of different sizes, ages and social statuses (Table 5).

Discussion

Timing and duration of the breeding season

The length of various components of the reproductive cycle of the southern elephant seal are essentially similar at all study sites for which data are available (Table 6). The peak in cow numbers on October 15th is similar to that reported for this population during the 1970's and early 1980's (Condy 1979, Skinner & Van Aarde 1983) and is similar to other islands of the Iles Kerguelen (Angot 1954, Barrat & Mougin 1978, Van Aarde 1980a) and Macquarie Island (Sorensen 1950, Hindell & Burton 1988b) stocks of southern elephant seals. The earlier dates of first arrival for cows and pups found in the present study, compared with those of Condy (1979) may have resulted from the weekly (previous study) as opposed to daily (present study) counts. However, the dates of last departure of cows and pups were similar to those seen in the 1970's (Condy 1979).

The later peak in pup numbers found by Condy (1979) is curious when the biology of the species is considered. Numbers of pups (unweaned, weaned and dead) at a beach necessarily increase to a peak value, then remain constant until these animals begin to disperse from their natal beaches (Condy 1979, Panagis 1981, Wilkinson & Bester 1990b). The earliest recorded movement between beaches at Marion Island is 25 October, with no other recorded changes prior to 5 November (Wilkinson & Bester 1990b). This means that throughout October it can confidently be assumed that pups on a given beach were born there. During November it is possible that pup numbers at a site may increase above October levels but this will be a consequence of immigration from other (neighbouring) sites not matched by any departures from the particular site. The peak numbers of pups must coincide with the date of the last birth, providing that the counts include unweaned, weaned and dead pups. Given the dates of last birth in the present study pup numbers must reach a peak during October. If daily checks are not made at a beach, and pups are not individually identifiable, peak numbers will be influenced by the immigration of pups from other beaches. It is therefore likely that this is

Table 5. Mean (± 1 S.D. of the mean, with sample sizes in parentheses) values for date of haulout, oestrus, first copulation, weaning, departure and intervals between haulout and birth, and birth and departure for southern elephant seal cows of different age, social rank, size at Trypot Beach, Marion Island between 1986 and 1988.

Maternal character	Date of Haulout	Date of parturition	Date of oestrus	Date of first copulation	Date of weaning	Date of departure	Haulout to birth interval	Birth to departure interval
Age 1	30 Sept ± 11,8 (24)	5 Oct ± 10,8 (23)	22 Oct ± 10,2 (22)	22 Oct ± 10,3 (22)	24 Oct ± 9,7 (19)	26 Oct ± 10,1 (24)	4,5 ± 2,2 (23)	21,8 ± 3,0 (23)
Age 2	4 Oct ± 9,3 (69)	8 Oct ± 8,5 (69)	27 Oct ± 8,1 (67)	27 Oct ± 8,0 (67)	30 Oct ± 8,2 (61)	30 Oct ± 8,4 (69)	4,4 ± 1,8 (69)	22,0 ± 2,3 (69)
Age 3	2 Oct ± 10,7 (44)	7 Oct ± 10,4 (44)	25 Oct ± 9,8 (44)	25 Oct ± 10,5 (44)	28 Oct ± 10,1 (42)	29 Oct ± 10,2 (44)	5,2 ± 2,1 (44)	21,6 ± 1,8 (44)
Small	28 Sept ± 8,8 (30)	3 Oct ± 8,1 (30)	22 Oct ± 7,6 (28)	22 Oct ± 7,5 (28)	25 Oct ± 8,1 (28)	25 Oct ± 7,9 (30)	5,1 ± 1,8 (30)	21,7 ± 2,1 (30)
Large	2 Oct ± 11,2 (30)	7 Oct ± 11,8 (30)	26 Oct ± 11,2 (30)	25 Oct ± 11,7 (30)	29 Oct ± 11,4 (29)	29 Oct ± 11,4 (30)	4,9 ± 1,9 (30)	22,2 ± 1,9 (30)
Low rank	3 Oct ± 10,0 (69)	7 Oct ± 9,1 (67)	25 Oct ± 8,1 (65)	25 Oct ± 8,1 (65)	29 Oct ± 8,4 (58)	29 Oct ± 8,8 (67)	4,4 ± 2,0 (67)	21,8 ± 2,6 (67)
High rank	2 Oct ± 10,5 (69)	7 Oct ± 10,1 (69)	26 Oct ± 9,8 (68)	26 Oct ± 10,3 (68)	30 Oct ± 10,0 (65)	29 Oct ± 9,9 (69)	5,0 ± 2,0 (69)	21,9 ± 1,9 (69)

Table 6. Summary of known data on the timing of events within the reproductive cycle of the southern elephant seal. Figures in parentheses, separated by hyphens indicate the range of values quoted, values after the ± sign are standard deviations of the mean, while the lone number, or that following the period refers to sample size.

Study site	Haulout to birth (days)	Birth to 1st copulation	Birth to weaning (days)	Birth to oestrus	Haulout to departure	Reference
Heard Island	3 - 5	End of lactation	3 weeks			Carrick & Ingham 1960
Macquarie Island	$4,8^{a}$ (67)	Few days before or immediately prior to weaning	21,7 (18-27,39)	3rd week of lactation	28 days	Carrick *et al.* 1962b
	$5,9^{b}$ (1-16,18)					
	$4,3^{c}$ (2-15,24)					
	$4,0^{d}$ (2-7,15)					
Marion Island	$6,1\pm4,3$ $(18)^{*}$		$22,5\pm3,5^{**}$ (18^{e})		28,6 days^{**}	Condy 1979^{*}
			$24,2\pm2,3^{**}$ (10^{f})			Condy 1980^{**}
Iles Crozet	7,0 (4-8)		23 (21-25)			Barrat & Mougin 1978
Iles Kerguelen	4 - 8		22,4±2,0 (12)	17-22 days	28-30 days	Van Aarde 1980a
	4 - 6	21 days				Angot 1954
South Georgia	$6,4\pm2,2^{g}$ (67)		$25,5\pm4,4^{h}$ (4)			McCann 1982
			$23,3\pm1,3^{i}$ (8)			
			$24,0^{j}$ (12)			
	8		23 (20-27)	18 days	31 days	Laws 1956a
Signy Island	5 (1-13,45)		19 (13-24)		28 days	Laws 1956a

a=cows aged 4-8 years; b=Primiparous 4 year old cows; c=Six year old cows; d=Eight year old cows; e=Mother-pup pairs at disturbed site; f=Mother-pup pairs at undisturbed site; g=67 of the first 130 cows arriving at the beach; h=Primiparous mothers; i=Multiparous mothers; j=Combined results of h & i.

the reason that Condy (1979) reported a peak in November.

The spread of births is similar to that previously recorded in this species (Carrick *et al.* 1962b, McCann 1985) with 80% occurring in three weeks, which implies similarities in the duration of the breeding season at different sites. Comment on any possible change in the length of the breeding season at Marion Island, between the 1970's and late 1980's is not possible using this method as the relevant data are not given by Condy (1979). However, based on periods during which cows were hauled out on the beaches in the two studies, it would seem that there has been no change.

Timing of events within the reproductive cycle

The synchrony in haulout dates between years in this and previous studies (Condy 1979) indicates the presence of a precise determining factor(s), a possible cue being the rate of change in day length which occurs synchronously at all localities on the same latitude (Ling 1969, Condy 1979, Griffiths & Bryden 1981, Temte 1985, Bester 1990b). In Antarctic fur seals, female haulout is precisely controlled by a constant and predictable environmental factor which will normally ensure that pups are born at a time which is favourable to their survival (Duck 1990). This timing can, however, be modified by changes to both the physical and biological components of the animals' environment, such as changes in food availability (Ribic 1984, Stewart 1989, Duck 1990). Given the synchrony between years in the present study it would seem unlikely that there were any major changes in food availability, despite the observed changes in the physical environment (sea and air temperatures) at Marion Island (Smith & Steenkamp 1990).

Pre and *post-partum* components of the breeding season haulout

The duration of the *pre-partum* period is very similar to previous figures (Table 6), while the inverse relationship seen between this period and the date of haulout, seen in the present study, has not previously been reported. At Macquarie Island the *pre-partum* period was related to age of the cows, with older animals spending a shorter period ashore prior to giving birth than younger cows, and this was ascribed to the older females' better ability to predict the timing of birth (Carrick *et al.* 1962b). Furthermore, at South Georgia younger cows hauled out earlier than older cows (McCann 1982). The above two findings would explain the change in length of the haulout period. However, no differences were seen either in haulout date or duration of *pre-partum* period in cows of different age, size or social status in the present study.

A possible explanation for the change in length of the *pre-partum* component of the cycle is the increase in visual, auditory, olfactory and tactile signals from other animals on the rookery. Bigg (1984) suggested that parturition in northern fur seals was triggered by arrival at the rookery, combined with the above mentioned signals from the other females present. If this is the case with southern elephant seals, then cows arriving early are exposed to few other females at the rookery, resulting in a longer haulout-birth interval than those arriving at an already crowded beach where levels of stimuli are high. A further possibility is that females have a set date on which they will give birth and some time their arrival better than others (Carrick *et al.* 1962b). Females could then possibly give birth while still at sea, and some mechanism to avoid this eventuality is of obvious advantage to these animals (Sergeant 1976, Bigg 1984).

The constant length of the *post-partum* period during the breeding season would appear to support the view that once hauled out, physiological reproductive mechanisms operate to maintain the synchrony of the cycle between individuals (Condy 1979).

The birth to weaning interval is similar to that reported for Macquarie Island by Carrick *et al.* (1962b) but is shorter than reported elsewhere (Barrat & Mougin 1978, Van Aarde 1980a, McCann 1982). This difference in length of lactation between studies is probably a consequence of the different observational methods used. In the present study, weaning was considered as that time when the final separation between mother and pup occurred, which was facilitated by the individual marking of cow and pup along with a regime of continuous daily observation. If rookeries are not watched on a daily basis, it is possible that weaning may occur a day or two prior to its actual recording. Given the interval between weaning and departure of the cow in the present study, in studies where a constant watch was not maintained on the colony, recorded lactation periods could be reduced by at least one day.

It is then clear that the change in length of haulout is a result of a shortening in the haulout-birth interval as the season progresses.

The post-lactation pelagic phase

The period spent at sea between lactation and the annual moult is important to the female as she must replace the resources lost during lactation. At South Georgia southern elephant seal cows lost an average of 34 percent of their initial mass during lactation (derived from McCann *et al.* 1989), while in northern elephant seals the figure is 42 percent (Costa, Le Boeuf, Huntley & Ortiz 1986).

No comparable data on the length of the post-lactation pelagic phase are available for southern elephant seals. However, one might expect that the period spent at sea would depend on the amount of resources used during lactation. Indeed northern elephant seals cows that successfully reared their pups, and therefore by implication used a far greater amount of their body fat reserves than those failing to rear their pups, stayed at sea significantly longer than unsuccessful cows (Stewart 1989). Only the period hauled out had a significant effect on the duration of the pelagic period in cows at Marion Island. If length of time spent ashore could be directly related to depletion of resources the result would afford support to Stewart's (1989) findings. However, that successful rearing of a pup did not influence the pelagic period probably rules against this.

The influence of maternal variables on the timing and spacing of events in the reproductive cycle

That timing of haulout, and spacing of events within the haulout period was independent of age, size or social effects of the cow concerned, has advantages to a female's reproductive success. Response to an environmental cue will permit a female to time her breeding haulout correctly from the beginning of her reproductive life, thus maximising her offsprings' chances of survival. If the timing had to be learned then a female may waste reproductive effort by producing young at a time of year which is not advantageous to their survival.

CHAPTER 4

POPULATION BIOLOGY

Introduction

The southern elephant seal population at Marion Island forms part of the Iles Kerguelen stock of these seals (Laws 1960). The driving forces behind the observed decline in the size of the population at Marion Island (Condy 1978, Skinner & Van Aarde 1983) as well as the other islands of the Southern Indian and Southern Pacific Oceans are poorly understood (see Chapter 1 for details), and many hypotheses have been offered to explain these declines (see Chapter 1 for references).

Comprehensive tagging studies which commenced at Marion Island in 1983 provide animals of known age which permit the first assessment of life history parameters such as age-specific survival, age-specific fecundity and age at maturity for females in the Marion Island population based on data collected at Marion Island. Previous comment on population characteristics for this population (Condy 1977) were largely based on statistics drawn from the populations at Macquarie Island (Carrick & Ingham 1962c) and South Georgia (Laws 1960).

This chapter describes the present status of the Marion Island population and analyses the population based on parameters derived from the 1983 cohort. These parameters can not tell us what the cause of the decline is, but can help highlight weak links within the elephant seal population at this site, at which future research can be directed.

Methods

Annual & weekly censuses

During the present study (1986 - 1989) weekly censuses were carried out on foot in the main study area (MSA) (Figure 8) in which numbers of bulls, cows, unweaned pups, weaned pups

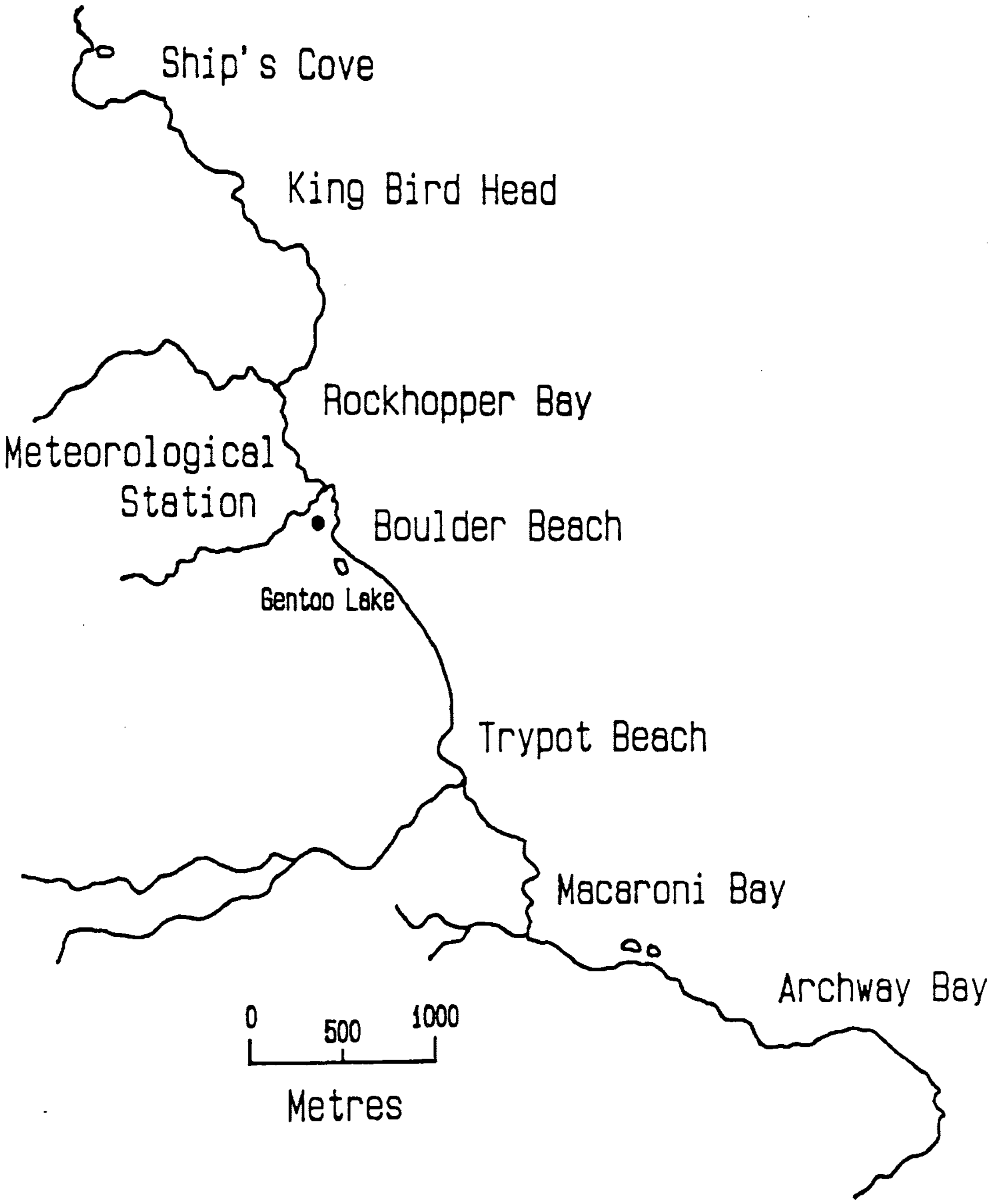

Figure 8. Map of the north east coast of Marion Island showing the main study area (MSA) beaches where southern elephant seals were counted at weekly intervals during the breeding seasons from 1974 to 1989.

and dead pups were recorded. To avoid counting a dead pup more than once, it was removed from the harem whenever possible, or marked in some way to facilitate subsequent identification. To allow comment on how numbers have changed over the period of intensive monitoring (from 1973 onwards) at Marion Island, other data on file at the Mammal Research Institute for the period 1974 - 1985 were also included. These data were collected in the same way as those of the present study and are thus comparable. Data collected in 1973 which have been used previously (Condy 1978, Skinner & Van Aarde 1983) have been omitted from the present analysis due to the late timing of census in that year making it incompatible with other years data. All beaches occupied by elephant seals were accessible by foot and even when counts had to be made from cliff tops animals were easily visible, either with the naked eye, or in the case of small pups with the aid of binoculars. The count for 1973 was excluded as it was conducted during mid-November by which time weaned pups are moving between beaches, and some have already departed the island (Wilkinson & Bester (1990b) which will result in underestimates of pup numbers, the count is therefore not comparable to the others between 1974 and 1989. However, a count in November 1951 by Rand (1962) has been included, despite it also being prone to the same inaccuracies as the 1973 count. The inclusion of the 1951 count, despite its inaccuracies, is justified as slight errors in numbers of pups on Marion Island at that time will have little effect on the estimated rate of decline of the population over the period from 1951 to 1989, and it provides an important indication of population size at that time.

In 1976 and for the years 1986 to 1989 counts of pups at all beaches on the island were conducted at the end of October to determine total pup production for the year. Counts of cows, weaned pups and dead pups at that stage provide a reliable estimate as a) no more cows hauled out after this time (see Chapter 3), b) weaned pups had not yet departed from their natal beach (Wilkinson & Bester 1990b), and therefore the numbers ashore of the three components represent total pup production. An error may occur in the case of mothers of weaned and dead pups that have not yet departed the rookery. A second estimate of pup production around the island was derived from the numbers of cows hauled out on the date of peak haulout (15 October at all Indian Ocean breeding sites - see Chapter 3). This assumes that the numbers of cows ashore on this date is equal to ≈95% of those that will come ashore, and thus the cow numbers represent ≈95% of pup numbers (see McCann 1985).

During the 1986, 1987 and 1988 seasons counts of bulls and cows were made on, or as close as possible to, 15 October at all beaches on the island, while in 1989 counts of cows only were made. This is the date of maximum haulout of cows (see Chapter 3), and is therefore assumed to be the time when the greatest number of bulls will be ashore (Hindell & Burton 1987). This assumption is made because males do not necessarily stay at one beach during the season (Laws 1956a, Jones 1981), in contrast to females, and so sequential counts of beaches will not produce total numbers hauling out during the season. At the time of these counts the size of harems was recorded as was the number of cows with or without a bull in attendance.

Social structure of the population was recorded in two ways, first as the ratio of bulls:cows in harems (McCann 1980) and second by grouping the bulls into the four categories: beachmaster, assistant beachmaster, challenger and bachelor after Carrick *et al.* (1962b).

The proportion of pups born in the MSA expressed as a percentage of the total island pup production was calculated for 1976 and for the years 1986 to 1989. Arcsine transformed values were compared using a Chi-squared test based on equal expected frequencies (Zar 1984), to determine if the proportion had changed.

Tagging

Between 1983 and 1989 weaned pups were double tagged, in their hind flippers, using 'Jumbo' rototags (Dalton Supplies Ltd, Henley-On-Thames, UK) with three digit numbers from 001 upwards and colour coded for year of application. Sex of the pup was recorded at the time of tagging.

Resighting of tagged animals

During the breeding season (mid-August to mid-November) all beaches on Marion Island were searched weekly for tagged animals. Outside the breeding season, beaches were visited once every 7-10 days. Whenever possible, tags were read without disturbing the animal, but when necessary the hind flippers were opened to permit reading of the tag. The number of the tag, the number of tags remaining (1 or 2), the location sighted, the date of sighting and stage of moult were all recorded.

Females sighted during the breeding season were recorded as either pregnant (confirmed by subsequent sighting with pup), parturient or not pregnant (hauled out only for purpose of mating). When animals were resighted during the moult, they were recorded as moulting (in thirds completed), fully moulted, or yet to moult.

Age-specific survival estimates

Jolly-Seber mark-recapture methods were employed to estimate "apparent" age-specific survival rates (mortality and emigration being indistinguishable).

The notation, following that of Seber (1982) is as follows:

R_x = number released with marks,
m_x = number with marks resighted after the initial release, and
n_x = total number sighted.

In this analysis $R_x = m_x = n_x$ as all refer to the same individuals. All animals that are sighted had to have had tags to be identifiable, and hence $n_x = m_x$. After resighting, the individuals are 'released' back in the population (R_x), and as no animals died within this fraction of time then:

$$R_x = m_x = n_x$$

In addition:
z_x = number of marks that were not resighted in a given sample, but resighted subsequently,
r_x = number released that were resighted,
M_x = estimated number of marks available for capture,
ϕ_x = survival estimate, corrected for tag retention,
θ_x = tag retention rate, and

p_x = sighting probability.

The estimated number of marks available for capture was calculated using the equation:

$$M_x = \frac{(R_x+1)z_x}{r_x+1} + R_x$$

The survival estimate, corrected for tag retention was determined from the equation:

$$\phi_x = \left(\frac{M_{x+1}}{M_x}\right)\theta_x$$

and the sighting probability estimated from the equation:

$$p_x = R_x/M_x$$

Multiple resightings in a single year were treated as a single sighting. Each year was assumed to begin on 15 October and thus animals seen after this date were treated as reaching the following age class. In the case of adult females seen during the breeding season which spans the 15 October "year end", those only seen prior to 15 October but on the breeding beaches are assumed to have survived to the next year class as they will leave the beach after 15 October.

Annual survival estimates (ϕ_x) were calculated for both males and females of each cohort. Probability of surviving to a given age (l_x) was calculated from the product of all values of ϕ prior to that age, *i.e.* survival to age five = $\phi_0 \times \phi_1 \times \phi_2 \times \phi_3 \times \phi_4$. Comparison of first year survival was made between different cohorts using estimates at one year of age. Values for survival assessed at year one were arcsine transformed (Zar 1984) and these values compared using χ^2 analysis for equal expected values (Zar 1984). Possible differences between years could be due either to differences in survival or to differences in resighting effort/success. Comparisons of resighting effort/success between seasons were checked by considering percentage improvement in first year survival estimates made at ages one and two. Percentage changes were transformed using arcsine transformations (Zar 1984) and the transformed values compared using a χ^2 test for equal expected values (Zar 1984), for both males and females. A comparable improvement between years suggests similar resighting effort/success. This assumes that the percentage improvement between years for the same component of the population will be similar.

The influence of subsequent years resightings on survival estimates of both male and female first year survival were calculated by modifying z_1 to include resightings in years two to six and then recalculating M_1 to obtain different estimates for m_1.

Life tables, with yearly intervals, were constructed for both males and females of the 1983 cohort, for which there was five years data available. Given the longitudinal nature of the data, no assumptions were necessary on rate of increase or stability of age distribution (Caughley 1977). The calculated l_x values were used to determined probability of dying ($d_x = l_x - l_{x+1}$), mortality rate ($q_x = d_x/l_x$), and the product of survival and fecundity ($l_x m_x$), without necessitating modification. Mortality was assumed to be constant after maturity (Harwood & Prime 1978) until a year or two before death (McCann 1985).

When compiling the female lifetable, fecundity rates (m_x) were assumed to remain constant after the age of full recruitment to the breeding population until death, with no reproductive senescence (Hindell & Little 1988). All cows were assumed to produce only one pup (Laws 1956a, Carrick *et al.* 1962b), with a proportion of 0,489 female pups (see results section), and female longevity was 23 years (Hindell & Little 1988).

Survivorship data for Marion Island were compared with data from both the stable South Georgia (McCann 1985, McCann & Rothery 1988), and declining Macquarie Island (Hindell & Burton 1987, Hindell 1991) population.

Tag loss corrections

Tag loss for individual tags was determined using the equation:

$$l = n_1/(n_1 + 2n_2)$$

where

l = estimated loss rate for a single independent tag,
n_1 = number returning in next period with only one tag, and
n_2 = number returning in next period with both tags.

(Eberhardt, Chapman & Gilbert 1979).

Overall retention rates (θ) were calculated from the equation:

$$\theta = 1 - ((m_1 l_1 + m_2 l_2)/m_1 + m_2)$$

where

θ = overall tag retention rate,
m_1 = marked seals sighted with one tag,
m_2 = marked seals sighted with two tags,
l_1 = probability of losing one tag, and
l_2 = probability of losing both tags.

where the probability of losing both tags, $(l_2) = (l_1)^2$, assuming tag loss rates to be independent (J.W. Testa *pers. comm.*[1])

Survival rates (ϕ) were corrected for tag loss following the method of Arnason & Mills (1981), using the equation:

---

[1] J.W. Testa, Institute of Marine Science, University of Alaska, U.S.A.

$$\phi^c = \phi/\theta$$

where ϕ = estimated survival from age x to $x+1$, ϕ^c = corrected survival rate, and θ = overall tag retention rate.

Fecundity rates

Fecundity rates were obtained by direct observation of females of known age during censuses. However, some females may not have been seen giving birth, either on Marion Island, where they were not detected due to the difficulty in reading tags in harems, or on neighbouring Prince Edward island where no checks for tagged animals were possible during breeding seasons. Given the above, an indirect method of determining fecundity rates for the population was used. This method was based on the following:

The dates of moult for females of age three and above were recorded, and then the date that they would have been ashore to breed calculated. Beaches were checked for moulting animals on a 7-10 day cycle and if a cow was seen prior to the onset of moult during a census she was assumed to have arrived midway between the current census and the previous one. From this date 62 days were subtracted to allow estimation of date of departure from the rookery if she was ashore. The period of 62 days that was chosen was based on the periods at sea of 50 females with known departure dates and approximate return dates to moult (see Chapter 3). All cows with estimated departure dates between early October and late November were possibly fecund in that particular year. This method allowed assessment of likelihood of pupping and combined with previous seasons data also allowed age at first pupping to be determined for each of the cows in the cohort.

When breeding data were available for the previous season, fecundity was determined from inter-annual changes in birth (and hence departure) date. Observations of cows at the study colony (Trypot beach) suggested that inter-annual differences in birth date of more than seven days were indicative of a failure to breed in that particular season. Cows with a difference of greater than seven days between parturition dates in successive years were assumed to have failed to pup.

Age-specific fecundity values were calculated by taking the numbers of cows (seen, or implied) producing pups at each age and dividing by the number of females alive at this age. For any differences in the numbers of females alive based on tag resights and those generated by the Jolly-Seber estimate it was assumed that the fecundity patterns were the same as for the observed females.

Age at first pupping

The average age of first pupping was calculated using the equation:

$$\bar{x} = \sum x r_x$$

with:

$$z_x = y_x / n_x$$

where:

x = the animal's age in years,

z_x = proportion of females at age x that had pups,

y_x = number of females at age x with pups in the sample, and

n_x = number of females in sample.

and:

$$r_x = z_x - z_{x-1}$$

where r_x = estimated probability that a female produces her first pup at age x. (York 1983)

The variance for x was:

(H.M. Dott *pers. comm.*[2])

---

[2] H.M. Dott. Mammal Research Institute, University of Pretoria, Pretoria, South Africa.

$$\bar{x}=\frac{\sum_{k=1}^{N_c}(A_c^{*}k)^2-\frac{(\sum_{k=1}^{N_c}A_c^{*}k)^2}{N_c}}{N_c(N_c-1)\sum_{k=1}^{N_c}A_c^{*}k}$$

where:

$$A_c^{*}k=N_cA_c-(N_c-1)A_ck$$

and A_ck = average age at first reproduction of the year class, using all but the *k*th individual in the sample.

Net reproductive rate (R_o)

The net reproductive rate (R_o) or 'finite rate of increase per generation' was calculated for females of the 1983 cohort using the equation:

$$R_o = \Sigma l_x m_x$$

where:

$\Sigma l_x m_x$ = the sum, of the product of the age-specific survival and fecundity values of females of a cohort (Caughley 1977).

Manipulation of variables to examine effects on R_o.

Variables influencing R_o include sex ratios of offspring, age-specific survival, and age-specific fecundity. The effect of changing these variables on R_o was investigated by substituting alternative values for each variable in turn while maintaining all the other variables as determined during the study.

Rates of population change

Rates of population change were calculated using the exponential equation:

$$N_t = N_o e^{rt}$$

where;

N_t = population number at time t,

N_o = population number at the start of the period,

e = Naperian logarithm,

r = intrinsic rate of increase, and

t = time interval in years between the first and last observation (Caughley 1977).

Results

Population size

Total pup production figures for Marion Island for the years 1986 to 1989 are shown in Table 7. Figures for total numbers of pups born on Marion Island obtained from direct counts of pups, and those derived from numbers of cows hauled out on October 15 (see methods) did not differ significantly (Table 7), and thus direct counts of pups were used in population estimates.

Table 7. Comparison of annual pup production figures for Marion Island based on direct counts in late October and extrapolations from the number of cows counted on 15 October (see McCann 1985). Differences in pup production figures were compared using χ^2 tests (Zar 1984) assuming expected values were equal to the average of the two pup production figures, with one degree of freedom. All values were non significant.

Year	Number of cows	Estimated pup production	Number of pups counted	% difference	χ^2 value
1986	640	674	690	-2,9	0,19
1987	599	631	625	2,2	0,03
1988	605	637	635	0,3	0,00
1989	547	576	585	-1,5	0,07

Rates of change in population size

The numbers of pups born in the MSA expressed as a percentage of the total island pup yield (28%) did not change for the years 1976 and 1986-1989 (χ^2_4=0,19; P>0,05) (Table 8).

Table 8. The numbers of elephant seal pups born in the main study area (MSA) at Marion Island for the years 1976 and 1986-1990 expressed as a percentage of the total island pup production. Island pup numbers are based on counts conducted at the end of October each year.

Year	Number of pups in MSA	Total number of pups on the island	Percentage of pups occurring in the MSA
1976	301	1114	27,0
1986	183	690	26,5
1987	177	625	28,3
1988	177	635	27,9
1989	184	585	31,5

The population size at Marion Island, based on pup production, declined at an exponential rate of 4,8% per annum over the period 1951 to 1989. (Figure 9). The rate of decline in the MSA from 1974 to 1989 was 4,8% ($y=101{,}4e^{-0{,}048x}$; t_{12}=9,83; P<0,001). Over the period 1974 to 1989 cow numbers declined at 5,2% per annum ($y=108{,}93e^{-0{,}052x}$; t_{12}=9,02; P<0,001)(Figure 10) and bull numbers followed no distinct trend over the same period ($y=64{,}8e^{-0{,}031x}$; t_{12}=1,45; P>0,05)(Figure 11). Maximum numbers of bulls, cows and pups in each year are given in Appendix II).

The numbers of pups born in the MSA declined exponentially at 1,9% per annum ($y=42{,}1e^{-0{,}019}$; t_5=2,79; P<0,05) between 1983 and 1989. Consideration of annual differences between 1974 and 1989 show three clear phases of decline (Figure 12), and the annual rates of increase (r), for pups, show the three phases during which the decline slowed, or reversed (Figure 13).

There was no significant correlation between the peak numbers of bulls and cows present in

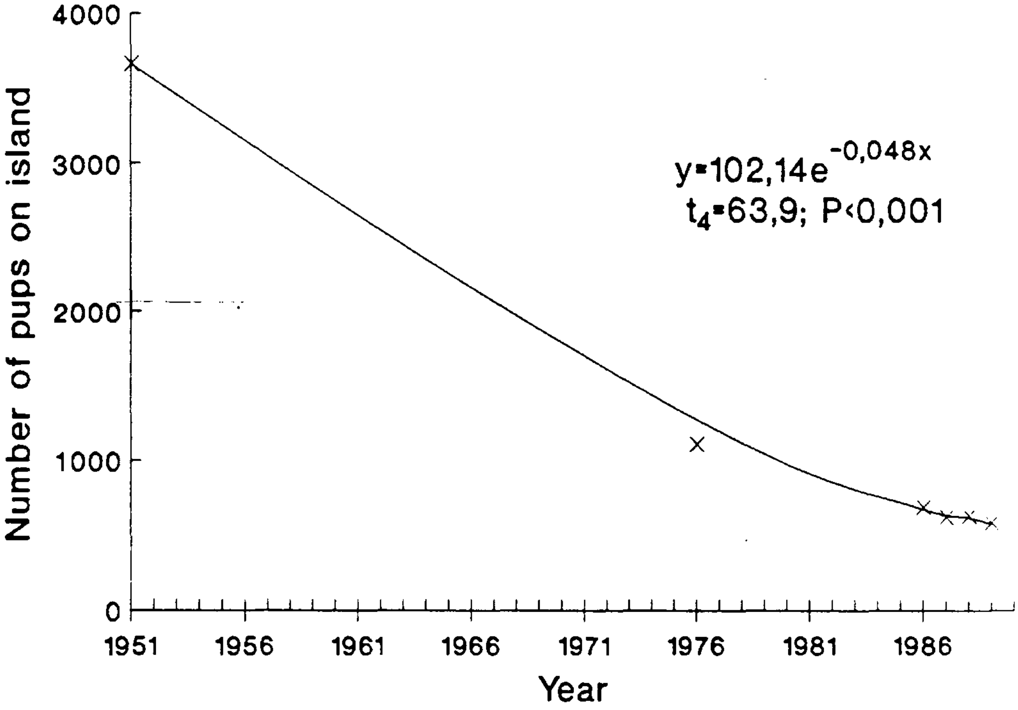

Figure 9. Trend in the numbers of southern elephant seal pups born at Marion Island from 1951 to 1989. Exponential curve fitted through least squares regression analysis.

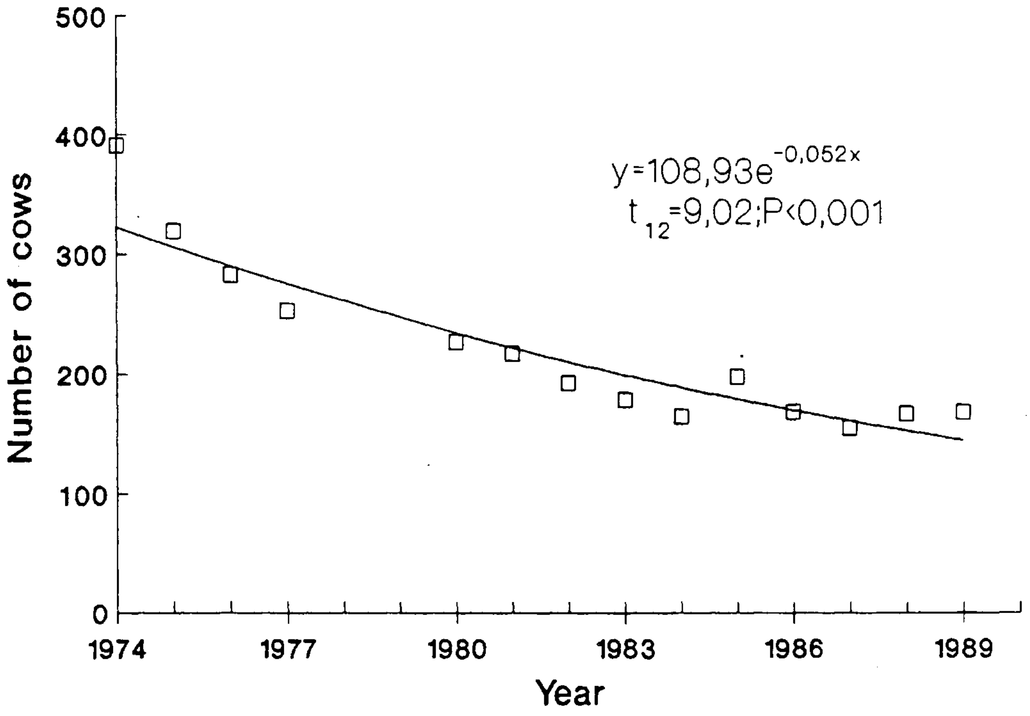

Figure 10. Maximum numbers of southern elephant seal cows present in the MSA, Marion Island, for the years 1974 to 1989. The slope of the exponential line differs significantly from zero.

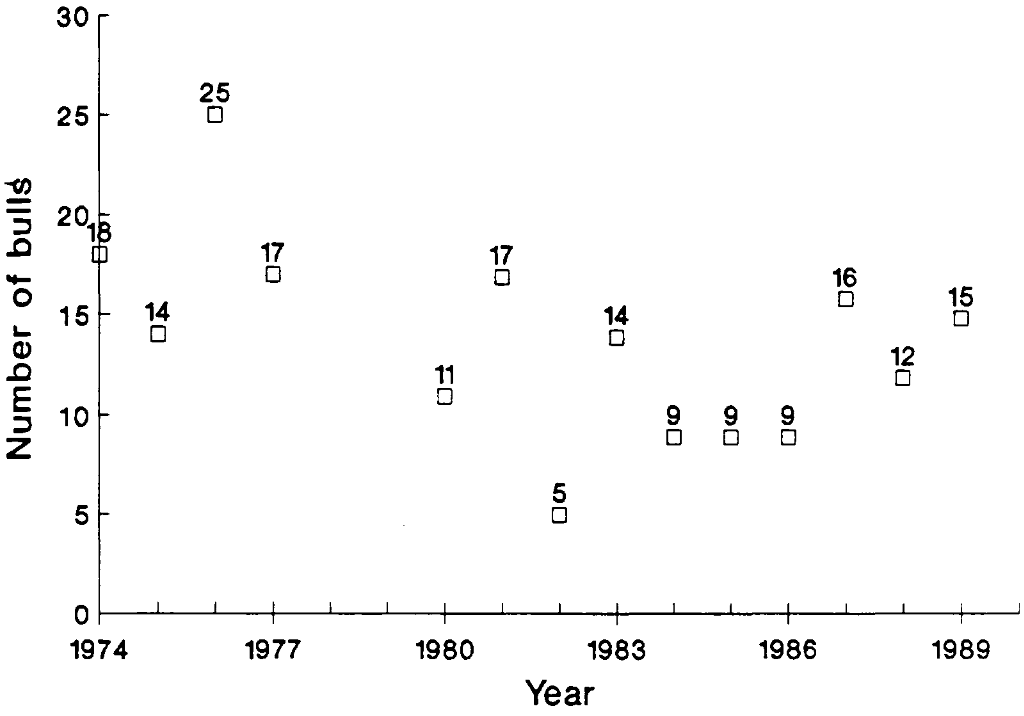

Figure 11. Maximum numbers of southern elephant seal bulls present in the MSA, Marion Island, at the time of peak cow numbers for the years 1974 to 1989.

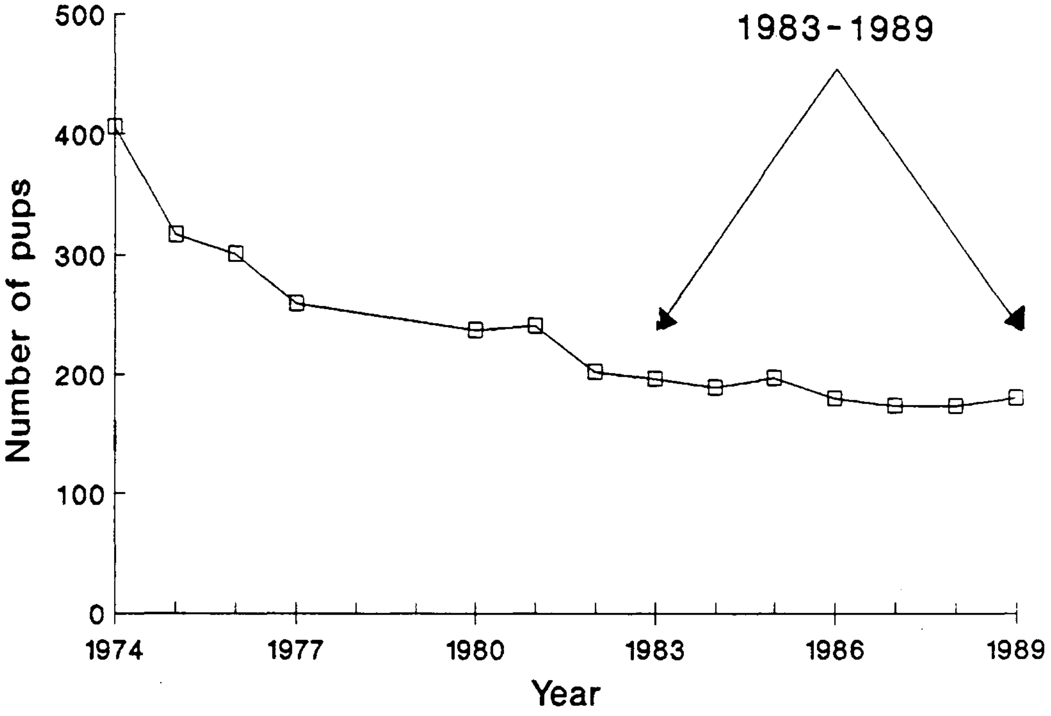

Figure 12. Annual pup production of southern elephant seals within the MSA, Marion Island, for the years 1974 to 1989. For the period 1983 to 1990 (defined by arrows) the population declined at an exponential rate of 1,9% per annum.

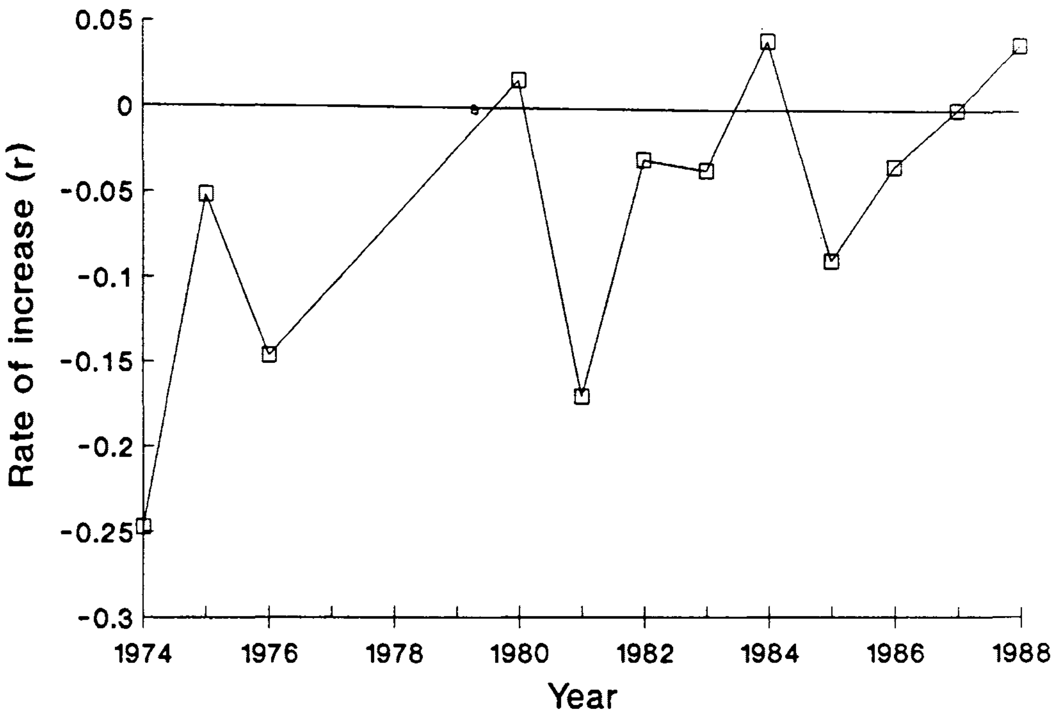

Figure 13. Intrinsic rates of increase (r) for the pup population in the MSA, Marion Island, for the years 1974 to 1989. The values at each point refer to the change occurring from that year to the next.

the MSA in the same year (r_{12}=0,50; P>0,05), nor was there a significant correlation between the number of bulls ashore in one season and the numbers of cows seen in the subsequent year (r_{10}=0,52; P>0,05).

Pre-weaning mortality

Pre-weaning mortality in the MSA ranged from 2,5% to 8,5% between 1974 and 1989. There was no correlation between pup mortality (expressed as a percentage of the pups born in the MSA) and the number of births (r_{10}=0,43; P>0,05) or between mortality and the number of bulls in the area (r_{10}=0,01; P>0,05). There was no correlation between numbers of births around the whole island and the mortality rate (r_2=0,68; P>0,05; Table 9).

Table 9. Pre-weaning mortality rates of southern elephant seal pups at Marion Island in the years 1986 to 1989.

Year	Number of births	Number of deaths	% mortality
1986	690	35	5,07
1987	625	14	2,24
1988	635	22	3,46
1989	585	20	3,42

Sex ratio of pups

A total of 1970 male pups and 1886 female pups were tagged between 1983 and 1989 (Table 10). The ratio of 1,04:1 (M:F) does not differ significantly from unity (χ^2_1=1,82; P>0,05).

Adult social structure during the breeding season

The adult sex ratio in the MSA (Figure 14) did not change significantly (χ^2_{13}=19,26; P>0,05) during the period 1974 to 1989. Adult sex ratio had no effect on either the proportional change (λ) in cow (Figure 15a) or pup (Figure 15b) numbers from the year the sex ratio was observed and the following year. Mean harem size in the MSA, was not significantly smaller

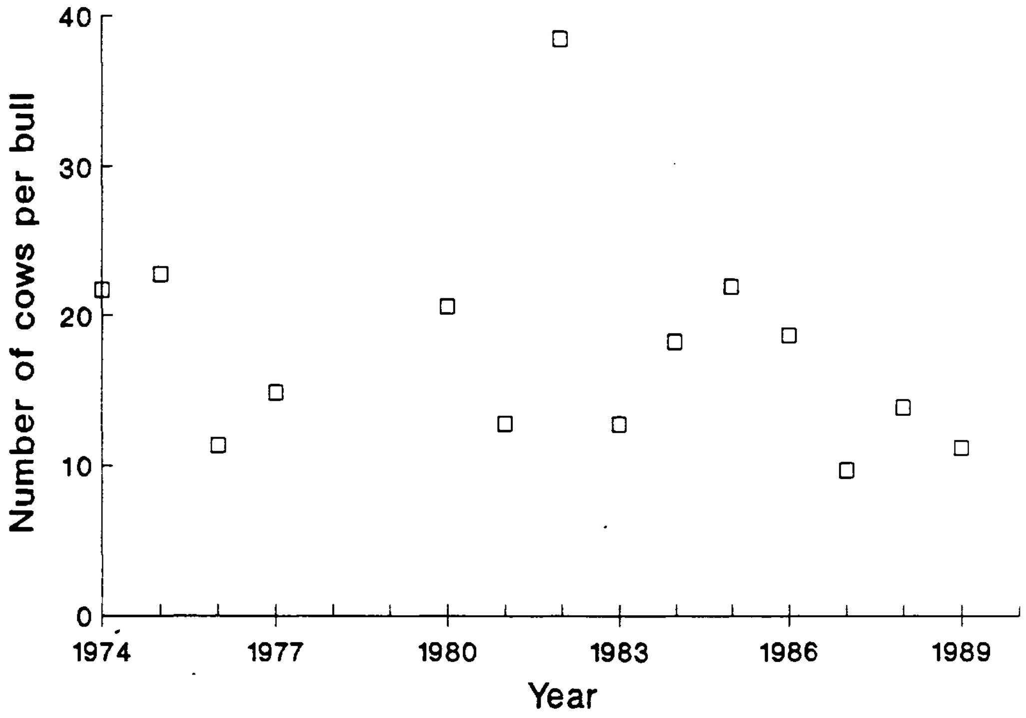

Figure 14. The ratio of cows per bull in the MSA, Marion Island, for the years 1974 to 1989. Ratios are of the maximum numbers of cows and bulls hauled out each year.

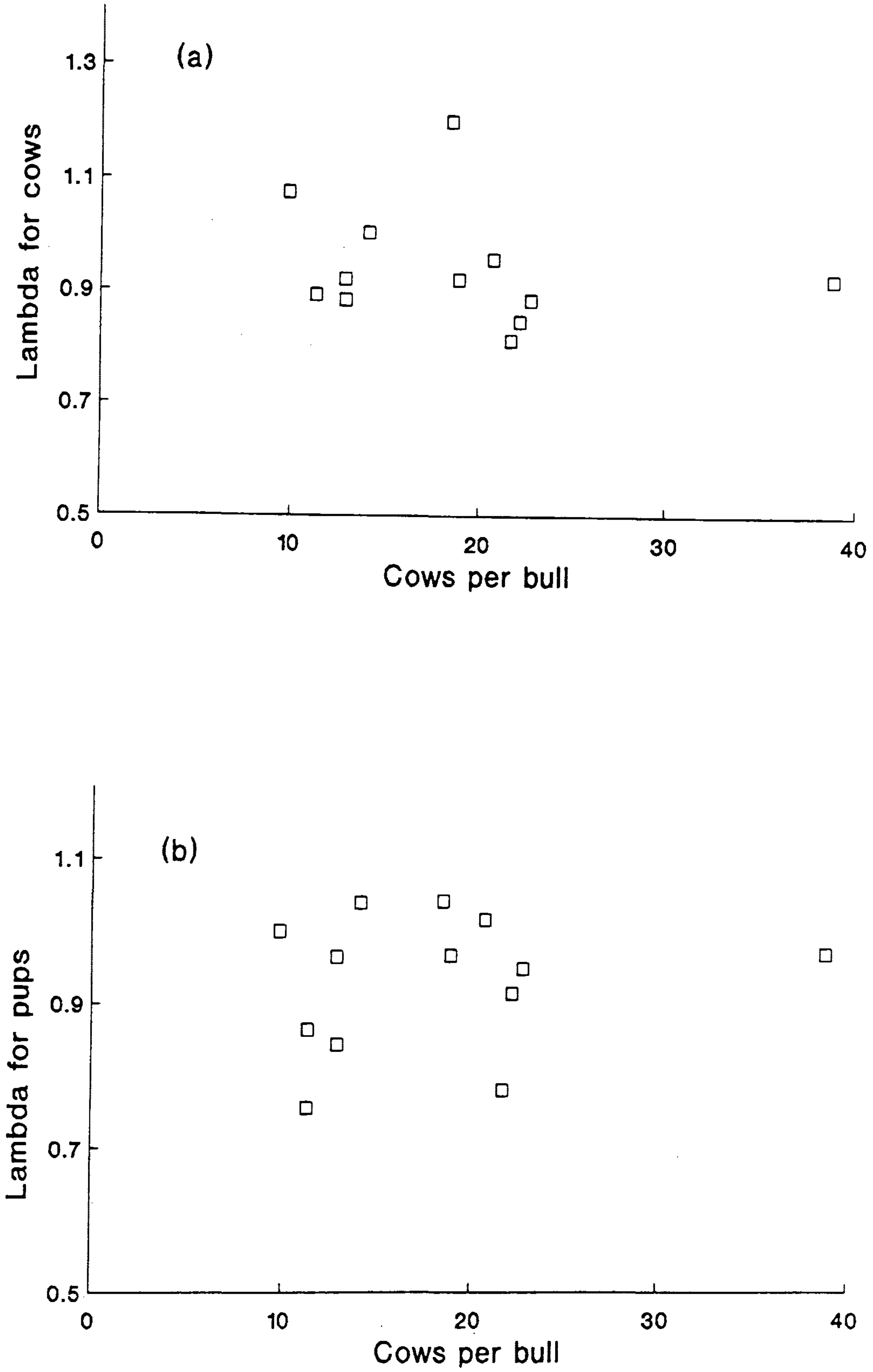

Figure 15. The relationship between the sex ratio (cows:bulls) in the MSA, Marion Island, and the value of λ for (a) cows and (b) pups, measured between 1974 and 1989. λ refers to the number of (a) cows and (b) pups present in the year following that when the sex ratio was determined, divided by the numbers in the same year the sex ratio was determined.

Table 10. The sex ratio of southern elephant seal pups tagged, at weaning, annually from 1983 to 1989 on Marion Island.

Year	Males	Females	Male:Female ratio
1983	207	200	1,04:1
1984	263	231	1,14:1
1985	355	345	1,03:1
1986	286	269	1,06:1
1987	308	300	1,03:1
1988	303	279	1,09:1
1989	248	262	0,95:1
Total	1970	1886	1,04:1

than the mean harem size for the whole island in 1986 (t_{29}=1,85; P>0,05), 1987 (t_{34}=0,64; P>0,05) or 1988 (t_{35}=1,76; P>0,05) (Tables 11 & 12). Mean harem size did not change significantly between 1974 and 1988 (t_{30}=1,81; P>0,05, Table 13). At least 95% of all the cows were found in the company of at least one adult male, either in a harem or singly with an attendant bull (Table 14). The ratio of bulls to cows ashore over the whole island between 1986 and 1988 ranged from 1:9 to 1:12.

Age-specific survival estimates

Jolly-Seber survival variables for males and females of the 1983 cohort are shown in Tables 15 & 16 respectively. Similar numbers of males and females survive to age one, but thereafter female survivorship is higher than that for males (Figure 16a). Mortality rate declines from age one to three in both sexes, after which it increases between age three and four, more noticeably among females. This increase is followed by a decrease, again of greater magnitude among females, to age five (Figure 16b). Lifetables for males and females are presented in Tables 17 & 18 respectively.

Figures 17a & 17b show survivorship curves for females and males at Marion Island, Macquarie Island (Hindell 1991) and South Georgia (McCann 1985). After similar survival to age one in the Marion Island and South Georgia populations, both juvenile and adult

Table 11. The social structure of the section of the Marion Island southern elephant seal population occurring within the MSA in the years 1986 to 1988. Data were obtained on the date of peak haulout of cows.

Year	Number of harems	Beachmaster	Challenger		Bachelor		Cows		Ratio of cows/bull
			Mean	S.D.	Mean	S.D.	Mean	S.D.	
1986	4	1	0,50	0,58	0,5	1,00	39,75	19,28	19,88
1987	6	1	1,00	0,89	0,33	0,52	23,67	19,43	10,16
1988	5	1	0,60	0,89	0,60	0,89	32,40	18,24	14,73

Table 12. The social structure of the southern elephant seal breeding population at Marion Island in the years 1986 to 1988. Data were obtained on the date of peak haulout of cows, and include all animals present on the island on that day.

Year	Number of harems	Beachmaster	Challenger		Bachelor		Cows		Ratio of cows/bull
			Mean	S.D.	Mean	S.D.	Mean	S.D.	
1986	27	1	0,48	0,58	0,11	0,42	23,10	16,45	14,53
1987	30	1	0,57	0,94	0,13	0,35	18,97	15,85	11,16
1988	32	1	0,59	0,88	0,31	0,74	18,69	15,66	9,84

Table 13. Maximum numbers of cows present in harems along the north east and south east coast of Marion Island during comparable counts conducted in 1974 and 1988.

Beach	Number of cows in harems	
	1974*	1988
Ship's Cove	65	49
	7	
Rockhopper Bay	10	9
Boulder beach	18	
Trypot beach	70	40
Macaroni Bay	70	17
	10	
Archway Bay	152	47
Hansen Point	13	5
Kildalkey Bay	130	50
	40	5
King Penguin Bay	18	27
	27	5
		17
Sea Elephant Bay	38	22
Blue Petrel Bay	18	9
Sealer's beach	80	45
	5	3
Total harems	17	15
Total cows	771	350
Mean harem size	45,35	23,33
SD of harem size	43,77	18,14

* Data from Condy (1978).

Table 14. Numbers of bulls and cows counted at Marion Island in the years 1986 to 1988 on the date of peak haulout of cows (and implied peak haulout of bulls). The numbers of cows with an attendant bull differ from the total as some cows hauled out away from breeding aggregations, or were in unattended harems. Sex ratios are based on total numbers of animals present on the island, irrespective of whether they were in a harem or not.

Year	Bulls ashore	Total cows ashore	Cows with attendant bulls	% of cows with bulls	Bulls:cows
1986	54	640	626	97,8	1:11,9
1987	67	599	569	95,0	1:8,9
1988	67	605	599	99,0	1:9,0

Table 15. Jolly-Seber survival analysis of male southern elephant seals born at Marion Island in 1983 and followed until six years old. **N.B.** The notation follows that of Seber (1982). The number released with marks (R_x) was equal to the number of animals with marks resighted (m_x) after the initial release and to the total number of animals sighted (n_x); in this analysis, R_x=m_x=n_x. The number of marked animals not resighted in a given sample that were resighted subsequently (z_x), the number released that were resighted (r_x), and the estimated number of marks available for recapture (M_x) are also shown. Survival estimates (ϕ_x) are corrected for tag retention rates (θ_x). S.E. and Cov. refer to standard error and covariance of the estimates, and sighting probabilities (p_x) are also shown.

Age (x)	R_x	r_x	z_x	M_x	θ_x	ϕ_x	S.E.(ϕ_x)	Cov. ($\phi_{x,x+1}$)	p_x
0	207	110	0	207,0	0,9999	0,5972	0,0434	-0,0008	
1	88	54	22	123,6	0,9996	0,6892	0,0635	-0,0014	0,7120
2	59	38	17	85,2	0,9994	0,7246	0,0774	-0,0020	0,6929
3	46	26	9	61,7	0,9986	0,6658	0,0981	-0,0046	0,7459
4	27	15	8	41,0	0,9946	0,6842	0,1349		0,6585
5	16	9	7	27,9					0,5735
6	16	0	0						

Table 16. Jolly-Seber survival analysis of female southern elephant seals born at Marion Island in 1983 and followed until six years old. **N.B.** The notation follows that of Seber (1982). The number released with marks (R_x) was equal to the number of animals with marks resighted (m_x) after the initial release and to the total number of animals sighted (n_x); in this analysis, $R_x = m_x = n_x$. The number of marked animals not resighted in a given sample that were resighted subsequently (z_x), the number released that were resighted (r_x), and the estimated number of marks available for recapture (M_x) are also shown. Survival estimates (ϕ_x) are corrected for tag retention rates (θ_x). S.E. and Cov. refer to standard error and covariance of the estimates, and sighting probabilities (p_x) are also shown.

Age (x)	R_x	r_x	z_x	M_x	θ_x	ϕ_x	S.E.(ϕ_x)	Cov. ($\phi_{x,x+1}$)	p_x
0	200	113	0	200,0	0,9999	0,6176	0,0414	-0,0006	
1	92	61	21	123,5	0,9988	0,7282	0,0581	-0,0011	0,7449
2	60	44	22	89,8	0,9979	0,7821	0,0634	-0,0009	0,6680
3	58	38	8	70,1	1,0000	0,7275	-0,0765	-0,0026	0,8274
4	31	23	15	51,0	0,9942	0,8240	0,0981		0,6078
5	34	17	4	41,8					0,8138
6	21	0	0						

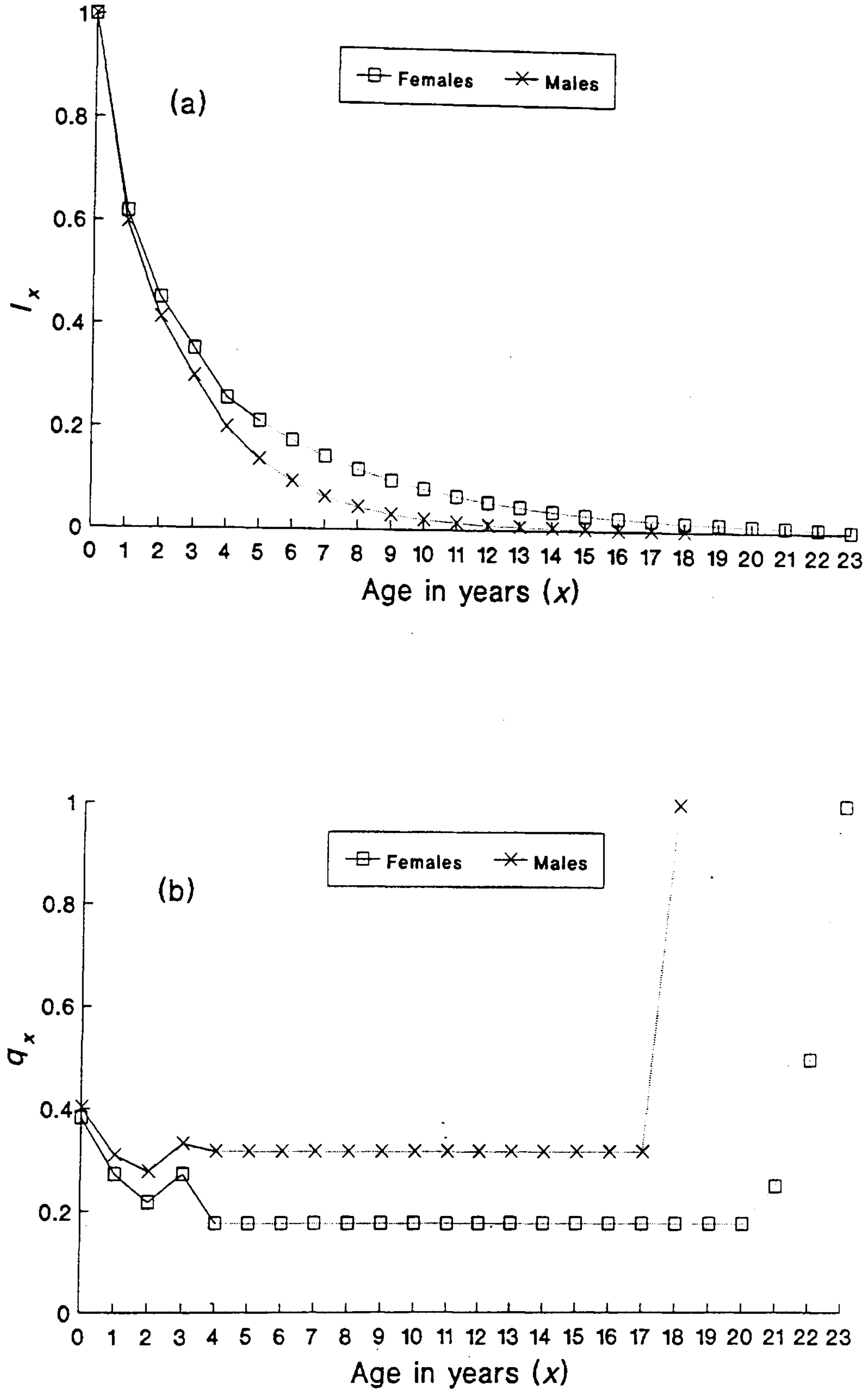

Figure 16. Age specific (a) survivorship (l_x), and (b) mortality rates (q_x) for male and female southern elephant seals at Marion Island. Dotted lines for both sexes after (a) age five and (b) age four, refer to estimated values.

Table 17. Lifetable of male southern elephant seals of the 1983 cohort at Marion Island.

Age (x)	Probability of surviving (l_x)	Probability of dying (d_x)	Mortality rate (q_x)
0	1,000	0,403	0,403
1	0,597	0,185	0,310
2	0,412	0,114	0,277
3	0,298	0,099	0,332
4	0,199	0,063	0,317
5	0,136	0,043	0,317
6	0,093	0,029	0,317
7	0,064	0,020	0,317
8	0,044	0,014	0,317
9	0,030	0,010	0,317
10	0,020	0,006	0,317
11	0,014	0,004	0,317
12	0,010	0,003	0,317
13	0,007	0,002	0,317
14	0,005	0,002	0,317
15	0,003	0,001	0,317
16	0,002	0,001	0,317
17	0,001	0,001	0,317
18	0,000	0,001	1,000

Table 18. Lifetable of female southern elephant seals of the 1983 cohort at Marion Island.

Age (x)	Probability of surviving (l_x)	Probability of dying (d_x)	Mortality rate (q_x)	Pregnancy rate	Fecundity (m_x)	l_xm_x
0	1,000	0,382	0,382	0,000	0,000	0,000
1	0,618	0,168	0,272	0,000	0,000	0,000
2	0,450	0,098	0,218	0,000	0,000	0,000
3	0,352	0,096	0,273	0,262	0,128	0,045
4	0,256	0,045	0,176	0,565	0,276	0,071
5	0,211	0,037	0,176	0,763	0,373	0,079
6	0,174	0,031	0,176	1,000	0,489	0,085
7	0,143	0,025	0,176	1,000	0,489	0,070
8	0,118	0,021	0,176	1,000	0,489	0,058
9	0,097	0,017	0,176	1,000	0,489	0,047
10	0,080	0,014	0,176	1,000	0,489	0,039
11	0,066	0,012	0,176	1,000	0,489	0,032
12	0,054	0,009	0,176	1,000	0,489	0,026
13	0,045	0,008	0,176	1,000	0,489	0,022
14	0,037	0,007	0,176	1,000	0,489	0,018
15	0,030	0,005	0,176	1,000	0,489	0,015
16	0,025	0,004	0,176	1,000	0,489	0,012
17	0,021	0,004	0,176	1,000	0,489	0,010
18	0,017	0,003	0,176	1,000	0,489	0,008
19	0,014	0,002	0,176	1,000	0,489	0,007
20	0,012	0,002	0,176	1,000	0,489	0,006
21	0,010	0,003	0,250	1,000	0,489	0,005
22	0,007	0,004	0,500	1,000	0,489	0,003
23	0,003	0,003	1,000	1,000	0,489	0,001
						R_o = 0,661

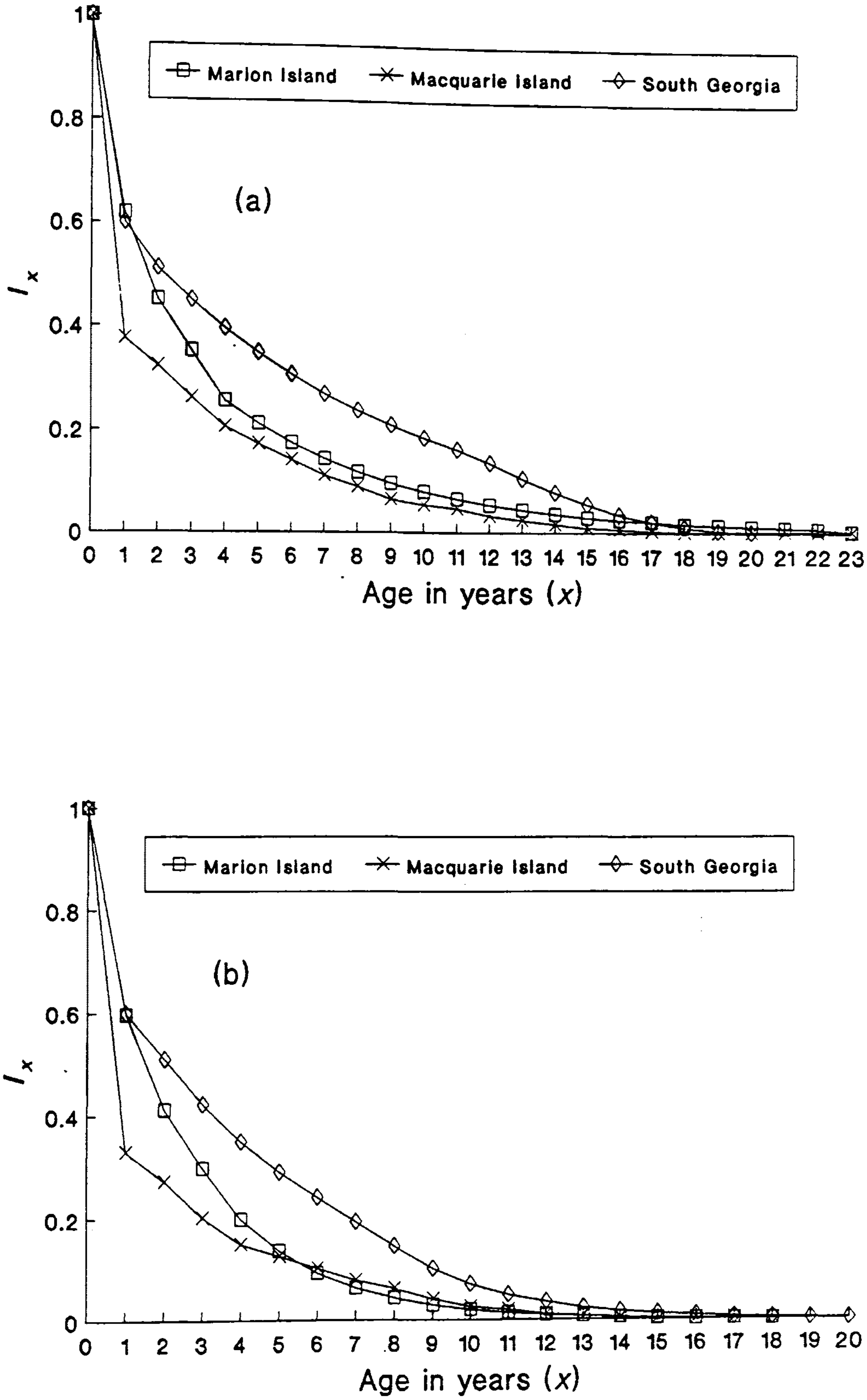

Figure 17. Survivorship curves for (a) female, and (b) male southern elephant seals at Marion Island (present study), Macquarie Island (Hindell 1991) and South Georgia (McCann 1985).

survival is lower at Marion Island. First year survival at Macquarie Island is lower than at both Marion Island and South Georgia, and after showing lower juvenile survival, adult survival is similar to that at Marion Island.

Inter-year comparisons of first year survivorship

Percentage improvement in first year survival estimates, between the estimate made at one year of age and that made at two years of age, did not differ for males (χ^2_4=2,29; P>0,05) or females (χ^2_4=2,58; P>0,05) between cohorts (Table 19), which suggests that the resighting effort/success was similar over the course of the study. Neither male, nor female, first year survival based on estimates at age one, differed within the six cohorts from 1983 to 1988 (Figure 18). Estimates of first year survival improved with subsequent years resightings in all cohorts for both males and females, with estimates at six years of age more than 30% greater than after one year (Figures 19a & 19b respectively).

Table 19. Comparison of percentage improvement in first year survival estimates made after resightings at 1 and 2 years of age. Resightings in the second year of life represent different years efforts for each cohort. Similar improvements in the estimates of first year survival over all of the cohorts is indicative of a constant inter annual search effort.

Cohort	Sex	1st year survival assessed at 1 year of age	1st year survival assessed at 2 years of age	% improvement
1983	Male	42,5	52,2	9,7
	Female	46,0	54,1	8,1
1984	Male	39,2	55,8	16,6
	Female	41,6	48,8	7,2
1985	Male	45,1	52,1	7,0
	Female	46,4	54,3	7,9
1986	Male	39,9	49,0	9,1
	Female	48,7	55,5	6,8
1987	Male	39,9	49,5	9,6
	Female	45,0	60,6	15,6

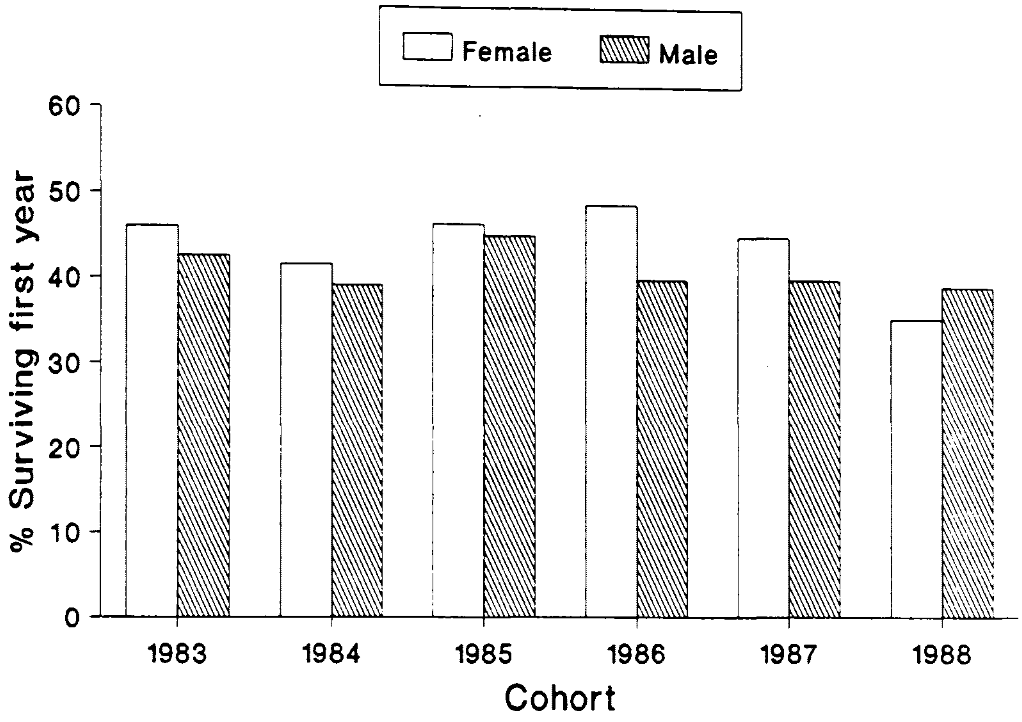

Figure 18. First year survival of male and female southern elephant seals at Marion Island between 1983 and 1989. All estimates are based on those made at one year of age, and do not take into account improvements likely with future years resightings.

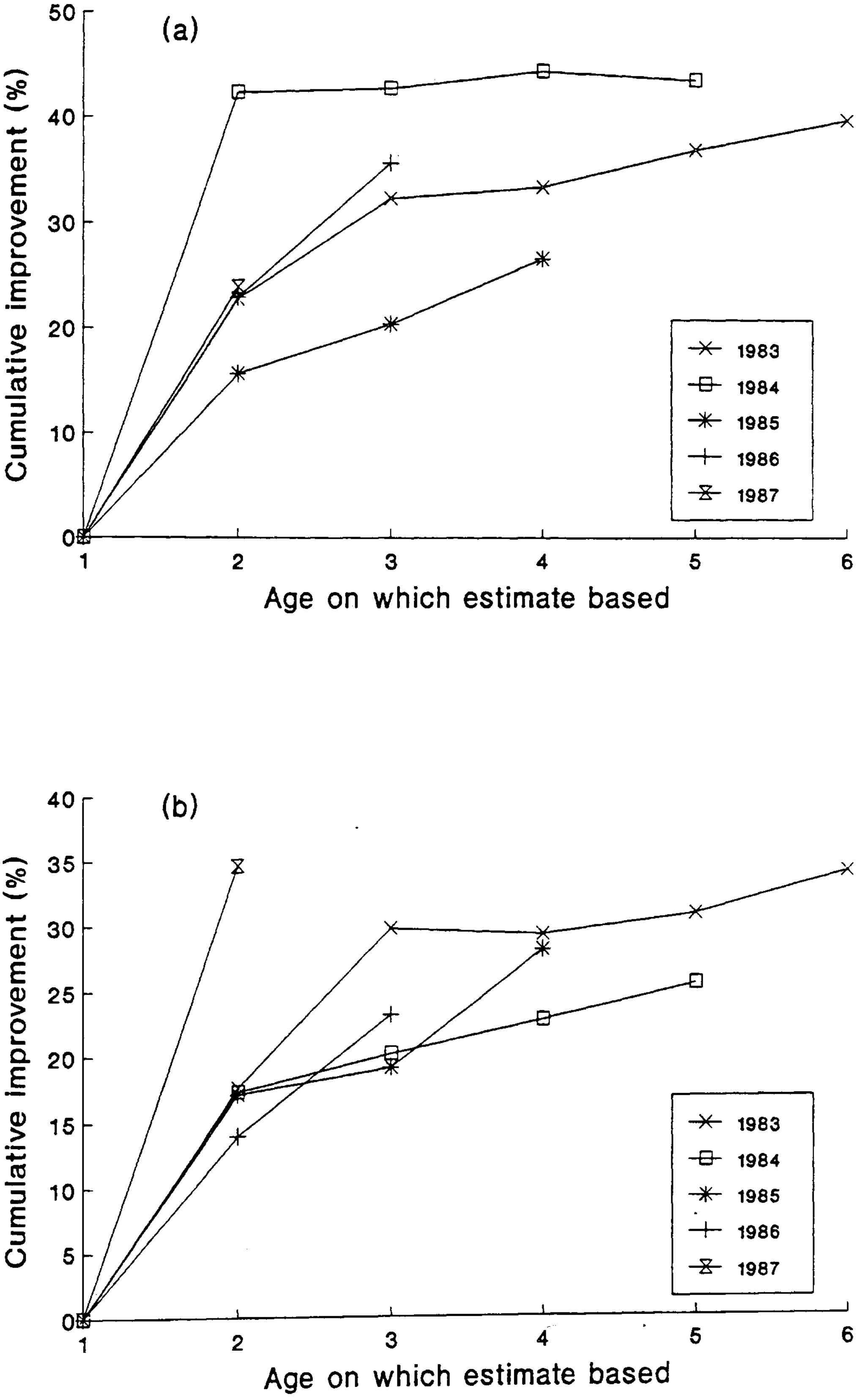

Figure 19. Cumulative improvement (%) in the estimate of (a) male and (b) female first year survival of five cohorts (1983 to 1987) at Marion Island. All values refer to the cumulative percentage improvement on the initial estimate of first year survival made when the animals were one year old.

Age at first pupping & age-specific pupping rates

Age-specific pupping rates are shown in Figure 20. Some cows (26,2%) gave birth at age three and all were believed to be parous by the age of six. The average age at first reproduction of the females in the 1983 cohort was 4,41 the variance of the estimate was 0,006. Given that 48,9% of pups are female, the values for age-specific fecundity (m_x) are zero at age one and two, 0,128 at 3, 0,276 at 4, 0,373 at 5 and 0,489 from age 6 onwards.

Net reproductive rate (R_o)

The value calculated for R_o using the sum of the $l_x m_x$ values was 0,661 (Table 17), with cows between the ages of four to seven contributing almost 50 percent of the $l_x m_x$ total (Figure 21).

Sex ratio of offspring would have to be skewed to almost three to one in favour of females to achieve an R_o of 1 (Table 20), and full recruitment would have to be realised by age four to achieve the same result. Five percent changes in first year survival (Table 21) produce similar changes in R_o, with a value in excess of 90% necessary to produce an R_o of 1. An annual adult survival rate of between 89 and 90% is necessary for R_o to reach one, with 1% changes in annual survival producing 5% differences in R_o (Table 22).

Table 20. The effect on net reproductive rate, R_o, of changing the proportion of female pups born to southern elephant seal cows at Marion Island, while maintaining age-specific pupping rates and age-specific survival rates at the levels seen in the lifetable (Table 18).

Percentage of female pups born	Net Reproductive Rate (R_o)
48,9	0,661
50,0	0,675
55,0	0,743
60,0	0,811
65,0	0,878
70,0	0,946
75,0	1,013

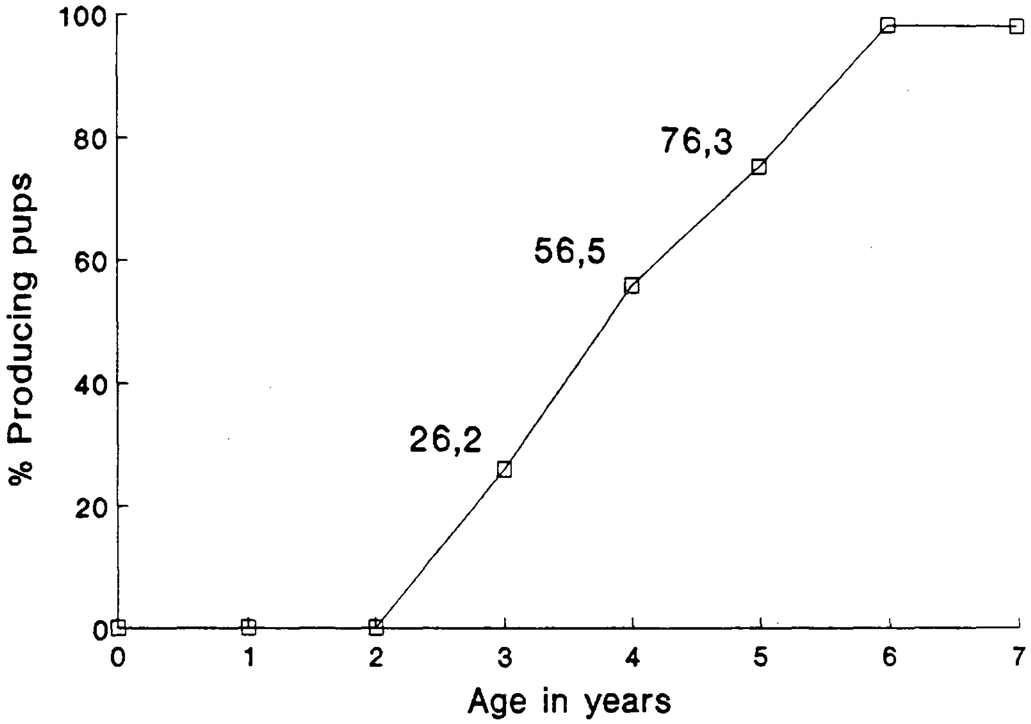

Figure 20. Percentage of southern elephant seal cows, of the 1983 cohort at Marion Island, producing pups at ages between zero and seven. All cows have pupped by age six. Values in the figure refer to percent of cows pupping at three, four and five years of age.

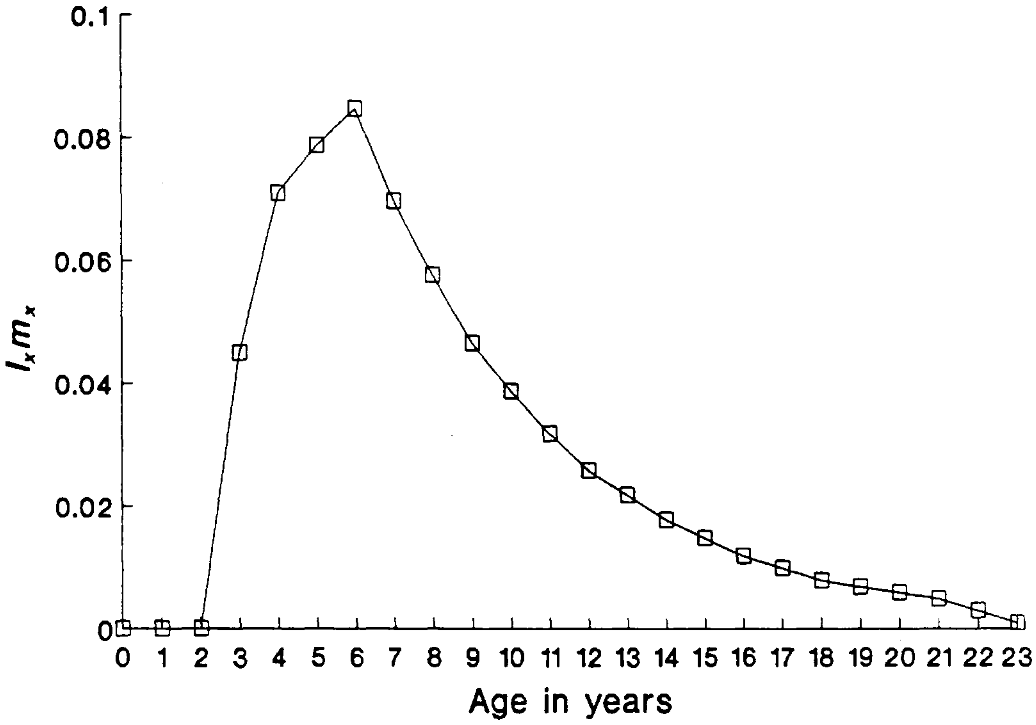

Figure 21. Age-specific changes in $l_x m_x$ values for southern elephant seal females born in 1983 at Marion Island.

Table 21. The effect on net reproductive rate, R_o, of changing the first year survival rate of southern elephant seals at Marion Island, while maintaining age-specific fecundity rates and age-specific survival rates after year one at the levels seen in the lifetable (Table 18).

Percentage of female pups surviving to age one	Net Reproductive Rate (R_o)
61,8	0,661
65,0	0,693
70,0	0,750
75,0	0,802
80,0	0,863
85,0	0,933
90,0	0,985
95,0	1,033
100,0	1,087

Table 22. The effect on net reproductive rate, R_o, of changing the annual adult (females aged five and over) survival rate of female southern elephant seals at Marion Island, while maintaining age-specific fecundity rates and age-specific survival rates up to age five at the levels seen in the lifetable (Table 18).

Annual survival rate of adult females	Net Reproductive Rate (R_o)
82,4	0,661
83,0	0,676
84,0	0,709
85,0	0,762
86,0	0,817
87,0	0,866
88,0	0,917
89,0	0,981
90,0	1,043

Discussion

The changes in the rates of increase (r) for the pup component of the population in the MSA may be the result of fluctuations around a lower asymptote at the end of a decline (Bester 1990a), or they may merely be a consequence of the small numbers involved. The MSA is not an isolated region and inter-annual movements of cows to different beaches could account for these apparent population increases. The largest of these changes involved eight of the pups born on the whole island, and it is therefore possible that it merely reflects a change in pupping site in that particular year.

Sex specific differences in rates of decline, or lack thereof

The observation that the adult sex ratio did not change over the period (1974-1989) under investigation suggests that despite the lack of an obvious trend in bull numbers during the period, the patterns of population change of bulls and cows did not differ greatly. This is in accordance with data for Macquarie Island over the period 1949-1985 (Hindell & Burton 1987), while contrasting previous findings for the Marion Island population (Skinner & Van Aarde 1983).

The ratio of bulls to cows ashore at Marion Island was as low as that reported for South Georgia (1:9; McCann 1980) and lower than reported for Iles Kerguelen (1:12,8; Bester & Lenglart 1982) and Macquarie Island (1:12, Hindell & Burton 1987). Given the similarity in the rates of decline at these sites and at Marion Island, along with the finding that sex ratio of adults ashore observed in one season had no effect on cow or pup lambda (λ) values, it would then seem unlikely that a shortage of males is responsible for the decline (see Skinner & Van Aarde 1983).

Social organisation at Marion Island differs from the other, larger breeding sites in the absence of the assistant beachmaster (ABM) category (Tables 11 & 12). Condy (1978) recorded an average of 0,53 ABM's per harem on Marion Island in 1974, and this social category generally only occurred in harems exceeding 50-60 cows. At Iles Kerguelen, Van Aarde (1980b) reported a mean harem size of 33 at which ABM's are admitted, while Bester and Lenglart (1982) suggested a value of 53 cows at the same site. From the above, it would seem that the present size of the harems at Marion Island are not of a size to allow the presence of an ABM.

Despite the observation that no significant reduction in mean harem size occurred between 1974 and 1988, the maximum harem size has decreased. In the present study no harem contained more than 60 cows, compared to the large (>100 cows) harems seen in 1974 (Condy 1978). This small harem size, combined with the discrete nature of the beaches on Marion Island allows the controlling bull to exclude other bulls from the harem. At other sites where harems are larger and situated on open beaches the beachmaster is unable to totally exclude other bulls from the harem (Condy 1978, Van Aarde 1980b).

Factors responsible for the decline

This section of the discussion will concentrate on the period 1983 to 1989, as it is for this period that life history parameters are available from tagged individuals.

Krebs (1985) noted that there are four fundamental variables which control the population size in any species, these being:

- recruitment from within the population (*i.e.* birth rate and juvenile survivorship),
- recruitment from outside the population (immigration),
- death of members of the population (mortality) and
- emigration.

Limited information from mark-recapture studies indicate that there is little, if any, intermixing of the different stocks of this species (Burton 1985, Bester 1989, Gales *et al.* 1989), and what intermixing does occur, does so at non-breeding sites. There are also no reports of new breeding colonies forming as a result of emigration from known sites and so it is unlikely that this is the cause of the decline.

The observed decline in the Marion Island population must then be the consequence of either changes in recruitment or mortality within the population. Factors contributing to the imbalance between birth and death rates may be low survival rates (in any age class), low pregnancy rates or delayed recruitment of females to the breeding population, or a combination of one or more of these factors.

Determination of age-specific survival estimates

The low tag loss rates in the present study (0,00% to 0,54%), result in calculations being based on known, as opposed to assumed values with a resultant increased confidence in the accuracy of the survival estimates.

The Jolly-Seber method relies on resightings of individuals in subsequent seasons to allow estimates of survival to be made. Consequently, estimates of age-specific survival improve with time. First year survival estimates (Figures 19a & 19b) improve by almost 50% with subsequent years resightings. This emphasizes the importance of long term data collection to the derivation of accurate population parameter estimates.

This is, to my knowledge, the second longitudinal study of southern elephant seals to rely on mark-recapture techniques to determine survival estimates. Studies at Macquarie Island followed several branded cohorts over their entire lifespan and survival estimates were based on the minimum numbers of individuals alive at each age (Hindell 1991). Resight effort did, however, differ between years and only covered a small fraction of the Macquarie Island coastline (Nicholls 1970, Hindell 1991).

The extent and consistency in search effort is important in view of the behaviour and demography of these animals. Because the mortality rates among juveniles (present study) are high, it is important to observe them each and every time they are ashore. If an animal is missed at one year of age, it may die before two but will be assumed to have died the previous year. The lack of fidelity to birth site of immatures (Wilkinson & Bester 1990b) emphasizes the importance of checking all beaches to determine survival rates. A further consideration is the timing of searches. Elephant seals have a well defined annual cycle (Carrick *et al.* 1962a, Condy 1979), and haulout periods of different age classes occur at different, but well synchronised, times of the year.

The differences in survival rates between the Macquarie Island and Marion Island populations may be the result of differences between island populations, differences in methodology, or may be linked to different factors involved in the decline of the species. No current data are available for Macquarie Island, nor are data available for Marion Island at the same time as when the Macquarie Island survival data were collected. It is therefore not possible to provide informed comment on the difference.

The use of the 1983 cohort to determine age-specific survivorship among females should provide accurate data as, by six years of age, all females are apparently recruited to the breeding population and should, therefore, be present on the island, and hence available for inclusion in the estimate. In addition, estimates of survival in younger female age classes will also have reached their peak (true) value. However, the possibility does exist that females will still arrive after this age which will inflate survival estimates. In contrast, the age-specific survival values for males are likely to be an underestimate as, by age six, not all males are recruited to the adult population. This may explain the observed sex differences in probabilities of survival (l_x). The presence of moulting subadult males in the Vestfold Hills, Antarctica (Tierney 1977) shows that these immature males do not necessarily haulout on their natal island during the year and so will not exist in the Jolly-Seber estimate. However, once the animal has attained social maturity (as opposed to sexual maturity) it will apparently return to its island of birth for breeding purposes, and thereafter to moult (Nicholls 1970).

Pre-weaning mortality

The values obtained for pre-weaning mortality are comparable with other reports for this species (4,5% at South Georgia; McCann 1985 and 5% at MacQuarie Island; Hindell & Burton 1987). That the Marion Island population has a comparable pre-weaning mortality rate to the stable population at South Georgia implies that mortality at this stage is not a driving force in the observed decline.

The lack of a relationship between pre-weaning mortality and cow (in terms of numbers of births) or bull density contrasts with findings in other populations of southern elephant seals (Carrick & Ingham 1962c, Van Aarde 1980b, Bester & Lenglart 1982) and in northern elephant seals, (Le Boeuf & Briggs 1977). A possible reason is that the effects of density related mortality agents only come into operation above a certain harem size, and the harems at Marion Island are below this size. Factors that have been implicated in pup mortality include trampling by males, wounds inflicted by females and starvation as a result of pups becoming separated from their mothers (Carrick *et al.* 1962b, Condy 1977, Le Boeuf & Briggs 1977, McCann 1982, Riedman & Le Boeuf 1982).

All the above mortality factors are exacerbated by high density conditions, and within the harems at Marion Island they will operate but not to the extent seen in larger harems at other sites. Male induced mortality will act as in larger harems, as bulls still fight for access to cows and pups will get trampled in the process. A mortality agent that probably exerts a lesser effect is that of pup starvation resulting from permanent separation (Le Boeuf & Briggs 1977).

The harems on Marion Island during the period of data collection (1974 onwards) were probably never of a size that the consequences of separation made themselves evident. Another possibility is that mortality rates in some of the large harems of the 1970's (Condy 1978), which were larger than during the present study, were underestimates. It is more difficult to count pups within larger harems and thus dead pups may have gone unnoticed. This is evidenced by the observation that at the larger breeding sites, where harems are larger than at Marion Island, cow numbers are used as an index of pup production as direct counting of pups is difficult (Hindell & Burton 1987, McCann & Rothery 1988). As harem size has declined the counts may have become more accurate and this has masked any density related changes in mortality.

First year survival

Figures for first year survival at Marion Island are similar to those at South Georgia (McCann 1985), while higher than that at Macquarie Island (Hindell 1991). Figures for the congeneric northern elephant seal are 58% for both sexes (Le Boeuf & Reiter 1988), while data for some otariids range from 50-60% (Kenyon, Scheffer & Chapman 1954, Lander 1981). No sexual differences are apparent in survival at this stage, which would support the view that the mortality factors acting on the two sexes are similar at this age.

Rates of first year survival did not differ for the six cohorts under consideration in the present study, which implies that during the period 1983 to 1989 there have been no major changes in factors influencing survival of this age group. At Macquarie Island first year survival declined from a mean of 47% during the 1950's to 28% in the 1960's, with the 1965 cohort showing less than 2% surviving to age one (Hindell 1991). These changes were attributed to factors influencing first year survival changing between the 1950's and 1960's at Macquarie Island. Inter-annual differences in resighting effort may have played a large part in the observed decline in survival rate. Yearlings haulout twice during the year, once to moult between mid November and January, and then again during autumn, with numbers peaking in April and May (Carrick *et al.* 1962a, Condy 1979). In both 1961 and 1962 no beaches at Macquarie Island were checked for marked seals (Nicholls 1970), which would result in underestimates of survival for one year old animals.

Immature & adult survival

Post first year survival figures at both Marion Island and Macquarie island are lower than those recorded at South Georgia (McCann 1985). The differences between Marion Island and Macquarie Island may be explained by the lower search effort at Macquarie Island (only a fraction of the island searched) or may reflect temporal differences as discussed earlier (see page 72).

Several northern phocids have adult female survival rates higher than the 83% seen in the present study. Survival rates for grey seals, *Halichoerus grypus*, (Harwood & Prime 1978), ringed seals, *Phoca hispida*, (Smith 1973), harp seals, *Phoca groenlandicus*, (Lett, Mohn & Gray 1981) and hooded seals, *Cystophora cristata*, (Jacobsen 1984) range from 88% to 97%. In Antarctic phocids, values for crabeater seals, *Lobodon carcinophagus*, are reported at 89% (Laws 1984), while those for Weddell seals, *Leptonychotes weddellii*, range from 74% to 97% (Siniff, De Master, Hofman & Eberhardt 1977, Croxall & Hiby 1983, Testa 1987).

Survival values for adult male southern elephant seals at South Georgia (McCann 1985) are considerably higher than at both Macquarie Island (Hindell 1991) and Marion Island (present study). However, given the polygynous breeding system of this species the consequences of male mortality will likely have a lesser effect than would female mortality until levels of male mortality increase to the extent that cows remain unattended in harems. In a rapidly expanding northern elephant seal population, annual mortality rates of 45% were reported for males (Le Boeuf 1974), indicating how few males are necessary to inseminate the available cows and permit population maintenance and growth.

Previous survivorship values reported for Marion Island (Condy 1977) were based on data from South Georgia (Laws 1960) and Macquarie Island (Carrick & Ingham 1962c). As comparisons have already been made with South Georgia and Macquarie Island, largely based on these figures, the data from the present study will not be compared with that of Condy (1977).

Age at first pupping & pupping rates

The mean age at first pupping and hence recruitment to the adult component of the population is similar for both Marion Island and the stable (McCann & Rothery 1988) South Georgia population (4,44, derived from data in McCann 1985), occurring a year earlier than at Macquarie Island (5,2 ± 1,8, Hindell 1991).

Pupping rates are higher at Marion Island than the figure of 85% quoted for the South Georgia population (McCann 1985). High natality rates, similar to those of the present study, are found in hooded seals (98%, Øritsland 1964 in Riedman 1990) and northern elephant seals (97,8%, Le Boeuf & Reiter 1988). The high proportion of cows pupping at Marion Island contradicts the suggestion that low numbers of bulls are limiting fertilisation success (see Skinner & Van Aarde 1983).

The fecundity of females in the present study has been assumed to remain unchanged until death at 23 years, there being no reproductive "senility". This assumption was based on observation of two 23 year old southern elephant seal cows at Macquarie Island which gave birth and successfully reared their pups (Hindell & Little 1988).

Net reproductive rate (R_o)

The R_o value derived from the survival/fecundity schedule suggests that we are dealing with a rapidly declining population. It is apparent that with each passing generation the population declines by 34%. As R_o is a composite of both survival and fecundity there are three factors which may influence it, age-specific survival, pregnancy rate and sex ratio of offspring.

Pupping rates would need to be advanced by two years, so that 100% pupping occurred at age four instead of six for R_o to reach 1. The age at first breeding has already decreased from the figure obtained for this population in the 1970's, when no three year olds bred (Condy 1977). Laws (1956b) suggested that the age at which a marine mammal reaches maturity is related to body size which is, in turn, affected by growth rate during the early years. Despite the necessity for the population at Marion Island to breed earlier to maintain itself, cows may be limited by their growth rates to their present pattern of reproduction. This may be indicative of reduced food resources preventing faster growth, despite the reduced numbers of animals competing for the available food. Although the age at first pupping is not early enough to permit replacement of the population, the proportion of females pupping after reaching maturity is as high as possible, given the fact that these animals only produce one offspring at a time.

Earlier primiparity can, in itself, produce some problems for a population. Northern elephant seal cows which produced their first pups at age four or five experienced lower mortality and higher fecundity rates than those that were primiparous at age three (Huber 1987, Reiter & Le Boeuf 1991). It was suggested that these effects were a consequence of the greater relative energetic costs of gestation and lactation incurred by the younger breeding females during a period in their development when growth was rapid (Reiter & Le Boeuf 1991). There is then a trade off between early breeding and the increased mortality resulting from it.

A second variable which could affect R_o is the sex ratio of offspring. The proportion of female pups seen in the present study is as high, or higher than that seen in other southern elephant seal populations. McCann (1985) reported an average figure of 47% female pups (assuming the sex ratio at weaning to be representative of that at birth). In the northern elephant seal 50,4% of 11073 weaned pups were female (Le Boeuf, Condit & Reiter 1989). In the presented model, a change in the proportion of females to 0,75 is necessary to raise R_0 to 1. It is also of interest to notice that the proportion of females recorded in the present study is higher than that used to produce an R_0 of greater than 1 at South Georgia (McCann 1985).

From the above discussion it would seem that it is survival which is driving down the R_0 value of this population. Higher survival rates would improve age specific $l_x m_x$ values and the resultant R_0 value.

The assumption of a constant adult survival rate until a year or two before death at age 23, will result in an inflated R_0 value in comparison to the data for South Georgia. McCann (1985) assumed, as did Laws (1960), that survival was constant from maturity until age 10 after which it decreased annually until death at age 20. This is in contrast to the findings for grey seals where female survival beyond the age of five was assumed to be constant (Harwood & Prime 1978). This assumption was supported by the goodness of fit of the data, from a shot sample, to a negative exponential curve (Harwood & Prime 1978). McCann (1985) argued that this could not be applied to southern elephant seals at South Georgia as it would require unrealistically high mortality rates to produce extinction at age 20. In the present study it was assumed that adult survival stayed constant until a year or two before extinction at age 23. If mortality increased from age five onwards then the R_0 value would be even lower than it already is, resulting in a faster rate of decline. Given the improvements seen in first year survival in the study with subsequent years resightings, the same is also probable for older age groups. Furthermore, as the numbers of animals remaining in the cohort decreases with age, the effect of the addition of relatively few individuals, on adult survival rates may be considerable.

The assumed annual adult survival rate of females (82,4%) is apparently not high enough to maintain the population, with a value between 89% and 90% necessary to realise an R_0 value of 1 in the presented model. If it is assumed that the observed adult survival rate is not abnormally low, then it may be the juvenile survival rates that are a problem. Although first year survival rates at Marion Island are comparable with those for South Georgia (McCann 1985), subsequent survival to age five differs markedly. If values for females up to the age of five are replaced with values reported for South Georgia, while maintaining survival from age five onwards at 82,4% the R_o reaches a value of one (Table 23).

The increase in female mortality rate between the ages of 3 and 4 (Figure 16b) comes at a crucial time for the Marion Island population. Although this age group is not the most reproductively valuable (Figure 21) a high mortality rate at this age will, combined with high juvenile mortality, reduce the level of recruitment to the adult population and thus affect the $l_x m_x$ schedule, lowering R_o. The sharp increase in the mortality rate between three and four years of age corresponds to the period when some of the females are maturing sexually, and may be exposed to increased physiological stress levels, resulting from gestation and lactation (Costa, Le Boeuf *et al.* 1986, Anderson & Fedak 1987).

Gestation and lactation impose increased energetic demands on the female, and these costs are relatively higher among young females (Reiter & Le Boeuf 1991) that are still in a more rapid phase of growth and development than their older counterparts (Laws 1953, Reiter *et al.* 1981). During the lactation period cows may lose up to 43% of their initial *pre-partum* mass (Costa *et al.* 1986). Cows at Marion Island in the present study that had recently weaned their pups were noticeably emaciated on their return to sea implying a severe drain on their body reserves. A second change which may occur among this group of females is a move from 'immature' to 'adult' feeding grounds. Haulout patterns show that during winter only immature individuals are to be found on Marion Island's beaches (MRI unpublished data). If we assume that only those animals who are in the proximity of the island haulout during this period then it would appear that adults are absent and are feeding in a different area during this period. There is, therefore, a possibility that the two groups forage in different areas. The young females which were the largest in their immature feeding areas are now the youngest and smallest in the new adult areas. This change in status may result in more stress in food acquisition (Carrick *et al.* 1962b). The combination of these two factors may explain the increase in mortality seen in this group.

Table 23. Lifetable of female southern elephant seals of the 1983 cohort at Marion Island. Mortality rates from age one to five have been replaced by those recorded at South Georgia (McCann 1985), while maintaining the estimated (present study) first year mortality rate and those after age five.

Age (x)	Probability of surviving (l_x)	Probability of dying (d_x)	Mortality rate (q_x)	Pregnancy rate	Fecundity (m_x)	l_xm_x
0	1,000	0,382	0,382	0,000	0,000	0,000
1	0,618	0,108	0,175	0,000	0,000	0,000
2	0,510	0,061	0,120	0,000	0,000	0,000
3	0,449	0,054	0,120	0,262	0,128	0,058
4	0,395	0,047	0,119	0,565	0,276	0,109
5	0,348	0,061	0,176	0,763	0,373	0,130
6	0,287	0,050	0,176	1,000	0,489	0,140
7	0,237	0,042	0,176	1,000	0,489	0,116
8	0,195	0,034	0,176	1,000	0,489	0,095
9	0,161	0,028	0,176	1,000	0,489	0,079
10	0,133	0,023	0,176	1,000	0,489	0,065
11	0,110	0,019	0,176	1,000	0,489	0,054
12	0,091	0,016	0,176	1,000	0,489	0,044
13	0,075	0,013	0,176	1,000	0,489	0,037
14	0,062	0,011	0,176	1,000	0,489	0,030
15	0,051	0,009	0,176	1,000	0,489	0,025
16	0,042	0,007	0,176	1,000	0,489	0,021
17	0,035	0,006	0,176	1,000	0,489	0,017
18	0,029	0,005	0,176	1,000	0,489	0,014
19	0,024	0,004	0,176	1,000	0,489	0,012
20	0,020	0,004	0,176	1,000	0,489	0,010
21	0,016	0,004	0,250	1,000	0,489	0,008
22	0,012	0,006	0,500	1,000	0,489	0,006
23.	0,006	0,006	1,000	1,000	0,489	0,003
						R_o = 1,072

CHAPTER 5

FACTORS AFFECTING REPRODUCTIVE SUCCESS

Introduction

The success of an individual, in an evolutionary sense, can be measured by the number of descendants it contributes to future generations which succeed in breeding (Wittenberger 1981). This fitness, or reproductive success, is measured over the entire life of an individual. Given the relatively long life span of large mammals, there are few studies which have measured lifetime reproductive success (see Clutton-Brock 1988). In many mammals, and especially pinnipeds, the survival of offspring to independence (i.e. weaning) is the only criterion of female reproductive success that can easily be measured (Doidge & Croxall 1989). A female can fail at two stages prior to the independence of her offspring. She may either fail to produce offspring, or she may give birth and the offspring will die prior to weaning.

A number of factors have been seen to affect survival of offspring in the post natal period prior to weaning. In red deer, maternal age, size and rank, along with date of birth and the body condition of the calf at birth all have an effect (Guinness, Clutton-Brock & Albon 1978, Clutton-Brock, Major, Albon & Guinness 1987, Clutton-Brock, Guinness & Albon 1982). Among pinnipeds, maternal age, size and rank (Reiter *et al.* 1981, McCann 1982, Ribic 1988), date of birth (Laws 1953, Carrick *et al.* 1962b, McCann 1982, Thomas & De Master 1983), birth weight and body condition (Carrick *et al.* 1962b, Thomas & De Master 1983, Calambokidis & Gentry 1985) and levels of maternal aggression (Christenson & Le Boeuf 1978, Ribic 1988) have all been seen to exert their effects.

Failure of a female to conceive may result from poor body condition (Stewart & Lavigne 1984) or because she is not mated while in oestrus. Female southern elephant seals are mated towards the end of lactation either within the harem in which they gave birth, or while on their way back to sea at the end of lactation (Laws 1956a, Carrick *et al.* 1962b). Matings outside the harem may be either by the controlling bull of the harem, or by subordinate bulls on the periphery of the harem (Laws 1956a, Carrick *et al.* 1962b). Skinner & Van Aarde

(1983) noted the apparent paucity of males in the Marion Island population and suggested that this may result in a number of females leaving the island after weaning their pups without being mated. Consequently, this shortage had a direct effect on the subsequent years pup production.

This chapter investigates factors affecting the survival of pups between birth and weaning and compares them with findings made for other southern and northern elephant seal breeding sites. In addition, cows studied over two or more seasons permit comment on how sexual behaviour at the end of their previous lactation period affected their chances of conception.

Methods

The study was carried out at Trypot beach, Marion Island. Observations were made on a dawn to dusk basis, from the day the first cow arrived (early September) until the last cow departed the rookery in mid-November, in 1986, 1987 and 1988. All bulls, cows, and pups were bleached marked (Lady Clairol 'Ultra Blue', Clairol Inc., Johannesburg, South Africa) to facilitate individual identification. Pups were given the same markings as their mothers. Cows were double tagged in their hind flippers and photographed to enable identification in subsequent seasons.

Maternal age, size and social status were determined as described in Appendix I.

Survival of pups to the age of weaning was related to the size, age and social rank of their mother, sex of the pup, date of birth, weight and condition at birth, length of suckling period, proximity of mother and pup (all variables which exerted an effect during their year of birth). It was also related to variables pertaining to the year in which it was conceived, these include: length of mother's haulout period, weaning weight of previous offspring and factors pertaining to sexual behaviour of the mother outlined below.

Mother-pup proximity and pup biting

The relative distance of all cows from their nearest neighbours in the study harem, and the distance of each pup from it's mother were recorded at hourly intervals during all three seasons. Distances were recorded as either (a) in contact, (b) less than one metre or (c) greater than one metre. When comparing nearest neighbour distances between pregnant and parturient females, and when comparing the amount of time surviving and non-surviving pups spent at various distances from their mother, categories (a) and (b) were combined.

When cows were seen to bite pups the identity of the pup and the attacking cow, along with the distance the pup was from it's mother at the time of the attack were recorded. In 1987 and 1988 all instances of pup biting were recorded, while in 1986 the numbers of animals on the beach precluded this form of data collection. The number of times a pup was bitten when at various distances from it's mother was compared with the number of times it would expect to be bitten, based on the proportions of time that mother spent at varying distances from their mothers. This also assumed that the distance a pup was from it's mother had no effect on it's chances of being bitten by another cow. Comparisons of numbers of bites received by pups of large and small cows, pups of high and low ranked cows, male and female pups, and pups surviving to weaning and those not, were made using the data for 1987 and 1988 only.

Sexual behaviour

The date of parturition, date of oestrus (cows were considered in oestrus if they assumed the lordotic posture when mounted by the bull, Figure 22), and all the copulations experienced by each cow (irrespective of which bull was involved) were recorded as events during continuous observations. From these events the following were calculated:

- birth to oestrus interval in days

- the duration of oestrus was defined as the interval, in days, from the first to the last day that cows exhibited lordosis.

- the total number of copulations occurring during a cow's oestrus period (experienced by all cows) involving only one (the dominant) bull.

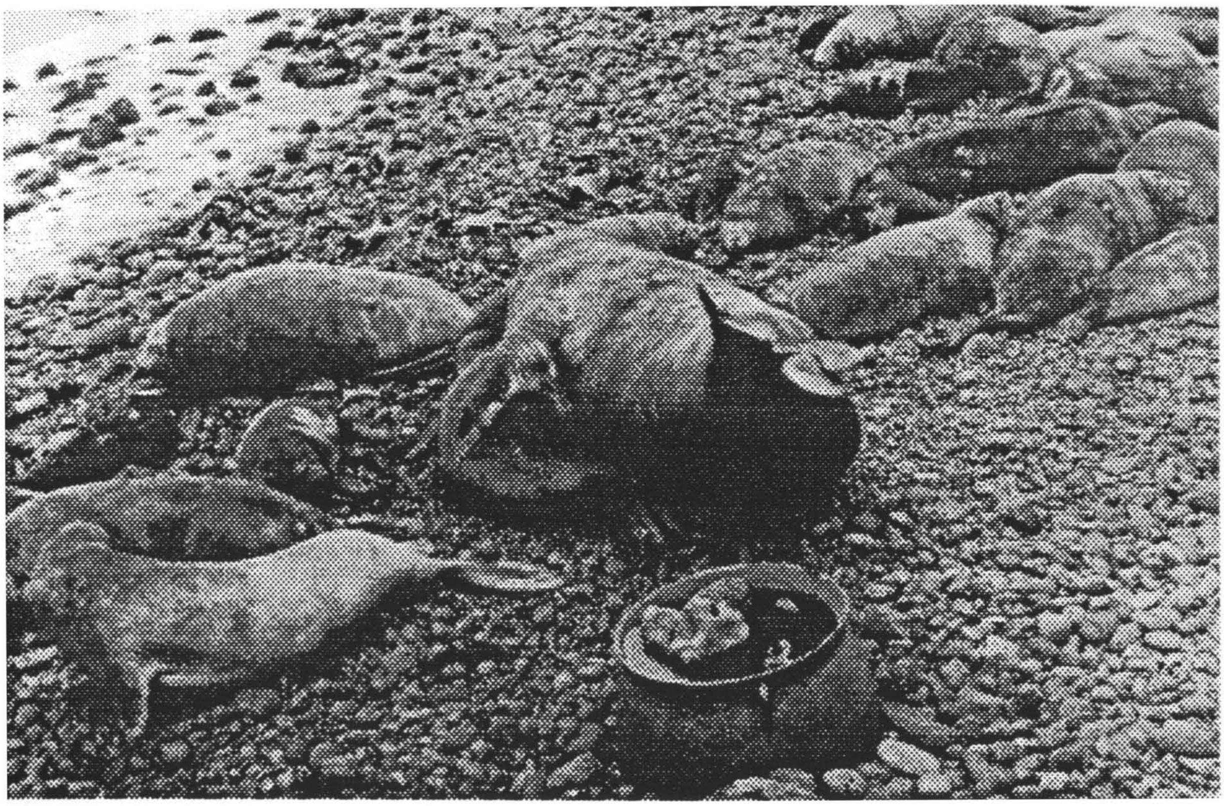

Figure 22. Southern elephant seal bull shown mounting an adult female exhibiting lordosis. The perineal region of the female is elevated and the hind flippers held apart to facilitate copulation.

- the number of cows in oestrus was defined as the mean number of cows (including the cow in question) in oestrus per day of the cows oestrus period.

- The number of copulations per day of a cow's oestrus period experienced from all the bulls at the beach.

- The number of copulations by a cow with a single (the dominant) bull, expressed as a proportion of the total number of copulations with all cows, involving that (dominant) bull, occurring during her oestrus period.

The aforementioned variables were compared for those cows conceiving and those not conceiving. As an indication of the level of sexual activity and fertility of the bulls, the number of copulations occurring on the beach (total numbers for all cows) for each day of the cow's oestrus period was calculated. For the purpose of this analysis only cows receiving copulations from the dominant bull alone were included. This analysis was limited to the 1986 season as only two cows from the 1987 season were observed to be barren the following year.

Pup mensuration

All pups were weighed within 24 hours of birth, most being weighed 6 hours after birth. Pups were removed from their mothers and weighed, to the nearest 0,5kg, in a sling using a Salter 150kg scale. Measures of curvilinear length and axillary girth were taken to the nearest centimetre (American society of mammalogists 1967). An index of body condition was determined from the relationship:

$$\frac{\text{Axillary girth} \times 100}{\text{Curvilinear length}}$$

Pups were given a bleach mark similar to their mothers and double tagged with 'Jumbo' rototags (Dalton Supplies Ltd., Henley-on-Thames, UK) in the interdigital webbing of their hind flippers. One day after weaning the weighing and measuring procedure was repeated.

Dates of birth, birth weights and weaning weights of pups seen alive at one year of age and those not seen (presumed dead) were compared.

Statistical procedures

Comparisons of two means were made using Student's *t* when variances were comparable, and comparisons of more than two means used one way ANOVA. When variances were not comparable Mann-Whitney 'U' tests were used in place of Student's *t*, and Kruskal-Wallis tests replaced ANOVA's. Ratios and proportions were compared using Chi-squared (χ^2) tests, Log-likelihood ratios (G), and Fisher's Exact test. Relationships between variable were compared using least squares regression analysis, and the resultant slopes tested for significant departures from zero using Student's *t*. Slopes of regression lines were compared using Student's *t*. All procedures follow Zar (1984). Footnotes in test results, *e.g.* r_{14} refer to number of degrees of freedom.

Results

Factors affecting survival which operated in the year of birth

Three of the 13 pups that died were separated from their mothers at birth, resulting in failure of the formation of the mother-pup bond. Two of these died at 10 and 14 days respectively without being very successful at obtaining milk from cows other than their mothers. The third suckled from 15 different females, and when 10 days old was successful in gaining milk from a cow which was still suckling her own pup. The cow permitted simultaneous suckling by the two pups for six days until she weaned her own pup. At this point she left the beach. The pup survived for 27 days before being killed to obtain samples for DNA analysis (not reported in this study). At the time of death it weighed the same as it did at birth.

Four pups were crushed by bulls in the harem, while another died from bite wounds inflicted by a low ranking bull after a failed attempt to copulate with it's mother. Two pups apparently died from starvation (weight at death was the same as at birth), despite the fact that they were never separated from their mothers. These mothers were small and the possibility exists that they did not produce any milk for their offspring.

Two pups were permanently separated from their mothers subsequent to the formation of the mother-pup bond. One of them was adopted by a cow, that had lost her own pup at birth, and reared to weaning. This pup was washed out to sea before it could be weighed and is presumed to have drowned. The second pup that was separated after the formation of the mother-pup bond was not observed to suckle from it's mother before separation, or from any other cow prior to it's death at the age of 12 days.

The thirteenth pup was washed into the sea when 19 days old, where it was seen to be eaten by killer whales.

Older cows weaned a greater proportion of their pups than did young cows, but the trend was not statistically significant (G=5,60; df=2; P>0,05; Figure 23). Large cows weaned a higher proportion of their pups than did small cows (100% *vs.* 93,4%) but this difference was not significant (Fisher's Exact, P=0,49).

Cows of known social status gave birth to 136 pups of which 124 (91,2%) were successfully reared to weaning. Of the 69 high ranking cows 66 (95,7%) reared their pups, while 58 (86,6%) of the low ranked cows reared their pups.This difference was not significant (G=0,786; df=1; P>0,05). During the study the number of mortalities were very low (n=13) and one of these was excluded from the above analysis as it's mother was not assigned a social rank. The cow in question remained apart from the harem, not interacting with other cows, from the date of her arrival until she departed 28 days later. She was small and apparently a first time breeder (deduced from the lack of scars on the neck). From Appendix I it follows that younger cows are low ranking. With the addition of this cow it is apparent that high ranking females are significantly more successful in rearing their young than low ranking females (G=4,49; df=1; P<0,05).

No significant sexual differences were observed in pre-weaning mortality at the study site, with 9 (12,0%) of 75 males and 4 (6,2%) of 62 females dying before weaning (G=1,25; df=1; P>0,05).

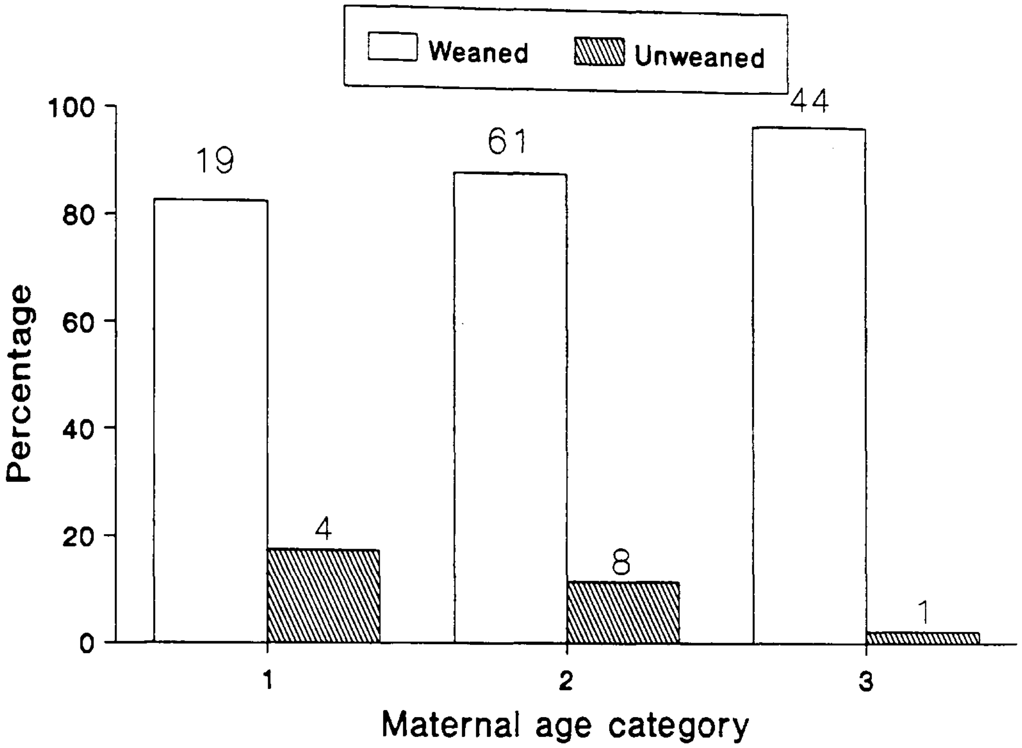

Figure 23. Percentage of southern elephant seal pups weaned by cows of three relative age categories at Trypot beach, Marion Island between 1986 and 1988 (numbers above bars indicate sample sizes).

Mortality rates before and after the median birth date did not differ significantly (G=0,44; df=1; P>0,05, Figure 24). Mortality rates of pups born within and outside the peak pupping period did not differ significantly (G=0,54; df=1; P>0,05).

Birth weights of male pups surviving to weaning were significantly greater (t_{60}=3,05; P<0,01) than those failing to wean, while in females no such relationship was evident (P>0,05). Curvilinear length (t_{127}=1,21; P>0,05), axillary girth (t_{127}=3,09; P<0,01) and body condition (t_{127}=1,99; P<0,05) were all greater, at birth, in pups that survived to weaning than those that did not (Table 24). The length of lactation was negatively correlated with the date of birth (r_{122}=-0,239; P<0,01).

Table 24. Comparisons of weights, curvilinear lengths, axillary girths and body condition at birth for southern elephant seal pups (at Trypot beach, Marion Island) surviving to weaning and those not surviving. Weights differed between males and females, but other parameters did not. Values were compared using Student 't' test (Zar 1984).

Parameter	Survived to weaning		Died prior to weaning or orphaned	
	Mean	S.D.	Mean	S.D.
Birth weight male (kg)**	40,9	5,1	35,4	5,5
Birth weight female (kg)	34,4	5,5	29,0	5,4
Curvilinear length (cm)	125,2	9,0	121,9	9,9
Axillary girth (cm)**	83,8	6,1	78,3	6,5
Body condition*	0,67	0,05	0,64	0,05

** = significant at P<0,01
* = significant at P<0,05

The nearest neighbour distance was significantly (χ^2_1=117,58; P<0,001) less among cows that had given birth than among pregnant cows. Pups that failed to reach weaning age spent, before they either died or were permanently abandoned, a greater percentage of their time at distances of greater than one metre away from their mothers than did pups that were reared to weaning (χ^2_1=169,90; P<0,001; Figure 25).

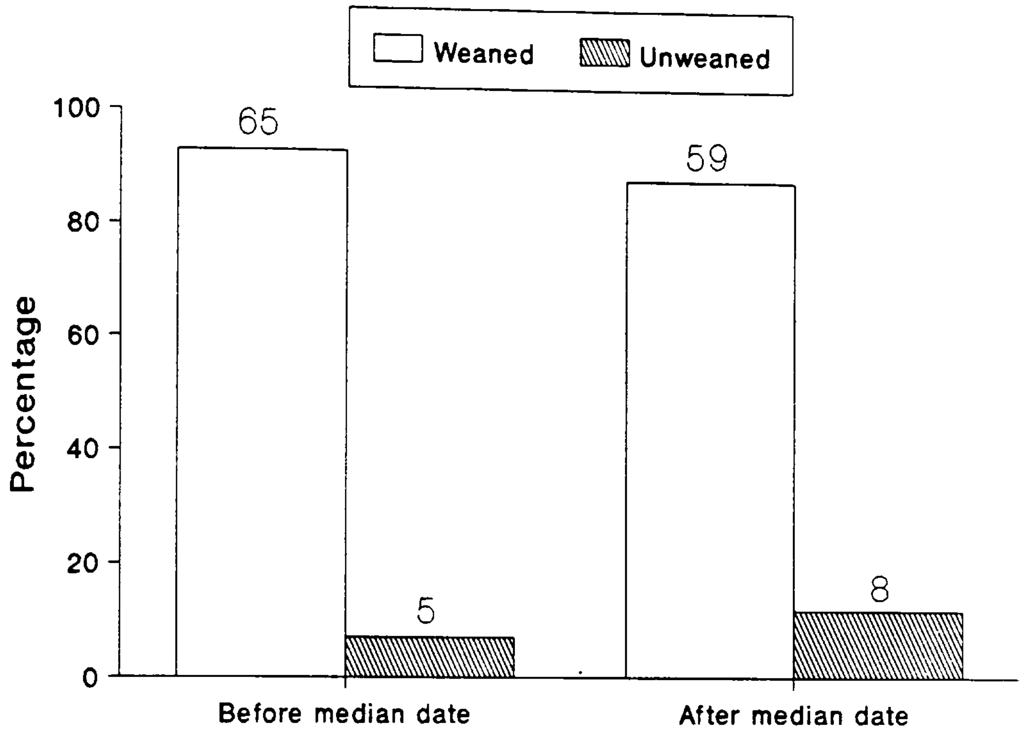

Figure 24. Pre weaning mortality rates of southern elephant seal pups born before and on or after the median recorded birth date at Trypot beach, Marion Island between 1986 and 1988 (numbers above bars indicate sample sizes).

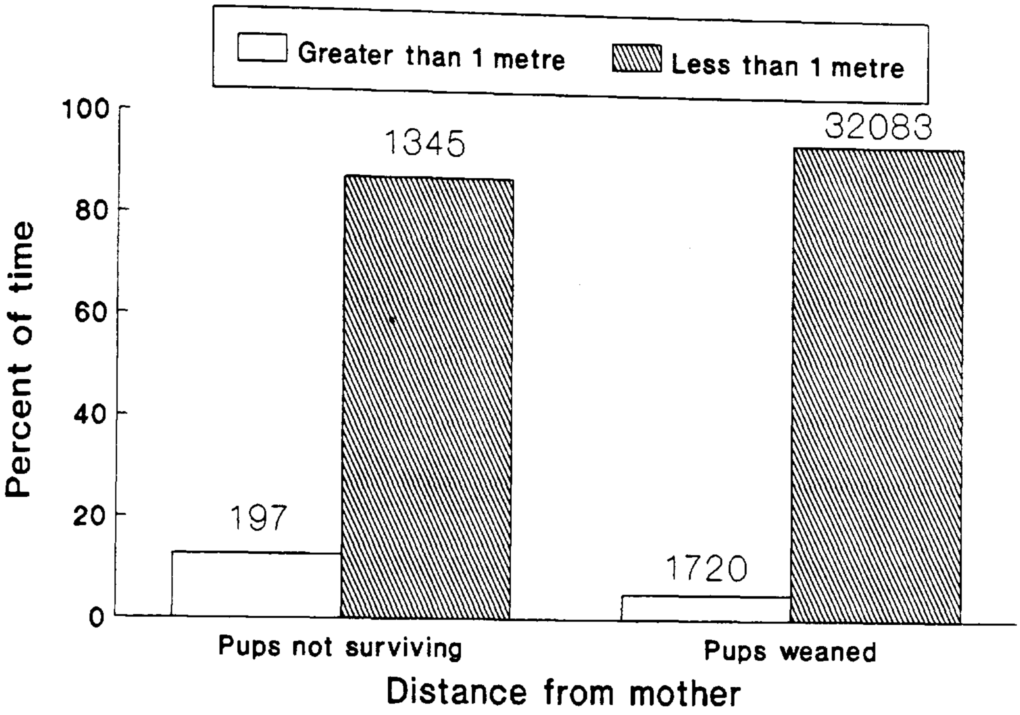

Figure 25. Percentage of time spent at distances of less than one metre, and greater than one metre, from their mother by southern elephant seal pups that survived to weaning, and those that died prior to weaning at Trypot beach, Marion Island between 1986 and 1988 (numbers above bars indicate numbers of scans).

Most mothers maintained close contact with their pups throughout lactation (Table 25), spending 42,4% of the time in direct contact, 52,2% within one metre and only 5,4% of the time more than one metre from the pup. These figures equal the expected frequencies in which pups are likely to be bitten when at these distances from their mothers, assuming that the chances of being bitten are unaffected by the pups proximity to it's mother. Observed frequencies of bites experienced by pups while at different distances from their mothers are shown in Table 26.

Table 25. Proximity of cow and pup southern elephant seals at Trypot beach, Marion Island in 1986, 1987 and 1988. Numbers refer to the number of scans when the animals were recorded in direct contact, less than one metre apart and greater than one metre apart.

Year	Proximity of cow and pup (number of scans)		
	In contact	< 1 metre	> 1 metre
1986	5187	8872	896
1987	3317	5330	415
1988	6464	4258	606
Total	14968 (42,4%)	18460 (52,2%)	1917 (5,4%)

Table 26. Number of bites received by southern elephant seal pups at Trypot beach, Marion Island in 1986, 1987 and 1988, while at varying distances from their mothers. Numbers of scans in which pups were observed at various distances from their mother is indicative of the time spent by the pups at these distances. The number of bites divided by the number of scans illustrates that pups are bitten more frequently while at greater distances from their mother.

Year	Number of bites		
	Proximity of cow and pup		
	In contact	< 1 metre	> 1 metre
1986	13	172	56
1987	130	274	61
1988	79	209	36
Total bites	222	655	153
Total scans	14968	18460	1917
Bites/Scans	0,015	0,035	0,080

Figure 26 shows a comparison between the frequency of bites observed on pups while at different distances from their mother and the numbers expected as explained above. Observed and expected values differed significantly ($\chi^2_2=299{,}9$; $P<0{,}001$), with pups in contact with their mothers being bitten less than expected while those not in contact were bitten more often, the disparity increasing with increasing distance from the mother.

The number of bites received by pups surviving to weaning and those not-surviving did not differ significantly (Mann Whitney U-test; $z=0{,}86$; $n_1=7$; $n_2=74$; $P>0{,}05$), and no significant difference existed between the number of bites received by male and female pups (Mann Whitney U-test; $z=0{,}28$; $n_1=35$; $n_2=46$; $P>0{,}05$). Of the three maternal variables, only cow size shows a significant difference (Mann Whitney U-test; $z=1{,}96$; $n_1=21$; $n_2=21$; $P<0{,}05$), with pups of smaller cows being bitten more frequently than those of large cows. There was a tendency for pups of young cows to be bitten more often than those of older cows (Kruskal Wallis; $H=5{,}25$; $n_1=11$; $n_2=43$; $n_3=27$; $P>0{,}05$), and those of low ranking cows were bitten more frequently than those of high ranking cows (Mann Whitney U-test; $z=1{,}54$; $n_1=39$; $n_2=41$; $P>0{,}05$), although neither difference is significant. (Table 27).

Table 27 The frequency with which southern elephant seal pups at Trypot beach, Marion Island (1986 to 1988) were bitten by other females within the harem in relation to maternal rank, maternal size, maternal age, sex of pup and whether the pup survived or not (M = median and n = sample size).

	Category		Category		Category	
	M	n	M	n	M	n
Maternal rank	Low		High			
	10	39	8	41		
Cow size	Small		Large			
	16	21	7	21		
Sex of pup	Female		Male			
	10	35	9	46		
Pup survival	Unweaned		Weaned			
	10	7	9	74		
Cow age	Age 1		Age 2		Age 3	
	16	11	10	43	7	27

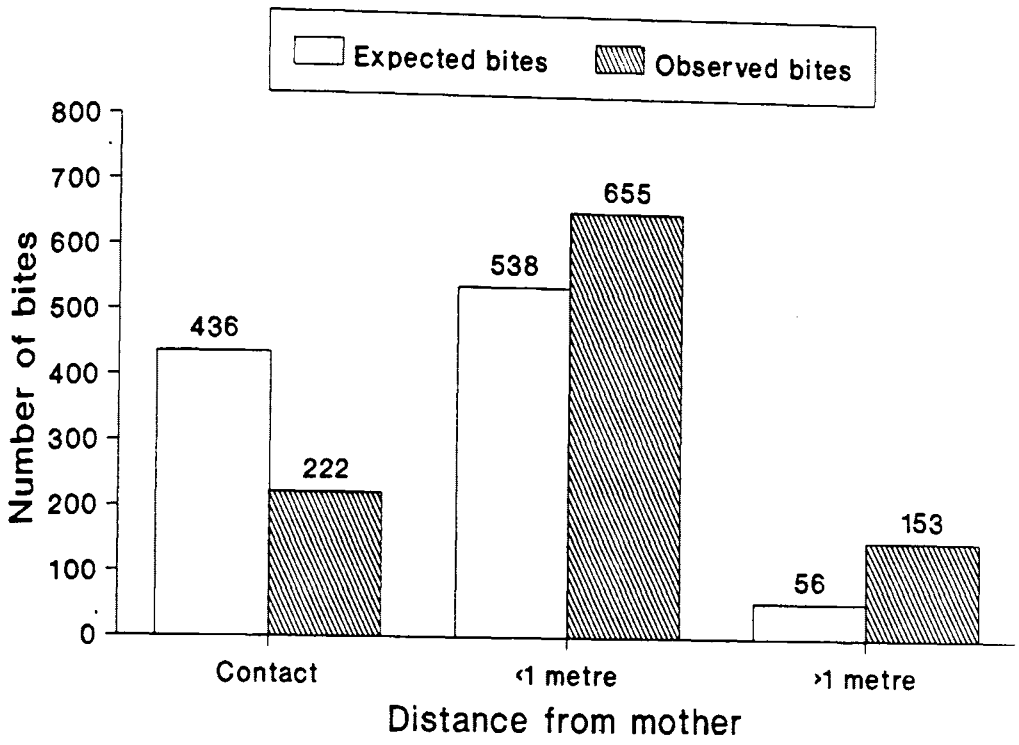

Figure 26. Number of times southern elephant seal pups were bitten while at various distances from their mothers at Trypot beach, Marion Island (1986 - 1988). Observed values are actual numbers of bites at each distance, while expected numbers are calculated from the amount of time the pups spent at each distance from their mother (numbers above bars indicate numbers of bites).

There was no correlation between the mean number of cows per day on the beach during a pup's dependent period and the frequency with which the pups were bitten (r_{79}=0,01; P>0,05).

Factors affecting survival which operated in the year of conception

There was no significant difference (Mann Whitney U-test; z=0,48; n_1=6; n_2=48; P>0,05) in the length of the haulout period in the year cows were mated between cows failing to conceive than those conceiving.

The weaning of a pup the previous season had no effect on whether the cow conceived (Table 28) or if she reared her next pup successfully (Table 29). Numbers were too small to test if investment, in terms of weaning weight, in a previous pup affected the survival of subsequent offspring. Only one reproductive failure was recorded for a cow whose previous reproductive performance was known.

Table 28. The influence of weaning a pup in year t, on the production of offspring in the following year, year t+1, among southern elephant seal cows at Trypot beach, Marion Island.

Weaned pup in year t	Produced pup in year t+1	No pup in year t+1
Yes	43	6
No	5	0

Fisher's Exact P=0,542

Table 29. The influence of weaning a pup in year t, on the successful weaning of a pup in the following year, year t+1, among southern elephant seal cows at Trypot beach, Marion Island.

Weaned pup in year t	Weaned pup in year t+1	Pup not weaned in year t+1
Yes	18	1
No	2	0

Fisher's Exact P=0,905

The six cows failing to produce pups in year t+1 weaned pups in year t that were lighter (Mann Whitney U-test; z=3,13; n_1=6; n_2=40; P<0,01), grew less between birth and weaning (Mann Whitney U-test; z=3,12; n_1=6; n_2=40; P<0,01) , and grew at a slower rate per day of lactation (Mann Whitney U-test; z=3,10; n_1=6; n_2=40; P<0,01), than those cows producing pups in year t+1 (Table 30).

Table 30. Weaning weights, weight increases between birth and weaning, and growth rates per day of lactation for pups of southern elephant seal cows at Trypot beach, Marion Island (1986 and 1987) which produced pups in the following season, compared with those cows that did not produce pups. Sample size is denoted by n.

	Cows producing pups n=40		Cows failing to produce pups n=6	
	Mean	S.D.	Mean	S.D.
Weaning weight (kg)*	106,9	15,0	83,3	11,3
Weight increase (kg)*	69,8	12,5	52,0	9,9
Weight increase per day (kg/day)*	3,31	0,58	2,44	0,55

* = Mann Whitney 'U' test, P<0,01

Over the three years of the study 617 (98,1%) of the 629 copulations observed, at the study beach, involved the dominant bull on the beach (Table 31). Levels of sexual activity, in terms of copulations per day of a cows' oestrus ($F_{2,131}$=20,36; P<0,001), total copulations on the beach per day of a cow's oestrus period ($F_{2,119}$=27,04; P<0,001), and the same parameter divided by the number of cows in oestrus ($F_{2,119}$=58,59; P<0,001) show an annual decline from 1986 to 1988 (Tukey's multiple range comparisons @ P<0,05). Other parameters showing differences were the number of copulations a cow received during oestrus (1986 differed from 1988, $F_{2,135}$=5,157; P<0,01), the proportion of copulations a cow received (the 1987 value was greater than both 1986 and 1988, $F_{2,119}$=4,30; P<0,05) and the numbers of cows in oestrus at a given time (1987 less than 1986 and 1988, $F_{2,131}$=18,89; P<0,001).(Table 31).

Given the above information that differences occurred between years, the analysis of the effect of sexual activity on subsequent fecundity was limited to the 1986 season, where four

Table 31. Inter-year comparisons of parameters relating to sexual activity among southern elephant seal cows at Trypot beach, Marion Island between 1986 and 1988. Differences between years were identified using one way analysis of variance (ANOVA), and significant differences, @ P<0,05, identified using the Tukey multiple range test (Zar 1984). Values in parentheses denote sample size unless otherwise stated. Parameters follow the definitions in the methods section.

Parameter	Year		
	1986	1987	1988
Total copulations	303	156	170
Number of bulls participating in breeding	5	2	2
Number of copulation by dominant bull (% of total copulations)	296 (97,4)	153 (98,1)	168 (98,8)
Number of cows only mated by dominant bull (% of total cows)	50 (89,3)	32 (91,4)	40 (87,0)
Mean number of copulations received per cow*	5,3 ± 0,4 (57)	4,3 ± 0,4 (35)	3,7 ± 0,4 (46)
Duration of oestrus (days)	3,3 ± 0,2 (56)	3,3 ± 0,3 (35)	4,0 ± 0,3 (43)
Proportion of copulations received*	0,21 ± 0,02 (50)	0,35 ± 0,05 (32)	0,22 ± 0,04 (40)
Number of cows in oestrus*	6,6 ± 0,3 (56)	4,2 ± 0,3 (35)	7,6 ± 0,5 (43)
Copulations received by a cow per day of her oestrus period*	1,8 ± 0,1 (56)	1,4 ± 0,1 (35)	1,1 ± 0,1 (43)
Birth to oestrus interval (days)	18,6 ± 0,3 (55)	18,2 ± 0,3 (35)	18,3 ± 0,3 (43)
Date of parturition	9 Oct ± 1,3 (56)	5 Oct ± 1,7 (35)	6 Oct ± 1,2 (46)
Date of oestrus	27 Oct ± 1,3 (56)	23 Oct ± 1,7 (35)	25 Oct ± 1,1 (43)
Total copulations by dominant bull for all cows/ duration of oestrus period of a single cow*	10,2 ± 0,4 (50)	5,4 ± 0,4 (32)	7,4 ± 0,5 (40)
(Total copulations/ duration of oestrus)/ number of cows in oestrus*	1,56 ± 0,04 (50)	1,30 ± 0,05 (32)	1,00 ± 0,03 (40)

* = significant differences between years.

cows failed to produce the following season. Statistical analysis was not possible on data for 1987 as the sample size of cows failing to conceive (n=2) prohibited this.

Level of sexual activity, measured as copulations per hour, was significantly related to the numbers of cows in oestrus (1986, $y=0{,}098x + 0{,}113$; $t_{41}=9{,}0$; $P<0{,}001$; 1987, $y=0{,}088x + 0{,}030$; $t_{41}=10{,}36$; $P<0{,}001$; 1988, $y=0{,}071x + 0{,}013$; $t_{41}=15{,}45$; $P<0{,}001$). The numbers of cows on the beach that were in oestrus simultaneously increased as the season progressed with higher numbers present in the latter part of the breeding period (Figure 27). Number of copulations per cow did not change with day of season, and neither did number of copulations/cow/day. The proportion of the total number of copulations during a cows oestrus period that she receives is negatively correlated to the number of other cows in oestrus at the same time ($r_{133}=-0{,}86$; $P<0{,}001$).

The total number of copulations (of the dominant bull) per day of a cow's oestrus period was correlated with the number of cows in oestrus on the beach ($r_{122}=0{,}81$; $P<0{,}001$), and the total activity on the beach (total copulations/duration of oestrus) did not differ between those cows conceiving and those not. This indicates that the fertilising capabilities of the bull were not reduced as a consequence of increased sexual activity.

No parameters measured in either 1986 (Table 32) or 1987 (Table 33) relating to sexual behaviour had any influence on the cows chances of conception.

The date a cow gave birth in any given year had no effect on her chances of conceiving that year (Mann Whitney U-test; $z=0{,}014$; $n_1=6$; $n_2=48$; $P>0{,}05$). The length of the birth-oestrus interval was the same in cows conceiving and those not conceiving (Mann Whitney U-test; $z=0{,}057$; $n_1=6$; $n_2=47$; $P>0{,}05$), and the date of oestrus did not influence likelihood of conception (Mann Whitney U-test; $z=0{,}056$; $n_1=6$; $n_2=47$; $P>0{,}05$).

The duration of oestrus (Figure 28) varied from 1 to 9 days but no differences were evident between cows conceiving and those barren. The number of copulations (Figure 29) received by a cow (range 1 to 15) was positively correlated with duration of oestrus ($r_{133}=0{,}59$; $P<0{,}001$), while the duration of oestrus was negatively correlated with the birth to oestrus

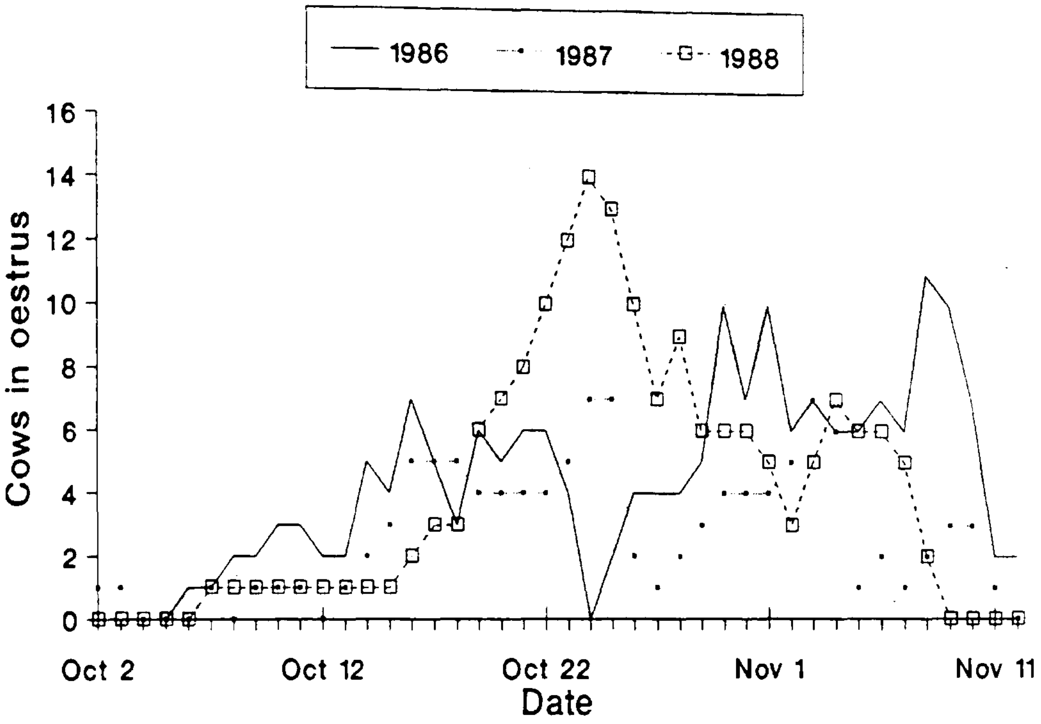

Figure 27. The number of cows in oestrus on each day of the 1986, 1987 and 1988 breeding seasons at Trypot beach, Marion Island.

Table 32. Comparison of mean values of parameters pertaining to sexual activity of southern elephant seals at Trypot beach, Marion Island in 1986, between cows conceiving and those not conceiving. S.D. and n refer to standard deviation of the mean and sample size respectively. Parameters are as defined in text. Mann Whitney 'U' tests (Zar 1984) revealed no significant differences for any of the parameters.

Parameter	Cows that conceived			Cows that did not conceive (n=4)	
	Mean	S.D.	n	Mean	S.D.
Number of copulations	5,4	0,7	28	5,0	1,5
Duration of oestrus (days)	3,2	0,3	27	3,0	0,7
Proportion of copulations received (%)	23,8	4,6	23	17,0	4,4
Number of cows in oestrus	6,4	0,4	27	6,3	1,0
Copulations per day of oestrus	1,9	0,2	27	1,6	0,2
Birth to oestrus interval (days)	18,6	0,4	27	19,3	1,4
Date of parturition	8 Oct	2,1	28	12 Oct	3,7
Date of oestrus	26 Oct	2,0	27	31 Oct	2,5
Total copulations per day of cows oestrus period	9,7	0,7	23	10,6	1,7

Table 33. Comparison of mean values of parameters pertaining to sexual activity of southern elephant seals at Trypot beach, Marion Island in 1987, between cows conceiving and those not conceiving. S.D. and n refer to standard deviation of the mean and sample size respectively. Parameters are as defined in the text. The low sample size of barren cows precluded statistical comparison.

Parameter	Cows that conceived			Cows that did not conceive (n=2)	
	Mean	S.D.	n	Mean	S.D.
Number of copulations	5,1	0,5	20	4,5	0,5
Duration of oestrus (days)	3,7	0,4	20	3,0	0,0
Proportion ofcopulations received (%)	35,4	6,8	17	58,7	41,3
Number of cows in oestrus	4,1	0,4	20	3,7	2,7
Copulations per day of oestrus	1,5	0,1	20	1,5	0,2
Birth to oestrus interval (days)	18,5	0,4	20	17,0	1,0
Date of parturition	6 Oct	2,3	20	26 Sept	
Date of oestrus	24 Oct	2,2	20	13 Oct	
Total copulations per day of cows oestrus period	5,6	0,5	17	4,6	3,0

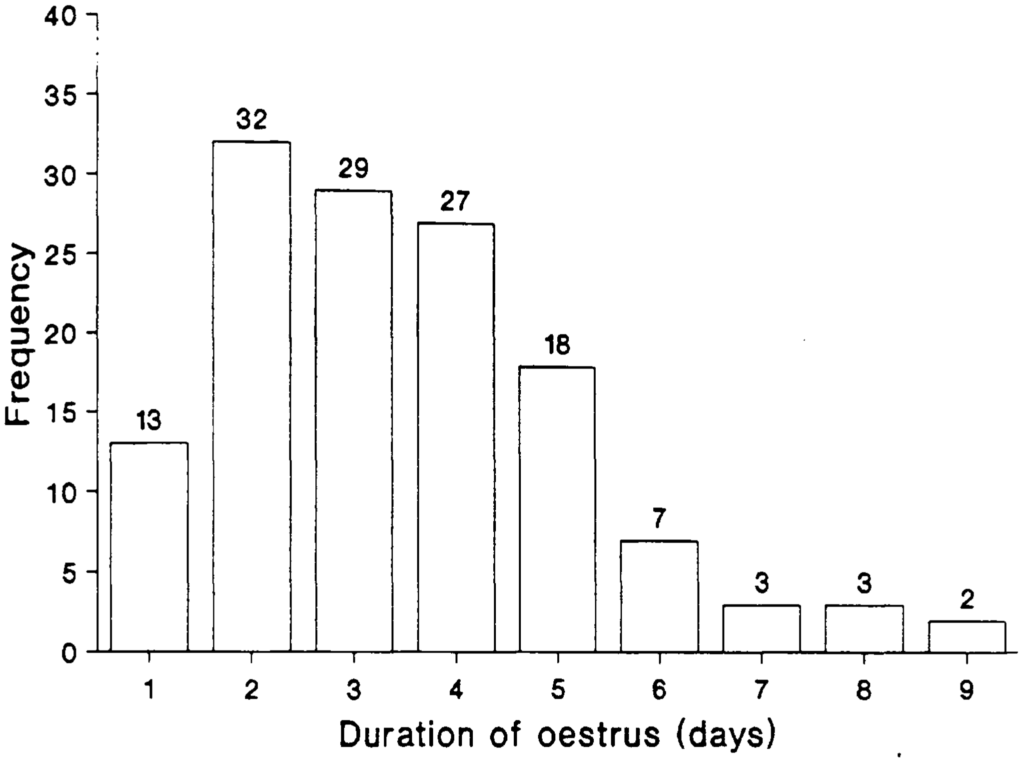

Figure 28. The number of days southern elephant seal cows were observed to remain in oestrus at Trypot beach, Marion Island (1986 - 1988).

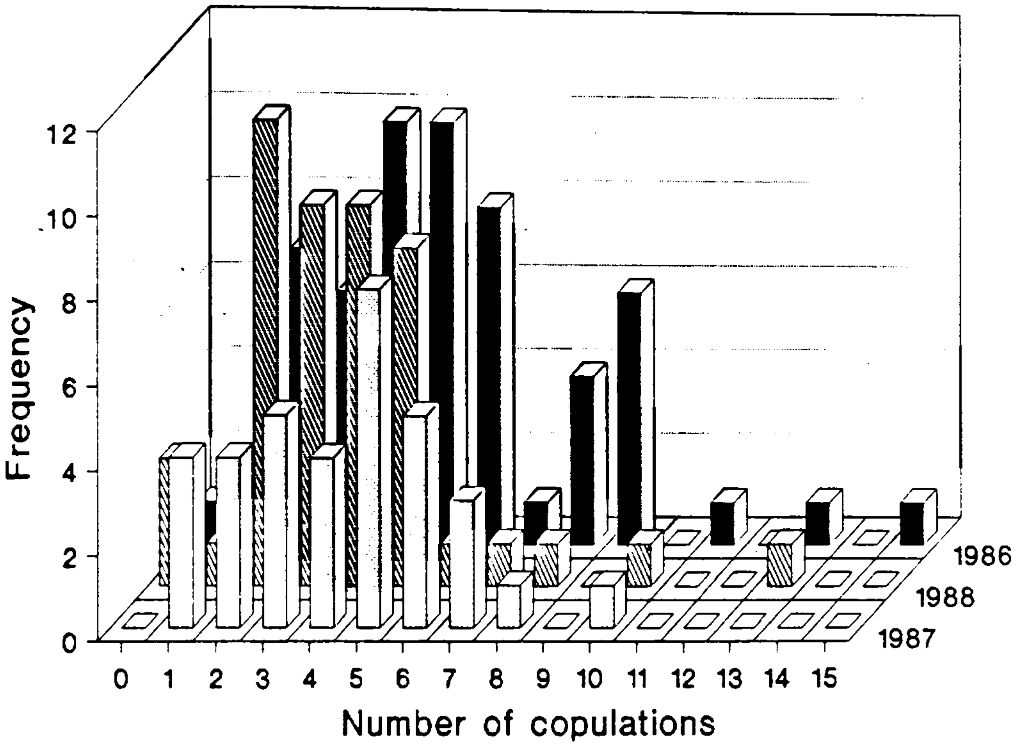

Figure 29. Frequency of copulation of southern elephant seal cows at Trypot beach , Marion Island during the breeding seasons of 1986, 1987 and 1988. Mean numbers of copulations received, differed significantly between seasons ($F_{2,135}$=5,15; P<0,01), and so are displayed separately.

interval (r_{132}=-0,42; P<0,001). No relationship was evident between date of oestrus and birth to oestrus interval.

Consequently, as duration of oestrus and number of copulations is positively correlated it is not surprising that there is no difference in number of copulations between conceiving and non-conceiving cows.

The number of cows in oestrus during the same period as the female in question, and the number of times a cow copulated during her oestrus period expressed as a proportion of the total copulations by the dominant bull did not effect her chances of conception.

Pups surviving to one year of age were heavier at both birth (t_{135}=2,18; P<0,05) and weaning (t_{118}=2,69; P<0,01) than those who were presumed dead. Date of birth however had no influence on survival (t_{135}=0,25; P>0,05). (Table 34).

Table 34. Comparison of dates of birth, birth weights and weaning weights of southern elephant seal pups born at Trypot beach, Marion Island that survived to one year of age and those that were presumed dead during their first year. S.D. and n refer to standard deviation of the mean and sample size respectively.

Parameter	Pups surviving to age 1			Pups presumed dead in first year		
	Mean	S.D.	n	Mean	S.D.	n
Birth weight	39,3	5,5	39	36,7	6,5	98
Weaning weight	113,1	17,2	38	103,1	19,8	82
Date of birth	7 Oct	8,9	39	7 Oct	9,8	98

Discussion

The trend in the current study for old, large, high ranking cows to successfully rear a higher percentage of offspring agrees with other studies on pinnipeds (Christenson & Le Boeuf 1978, Reiter *et al.* 1981, McCann 1982, Ribic 1988). It should be noted, however, that in the present study the tendency was not statistically significant.

The increased levels of male pre-weaning mortality that might be expected in a highly sexually dimorphic, polygynous species (Fisher 1930) such as the southern elephant seal were not observed in the present study. This is perhaps not surprising as the basis for this assumption, that males cost more to rear than females, did not hold true (see Chapter 6). Had it been the case that differential mortality was evident then the fact that smaller cows produce more daughters would have resulted in a lower reproductive success among these individuals. A similar finding of no differential pre-weaning mortality between sexes has been reported for both northern elephant seals (Le Boeuf & Briggs 1977) and red deer (Clutton-Brock, Albon & Guinness 1981).

Time of birth and survival

The date of birth is known to influence reproductive success in southern elephant seals (Laws 1953, McCann 1982), northern elephant seals (Reiter *et al.* 1981) and Weddell seals (Thomas & DeMaster 1983). Carrick *et al.* (1962b) and McCann (1982) reported an increase in birth weight of southern elephant seals at both Macquarie Island and South Georgia during the season, which combined with the observations in other species (Thomas & DeMaster 1983, Calambokidis & Gentry 1985, Clutton-Brock *et al.* 1987) that animals in poor condition, or low mass at birth are more likely to die before weaning, implies that it is advantageous to give birth later in the season. However, in the present study there was no relationship between birth weight or condition and date of birth. At South Georgia, pups born very early in the season melted deep holes in snow covering tussock grass, *Poa flabellata*, became trapped and subsequently starved (McCann 1982). Mortality rates of up to 30% from this cause were noted in some areas by Laws (1953).

Conversely, in the northern elephant seal early birth often confers an advantage on the pups as, once weaned, they have a longer period to steal milk to supplement their reserves at weaning (Reiter *et al.* 1981). Disadvantages in late births were highlighted by Condy (1977), who noted that late born pups at Marion Island were weaned up to nine days earlier than their early born counterparts. This shortening of the lactation period would result in lighter weaning masses with its consequences for post weaning mortality. In the present study the shortening of lactation between the first and last recorded births amounted to two days, which would result in a mass difference of around 4kg at weaning. This is unlikely to affect first year survival to the extent that the reduction reported by Condy (1977) would have. The post-weaning milk stealing behaviour exhibited by northern elephant seal weaners was only seen in one pup at Marion Island, and it would seem that this behaviour plays a much less significant role than in the northern species.

Pups born during the peak in cow numbers will be exposed to more intense density dependent mortality factors, *e.g.* more aggressive females, increased bull activity in and around harems with the resultant increased possibility of injury or death, and increased incidence of mother-pup separation and it's consequences (Le Boeuf & Briggs 1977). The finding that survival to weaning is not affected by date of birth is surprising both in terms of previously reported findings and from a theoretical view point. The seasonal nature of breeding in the southern elephant seal should be reinforced by stabilizing selection (Krebs 1985). Cooke & Findlay (1982) found that clutches of snow goose eggs hatching either side of the peak hatching period showed lower brood sizes at fledging than those hatched during the peak. This resulted from the increased effects of predation on smaller numbers on either side of the peak. In Weddell seals at McMurdo Sound, Antarctica, pups born very early and very late in the season had lower survival rates than those born at the peak of pupping (Thomas & DeMaster 1983).

Birth weight and condition

Data for red deer show that light born calves are more likely to die during their first summer than heavier calves (Guinness *et al.* 1978, Clutton-Brock *et al.* 1987), and in northern fur seals, *Callorhinus ursinus*, pups that died from all causes were significantly lighter at birth than the total population (Calambokidis & Gentry 1985). The pups dying in the present study were lighter than the mean birth weight of their peers.

How a bull crushing a pup can be influenced by the pup's birth weight is uncertain, but in the case of pups that are abandoned or starved the reasons are clearer. It is, therefore, possible that deaths of these smaller pups result from a combination of factors. In the present study, older, larger and higher ranking cows produced heavier pups than other cows, and these four factors were correlated with improved pup survival during the lactation period. In studies of northern elephant seals (Christenson & Le Boeuf 1978, Reiter *et al.* 1981, Riedman & Le Boeuf 1982) these maternal parameters were significantly related to survival of the pup. Larger, high ranking cows afforded their pups more protection than smaller, low ranking cows, which affected survival of their offspring. Thus low mass at birth may not, in itself, result in higher pre-weaning mortality, but rather may be a consequence of many other factors which, when combined, result in higher mortality.

Biting of pups

On Marion Island pups are more likely to be bitten by strange females when they are more than a metre apart from their mother, and pups that failed to survive until weaning spent proportionally more time away from their mother than did those that survived. This supports the view that maintenance of close contact between a mother and her pup affords protection to the pup. (Christenson & Le Boeuf 1978, Ribic 1988).

Permanent mother-pup separations which, in some northern elephant seal colonies is usually the prelude to the death of the pup (Le Boeuf & Briggs 1977, Riedman & Le Boeuf 1982) were not common in the present study. The low density of females present on the study beach probably facilitated the rapid reunion of mother and pup, as pups are rarely totally isolated from their mother by other females. In the high density harems of northern elephant seals, pups are often prevented from returning to their mother by hostile females (Le Boeuf & Briggs 1977), and die from starvation and wounds inflicted by these females.

Results of previous studies have shown that pups of high ranking cows are bitten less frequently than those of low ranking cows (*M. angustirostris*; Christenson & Le Boeuf 1978, *M. leonina*; McCann 1982). It was further shown in both cases that pups failing to survive to weaning age were bitten more frequently than those surviving. This suggests that maternal rank is correlated with pup survival. In the present study neither of the above relationships was evident, corroborating the findings in northern elephant seals by Ribic (1984), while a weak inverse relationship existed between cow size and biting frequency. One would expect that as the numbers of cows on the beach increases the frequency of agonistic encounters between them would increase, and as a result the number of occasions on which pups are bitten should also increase. The discrepancy with the present findings may be a consequence of the low numbers involved.

Biting of pups was not an important source of mortality in a northern elephant seal study at Southeast Farallon Island (SEFI), and the differences between that study and others carried out on northern elephant seals at Año Nuevo Island (ANI)(Christenson 1974, Le Boeuf & Briggs 1977, Christenson & Le Boeuf 1978) were ascribed to differences in cow density during the breeding season (Ribic 1988). This is supported by the observation that in 1983 when the breeding population of cows on SEFI reached a peak, the level of aggression and biting had the greatest influence on pup survival (Ribic 1988). There may be a threshold density above which the frequency of biting increases and the lack of a relationship between frequency of biting and the number of females seen in the present study may indicate that harems at Marion Island are not of a size at which density dependent factors operate.

The causes of death of pups in the present study are similar to those seen in other studies. The commonly occurring separations in northern elephant seal colonies (Le Boeuf & Briggs 1977, Riedman & Le Boeuf 1982, Ribic 1984, Stewart 1989) were not common at Marion Island, with only two pups being permanently separated after the formation of the mother-pup bond. The most common cause of mortality in the present study was male induced, or presumed to be so. The lower numbers of cows in the harems at Marion Island will reduce the incidence of separation and subsequent death of pups. Notwithstanding this reduction in mortality, the presence of bulls in and around the harem will result in pup mortalities, and this agent of mortality will assume a relatively greater importance than has been reported elsewhere.

Influence of previous investment on reproductive success

The apparent lowered conception rates following low levels of investment by cows in the present study are in contrast to what might be expected (Clutton-Brock, Albon & Guinness 1989). It is possible that poor condition in these cows results in the poor growth of their pups and this drain of rearing the offspring reduces body condition to such a point that either conception does not occur, or the pregnancy is terminated. The influence of poor body condition on chances of conception has been recorded in both harp seals (Stewart & Lavigne 1984) and red deer (Clutton-Brock *et al.* 1989).

Time of mating and its effect on conception

The difference in the level of sexual activity seen between seasons in the present study may be a consequence of individual differences in the reproductive effort of the bulls in different years, as is the case with other pinnipeds (Anderson & Fedak 1985, Bartsch, Johnston & Siniff 1991, Deutsch, Haley & Le Boeuf 1991). This would explain the difference between 1986 and 1987 when the dominant males were different individuals, but the bull in 1988 was the same as in 1987. A feasible explanation for this is that the injury to the left front flipper (cause unknown) of the beachmaster which occurred on 2nd November 1988 hindered him in his attempts to mate with cows. This bull appeared to favour his left flipper when mounting and was not as successful in mounting cows using his right flipper. In addition his locomotory capabilities were greatly reduced and many females were able to evade his mating attempts. Unfortunately, the consequences of this disability on conception rates could not be determined as these cows were not studied in the subsequent season.

The ability of this bull to retain control of the beach while apparently incapacitated probably results from the well established male hierarchy at the beach, and the low numbers of adult males at the site. By the stage of the season when the injury occurred the bull was secure in his social position and he was able to fend off rivals by roaring, or merely looking in their direction (see Sandegren 1976, McCann 1981a). If inter-male competition was more intense he would probably have been deposed. The tactic of fighting a weakened opponent has been observed in both northern and southern elephant seals (Laws 1956a, Carrick *et al.* 1962b, Le Boeuf 1974), this can either occur when a male is challenged immediately after he has just been fighting, or when a male arriving late in the season deposes a bull that has been weakened by fighting to keep his harem.

That sexual activity had no effect on the chances of conception indicates that the bull present at the site is more than capable of inseminating the cows that are present. The observation that the first and last cows mated by the dominant bull in both 1986 and 1987 produced offspring in the following season indicates that he was fertile at the beginning and end of the season. It does not, however, preclude the possibility that during the peak of sexual activity, within the season, frequent ejaculation may result in lowered fertilisation capability.

Studies in chimpanzees, *Pan troglodytes troglodytes*, have shown that sperm counts are lowered, but not significantly, by frequent ejaculation (Marson, Gervais, Meuris, Cooper & Jouannet 1989). It was reported that even after six ejaculations the epididymal sperm reserves were not completely depleted. Marson *et al.* (1989) suggested that the large reserve capacity of the epididymis was an adaptation to the multi-male breeding system of chimpanzees. Each male mates frequently with the oestrous females and has to deposit enough sperm to compete with that of the other males.

That levels of sexual activity, measured in total copulations by the dominant bull per day of a given cows oestrus period had no effect on whether or not the cow conceived, indicates that the bull was fertile for the entire duration of the period during which cows were in oestrus. It is not possible to say up to what harem size a single bull can successfully inseminate all cows, but in the present study a harem of up to 50 cows was successfully 'managed'. Given that there have been no changes in mean harem size between the 1970's and late 1980's, this finding rules out the possibility that low numbers of males are limiting fertilisation success as suggested by Skinner & Van Aarde (1983) for this population.

The frequency of copulation has been shown to affect the chances of conception in the ewe, *Ovis aries*. Depending on the time of insemination in relation to the stage of oestrus, single or multiple matings were required for fertilisation to occur (Jewell, Hall & Rosenberg 1986). Matings within the first three hours of the onset of oestrus did not result in fertilization, therefore multiple mating would be required. The most successful copulations occurred between 9 and 15 hours after the onset of oestrus, and if performed during this period only a single mating is required for fertilisation to occur. It was not possible to detect in the present study precisely when oestrus began, as determination was dependent on the behaviour of the bull. The results however, show that frequency of copulation received by cows had no influence on conception rates.

The frequency of copulation on the study beach at Marion Island was higher that at South Georgia (McCann 1981b) and for northern elephant seals at Año Nuevo Island (Le Boeuf 1972). At Año Nuevo Island between 1968 and 1970 the number of copulations per female, measured as total copulations divided by total females, ranged from 0,95 to 1,84, while at South Georgia the comparable statistic was 1,32. The corresponding values in the present study ranged from 3,7 to 5,3 copulations per cow. It seems strange that the values at Marion Island were so much higher than previously recorded, but may be the combined effect of small harem size and few attending males. The small, isolated harems are easily defended from peripheral bulls, who, as has been mentioned above, form a social hierarchy early in the season. Consequently the beachmaster can repel these bulls by ritualised postures as opposed to actual conflict. This leaves much more time for copulation by the bull.

At both South Georgia (McCann 1981b) and Año Nuevo (Le Boeuf 1972) the harems were very large, ranging from 100 to 300 females, and contained, and were surrounded by, many bulls. The bulls controlling these harems have to constantly repel intruders both entering the harem and attempting to mate cows within. McCann (1983) and Deutsch *et al.* (1991) reported in southern and northern elephant seals respectively that higher ranked males are more active than lower ranked ones. This increased level of vigilance at these sites may explain the apparent difference in copulatory frequency, however, until such time that comparable data are available for animals at Marion Island this remains speculative.

The practice of multiple mating observed in this study is common to both southern and northern elephant seals. Le Boeuf (1972) thought that multiple matings in elephant seals were due to the fact that matings are frequently interrupted and thus multiple copulation may be necessary to ensure insemination and pregnancy. In contrast to this view McCann (1981a) suggested that the first male to copulate with a cow is the one most likely to cause fertilization. This being the case, there should be a concerted effort by the beachmaster to prevent other bulls mating with cows, thus improving his own chance of being the first to do so. Multiple matings may then be a result of the bulls exclusion of others combined with an inability to determine which cows have already been mated.

The long duration of oestrus in cows would at first seem to be greater than necessary if only one mating was required for fertilisation. However, as these cows may aggregate in large harems, if they were in oestrus for only one day, it is possible that the chance of being mated would be low. So the length of oestrus could be viewed as a means of ensuring fertilisation. An alternative is that by lengthening oestrus the cow increases her chances of mating with the dominant bull. The longer a cow remains in oestrus, the more frequently she will be mated, and given the high percentage of matings achieved by dominant males, she will increase her chances of multiple matings, and of those matings coming from a dominant bull. Studies in laboratory rats have shown that the male mating last, or most frequently, has a significant reproductive advantage over the male mating first (Dewsbury & Hartung 1980). How many matings are required to ensure fertilisation can not be determined, however, the five (3,6% of the total cows) cows receiving only a single mating appear to indicate that one mating is adequate. Given that the population at South Georgia is replacing itself (McCann & Rothery 1988) then it would seem that one copulation per female is sufficient for fertilisation.

As males are known to remain fertile for the duration of the breeding season, it does not seem so critical as to the time the cow comes into oestrus. As the season progresses the numbers of receptive cows increase, and the males reproductive effort increases proportionally. This increase in activity combined with the increase in number of receptive cows results in a decrease in the proportion of matings a given cow receives. This proportion of matings is the only parameter which really changes with time of season, and as it does not affect conception, time of mating appears to be unimportant.

CHAPTER 7

CONCLUSIONS

In conclusion, this study has highlighted the continued decline in numbers of southern elephant seals at Marion Island. The slowing of the rate of decline may indicate that the population is levelling off at the tail of an exponential decline as has been reported at Gough Island (Bester 1990a). In the most recent suggestion as to the cause of the declines, Hindell (1991) suggested that the populations at both Macquarie Island and Iles Kerguelen may be returning to pre-sealing levels after rising to abnormally high levels at the end of exploitation. This was based on the observation that, after reaching a figure of 156,000 seals in the 1950's, the Macquarie Island population declined to approximately 90,000 in 1985, which is similar to the estimated pre-sealing population size of 90,000 - 110,000 (Hindell & Burton 1988a). Given the magnitude of the decline observed at Marion Island, an 84% reduction in the number of pups born between 1951 and 1989, it seems unlikely that the population could have overshot its original size by a factor of seven. Furthermore, it would also imply that the sealers who harvested southern elephant seals at Marion Island up until 1930 (Marsh 1948) were utilising a population that produced only 600 pups per year, which would have been uneconomical. Given the above, the observed decline is real.

The observations of animals over the three years of the study showed that factors which may affect the reproductive success of cows at Marion Island, such as maternal age, size, social status as well as the dates of birth, weaning, oestrus, and the number of copulations a cow received had no effect, despite the fact that these factors operate in other elephant seal populations (Laws 1953, Carrick *et al.* 1962b, Christenson & Le Boeuf 1978, Reiter *et al.* 1981, McCann 1982). Many of the problems associated with these factors are exacerbated by high density conditions, while almost absent at low densities. An example would be the effects of separation of a mother and her pup, in high density harems this situation frequently leads to permanent separation and ultimately death of the pup, while in low density harems mother and pup are usually reunited. The reduction in population size has given rise to the low densities of harems at Marion Island providing a favourable environment in which to raise offspring, evidenced by the high reproductive success of cows at the site.

To produce a pup in the first place a cow must be fertilised and conceive during the previous season. The suggestion that the absence of adult males on the periphery of harems at Marion Island was having a negative effect on fecundity rates (Skinner & Van Aarde 1983) is untenable in view of the high fecundity rates seen and the observation that levels of prior sexual activity have no effect on the success of copulations by the bull. Given the observed capabilities of the breeding bulls, it would appear that given the present size of the harems at Marion Island, these beachmasters are, alone, more than able to ensure the production of the following years pups by the vast majority of cows.

Notwithstanding the limitations of the mark recapture data (in that it does not span the entire lifespan of the cohort in question) it would appear that the decline at Marion Island is being driven by factors which affect the survival of immature and young adult females. First year survival is good, which indicates that cows are weaning healthy young. The observed high fecundity rates and already declining age at sexual maturity of cows indicates that they are reproducing as fast as they are able to. Adult survival rates are not especially low given the improved estimates expected with subsequent years resightings, and thus the recruitment of females to the adult age classes appears to be the problem. Despite the high fecundity rates and the early maturation of females, too few are surviving to adulthood to maintain the population.

The identification of sub-adult and newly mature cows as the vulnerable component of the population, along with the findings of the reproductive success study focus attention away from the intensely studied terrestrial component of the southern elephant seal's life history. Modern technological advancements have made the study of at-sea behaviour of these animals possible (Le Boeuf *et al.* 1988, Hill 1991, Hindell, Burton & Slip 1991) and it is during this pelagic phase that the key to the decline must be sought. Comparison of the at-sea behaviour and foraging areas of these young females with their older counterparts may identify important differences pertinent to the decline.

The lack of evidence of differential investment between the sexes in terms of lowered fecundity, or differences in birth and weaning weights or daily growth rates was surprising in a species such as the southern elephant seal, which exhibits extremes of sexual dimorphism and polygyny. Cows do, however, apparently 'manipulate' the sex ratio of offspring in favour of the sex which they are best suited to nourish, with larger/older cows producing more males and smaller/younger cows more females. The mechanism by which this manipulation is achieved is, however, not yet understood. Accepting the weak link between size at weaning and adulthood, manipulation of the sex ratio in these cows allows them to maximise their reproductive success dependant on their abilities. Cows in a position to invest heavily in offspring should produce males as in a polygynous species they can achieve a higher reproductive success. The lack of unequivocal support for theoretical expectations suggest that, in agreement with the views expressed by McCann *et al.* (1989), sexual selection may not be the most important factor shaping maternal investment patterns in this species. That sexual selection is operative in this species, given its characteristics, is not in doubt, but the extent of its role in the control of investment patterns, in this population at least, may be.

CHAPTER 6

FACTORS AFFECTING SEX OF OFFSPRING AND IT'S CONSEQUENCES

Introduction

The sex, and patterns of care, of offspring have been of great interest to evolutionary biologists (Trivers & Willard 1973, Maynard Smith 1980). Where reproductive success varies more widely among offspring of one sex, and is influenced by parental investment, parents should invest in that sex. This can be done either by skewing the sex ratio at birth towards the more valuable sex (Trivers & Willard 1973) or by producing a 1:1 sex ratio at birth, and then investing differentially in the most valuable offspring (Maynard Smith 1980).

Investment in offspring comes from both parents, but some forms are, of necessity, the prerogative of one parent only. Investment in mammals can include, production of primary germ cells, gestation, den building or modification, parturition, lactation, feeding and protection of young (Trivers 1972).

Southern elephant seals are among the most sexually dimorphic and polygynous of all mammals, males may be more than 10 times the weight of a reproducing female (McCann *et al.* 1989). Some 90% of adult males die before reaching social maturity, and of those males reaching this age only the largest and strongest succeed in breeding (Jones 1981, Le Boeuf & Peterson 1969). These males, depending on location, may be successful in breeding in only one season or for at least five seasons (Marion Island, MRI records). In this time the male may sire more than 100 offspring (Le Boeuf 1974). In comparison, virtually all females breed from the time they reach sexual maturity at age 3 or 4, annually until death at about 20 years. Twins are extremely rare, so females may produce up to 17 pups in their lifetime (assuming no missed pregnancies).

Thus it is clear that the variation in reproductive success is far greater among male offspring than female offspring. In northern elephant seals such variation among males is four times that of females (Le Boeuf & Reiter 1988), and male mating success is strongly correlated with size.

Estimation of parental investment in southern elephant seals is simplified by the following:

- males invest nothing but sperm in offspring.

- females breed on island beaches and are easily observable throughout the course of maternal investment, a 21 day period during which the lactating mothers fasts.

- all nourishment for the pups comes from the mother's milk and thus weaning weight should provide an indicator of investment.

- it is unlikely that post-weaning investment occurs, since female southern elephant seals go to sea after weaning and mother-pup contact is ended.

Given the above, evolution would favour greater investment in males than females (see Le Boeuf *et al.* 1989). Mothers in good condition could achieve this greater investment by diverting more resources to individual sons than daughters, or by modifying the sex ratio, or by a combination of these methods.

To this end this study set out to identify which of these options cows at Marion Island utilise, if any. In addition, in view of the declining population numbers at this site, comparisons of levels of investment with those at other breeding localities of this species are pertinent.

Methods

Cow and pup identification

All cows coming ashore on Trypot Beach in the 1986 - 1988 breeding seasons were marked with bleach to facilitate individual identification, and tagged in their hind flippers to allow inter-season identification. Pups were given similar marks to their mothers when handled for the purposes of weighing soon after birth. The methods used in the division of cows into size categories, and their parity is described in Appendix I. Methods relating to sexual activity are described in Chapter 5.

Gestation length

Gestation length was calculated for a number of cows present at the study colony over more than one season. The period was taken as the interval (in days) between the date of birth and the first observed copulation in the previous year. The Mann-Whitney 'U' test (Zar 1984) was used to compare gestation lengths of male and female pups.

Maternal survival and fecundity

Reasons for not seeing cows in subsequent seasons include, tag loss and thus loss of identification, dispersal to other islands or mortality. When comparing resightings of females over 1 or 2 years, after the production of a pup, as in the present study, differences between mothers of male and female pups are assumed to result from differences in mortality, as there is no reason to suspect that either tag loss or the tendency to move to another island should differ between these maternal categories.

Fecundity of cows was determined by using a combination of direct sightings and estimation from moult dates and shifts in departure date as described in Chapter 4.

Pup mensuration

All pups were weighed to the nearest kilogram within six hours of birth, and their axillary girth and curvilinear length measured. Standard length was not measured as pups could not be immobilised to facilitate this measurement. These pups were reweighed within 24 hours of weaning and the weight gain determined. Weaning was determined as the date on which the cow and pup became permanently separated. Growth rates for the pups were calculated by dividing the weight gained by the duration of lactation (assuming growth was linear during this period). One way analysis of variance (Zar 1984) indicated that no differences existed between the data for birth weight, weaning weight and growth rate between seasons. As a result all data were pooled for analysis.

Birth weights were compared with data for Macquarie Island (Little, Bryden & Barnes 1987) and South Georgia (McCann *et al.* 1989) using single factor ANOVA (Zar 1984) and Tukey multiple range test (Zar 1984) to identify differing groups. Mean weaning weights and daily growth rates were compared with those at South Georgia using Student's *t* (Zar 1984). Pups at the study site were sexed at the time of weighing, while those at beaches between Blue Petrel Bay and Archway bay were sexed when tagged within a few days of weaning.

Date of birth

The possible relationship between date of birth and offspring sex was investigated in two ways. First, by looking at animals at the study site whose exact birth date was known and second by looking at the sex ratio of pups tagged between Blue Petrel Bay and Archway bay (in 1987 and 1988), where beaches were checked every second or third day for newly weaned pups. Sex ratios of pups at the study site were compared before and after the median birth date, while at the other sites the tagging period was divided into four quarters, and the sex ratio for each of these periods was checked according to the method used by Stirling (1971).

Suckling behaviour

During 1987 all pups were observed daily, from birth to weaning, to determine time spent suckling. The colony was scanned at five minute intervals and each pup was recorded as not suckling, suckling their filial mother, suckling another female, visible but activity undetermined, and not visible during the scan.

If pups were seen suckling on two consecutive scans they were considered to have suckled during the interim period also. Thus, the percentage of scans encompassing each activity were taken to be indicative of the daily pattern. Percent of each day spent suckling was calculated and then total time during the period of parental care spent suckling was determined from the average of these daily values multiplied by the duration of lactation. This value was then expressed in suckling days. The relation between age and suckling intensity was determined by averaging all values for males and females of a specific age and plotting the arcsine transformation of this value against age in days. The slopes of the regression lines for males and females were then compared using Student's *t* (Zar 1984) to allow comment on whether males suckle more frequently than females.

Longitudinal observations on individual cows

Seventeen cows were observed at the study site in more than one season and data on sex of offspring, birth weights, weaning weights, growth rates and duration of lactation permit comment on the possible occurrence of differential investment in individual females.

General statistical procedures

Comparisons of means were made using Student's *t*, unless variances were not comparable in which case Mann-Whitney 'U' tests were used. Ratios and proportions were compared using Chi-squared (χ^2) tests. Relationships between variables were compared using least squares regression analysis, and the resultant slopes tested for significant departures from zero using Student's *t*. Slopes of regression lines was compared using Student's *t*. All procedures follow Zar (1984). Footnotes in test results, *e.g.* r_{14} refer to number of degrees of freedom.

Results

Sex ratio

During the study 75 male pups and 62 females were born giving a sex ratio of 1,21:1. This ratio did not differ significantly from unity (χ^2_1=1,24; P>0,05). Between 1983 and 1989, 3856 pups were tagged (at weaning) as part of long term study of the population parameters of the Marion Island population (Table 10). The ratio of males (n=1970) to females (n=1886) tagged was 1,04:1 and did not differ significantly from unity (χ^2_1=1,82; P>0,05). The sex ratio of pups born on the study beach and those born on the island during the same years did not differ significantly (χ^2_1=0,57; P>0,05)

There was a significant trend for large cows (n = 30) to produce more male than female pups and for small cows (n = 30) to show the opposite trend (χ^2_1=9,6; P<0,01). Primiparous cows (n = 23) produced significantly more females and multiparous cows (n = 114) significantly more males (χ^2_1=12,15; P<0,001) (Figure 30).

Pre-natal investment

Gestation length in males ($\bar{x}$=343,8 ± 3,1 days; n=13) was not significantly (Mann Whitney U-test; z=-0,80; n_1=7; n_2=13; P>0,05) different to that of females ($\bar{x}$=344,9 ± 3,2 days; n=7). There was no relationship between the date of first copulation and the length of gestation (r_{18}=0,137; P>0,05).

Male pups were significantly (t_{135}=6,536; P<0,001) heavier ($\bar{x}$=40,3 ± 5,4 kg, n=75) at birth than females ($\bar{x}$=34,1 ± 5,6 kg, n=62). Large cows (see Appendix I for definition) produced pups (both male and female) of significantly greater birth weight than small cows (Table 35). Birth weights of male pups at Marion Island were significantly lower than those for South Georgia ($F_{2,121}$=5,488; P<0,05; Tukey multiple range test @ P<0,05; Table 36), while for females Marion Island differed from both Macquarie Island and South Georgia ($F_{2,100}$=13,777; P<0,001; Tukey multiple range test @ P<0,05; Table 36), but the latter two sites did not differ.

Post-natal investment

Length of lactation in cows producing males ($\bar{x}$=21,2 ± 1,7 days, n=66) and females ($\bar{x}$=21,5 ± 2,0 days, n=57) did not differ significantly (t_{121}=0,88; P>0,05). Length of lactation for large cows ($\bar{x}$=21,4 ± 2,3; n=28) and small cows ($\bar{x}$=22,0 ± 1,7; n=29) did not differ significantly (t_{55}=1,08; P>0,05).

Daily growth rate (kg/day) during the lactation period were significantly (t_{118}=2,835; P<0,001) higher in males ($\bar{x}$=3,4 ± 0,7 kg/day, n=66) than females ($\bar{x}$=3,0 ± 0,7 kg/day, n=54). Rates

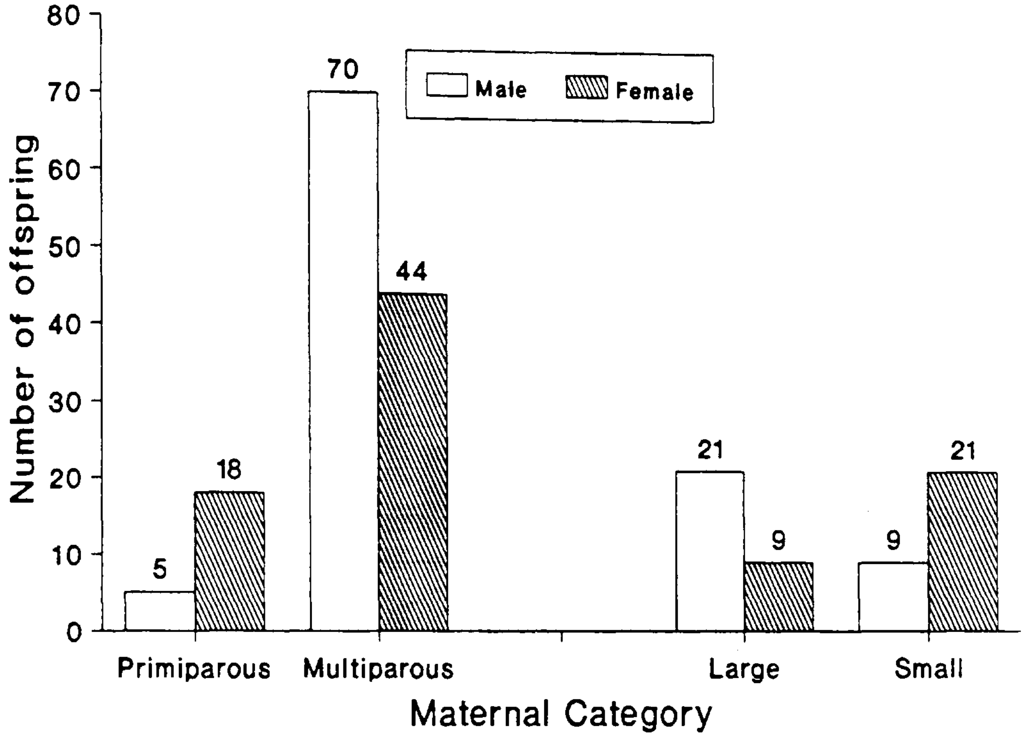

Figure 30. Sex of southern elephant seal pups born to mothers of different reproductive and size categories at Trypot beach, Marion Island between 1986 and 1988 (numbers above bars denote sample sizes).

Table 35. Comparison of mean birth weights (BWT) and weaning weights (WWT) for male and female southern elephant seal pups of large and small cows at Trypot beach, Marion Island, between 1986 and 1988. Means, standard deviations (S.D.) and sample sizes (n) are given.

Sex	Birth weight (BWT) or weaning weight (WWT)	Large cow			Small cow			't' value
		Mean	S.D.	n	Mean	S.D.	n	t
Male	Bwt**	44,0	4,4	21	35,0	4,2	9	5,14
Female	Bwt**	40,4	3,4	9	30,0	4,6	21	6,18
Male	Wwt*	122,6	21,4	21	98,5	14,8	8	2,91
Female	Wwt**	115,5	18,3	7	85,4	11,3	20	5,15

** = Significant at P<0,001
* = Significant at P<0,01

Table 36. Comparisons between birth weights, weaning weights and growth rates of southern elephant seal pups on three different islands. S.D. and n refer to standard deviation of the mean and sample size respectively.

Measurement	Age (days)	Sex	Marion Island			South Georgia			Macquarie Island		
			Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n
Weight (kg)	0	Male	40,3	5,4	75	45,1	6,9	16	42,2	5,3	33
		Female	34,1	5,6	62	40,2	4,3	13	39,4	4,9	28
Weight (kg)	21-22	Male	113,3	18,4	66	119,0	15,0	23			
		Female	97,6	17,5	54	112,0	21,0	24			
Growth rate (kg/day)	0-22	Male	3,4	0,7	66	3,6	0,7	23			
		Female	3,0	0,7	54	3,6	0,9	23			
Source			Present study			McCann *et al.* 1989			Little *et al.* 1987		

of growth for female pups were significantly (t_{25}=2,51; $P<0,05$) faster in large mothers ($\bar{x}$=3,3 ± 0,9 kg/day, n=7) than in small mothers ($\bar{x}$=2,6 ± 0,6 kg/day, n=20). The difference for male pups was not significant (t_{27}=1,667; $P>0,05$), with male pups of small cows growing at 3,1 ± 0,8 kg/day (n=8) and those of large cows at 3,6 ± 0,8 kg/day (n=21).

The growth rate of pups was positively, and significantly, related to their weight at birth in both males ($y=0,043x + 25,51$; t_{64}=2,67; $P<0,01$; Figure 31a) and females ($y=0,046x + 1,48$; t_{52}=2,61; $P<0,05$; Figure 31a), however, comparison of the two slopes showed no significant differences (t_{118}=1,68; $P>0,05$). Growth rates of male pups did not differ between Marion Island and South Georgia (t_{87}=1,181; $P>0,05$), while females grew at a faster rate (t_{75}=3,154; $P<0,01$) at South Georgia then at Marion Island (Table 36).

Birth weight was significantly related to weaning weight in both males ($y=2,12x + 26,67$; t_{64}=5,76; $P<0,001$; Figure 31b) and females ($y=2,13x + 25,51$; t_{52}=6,13; $P<0,001$; Figure 31b) but the slopes of the two regression lines did not differ significantly (t_{118}=0,124; $P>0,05$). When large and small cows were compared (sexes combined) the slope of pups of large cows ($y=2,55x + 10,77$; t_{26}=3,36; $P<0,01$; Figure 32) was significantly greater (t_{52}=7,979; $P<0,001$) than for pups of small ($y=1,66x + 36,43$; t_{26}=3,73; $P<0,001$; Figure 32) cows.

Male pups were significantly (t_{118}=4,74; $P<0,001$) heavier at weaning ($\bar{x}$=113,3 ± 18,4 kg, n=66) than females ($\bar{x}$=97,6 ± 17,5 kg, n=54), a result which persisted when mothers were divided into large and small categories (Table 35). Weaning weights of male pups at Marion Island did not differ significantly from those at South Georgia (t_{87}=1,337; $P>0,05$) while females at South Georgia were significantly (t_{76}=3,15; $P<0,01$) heavier than those at Marion Island.

Suckling intensity (time spent suckling) increased linearly (Figure 33) with increasing age in both males (r_{21}=0,91; $P<0,001$) and females (r_{21}=0,86; $P<0,001$). No significant difference was evident between the slopes (t_{42}=0,194; $P>0,05$). There was no correlation between the time a pup was observed to suckle and the amount of weight it gained during lactation, for either females (r_{51}=0,13; $P>0,05$) or males (r_{64}=0,13; $P>0,05$) (Figure 34).

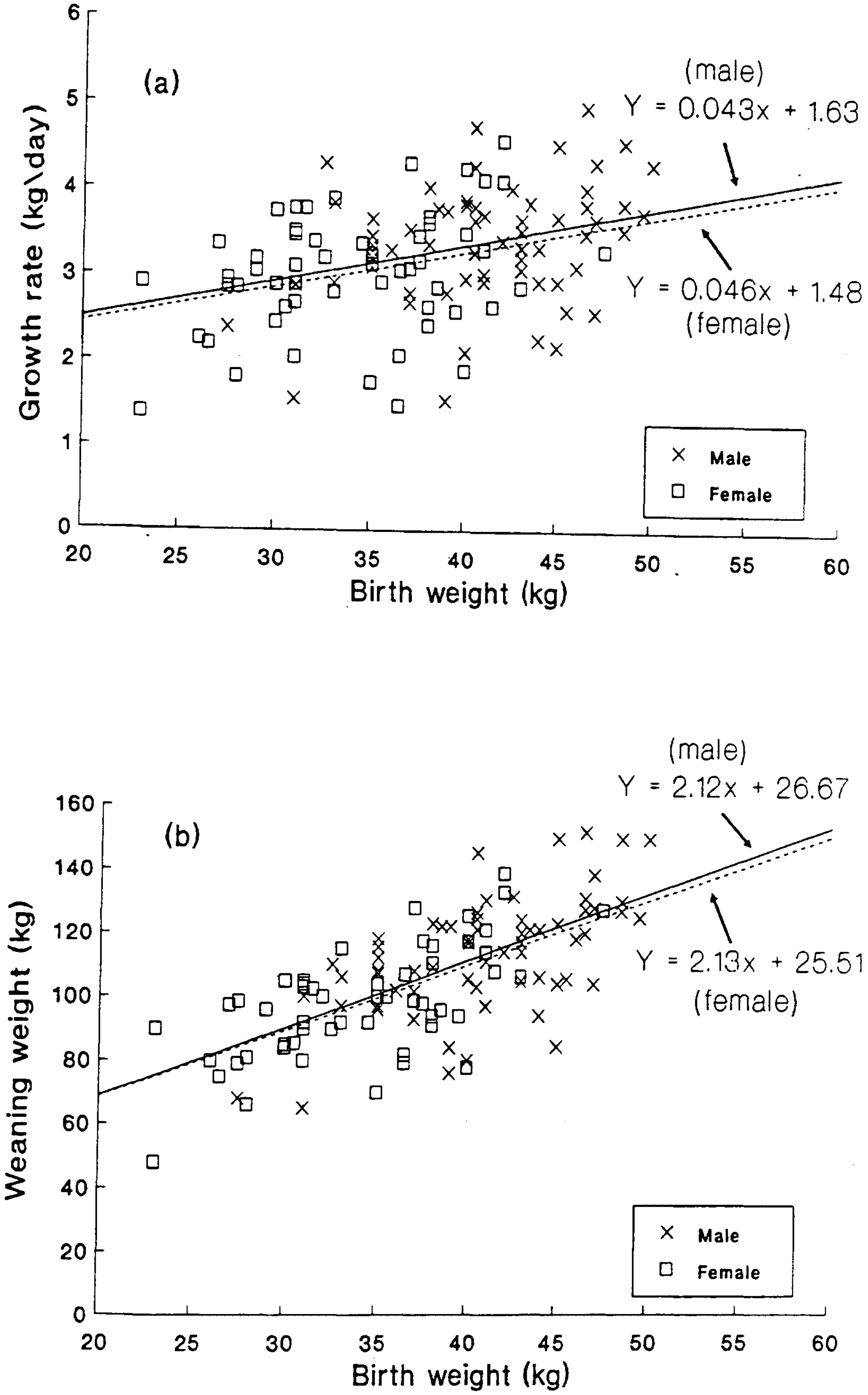

Figure 31. The relationship between birth weight and (a) growth rate and (b) weaning weight for male and female southern elephant seal pups at Trypot beach, Marion Island, between 1986 and 1988. Lines were fitted through least squares regression analysis.

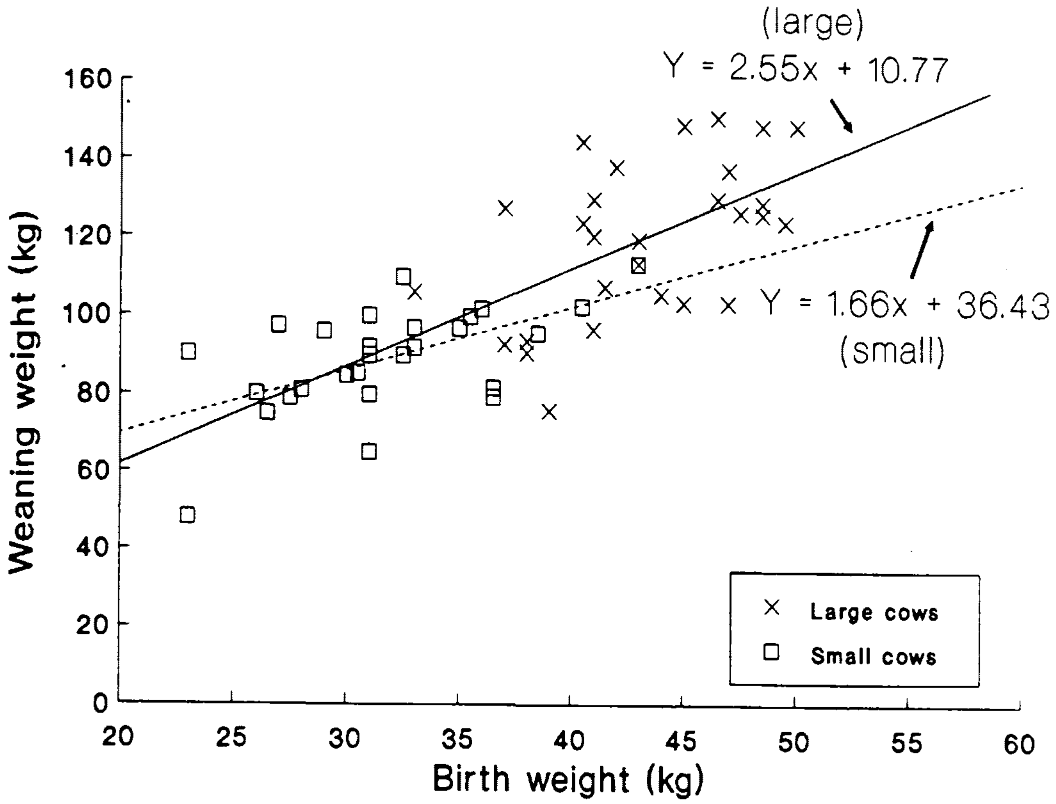

Figure 32. The relationship between birth weight and growth rate for southern elephant seal pups (sexes combined) with large and small mothers at Trypot beach, Marion Island, between 1986 and 1988. Lines were fitted through least squares regression analysis.

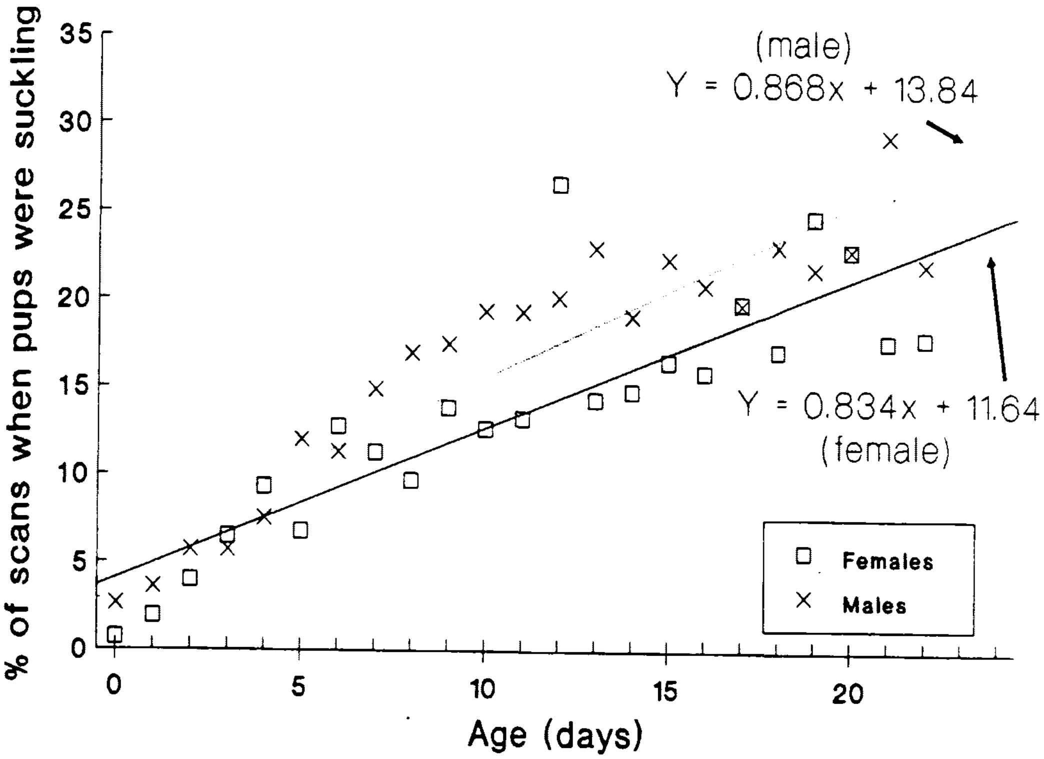

Figure 33. The relationship between time spent suckling (% of daily scans) and age of the pup in southern elephant seal pups at Trypot beach, Marion Island during 1987. The least squares linear regression analyses are based on arcsine tranformations (Zar 1984) of the suckling data, and thus the values for the Y intercept in the equations do not correspond with figures on the graph.

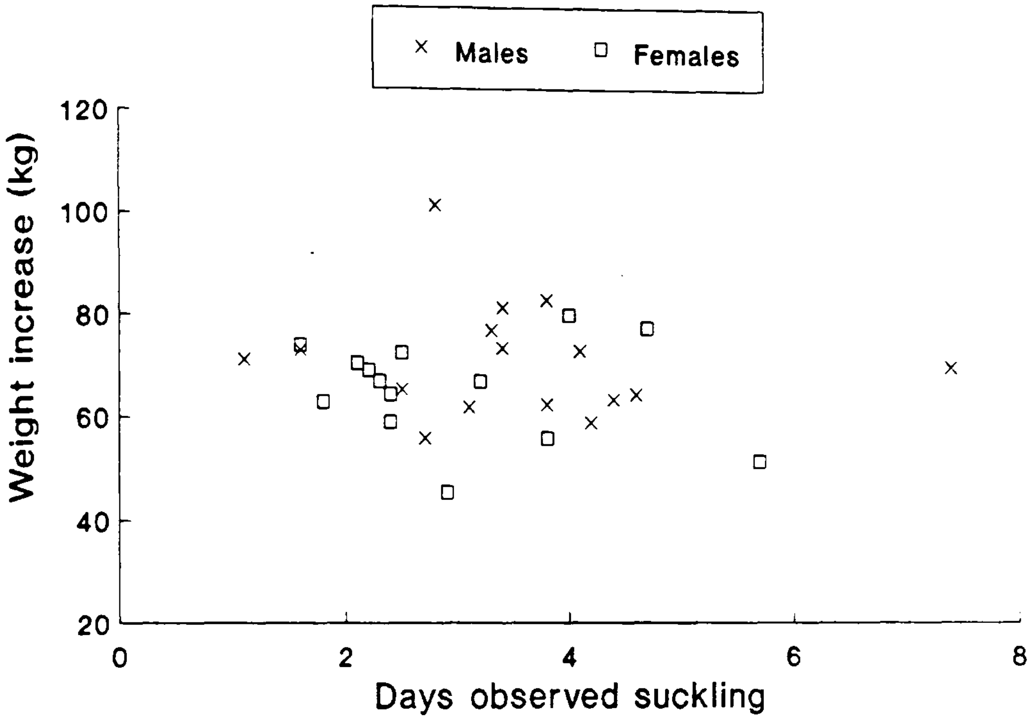

Figure 34. Total suckling time (suckling days) and its relationship with weight increase from birth to weaning in southern elephant seal pups at Trypot beach, Marion Island, in 1987 (see text for explanation).

Influence of prior investment on offspring sex ratio

The sex of the pup produced in one year had no influence (χ^2_1=0,01; P>0,05) on the sex of pup produced in the following year in the 47 cases recorded during the study. Eleven of 25 cows producing male pups one year produced males the following season, while 12 of 22 cows producing female pups in one season produced females in the next season.

Cows producing male pups in year 't+1' weaned heavier (t_{37}=2,26; P<0,05) pups in year 't' than those producing female pups (Table 37). Birth weight, growth from birth to weaning and the amount of time spent suckling by pups, events occurring in the year of conception, had no effect on the sex of the next seasons offspring (Table 37).

The sex ratio at birth of pups conceived before the median date of first copulation was 10 males to 7 females and after the median date 7 males and 11 females. Date of conception had no significant (χ^2_1=0,71; P>0,05) effect on sex of offspring.

No evidence was found for sex differences in the timing of birth (χ^2_1=0,05; P>0,05) among pups at the study site, with births of males and females distributed evenly, either side of the median birth date. Similar results were found for a larger sample of tagged pups in the area of coastline between Blue Petrel Bay and Archway Bay (χ^2_3=5,84; P>0,05; Table 38).

No relationship existed between date of copulation and sex of subsequent offspring. Cows producing male pups received the same number of copulations as those producing females (t_{43}=0,45; P>0,05).

Table 37. The influence of previous investment on the sex of subsequent offspring. All measures of investment refer to the pup the cow reared in the year prior to giving birth to either a male or female pup. For example, cows giving birth to male pups gave birth to heavier pups in the previous year than cows bearing females. S.D. and n refer to standard deviation of the mean and sample size respectively.

Measure of previous investment	Sex of subsequent offspring						Students '*t*' value
	Male			Female			
	Mean	S.D.	n	Mean	S.D.	n	
Birthweight (kg)	38,1	6,9	22	36,1	6,3	23	1,02
Weaning weight (kg)*	114,7	18,1	19	102,9	14,3	20	2,26
Weight increase birth to weaning	76,2	13,4	19	68,1	15,4	20	1,76
Investment in suckling days from scan samples	3,4	1,3	19	2,8	1,3	21	1,58

* = Significant at P<0,05

Table 38. Numbers of recently tagged male and female southern elephant seal pups between Blue Petrel Bay and Archway Bay, Marion Island, in 1987 and 1988. The total is divided into quarters corresponding to the periods during which tagging was carried out. The percentage of males in the tagged animals for each quarter is shown.

Sex of pup	First quarter	Second quarter	Third quarter	Fourth quarter
Male	68	73	67	55
Female	59	54	60	73
% male	53,5	57,5	52,8	43,0

Effect of previous investment on maternal survival and fecundity

Of the 80 cows giving birth to male pups during the study, 56,3% (45) were observed in following seasons, while 49,4% (38) of 77 cows producing female pups were seen, these figures indicate that sex of offspring has no influence on short term maternal survival. Fecundity was also unaffected by sex of offspring produced the previous season. Twenty seven (90%) of thirty cows producing male pups were seen, or predicted to have pupped, in the following season, while 22 (88%) of 25 producing female pups gave birth in the following season.

Longitudinal data for individual females

Data for 17 cows, seen in more than one season, for sex of pup, birth weight, weaning weight, growth rate and length of lactation are shown in Table 39. Of 12 cows that produced at least on pup of each sex during the study, lactation was longer for the male pup in one case, longer for the female pup in 10 cases and one case where there was no clear relation.

Birth weights, growth rates and weaning weights were all greater for males than female pups born to individual cows in this longitudinal data set, with one or two exceptions in each case. Whenever cows produced two pups of the same sex during the study, the second born was, with two exceptions, heavier at birth than the first. Values were not compared statistically due to the limited sample size.

Table 39. Sex (male/female), birthweight (kg), weaning weight (kg), growth rate (kg/day) and duration of lactation (days) for offspring produced by 17 southern elephant seal cows at Trypot beach, Marion Island, that were present in consecutive years during the study. Longitudinal data such as this may show up inter-annual differences in investment that a cross-sectional study can not.

Female	Year	Pup sex (M/F)	Birth weight	Weaning	Growth rate	Lactation
AL86	1986	F	30,0	105,0	3,75	20
	1987	M	33,0	106,0	3,84	19
	1988	M	35,0	96,0	3,21	19
AT86	1986	M	35,0			DIED
	1987	F	37,5	117,5	3,48	23
AV86	1986	M	35,0	112,0	3,67	21
	1987	F	31,0	105,0	3,52	21
	1988	M	40,5	126,5	4,30	20
CL286	1986	M	37,0			DIED
	1987	M	40,5	121,0	3,83	21
CN86	1986	F	45,0			23
	1987	F	47,5	127,5	3,33	24
	1988	M	46,5	152,0	5,02	21
CT86	1986	F	41,0			22
	1987	M	41,0	97,0	2,95	19
DT86	1986	F	33,0	115,0	3,90	21
	1987	M	35,0			DIED
	1988	M	42,5	131,5	4,05	22
LD86	1986	M	36,0	102,0	3,30	20
	1987	F	35,5	100,0	2,93	22
LN86	1986	M	38,0	123,0	4,05	21
	1987	F	35,0	104,0	3,14	22
	1988	F	34,5	92,0	3,38	17
NC86	1986	M	42,0	114,0	3,43	21
	1987	M	44,0	106,0	2,95	21

Table 39 continued.

Female	Year	Pup sex (M/F)	Birth weight	Weaning	Growth rate	Lactation
TD86	1986	M	33,0			DIED
	1987	M	35,0	108,0	3,32	22
ZD86	1986	F	42,0	133,0	4,14	22
	1987	M	48,5	150,0	4,61	22
	1988	M	47,0	138,5	4,36	21
AV87	1987	F	23,0	90,0	2,91	23
	1988	M	35,0	115,5	3,36	21
DA87	1987	M	35,0	108,0	3,32	22
	1988	M	39,0	122,0	3,77	22
DC87	1987	M	43,0	106,5	2,89	22
	1988	F	31,5	102,5	3,79	24
LV87	1987	M	43,0	120,0	3,35	23
	1988	F	36,5	107,0	3,07	23
NT87	1987	F	38,0	94,0	2,43	23
	1988	M	45,0	84,5	2,19	18

Discussion

Postnatal maternal investment in the southern elephant seal takes the form of milk transferred from mother to offspring. That there was no relation between observed suckling time and weight gain in the pups during the present study suggests that the relationship between observed suckling time and weight gain is a poor measure of investment. Numerous studies have cited increased suckling time of males as evidence of increased investment (Reiter, Stinson & Le Boeuf 1978, Clutton-Brock *et al.* 1982, Trillmich 1986, Wolff 1988) assuming that increased suckling implied increased milk intake (Clutton-Brock *et al.* 1982). This was questioned by Mendl & Paul (1989) after observations in mice and domestic cats showed an inverse relationship between suckling frequency and growth rate.

There are a number of possible reasons for the lack of a relationship between suckling time and weight gain. First, observed suckling times may be poor indicators of milk (energy) transfer rate, as rate of milk release and suckling vigour may vary between individuals, as might the energy value of milk of different mothers. Furthermore, possible differences in metabolism between individuals will result in differing efficiency of growth, and may mask the relationship between suckling behaviour and growth (Mendl & Paul 1989). Since pups were recorded as suckling when they were in contact with the nipple and 'active' suckling was not the criteria used in the study, any propensity for a pup to rest "on the nipple" would bias results. In view of the above, the use of suckling time as an index of investment is too simplistic in its approach and should be ignored.

Sex ratio

The observation that older and larger southern elephant seal cows at Marion Island produce an excess of male pups is in contrast to the expectations of Maynard Smith's (1980) theory, suggesting differential investment after producing offspring at a ratio of 1:1 (male:female), but fits the expectations of a model, which states that females able to produce good males should do so (Trivers & Willard 1973). Older cows tend to be larger than younger cows (Appendix I) and these larger females will, conceivably, have more resources available for their newborn young during both gestation and lactation. This is in contrast to the situation for southern elephant seals at South Georgia where cows above and below the median preparturient weight gave birth to equal numbers of male and female offspring (McCann *et al.* 1989). If we assume that the larger cows are heavier (and there is no reason to believe this is not the case) then a broad comparison can be made between the heavy cows at South Georgia (McCann *et al.* 1989) and the "large" cows in the present study. The "small" cows will fit the lower end of the size continuum at South Georgia. The lack of "mid-range" cows in the present study may explain the contrast in findings in the two studies. The South Georgia sample represents a size continuum and cows of intermediate size may have masked any size related sex differences.

The even sex ratio seen among tagged weaned pups between 1983 and 1989 concurs with data from northern elephant seals (Le Boeuf *et al.* 1989), while contrasting the significant male bias (1,32:1) in a sample of 27,946 six week old Cape fur seal, *A. pusillus*, pups (Shaughnessy in press). This large male bias was assumed by Trillmich (1986) to reflect the situation at birth in this species, however, evidence from Namibia suggest that the birth sex ratio is approximates 1:1, but disproportionately high, early, mortality among females, which are born earlier in the season, skew the sex ratio (J.P.Roux *pers. comm.*[3]).

The earlier birth of female Cape fur seals in Namibia contrasts the situation seen in some phocids, where sex ratio is skewed toward males in the beginning of the season (Coulson & Hickling 1961, Boyd & Campbell 1971). In the present study the lack of a relationship between date of birth and sex of offspring, in view of the fact that duration of gestation did not differ between sexes, corroborates the finding that date of conception had no effect on sex ratio at birth.

Timing of implantation following the period of delayed implantation in grey seals was earlier in females of larger than average body size and correlated with the time during spring when body condition improved after the drain of lactation and the moult (Boyd 1984). A similar relationship between timing of conception and body condition in evident in red deer (Mitchell & Lincoln 1973). These findings may explain the earlier births of male offspring in grey seals and red deer, assuming body condition influences sex ratio. The lack of a tendency for earlier male births in southern elephant seals at Marion Island may be due either to the fact that a similar relationship between timing of implantation and body condition does not exist in this species, or if it does, then trying to relate maternal condition directly to sex ratio is perhaps naive (Clutton-Brock *et al.* 1982).

The timing of insemination with respect to ovulation has been implicated in sex ratio adjustment (see James 1989). In humans, more males are born as a consequence of natural inseminations shortly before, or shortly after, ovulation (Guerrero 1974, 1975). Other data supporting this relationship are available for rhesus monkeys, *Macaca mulatta*, (Simpson & Simpson 1982) and white tailed deer, *Odocoileus virginianus*, (Verme & Ozoga 1981). James (1980, 1989) suggested that this trend, in humans at least, may result from maternal

---

[3] J.P. Roux, Department of Sea Fisheries, P.O.Box 394, Lüderitz, Namibia

gonadotrophin levels peaking around the time of ovulation, thus activating the female reproductive tract and preventing the separation of X-bearing and Y-bearing sperm through gravitation (Roberts 1972, 1978). In the present study there was no means of determining exactly how long after the onset of oestrus a cow was mated. Consequently, this theory can not be commented upon.

James (1986) hypothesized that coital rate can influence the sex ratio of offspring. Male biased sex ratios have also been reported when testosterone was added to the semen of bulls, rams, rabbits and boars (see James 1986). Prolonged periods of frequent copulations lower the levels of testosterone in semen and thus produce an excess of females, although the way in which this mechanism operates is not understood (James 1986). If this relationship is applicable to southern elephant seals, then we would expect high proportions of male births early in the season, as seen in some other phocids. The apparent lack of such a tendency in the present study argues against the views of James (1986).

Despite the relatively small sample sizes involved, cows at Marion Island appear to "manipulate" the sex ratio in relation to their physical capabilities to maximise their reproductive success. All considerations of which sex to produce rely on the assumption that the nutrition provided at this early age will directly affect the offspring's reproductive abilities. Assuming this to be the case, then the period of maternal investment is vitally important in determining the offspring's future success.

Assuming then, that southern elephant seal cows at Marion Island skew the sex ratio of their offspring toward the most suitable for them to produce at any given time, what differences in investment, if any, occur between the sexes pre and post natally?

Parameters such as duration of gestation and lactation, birth and weaning weights, growth rates, and intensity/frequency of suckling have all been used by various authors to demonstrate increased maternal investment in either male or female offspring (Reiter *et al.* 1978, Clutton-Brock *et al.* 1981, Gosling, Baker & Wright 1984, Kovacs & Lavigne 1986a, Anderson & Fedak 1987, Ono, Boness & Oftedal 1987, Higgins, Costa, Huntley & Le Boeuf 1988, Wolff 1988, Verme 1989, Byers & Moodie 1990).

The observed differences in birth weights of males and females in the present study are apparently not the result of differences in the duration of gestation. This contrasts the situation in red deer where higher male birth weights were associated with a longer gestation period (Clutton-Brock *et al.* 1982). It may be that the sample size in the present study was insufficient to demonstrate a sexual difference in gestation length. The implication in the red deer study is that, in view of the fact that the foetus grows faster at the end of gestation (Frazer & Huggett 1974), the longer period *in utero* results in the higher birth weight. Consequently, it would appear that sex differences in birth weight result from either differential provision of maternal resources or differences in the abilities of foetuses of each sex to utilize these nutrients. The increased anabolic properties of androgens, in comparison to oestrogens (MacGillivray 1986) may explain the differences in pre-natal growth between the two sexes, as males are exposed to higher levels of testosterone *in utero* (Rigaudiere 1979).

The higher birth weights of males at Marion Island correspond to the findings at Macquarie Island (Little, Bryden & Barnes 1987) and South Georgia (McCann *et al.* 1989). Increased birth weights among males are also found in grey seals (Kovacs & Lavigne 1986a, Anderson & Fedak 1987) and several otariids (Trillmich 1986, Boyd & McCann 1989). This disparity in the birth weights of the two sexes has been taken as evidence that males are more costly to produce for the mother than females. This is, however, based on the assumption that metabolic rates and assimilation efficiencies, in respect of maternal nutrients, of male and female foetuses are similar.

Birth weight increased with increasing maternal size, a finding observed for southern elephant seals at South Georgia (McCann *et al.* 1989) and in Antarctic fur seals (Costa, Trillmich & Croxall 1988, Boyd & McCann 1989). That increased maternal size had a greater influence on female birth weights than those of males (35% *vs.* 26%) agrees with observations at South Georgia where female birth weights increased significantly in relation to increased maternal weight at parturition, while the birth weights of male pups bore no such relation. This implies that female foetuses are directly limited in their growth potential by the maternal resources available to them, while male foetuses can exploit maternal resources more efficiently and grow at a greater rate than their female counterparts. Males, however, may already be growing at a higher plane and thus increased levels of available nutrients will have a lesser effect on their growth than that of females.

Post-natal investment

Growth rates of both males and females were significantly related to birth weight. This corresponds to findings for southern elephant seals at Macquarie Island (Bryden 1968a) and for Weddell seals in McMurdo Sound (Hill 1987), while contrasting the findings in Antarctic fur seals (Doidge & Croxall 1989). This difference may result from phocid mothers feeding their young entirely from finite stored food reserves at the time of parturition. Otariid mothers, in contrast, spend time at sea feeding in between feeding their young (Croxall & Gentry 1987). Consequently, otariid mothers are vulnerable to fluctuations in food availability during the period of offspring dependence, which may influence growth rates of their pups (Ono *et al.* 1987).

That weaning weights and growth rates of male pups did not differ between Marion Island and South Georgia, and that values for both these parameters were lower in female pups at Marion Island than at South Georgia corresponds to the data in other studies where growth rates and weaning weights of female pups showed a stronger correlation with maternal size than did that of males (Anderson & Fedak 1987, McCann *et al.* 1989). A possible explanation for this is that male progeny are able to extract resources from their mothers, regardless of maternal size up to a limit imposed by the finite levels of maternal resources (Anderson & Fedak 1987).

Since growth rate was related to birth weight, it is not surprising that males, which are heavier at birth, grow at a faster mean rate than females. However, the slopes of the regression lines describing the relationship between birth weight and growth rate were similar for the sexes. This shows that for a given birth weight males and females grow at the same rate. This is supported by the observation on northern elephant seals that metabolic costs for male and female pups are similar (Kretzman, Costa & Le Boeuf 1989), indicating that efficiency of utilisation of maternal resources by pups of both sexes is similar after birth. Studies on the northern fur seal also showed that milk intake was more strongly correlated with body weight than either sex or age of the pup (Costa & Gentry 1986), which partly explains the faster growth of males than females at a given age in that study. Male and female California sea lion, *Zalophus californianus*, pups also have similar milk intake rates when expressed in terms of body weight (Oftedal, Iverson & Boness 1987).

The steeper slope of the birth weight versus weaning weight regression for large cows indicates that growth rates of pups of large cows were higher than that of small cows. The small sample size does not permit comment of the influence of the sex of the pup on this relationship. The assumed greater stored reserves of the large cows may permit a faster growth rate of pups and thus a greater weaning weight than in pups of small mothers.

The relationship between maternal size and growth rate can be explained in two ways. First, that large cows produce large neonates which will then exhibit high growth rates as a result of size specific growth rates (Costa & Gentry 1986, Oftedal *et al.* 1987, present study). The second option is that a larger cow has more resources available to give her pup. This relationship should only hold up to a certain size of cow, as after a certain size is reached there is evidence to suggest that the pup will be unable to assimilate further nutrients (McCann *et al.* 1989).

The rate of growth in female pups at South Georgia is greater than those at Marion Island, which probably results from the combined effects of the higher birth weights and larger maternal size at South Georgia. Lack of data on birth weight *vs.* growth rate from South Georgia preclude a comparison of the regression slopes and thus a firm comment on the reason for the inter-island differences.

The similarity in weaned weights of male pups at Marion Island and South Georgia, despite the heavier birth weight at South Georgia, probably results from the inability of males at South Georgia to fully utilise their growth potential, owing to the limitations of milk assimilation mentioned above (McCann *et al.* 1989). The disparity in female weights possibly result from the tendency of smaller cows at Marion Island to produce females. These pups will be limited in their growth by the low levels of maternal resources. In contrast, the South Georgia females are heavier at birth and, on average, probably have larger mothers than their Marion Island counterparts. These combined effects produce higher growth rates, and even if they are limited by their abilities to assimilate milk energy, the weaned weight obtained will be significantly higher than that possible for pups at Marion Island.

Studies at Heard Island showed that southern elephant seal cows came ashore with blubber stores that varied greatly while at the end of lactation these stores were very similar (Gales & Burton 1987). This implies that each cow has a finite level of resource she can pass on to her pup after which she must return to sea to feed and replace these resources. It is then probable that a pup's growth is limited by the amount of milk available. In sharp contrast to this, some cows at South Georgia were observed to return to sea with substantial stores of blubber after rearing their pup (McCann *et al.* 1989). The pups of these cows were no heavier at weaning than those of smaller cows (McCann *et al.* 1989). In this case the growth potential of the pup appears to be limited by its own ability to convert the milk provided into tissue. Thus the pup will take what it wants/can rather than the cow giving what she can. This reverses the previous trend of thought that it was the mother that controlled the passage of nutrients (Trivers & Willard 1973, Clutton-Brock *et al.* 1982). However, in mothers with low levels of resources the pup may take all that it is possible to take, while in large mothers the pup is limited by its own ability to assimilate the milk. These two cases occur in a potentially nutritionally stressed population (*e.g.* Heard Island: Burton 1986, Hindell & Burton 1987) and one where food is unlikely to be limiting (*i.e.* South Georgia: Hindell & Burton 1987, McCann & Rothery 1988).

The situation at Heard Island is probably similar to that at Marion Island where cows are possibly foraging in nutritionally poor areas (Burton 1986, McCann & Rothery 1988). Cows departing the breeding beaches during the present study appeared emaciated, thus they were apparently stressed by lactation. Given that this is the case, weaning weight may be related to maternal size in populations within the southern Indian ocean while at South Georgia (South Atlantic Ocean) females in the lower end of the size range should wean pups in relation to maternal size, but once over a certain size threshold the pups will not increase in size (Figure 35).

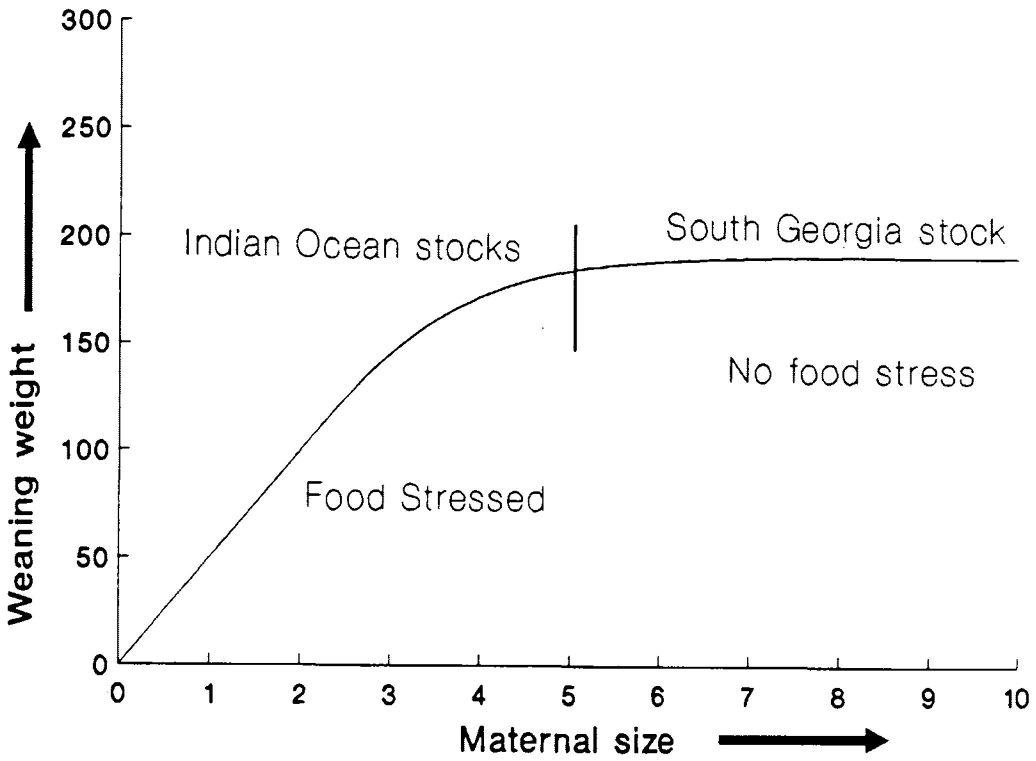

Figure 35. The hypothetical relationship between maternal size and weaning weight of southern elephant seal pups, in populations where food is limiting (Indian Ocean sites) and those where it is not (South Georgia). Weaning weight will increase proportionaly to increased maternal size until an upper limit is reached beyond which pups are unable to assimilate the increased amount of milk provided (further details in text).

The applicability of sexual selection theory to southern elephant seals

The data collected in the present study show that cows apparently skew the sex ratio of their offspring toward that which they are best suited to nourish, while consideration of whether they divert more resources to individual sons than daughters is dependent on interpretation of the data. If we consider higher birth weights, growth rates and weaning weights as evidence of increased investment (as is the case in many studies of pinnipeds and other mammal groups: Trillmich 1986, Anderson & Fedak 1987, Boyd & McCann 1989, Kojola 1989, Le Boeuf *et al.* 1989, Byers & Moodie 1990) then southern elephant seals at Marion Island would appear to invest differentially in sons and daughters. However, post natal growth rates and weaning weights are birth weight specific and independent of sex. If, in addition, it is assumed that there are differential efficiencies in utilisation of maternal nutrient supply *in utero* (which has also been postulated by Kovacs & Lavigne 1986a) resulting in differences in birth weight, then differences in birth weights, growth rates and weaning weights are not indicative of increased levels of maternal investment. Pre-weaning mortality in males and females in the present study is similar, suggesting equality in costs to the mothers.

Lack of differential investment support the view of Trivers & Willard (1973) that mothers that are in good condition (large size) should produce offspring that will benefit most from increased levels of maternal investment. The enhanced growth rates of pups of these mothers is further evidence that male pups can get a "good start" if they are born to large mothers.

Trivers & Willard's (1973) model depends on the following three assumptions:

- that the condition of the young at the end of the period of parental investment (PI) will tend to correlate with the condition of the mother during PI.

- that differences in the condition of young at the end of the period of PI will tend to endure into adulthood.

- adult males will be differentially helped in their reproductive success (compared to adult females) by slight advantages in condition.

The relationship between maternal size and weaning weight in the present study supports the first assumption. The second assumption is more difficult to support. McCann *et al.* (1989), however, noted that there was no correlation between birth and weaning weights of elephant seals at South Georgia (r^2=4%) and cautioned against the assumption that the apparent difference in investment during gestation (different birth weights between sexes) was the result of sexual selection. The findings at Marion Island contrast those for South Georgia in that a significant correlation existed between birth and weaning weight (r^2=47,4%; $P<0.001$). The relationship is even stronger for females than males.

At Marion Island birth differences in weight persist until weaning, but for how long thereafter?. No empirical data exists for any phocid which compares size at birth or weaning to adult size (McCann *et al.* 1989). Morris, Le Boeuf & Ortiz (1989) reported that increased weaning size of northern elephant seal pups conferred a survival advantage on them, and that weight at weaning was correlated with weight at one year of age. This then considers what happens in the first year of life, but what happens thereafter?. One observation for northern elephant seals provides circumstantial evidence for a correlation between sizes at the different ages. A bull seen at Año Nuevo Island was noted as being noticeably small for a beachmaster. This male was weighed at weaning in 1964 and was of smaller than average size for his cohort (Le Boeuf & Reiter 1988). It would then seem that size at weaning affected adult size in this animal, however, more data will be required before a conclusive statement can be made.

Despite the paucity of data on the relationship between early size and adult size in pinnipeds, Hill (1987) erroneously applied the assumption to all polygynous mammals. However, data do exist to show that mammals that grow slowly during the first months of life can seldom compensate during later years and often show reduced adult size and weight (Gunn 1965, Fraser & Morley Jones 1975, Russell 1976). Body size (based on antler size) of thirteen red deer stags at 16 months was correlated with their body size at six years of age (Clutton-Brock *et al.* 1982), thus lending support to the notion that maternal investment influences adult size.

The third and final assumption of the model seems applicable to southern elephant seals as the species is highly polygynous and access to females is strongly related to adult body size and competitive ability (McCann 1981). In contrast, all females of what ever size will breed once they reach breeding age (Le Boeuf & Reiter 1988).

Trivers & Willard (1973) assume that "sex ratio at birth in mammals is a measure of tendency to invest in one sex more than in another". In addition Trivers (1972) defined parental investment as *"any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring"*. This increased investment in males (in terms of producing more males at birth) should then translate into a cost component to the mother (measured in terms of lowered fecundity or survival), but in the present study none is evident, and therefore the results appear at odds with theoretical expectations.

This contradiction can be resolved in one of two ways. First, the correct cost component was not measured during the course of the study and second, that the production of a male, in contrast to Trivers & Willard's (1973) contention, does not imply a greater tendency for investment in males.

The measurement of lowered fecundity and/or survival following the rearing of male offspring has been used as an indication of increased cost in studies of red deer (Clutton-Brock *et al.* 1982) and bison, *Bison bison*, (Wolff 1988). However, no evidence for this is known of for pinnipeds (Trillmich 1986, Le Boeuf *et al.* 1989, present study), despite numerous studies which report apparent differential investment between the sexes in species exhibiting polygyny (Reiter *et al.* 1978, Payne 1979, Kovacs & Lavigne 1986a & 1986b, Trillmich 1986, Anderson & Fedak 1987, Little *et al.* 1987, Costa *et al.* 1988, Boyd & McCann 1989, Doidge & Croxall 1989, McCann *et al.* 1989).

Le Boeuf *et al.* (1989) suggest that northern elephant seal cows do not exhibit lowered fecundity/survival after rearing a male pup because they are more than able to offset the drain on their resources during the post lactation visit to sea. In contrast red deer and bison may have difficulty obtaining adequate food to replenish their fat stores during the harsh winter period.

With respect to the above, and assuming that maternal investment in males, in terms of skewed sex ratio, is indeed greater than females, it would seem that observation of fecundity/survival rates over one or two years are an inadequate measure of cost to a female pinniped. Because of phocid females apparent ability to buffer the short term cost of rearing a pup by rapid recovery of resources (Le Boeuf, Costa, Huntley & Feldkamp 1988), costs with respect to future reproductive success may only become apparent after considering the animal's entire life.

Reiter (1984) and Huber (1987) showed that northern elephant seal cows that bred for the first time at three years of age had a lower life expectancy than those breeding for the first time at four or five. Huber, McElroy, Boekelheide & Henderson (1983) showed that cows pupping first at three produced fewer pups over the subsequent four years than those delaying first breeding until four or five. Stewart (1983 in Riedman 1990) found that young harp seal females utilise more of their body reserves in rearing a pup that do older females. Young mothers deplete their blubber reserves to the minimum critical level needed for survival. This relatively high level of resource depletion has been seen in mothers of male pups in grey seals (Anderson & Fedak 1987) and southern elephant seals (McCann *et al.* 1989) and similar findings may occur to those seen in northern elephant seals.

In view of the above, it may only be possible to detect the costs involved in differential investment by monitoring reproductive histories of individual females over their entire life span. .

Assuming that the correct cost component has been measured, how then can the data indicating no differences in investment be reconciled with theory?

If there is no difference in the cost of producing males and females, then there will be no resulting differences in the costs to the mother. Even if this is the case, it does not undermine the advantages in mothers in good condition producing an excess of males, as their sons will be more successful in adulthood than those of small mothers. This is in agreement with Armitage (1987) who hypothesized that females should produce the sex that has a higher probability of future reproductive success, regardless of the costs involved in its production.

Thus, it is not the cost of producing sons or daughters that is the critical factor, but the probable survival and reproduction of offspring that is of paramount importance (Armitage 1987).

The apparent equality in investment between the sexes found in the present study is in accordance with recent studies at South Georgia (McCann *et al.* 1989) and on northern elephant seals at Año Nuevo Island (Kretzmann *et al.* 1989, Le Boeuf *et al.* 1989). This supports the view that pups are utilising nutrients to the best of their abilities, regardless of sex.

The sex ratio of southern elephant seal underyearlings hauling out for the autumn rest period at Marion Island was similar to that at the time of tagging (Wilkinson & Bester 1990b). Assuming that animals haul out in the autumn on an island close to where they are feeding at that time, then it would appear that underyearling males and females forage in the same areas. If this is indeed the case, males and females will compete directly for the same food resources if/when food is in short supply. It would therefore seem maladaptive to invest less in a female pup and put her at a disadvantage during her first year of life when competing with males.

McCann *et al.* (1989) suggested that the lack of correlation between their data and theoretical expectations may be a consequence of the cross-sectional nature of their study, and that differences in investment may be detectable in the same female from year to year if she had some pups of each sex.

That the sex of previous offspring had no effect on the sex of subsequent offspring probably results from the relative costs of males and females being similar, and thus cows producing males in one season are not disadvantaged in comparison with those producing females. Cows producing males in year t+1 weaned heavier pups, and is probably a result of the fact that older and larger mothers are more likely to produce males, and they also produce heavier pups. The lack of effect of time of suckling can be explained by the finding that observed suckling time bore no relation to weight increase and thus investment, while that of birth weight and growth rate imply that either this difference in cost of investment is negligible, or that there is no tendency to produce pups of one or other sex as a consequence of differential drain on maternal resources.

Longitudinal data in the present study parallel that seen for the cross-sectional data in the present study, with one exception, the longer lactation period for female pups. The lack of a negative relationship between the sexes of consecutive offspring is explained by the apparent lack of difference in the cost of producing sons and daughters.

SUMMARY

The decline in the southern elephant seal population at Marion Island and the speculation on the cause of the decline was the driving force behind the initiation of this research. The project aimed at determining the present size and demographic parameters of the population, to examine the factors influencing pup production and subsequent reproductive success of female southern elephant seals at Marion Island, to investigate patterns of parental investment in this species, and how these patterns agree or disagree with current theories on reproductive investment and sexual selection.

Consideration of aspects of reproductive behaviour necessitated an investigation of the sequence and timing of the reproductive cycle of southern elephant seals. The peak in cow numbers occurred on 15 October, as at other Indian Ocean breeding sites, 80% of the pups were born over a 24 day period, and the interval between the arrival of the first cow and departure from the rookery of the last cow was 63 days. It would appear that the length of the season is similar to other islands of the Kerguelen and Macquarie stocks, and that no major change in the length of the season has occurred at Marion Island since the 1970's. Dates of haulout during the present study did not differ between years, and were similar to those reported for this population in the 1970's. This synchrony suggests that a precise determining factor, such as photoperiod, is operating. Observed changes in the physical environment (climatic change) and biotic (*i.e.* food availability) components (if any) of these animals environment do not appear to have affected this photoperiodic control.

Cows gave birth 4,7 ± 2,0 days after hauling out on the island, came into oestrus 18,4 ± 1,9 days after parturition, weaned their pups after 21,4 ± 1,9 days, and departed the rookery 26,5 ± 3,2 days after arriving. The length of a cow's haulout period was inversely related to the date on which she hauled out, a result of the shortening of the *pre-partum* period with later haulout. This may result from the increased visual, tactile, auditory and olfactory signals received from other animals in the rookery later in the season inducing earlier birth, or from cows having a fixed parturition date and some are better able to time their arrival than others.

Maternal variables such as size, age and social status had no effect on the timing or spacing of events within the reproductive cycle. The ability to respond to environmental cues from an early age will maximise a female's future reproductive success.

Total numbers of pups born in the main study area at Marion Island between 1974 and 1989 declined at a rate of 4,8% per annum. The rate slowed between 1983 and 1989 to 1,9% per annum. Pre-weaning mortality ranged from 2,5% to 8,5% (between 1974 and 1989) and appeared unrelated to numbers of pups born, or numbers of bulls attending harems. The sex ratio of pups tagged from 1983 to 1989 did not differ significantly from unity. Adult sex ratio did not change between 1974 and 1989, there was no difference in mean harem size between 1974 and 1988, at least 95% of cows were attended by at least one bull during the present study, and the ratio of adult males to cows ashore around the whole island was approximately 1:10.

Intensive tagging since 1983 provided animals of known age from which population parameters could be determined. Based on analysis of the 1983 cohort, survival of female to age one was 61,8% and males 59,7%, the highest figure reported for this species. There were no changes in first year survival for the cohorts tagged from 1983 to 1988. Mortality rates declined from age one to three in both sexes, after which it increased between age three and four, more noticeably among females. This increase was followed by a decrease, again more noticeable among females to age five after which it is assumed constant until a year or two before the assumed death in both sexes (females at 23, males at 18). Females pupped for the first time at age three and all cows were mature by age six, mean age at first pupping was 4,41 years. All cows aged six and seven produced pups, and 100% pupping was assumed for all females above the age of five. The Net Reproductive Rate (R_o) calculated from a lifetable of females was 0,661, where a value of 1 implies a zero rate of increase. Manipulation of the lifetable shows that first year survival would have to be increased to 95%, or adult survival would have to increase from the observed 82,4% to 90%, or the proportion of female pups produced increase to 75% from the present 48,9%, or full recruitment of cows to the breeding population advance by two years to age 4, or juvenile survival would have to increased to realise an R_o of 1. The already high first year survival value, early age of first reproduction and almost 50% production of female offspring indicate that adult or sub-adult survival may be the key to the decline. The high mortality rate of three year old females may be ascribed to physiological stresses of gestation and lactation, and/or stresses from a possible change in feeding area at this age.

The trend in the present study for old, large, socially high ranking females to successfully rear a higher proportion of their offspring than other females agreed with other pinniped studies, however, the trend was not statistically significant. That timing of birth did not influence survival is assumed to result from the fact that mortality agents which normally operate in elephant seal harems were ameliorated by the low densities currently present at Marion Island. The mother-pup separations common in other breeding sites were rare in the present study, and the effects of biting of pups on survival was not evident, both probably the result of the low density harems.

Observations of sexual behaviour showed that beachmasters dominated mating activities on the beaches, achieving 98% of all the copulations. Cows received multiple matings, averaging 5,3 ± 0,4 per cow in 1986, to 3,7 ± 0,4 per cow in 1988, which is higher than previously reported for this species or the northern elephant seal. Cows remained in oestrus for an average of 3,3 ± 0,2 days in 1986, 3,3 ± 0,3 days in 1987 and 4,0 ± 0,3 days in 1988, and the numbers of copulations by the cow was directly related to the length of this period. Frequency of copulations had no effect on chances of conception, nor did the level of sexual activity by the dominant bull appear to affect his ability to successfully inseminate the cows on the beach, contradicting the suggestion that the low numbers of adult bulls at Marion Island are limiting fertilisation success. The level of sexual activity of the bulls was directly related to the numbers of oestrous cows on the beach. The small size of harems at Marion Island, and the fact that they are easily defendable from other bulls allows dominant bulls more time for sexual activity than at other sites, possibly explaining the higher frequency of copulations at Marion Island. The length of oestrus in cows is thought to be a means of ensuring fertilisation, and also may be a means of ensuring that she will be inseminated by the dominant bull on the beach.

Large cows produced significantly more male pups than did small cows. Gestation length for male and female pups was similar and gestation was not affected by date of copulation. Male pups were significantly heavier than females at birth, and large cows produced heavier pups (male and female than small cows). There was no difference in the length of lactation between males and females, and size of mother did not affect the length of lactation. Growth rates of male pups were faster than females, with rates for female pups of large mothers faster than in small mothers. Growth rates were positively related to birth weights in both sexes, with the higher birth weights of male pups explaining the faster growth rates. Birth weights were related to weaning weights with the proportional increase greater for larger mothers than small mothers. Previous investment did not lower future maternal survival or fecundity.

Cows at Marion Island appear to "manipulate" the sex ratio of their offspring in relation to their physical capabilities to maximise their reproductive success. Differences in birth weight between sexes may result from differences in the ability of foetuses to utilise maternal nutrients *in utero*, and thus is not indicative of differences in pre-natal investment. As weaning weight is related to birth weight, and growth rate dependent on birth weight, differences in post-natal investment are birth weight, as opposed to sex dependant. Maternal size influenced offspring size, but apparently only up to a certain level.

The lack of a cost component to maternal investment in terms of lowered fecundity and survival may be the consequence of the fact that in the short term cows can buffer the cost of rearing a pup by rapid recovery of resources, and so effects would only be seen in the long term. Alternatively, there may be no difference in the costs of rearing male and female offspring. In the absence of differential costs between sexes, mothers should still produce the sex that has the higher probability of future reproductive success, which in polygynous species is the male.

OPSOMMING

Die afname in die suidelike olifantrobbevolking op Marioneiland en bespiegeling oor die faktore verantwoordelik vir dié afname het as motivering vir die onderneming van die huidige studie gedien. Die projek het dit ten doel gestel om die huidige grootte en demografiese parameters te bepaal, faktore wat kalfproduksie en gevolglike voortplantingsukses van vroulike suidelike olifantrobbe op Marioneiland beïnvloed te ondersoek, asook patrone van ouerlike belegging na te speur en in verband te bring met huidige teorieë aangaande voortplantingsbelegging en geslagseleksie.

Oorweging van aspekte van voortplantingsgedrag berus op 'n ondersoek van die volgorde en tydsberekening van die voortplantingsiklus van suidelike olifantrobbe. Koeigetalle het op 15 Oktober gepiek en soos op ander teelgronde in die Indiese Oseaan is 80% van die kalwers oor 'n tydperk van 24 dae gebore. Drie-en-sestig dae het verloop vanaf die aankoms van die eerste koei tot die vertrek van die laaste koei. Die lengte van die teelseisoen is skynbaar dieselfde as dié op ander eilande van die Kerguelen en Macquarie stamme en op Marioneiland het geen groot verandering in die lengte van dié seisoen sedert die sewentiger jare plaasgevind nie. Die datum van aankoms op die eiland het nie van jaar tot jaar gedurende die studietydperk verander nie en was ook dieselfde as wat dit gedurende die 1970s was. Hierdie sinkronisasie dui daarop dat 'n eksakte bepalingsfaktor, soos byvoorbeeld dagliglengte, funksioneer. Waargenome veranderinge in die fisiese (klimaatsveranderinge) en biotiese (byvoorbeeld voedselbeskikbaarheid - indien enige) omgewings van die diere beïnvloed skynbaar nie die fotoperiodiese beheer nie.

Koeie het 4,7 ± 2,0 dae na hul aankoms op die eiland geboorte gegee, estrus 18,4 ± 1,9 dae na welping beleef, hul welpies 21,4 ± 1,9 dae na hul geboorte gespeen, en die teelgebied 26,5 ± 3,2 dae na aankoms verlaat. Die tydperk van verblyf op die teelgebied was omgekeerd gekorreleerd met die datum van aankoms. Dié was die gevolg van 'n verkorting van die voorgeboortelike tydperk met 'n vertraging van die datum van aankoms. Dit mag die gevolg wees van 'n toename in visuele, tasbare, auditoriese en olfaktoriese seine wat van ander diere op die teelgrond later in die seisoen ontvang word en wat vroeër geboorte kan induseer of van koeie wat 'n bepaalde geboortedatum handhaaf en wat hul aankoms beter as ander koeie

bereken. Moederlike veranderlikes soos liggaamsgrootte, ouderdom en sosiale status het geen invloed op tydsbepaling en spasiering van gebeurtenisse in die voortplantingsiklus gehad nie.

Die aantal welpies wat in die hoofstudiegebied op Marioneiland van 1974 tot 1989 gebore is het teen 'n tempo van 4,8% per jaar afgeneem. Hierdie tempo het vanaf 1983 tot 1989 verminder na 1,9% per jaar. Mortaliteit voor spening het vanaf 1974 en 1989 tussen 2,5% en 8,9% gewissel en het geen verband gehou met die hoeveelheid welpies wat gebore is nie, of met die hoeveelheid bulle in en om die harems nie. Die geslagsverhouding van welpies wat vanaf 1983 tot 1989 gemerk is het nie betekenisvol van die verwagte 1:1 verhouding afgewyk nie. Die geslagsverhouding van volwasse robbe het nie vanaf 1974 tot 1989 verander nie maar die grootte van harems het oor die tydperk verklein. Ten minste 95% van al die koeie was gedurende die studietydperk in die teenwoordigheid van 'n bul of bulle en die verhouding van volwasse bulle tot koeie teenwoordig op die eiland was 1:10.

'n Intensiewe merkprogram sedert 1983 het diere van bekende ouderdom, waarvandaan bevolkingsparameters bepaal kon word, gelewer. Gebaseer op 'n ontleding van die 1983 welpiegroep was die oorlewingstempos van koeie (61,8%) en bulle (59,7%) tot op die ouderdom van een jaar hoër as die voorheen bekend vir die spesies. Daar was geen verandering in oorlewing gedurende die eerste jaar vanaf 1983 tot 1988 nie. Mortaliteitstempos het vanaf die ouderdom van een tot drie jaar vir beide geslagte afgeneem, waarna dit tussen ouderdom drie en vier toegeneem het. Die toename was meer opvallend vir wyfies. Hierdie toename in mortaliteit was gevolg deur 'n afname wat weereens meer opvallend was vir koeie as bulle tot op die ouderdom van vyf jaar. Dit is aanvaar dat mortaliteitstempos hierna tot een of twee jaar voor sterfte (koeie op 23, bulle op 18) konstant bly. Koeie het vir die eerste keer op die ouderdom van drie jaar geboorte gegee en alle koeie was volwasse op die ouderdom van ses jaar. Die gemiddelde ouderdom van eerste geboorte was 4,41 jaar. Alle koeie ses tot sewe jaar oud het welpies geproduseer en dit is aanvaar dat alle koeie ouer as vyf welpies geproduseer het. Die netto voortplantingstempo (R_0) is deur die gebruik van 'n lewenstabel op 0,661 bereken, waar 'n waarde van 1 dui op 'n zero tempo van verandering. Manipulasie van die lewenstabel dui daarop dat oorlewing gedurende die eerste lewensjaar na 95% sal moet verhoog, óf dat oorlewing van volwassenes sal moet toeneem vanaf 82,4% tot 90%, óf dat die fraksie wyfie diere wat geproduseer word vanaf 48,9% tot

75% sal moet toeneem, óf dat insluiting van alle koeie tot die teelbevolking met twee jaar tot ouderdom 4 vervroeg word, óf dat oorlewing van welpies sal moet toeneem om 'n R_0 waarde van 1 te bereik. Die alreeds hoë oorlewingstempo van jaarlinge, die vroeë ouderdom van geslagsrypheid en die byna 50% produksie van wyfies by geboorte dui daarop dat volwasse of onvolwasse oorlewingstempos die sleutel tot die afname in die bevolking mag wees. Die hoë mortaliteitstempo van koeie gedurende die derde jaar van hul lewe kan toegeskryf word aan fisiologiese spanning van dragtigheid en laktasie, en/of as gevolg van spanning weens veranderinge in die voedingsgebied van die diere.

Die neiging van ou, groot en sosiaal dominante koeie om meer nakomelinge suksesvol te speen is in ooreenstemming met ander studies op robbe. In die huidige studie was die neiging egter nie statisties betekenisvol nie. Die lae digtheid van olifantrobbe op Marioneiland is skynbaar die rede waarom mortaliteitsagente wat bekend is vir ander olifantrobbevolkings nie hier funksioneer nie. Gevolglik was oorlewing nie deur die datum van geboorte beïnvloed nie. Die skeiding van moeders en welpies, bekend vir ander teelgronde, is slegs soms gedurende die huidige studie waargeneem. Oorlewing van welpies is ook nie deur bytery beïnvloed nie, beide eienskappe waarskynlik as gevolg van harems van lae digtheid.

Waarnemings aangaande geslagsgedrag het aangetoon dat strandmeesters verantwoordelik was vir meeste (98%) van die parings. Paringsfrekwensie vir koeie wat meer as een keer gepaar het, het vanaf 5,3 ± 0,4 keer gedurende 1986 tot 3,7 ± 0,4 keer in 1988 gewissel en was hoër as frekwensies waargeneem vir ander studies op olifantrobbe, insluitende die noordelike spesies. Koeie was in estrus vir 3,3 ± 0,2 dae gedurende 1986, 3,3 ± 0,3 dae gedurende 1987 en 4,0 ± 0,3 dae gedurende 1988 en die tydperk van estrus het die paringsfrekwensie beïnvloed. Paringsfrekwensie het nie die waarskynlikheid van bevrugting beïnvloed nie. Die vlak van seksuele aktiwiteit van die dominante bul het ook nie sy vermoë om koeie te bevrug beïnvloed nie en is gevolglik teenstrydig met die voorstel dat die lae digtheid van volwasse bulle bevrugtingsukses kan beperk. Die vlak van seksuele aktiwiteit van bulle het direk verband gehou met die hoeveelheid koeie wat op die teelstrand in estrus was. Die klein harems op Marioneiland en die gemak waarmee dit teen ander bulle verdedig kan word, kan moontlik verklaar waarom bulle op Marioneiland meer tyd het vir seksuele aktiwiteite as bulle op ander teelstrande. Die lengte van die estrustydperk is waarskynlik 'n wyse waarop bevrugting asook inseminasie deur die dominante bul op die strand verseker word.

Groot koeie het betekenisvol meer mannetjies as wyfies geproduseer. Die draagtydperk vir welpies van die twee geslagte was ook soortgelyk en is nie deur die dag van paring beïnvloed nie. Mannetjies was by geboorte betekenisvol swaarder as wyfies en die welpies (beide geslagte) van groot koeie was swaarder as die van klein koeie. Die laktasie-tydperk vir mannetjies en wyfies was soortgelyk en is ook nie beïnvloed deur die grootte van die moeder nie. Groeitempo van mannetjies was hoër as die van wyfies en tempo vir wyfies van groot koeie was ook hoër as die van klein koeie. Groeitempo was ook positief verwant aan die geboortegewig vir beide geslagte, waar die hoër geboortegewig van mannetjies hul hoër groeitempos verduidelik. Geboortegewig het verband gehou met gewig by spening met die proporsionele toename hoër in groot dan in klein koeie. Vorige belegging het geen invloed op toekomstige oorlewing of fekunditeit gehad nie.

Dit lyk asof koeie op Marioneiland die vermoë het om die geslag van hul nakomelinge te manipuleer na gelang van hul fisiese vermoëns om sodoende hul voortplantingsukses te maksimaliseer. Verskille in geboortegewigte van die geslagte is waarskynlik die gevolg van verskille in die vermoë van die fetusse om materne voedingstowwe in utero te gebruik, en is dus nie 'n aanduiding van verskille in prenatale belegging deur die moeder nie. Gewig by spening hou verband met gewig by geboorte, en omdat groeitempo afhanklik is van geboortegewig is verskille in nageboortelike belegging afhanklik van geboortegewig en nie van die geslag van die welpie nie. Materne grootte het 'n invloed op die grootte van nakomelinge maar oënskynlik slegs tot op 'n sekere vlak.

Die afwesigheid van 'n koste komponent in moederlike belegging in terme van 'n verlaging in fekunditeit en oorlewing kan die gevolg wees van die vermoë van koeie om die koste verbonde aan die grootmaak van 'n welpie te buffer deur die vinnige hernuwing van bronne. Effekte sal dus slegs oor die langtermyn gesien kan word. Alternatiewelik is daar waarskynlik geen verskille verbonde aan die grootmaak van welpies van verskillende geslagte nie. In die afwesigheid van differensiële koste tussen geslagte behoort moeders steeds dié geslag te produseer wat die hoogste waarskynlikheid van toekomstige voortplantingsukses het. In 'n poligame spesies behoort dit oorlewende manlike diere te wees.

REFERENCES

AMERICAN SOCIETY OF MAMMALOGISTS. 1967. Standard measurements of seals. *J. Mammal.* 48: 459 - 462.

ANDERSON, Sheila S. & FEDAK, M.A. 1985. Grey seal males: energetic and behavioural links between size and sexual success. *Anim. Behav.* 33: 829 - 838.

ANDERSON, Sheila S. & FEDAK, M.A. 1987. Grey seal, *Halichoerus grypus*, energetics: females invest more in male offspring. *J. Zool., Lond.* 211: 667 - 679.

ANGOT, M. 1954. Observations sur les mammifères marins de l'archipel de Kerguelen - avec une étude détaillée de l'Eléphant de mer, *Mirounga leonina* (L.). *Mammalia* 18: 1 - 111.

ARMITAGE, K.B. 1987. Do female yellow-bellied marmots adjust the sex ratios of their offspring? *Am. Nat.* 129: 501 - 519.

ARNASON, A.N. & MILLS, K.H. 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. *Can. J. Fish. Aquat. Sci.* 38: 1077 - 1095.

BARRAT, A. & MOUGIN, J.L. 1978. L'Eléphant de mer *Mirounga leonina* de l'île de la Possession, archipel Crozet (46°25'S, 51°45'E). *Mammalia* 42: 143 - 173.

BARTHOLOMEW, G.A. & COLLIAS, N.E. 1962. The role of vocalization in the social behaviour of the northern elephant seal. *Anim. Behav.* 10: 7 - 14.

BARTSCH, Sherie S., JOHNSTON, Shirley D. & SINIFF, D.B. 1991. Territorial behaviour and breeding frequency in relation to age, size and serum testosterone and cortisol concentrations in male Weddell seals. *Can. J. Zool.* (IN PRESS).

BESTER, M.N. 1989. Movements of southern elephant seals and subantarctic fur seals in relation to Marion Island. *Mar. Mamm. Sci.* 5: 257 - 265.

BESTER, M.N. 1990a. Population trends of subantarctic fur seals and southern elephant seals at Gough Island. *S. Afr. J. Antarct. Res.* 20: 9 - 12.

BESTER, M.N. 1990b. Reproduction in the male sub-Antarctic fur seal *Arctocephalus tropicalis*. *J. Zool., Lond.* 222: 177 - 185.

BESTER, M.N. & LENGLART, P-Y. 1982. An analysis of the Southern elephant seal *Mirounga leonina* breeding population at Kerguelen. *S. Afr. J. Antarct. Res.* 12: 11 - 16.

BIGG, M.A. 1984. Stimuli for parturition in northern fur seals (*Callorhinus ursinus*). *J. Mammal.* 65: 333 - 336.

BOYD, I.L. 1984. The relationship between body condition and the timing of implantation in pregnant grey seals (*Halichoerus grypus*). *J. Zool., Lond.* 203: 113 - 123.

BOYD, I.L. & McCANN, T.S. 1989. Pre-natal investment in reproduction by female Antarctic fur seals. *Behav. Ecol. Sociobiol.* 24: 377 - 385.

BOYD, J.M. & CAMPBELL, R.N. 1971. The grey seal (*Halichoerus grypus*) at North Rona 1959-68. *J. Zool.,Lond.* 164: 469 - 512.

BRYDEN, M.M. 1968a. Lactation and suckling in relation to early growth of the southern elephant seal, *M. leonina* (L.). *Aust. J. Zool.* 16: 739 - 748.

BRYDEN, M.M. 1968b. Control of growth in two populations of elephant seals. *Nature, Lond.* 217: 1106 - 1108.

BURTON, H.R. 1985. Tagging studies of male southern elephant seals (*Mirounga leonina* L.) in the Vestfold Hills area, Antarctica, and some aspects of their behaviour. In: Sea mammals of South Latitudes. (eds) L.K. Ling & M.M. Bryden. *Proc. symp. ANZAAS Congress* No. 52:

19 - 30. South Australian Museum.

BURTON, H.R. 1986. A substantial decline in the numbers of the southern elephant seal at Heard Island. *Tas. Nat.* 86: 4 - 8.

BUSCH, B.C. 1985. The War Against the Seals. Gill-Queens University Press, Canada.

BYERS, J.A. & MOODIE, J.D. 1990. Sex-specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. *Behav. Ecol. Sociobiol.* 26: 157 - 164.

CALAMBOKIDIS, J. & GENTRY, R.L. 1985. Mortality of northern fur seal pups in relation to growth and birth weights. *J. Wildl. Dis.* 21: 327 - 330.

CARRICK, R. & INGHAM, Susan, E. 1960. Ecological studies of the southern elephant seal, *Mirounga leonina* (L.), at Macquarie Island and Heard Island. *Mammalia* 24: 325-342.

CARRICK, R. & INGHAM, Susan E. 1962c. Studies on the southern elephant seal, *Mirounga leonina* (L.), V. Population dynamics and utilization. *CSIRO Wildl. Res.* 7: 198-206.

CARRICK, R., CSORDAS, S.E. & INGHAM, Susan E. 1962b. Studies on the southern elephant seal, *Mirounga leonina* (L.), IV. Breeding and development. *CSIRO Wildl. Res.* 7: 161-197.

CARRICK, R., CSORDAS, S.E., INGHAM, Susan E. & KEITH, K. 1962a. Studies on the southern elephant seal, *Mirounga leonina* (L.), III. The annual cycle in relation to age and sex. *CSIRO Wildl. Res.* 7: 119-160.

CAUGHLEY, G. 1977. Analysis of Vertebrate Populations. John Wiley & Sons, New York.

CHRISTENSEN, T.E. 1974. Aggressive and maternal behaviors of the female northern elephant seal. PhD thesis, University of California, Berkeley.

CHRISTENSEN, T.E. & Le BOEUF, B.J. 1978. Aggression in the female northern elephant seal, *Mirounga angustirostris*. *Behaviour* 64: 158 - 172.

CLUTTON-BROCK, T.H. 1988. Reproductive success. In: Reproductive Success. (ed.) T.H. Clutton-Brock. University of Chicago press, Chicago. pp. 472 - 486.

CLUTTON-BROCK, T.H., ALBON, S.D. & GUINNESS, Fiona E. 1981. Parental investment in male and female offspring in polygynous mammals. *Nature, Lond.*, 289: 487 - 489.

CLUTTON-BROCK, T.H., ALBON, S.D. & GUINNESS, Fiona E. 1989. Fitness costs and lactation in wild mammals. *Nature, Lond.* 337: 260 - 262.

CLUTTON-BROCK, T.H., GUINNESS, Fiona E. & ALBON, S.D. 1982. Red Deer: the Behaviour and Ecology of Two Sexes. University of Chicago Press, Chicago.

CLUTTON-BROCK, T.H., MAJOR, M., ALBON, S.D. & GUINNESS, Fiona E. 1987. Early development and population dynamics in red deer. I. Density dependent effects on juvenile survival. *J. Anim. Ecol.* 56: 53 - 67.

CONDY, P.R. 1977. The ecology of the southern elephant seal *Mirounga leonina* (Linnaeus 1758), at Marion Island. D.Sc. thesis, University of Pretoria, Pretoria.

CONDY, P.R. 1978. The distribution and abundance of southern elephant seals *Mirounga leonina* (Linn.) on the Prince Edward Islands. *S. Afr. J. Antarct. Res.* 8: 42 - 48.

CONDY, P.R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *S. Afr. J. Zool.* 14: 95 - 102.

CONDY, P.R. 1980. Postnatal development and growth in southern elephant seals (*Mirounga leonina*) at Marion Island. *S. Afr. J. Wildl. Res.* 10: 118 - 122.

CONDY, P.R. 1981. Annual food consumption and seasonal fluctuations in biomass of seals at Marion Island. *Mammalia* 45: 21 - 30.

CONDY, P.R. 1984. The population of the southern elephant seal, *Mirounga leonina*, at Marion Island, 1973 - 1983. *S. Afr. J. Sci.* 80: 26 - 27.

CONDY, P.R., VAN AARDE, R.J. & BESTER, M.N. 1978. The seasonal occurrence and behaviour of killer whales *Orcinus orca*, at Marion Island. *J. Zool., Lond.* 184: 449 - 464.

COOKE, F. & FINDLAY, C.S. 1982. Polygenic variation and stabilizing selection in a wild population of lesser snow geese (*Anser caerulescens caerulescens*). *Am. Nat.* 120: 543 - 547.

COSTA, D.P. & GENTRY, R.L. 1986. Free-ranging energetics of northern fur seals. In: Fur Seals: Maternal Strategies on Land and at Sea. (eds) R.L. Gentry & G.L. Kooyman. Princeton University Press, Princeton. pp 79 - 101.

COSTA, D.P., TRILLMICH, F. & CROXALL, J.P. 1988. Intraspecific allometry of neonatal size in the Antarctic fur seal (*Arctocephalus gazella). Behav. Ecol. Sociobiol.* 22: 361 - 364.

COSTA, D.P., Le BOEUF, B.J., HUNTLEY, A.C. & ORTIZ, C.L. 1986. The energetics of lactation in the northern elephant seal, *Mirounga angustirostris. J. Zool., Lond.* 209: 21 - 33.

COULSON, J.C. & HICKLING, G. 1961. Variation in the secondary sex-ratio of the grey seal *Halichoerus grypus* (Fab.) during the breeding season. *Nature, Lond.*, 190: 281.

CROXALL, J.P. & GENTRY, R.L. 1987. The 1984 fur seal symposium: An introduction. In: Status, Biology and Ecology of Fur Seals. (eds) J.P. Croxall & R.L.Gentry. *N160AA Tech. Rep. NMFS.* 51: 1 - 8.

CROXALL, J.P. & HIBY, L. 1983. Fecundity, survival and site fidelity in Weddell seals, *Leptonychotes weddelli. J. Appl. Ecol.* 20: 19 - 32.

DEUTSCH, C.J., HALEY, M.P. & Le BOEUF, B.J. 1991. Reproductive effort of male northern elephant seals: estimates from mass loss. *Can. J. Zool.* 68: 2580 - 2594.

DEWSBURY, D.A. & HARTUNG, T.G. 1980. Copulatory behaviour and differential reproduction of laboratory rats in a two-male, one-female competitive situation. *Anim. Behav.* 28: 95 - 102.

DOIDGE, D.W. & CROXALL, J.P. 1985. Diet and energy budget of the antarctic fur seal *Arctocephalus gazella*. In: Antarctic Nutrient Cycles and Food Webs. (eds) W.R.Siegfried, P.R.Condy & R.M.Laws. Springer-Verlag, Berlin. pp. 543 - 550.

DOIDGE, D.W. & CROXALL, J.P. 1989. Factors affecting weaning weight in Antarctic fur seals *Arctocephalus gazella* at South Georgia. *Polar Biol.* 9: 155 - 160.

DUCK, C.D. 1990. Annual variation in the timing of reproduction in Antarctic fur seals, *Arctocephalus gazella*, at Bird Island, South Georgia. *J. Zool., Lond.* 222: 103 - 116.

EBERHARDT, L.L., CHAPMAN, D.G. & GILBERT, J.R. 1979. A review of marine mammal census methods. *Wildl. Monogr.* 63: 1 - 46.

EVERSON, I. 1977. The Living Resources of the Southern Ocean. FAO United Nations Southern Ocean Fisheries Programme, GLO/SO/77/1, 156 pp.

FISHER, R.A. 1930. The Genetical Theory of Natural Selection. Oxford University Press, Oxford.

FRASER, J.F.D. & HUGGET, A. St G. 1974. Species variations in the foetal growth rates of eutherian mammals. *J. Zool., Lond.* 174: 481 - 509.

FRASER, D. & MORLEY JONES, R. 1975. The "teat order" of suckling pigs. I. Relation to birth weight and subsequent growth. *J. Agric. Sci. Camb.* 84: 387 - 391.

GALES, N.J. & BURTON, H.R. 1987. Ultrasonic measurement of blubber thickness of the southern elephant seal, *M. leonina* (Linn.). *Aust. J. Zool.* 35: 207 - 217.

GALES, N.J., ADAMS, M & BURTON, H.R. 1989. Genetic relatedness of two populations of the southern elephant seal, *M. leonina. Mar. Mamm. Sci.* 5: 57 - 67.

GOSLING, L.M., BAKER, S.J. & WRIGHT, K.M.H. 1984. Differential investment by female coypus (*Myocastor coypus*) during lactation. *Symp. zool. Soc. Lond.* 51: 273 - 300.

GRIFFITHS, D.J. & BRYDEN, M.M. 1981. The annual cycle of the pineal gland of the elephant seal (*Mirounga leonina*). In: Pineal Function. (eds) C.D. Matthews & R.F. Seamark. Elsevier/North Holland biomedical press, Holland. pp. 57 - 65.

GUERRERO, R. 1974. Association of the type and time of insemination within the menstrual cycle with the human sex ratio at birth. *New Engl. J. Medi.* 29: 10 - 56.

GUERRERO, R. 1975. Type and time of insemination within the menstrual cycle and the human sex ratio at birth. *Studies in Family Planning* 6: 367 - 371.

GUINNESS, Fiona E., CLUTTON-BROCK, T.H. & ALBON, S.D. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). *J. Anim. Ecol.* 47: 817 - 832.

GUNN, R.G. 1965. Levels of first winter feeding in relation to performance of Cheviot hill ewes. III. Tissue and joint development to 12-18 months of age. *J. Agric. Sci. Camb.* 64: 311 - 321.

HARWOOD, J. & PRIME, J.H. 1978. Some factors affecting the size of British grey seal populations. *J. Appl. Ecol.* 15: 401 - 411.

HIGGINS, Lesley V., COSTA, D.P., HUNTLEY, A.C. & Le BOEUF, B.J. 1988. Behavioral and physiological measurements of maternal investment in the Steller sea lion, *Eumetopias jubatus. Mar. Mamm. Sci.* 4: 44 - 58.

HILL, Suzanne E.B. 1987. Reproductive ecology of Weddell seals (*Leptonychotes weddelli*) in McMurdo Sound, Antarctica. PhD thesis, University of Minnesota, Minneapolis.

HILL, R.D. 1991. Geolocation by light-level readings. Wildlife Computers Geolocation Instruction Manual, Woodinville, U.S.A. 23pp.

HINDELL, M.A. 1991. Some life-history parameters of a declining population of southern elephant seals, *Mirounga leonina*. *J. Anim. Ecol.* 60: 119 - 134.

HINDELL, M.A. & BURTON, H.R. 1987. Past and present status of the southern elephant seal (*Mirounga leonina* Linn) at Macquarie Island. *J. Zool., Lond.* 213: 365 - 380.

HINDELL, M.A. & BURTON, H.R. 1988a. The history of the southern elephant seal industry at Macquarie Island and an estimate of the pre-sealing numbers. *Pap. Proc. Royal Soc. Tasman.* 122: 159 - 176.

HINDELL, M.A. & BURTON, H.R. 1988b. Seasonal haul-out patterns of the southern elephant seal (*Mirounga leonina* L.), at Macquarie Island. *J. Mammal.* 69: 81-88.

HINDELL, M.A., BURTON, H.R. & SLIP, D.J. 1991. Foraging areas of southern elephant seals, *Mirounga leonina*, as inferred from water temperature data. *Aust. J. Freshwat. Res.* 42: 115 - 128.

HINDELL, M.A. & LITTLE, G.J. 1988. Longevity, fertility and philopatry of two female southern elephant seals (*Mirounga leonina*) at MacQuarie Island. *Mar. Mamm. Sci.* 4: 168 - 171.

HUBER, Harriet H. 1987. Natality and weaning success in relation to age of first reproduction in northern elephant seals. *Can. J. Zool.* 65: 1311 - 1316.

HUBER, Harriet H., McELROY, Teresa, BOEKELHEIDE, R.J. & HENDERSON, P. 1983. Studies of Marine Mammals at the Farallon Islands, 1981-1982. *NMFS Administrative report*

No. LJ-83-09- C. La Jolla, California.

JACKA, T.H., CHRISTOU, L. & COOK, B.J. 1984. A data bank of mean monthly annual surface temperatures for Antarctica, in the Southern Ocean and South Pacific Ocean. *ANARE Res. Notes* 22: 1 - 98.

JACOBSEN, N.O. 1984. Estimates of pup production, age at first parturition and natural mortality for hooded seals in the West Ice. *Fiskeridir. Skr. Ser. Havunders.* 17: 483 - 498.

JAMES, W.H. 1980. Gonadotrophin and the human secondary sex ratio. *Br. Med. J.* 281: 711 - 713.

JAMES, W.H. 1986. Hormonal control of sex ratio. *J. theor. Biol.* 118: 427 - 441.

JAMES, W.H. 1989. Parental hormone levels and mammalian sex ratios at birth. *J. theor. Biol.* 139: 59 - 67.

JEWELL, P.A., HALL, S.J.G. & ROSENBERG, M.M. 1986. Multiple mating and siring success during natural oestrus in the ewe. *J. Reprod. Fert.* 77: 81 - 89.

JONES, E. 1981. Age in relation to breeding status of the male southern elephant seal, *Mirounga leonina* (L.), at Macquarie Island. *Aust. Wildl. Res.* 8: 327 - 334.

KENYON, K.W., SCHEFFER, V.B. & CHAPMAN, D.G. 1954. A population study of the Alaska fur seal herd. *U.S. Fish Wildl. Serv., Spec. Sci. Rep. Wildl.* 12: 1 - 77.

KERLEY, G.I.H. 1983. Relative population sizes and trends, and hybridization of fur seals *Arctocephalus tropicalis* and *A. gazella* at the Prince Edward Islands. *S. Afr. J. Zool.* 18: 388 - 392.

KING, Judith E. 1983. Seals of the World. Oxford University Press, Oxford.

KOJOLA, I. 1989. Mother's dominance status and differential investment in reindeer calves. *Anim. Behav.* 38: 177 - 185.

KOVACS, Kit M. & LAVIGNE, D.M. 1986a. Growth of grey seal (*Halichoerus grypus*) neonates: differential maternal investment in the sexes. *Can. J. Zool.* 64: 1937 - 1943.

KOVACS, Kit M. & LAVIGNE, D.M. 1986b. Maternal investment and neonatal growth in phocid seals. *J. Anim. Ecol.* 55: 1035 - 1051.

KREBS, C.J. 1985. Ecology: The Experimental Analysis of Distribution and Abundance. Harper & Row, New York.

KRETZMANN, M.B., COSTA, D.P. & Le BOEUF, B.J. 1989. Milk intake, metabolic rate and mass change in northern elephant seal pups: evidence for sexual equality. In: *Proceedings of the eigth biennial conference on the biology of marine mammals*. Dec. 7 - 11, Pacific Grove, California.

LAMB, H.H. 1977. Climate: Present, Past and Future. 2: Climatic History and the Future. Methuen, London.

LANDER, R.H. 1981. A lifetable and biomass estimate for Alaskan fur seals. *Fish. Res.* 1: 55 - 70.

LAWS, R.M. 1953. The elephant seal (*Mirounga leonina* Linn.). I. Growth and age. *Sci. Rep. Falkland Is. Dep. Surv.* 8: 1 - 62.

LAWS, R.M. 1956a. The elephant seal (*Mirounga leonina* Linn.). II. General, social and reproductive behaviour. *Sci. Rep. Falkland Is. Dep. Surv.* 13: 1-88.

LAWS, R.M. 1956b. Growth and sexual maturity in aquatic mammals. *Nature, Lond.* 178: 193 - 194.

LAWS, R.M. 1960. The southern elephant seal (*Mirounga leonina* Linn.) at South Georgia. *Norks Hvalfangsttid* 49: 466 - 476, 520 - 542.

LAWS, R.M. 1977. Seals and whales of the southern ocean. *Phil. Trans. R. Soc. Lond. B* 279: 81 - 96.

LAWS, R.M. 1984. Seals. In: Antarctic Ecology. (ed.) R.M.Laws. Academic Press, Lond. 2: 621 - 715.

Le BOEUF, B.J. 1972. Sexual behaviour in the northern elephant seal, *Mirounga angustirostris. Behaviour* 41: 1 - 26.

Le BOEUF, B.J. 1974. Male-male competition and reproductive success in elephant seals. *Am. Zool.* 14: 163 - 176.

Le BOEUF, B.J. & BRIGGS, K.T. 1977. The cost of living in a seal harem. *Mammalia* 41: 167 - 195.

Le BOEUF, B.J. & PETERSON, R.S. 1969. Social status and mating activity in elephant seals. *Science* 163: 91 - 93.

Le BOEUF, B.J. & PETRINOVICH, L.F. 1974. Elephant seals : interspecific comparisons of vocal and reproductive behaviour. *Mammalia* 38: 16-32.

Le BOEUF, B.J. & REITER, Joanne. 1988. Lifetime reproductive success in northern elephant seals. In: Reproductive Success. (ed.) T.H. Clutton-Brock. University of Chicago press, Chicago. pp. 344 - 362.

Le BOEUF, B.J., CONDIT, R. & REITER, Joanne 1989. Parental investment and the secondary sex ratio in northern elephant seals. *Behav. Ecol. Sociobiol.* 25: 109 - 117.

Le BOEUF, B.J., COSTA, D.P., HUNTLEY, A.C. & FELDKAMP, S.D. 1988. Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Can. J. Zool.* 66: 446 - 458.

LETT, P.F., MOHN, R.K. & GRAY, D.F. 1981. Density-dependent processes and management strategy for the northwest Atlantic harp seal population. In: Dynamics of Large Mammal Populations. (eds) C.W. Fowler & T.D. Smith. John Wiley & Sons, New York. pp. 135 - 158.

LING, J.K. 1969. A review of ecological factors affecting the annual cycle in island populations of seals. *Pacif. Sci.* 23: 399 - 413.

LING, J.K. & BRYDEN, M.M. 1981. Southern elephant seal *Mirounga leonina* Linnaeus, 1758. In: Handbook of Marine Mammals, volume 2: Seals. (eds) S.H. Ridgeway & R.J. Harrison. Academic press, London. pp. 297 - 327.

LITTLE, G.L., BRYDEN, M.M. & BARNES, A. 1987. Growth from birth to 20 days in the elephant seal, *Mirounga leonina*, at MacQuarie Island. *Aust. J. Zool.* 35: 307 - 312.

MacGILLIVRAY, Margaret H. 1986. Disorders of growth and development. In: Endocrinology and Metabolism. (eds) P. Felig, J.D. Baxter, A.E. Broadus & L.A. Frohman. 2nd edition. McGraw-Hill, New York. pp. 1581 - 1628.

MARSH, J.H. 1948. No Pathway Here. H.B. Timmins, Cape Town.

MARSON, J., GERVAIS, D., MEURIS, S., COOPER, R.W. & JOUANNET, P. 1989. Influence of ejaculation frequency on semen characteristics in chimpanzees (*Pan troglodytes*). *J. Reprod. Fert.* 85: 43 - 50.

MAYNARD SMITH, J. 1980. A new theory of sexual investment. *Behav. Ecol. Sociobiol.* 7: 247 - 251.

McCANN, T.S. 1980. Population structure and social organization of southern elephant seals, *Mirounga leonina* (L.). *Biol. J. Linn. Soc.* 14: 133-150.

McCANN, T.S. 1981a. Aggression and sexual activity of male southern elephant seals, *Mirounga leonina. J. Zool., Lond.* 195: 295 - 310.

McCANN, T.S. 1981b. The social organisation and behaviour of the southern elephant seal, *Mirounga leonina* (L.). PhD thesis, University of London, London.

McCANN, T.S. 1982. Aggressive and maternal activities of female southern elephant seals (*Mirounga leonina*). *Anim. Behav.* 30: 268 - 276.

McCANN, T.S. 1983. Activity budgets of southern elephant seals, *Mirounga leonina*, during the breeding season. *Z. Tierpsychol.* 61: 111 - 126.

McCANN, T.S. 1985. Size, status and demography of southern elephant seal *Mirounga leonina* populations. In: Sea Mammals of South Latitudes. (eds) L.K. Ling & M.M. Bryden. *Proc. symp. ANZAAS Congress* No. 52: 1 - 17. South Australian Museum.

McCANN, T.S. & ROTHERY, P. 1988. Population size and status of the southern elephant seal (*Mirounga leonina*) at South Georgia, 1951 - 1985. *Polar Biol.* 8: 305 - 309.

McCANN, T.S., FEDAK, M.A. & HARWOOD, J. 1989. Parental investment in southern elephant seals, *Mirounga leonina. Behav. Ecol. Sociobiol.* 25: 81 - 87.

MENDL, M. & PAUL, Elizabeth S. 1989. Observation of nursing and sucking behaviour as an indicator of milk transfer and parental investment. *Anim. Behav.* 37: 513 - 514.

MITCHELL, B. & LINCOLN, G.A. 1973. Conception dates in relation to age and condition in two populations of red deer in Scotland. *J. Zool., Lond.* 171: 141 - 152.

MORRIS, P.A., Le BOEUF, B.J. & ORTIZ, C.L. 1989. Effects of weaning mass on survival and size of yearling northern elephant seals. In: *Proceedings of the eigth biennial conference* *on the biology of marine mammals*. Dec 7 - 11, Pacific Grove, California.

MURRAY, M.D. 1981. The breeding of the southern elephant seal, *Mirounga leonina* L., on the Antarctic continent. *Polar Rec.* 20: 370 - 371.

NICHOLLS, D.G. 1970. Dispersal and dispersion in relation to the birthsite of the southern elephant seal, *Mirounga leonina* (L.) of Macquarie Island. *Mammalia* 34: 598 - 616.

OFTEDAL, O.T., IVERSON, Sara J. & BONESS, D.J. 1987. Milk and energy intakes of suckling california sea lion *Zalophus californianus* pups in relation to sex, growth, and predicted maintenance requirements. *Physiol. Zool.* 60: 560 - 575.

ONO, Kathryn A., BONESS, D.J. & OFTEDAL, O.T. 1987. The effect of natural environmental disturbance on maternal investment and pup behaviour in the california sea lion. *Behav. Ecol. Sociobiol.* 21: 109 - 118.

PANAGIS, K. 1981. Local movement of southern elephant seal pups *Mirounga leonina* (Linn.) at Marion Island. *S. Afr. J. Antarct. Res.* 10/11: 28 - 31.

PASCAL, M. 1979. Essai de dénombremont de la population d'éléphants de mer (*Mirounga leonina* (L.)) des Iles Kerguelen (49°S,69°E). *Mammalia* 43: 147-159.

PASCAL, M. 1985. Numerical changes in the population of elephant seals (*Mirounga leonina* L) in the Kerguelen Archipelago during the past 30 years. In: Marine Mammal Fishery Interactions. (ed.) J.R. Beddington, R.J.H. Beverton & D.M. Lavigne. George Allen & Unwin, London. pp. 170 - 186.

PAYNE, M.R. 1979. Growth in the antarctic fur seal *Arctocephalus gazella*. *J. Zool., Lond.* 187: 1 - 20.

RAND, R.W. 1956. Notes on the Marion Island fur seal. *Proc. zool. Soc. Lond.* 126: 65 - 82

RAND, R.W. 1962. Elephant seals on Marion Island. *Afr. Wildl.* 16: 191 - 198.

REITER, Joanne 1984. Studies of female competition and reproductive success in the northern elephant seal. PhD thesis, University of California, Santa Cruz.

REITER, Joanne & Le BOEUF, B.J. 1991. Life history consequences of variation in age at primiparity in northern elephant seals. *Behav. Ecol. Sociobiol.* 28: 153 - 160.

REITER, Joanne, PANKEN, Kathy J. & Le BOEUF, B.J. 1981. Female competition and reproductive success in northern elephant seals. *Anim. Behav.* 29: 670 - 687.

REITER, Joanne, STINSON, Nel L. & Le BOEUF, B.J. 1978. Northern elephant seal development : the transition from weaning to nutritional independence. *Behav. Ecol. Sociobiol.* 3: 337 - 367.

RIBIC, Christine A. 1984. Growth of a northern elephant seal (*Mirounga angustirostris*) colony. PhD thesis, University of Minnesota, Minneapolis.

RIBIC, Christine A. 1988. Maternal aggression in northern elephant seals: the effect of the pup. *Can. J. Zool.* 66: 1693 - 1698.

RIEDMAN, Marienne L. 1990. The Pinnipeds: Seals, Sea Lions and Walruses. University of California Press, Berkeley.

RIEDMAN, Marienne L. & Le BOEUF, B.J. 1982. Mother-pup separation and adoption in northern elephant seals. *Behav. Ecol. Sociobiol.* 11: 203 - 215.

RIGAUDIERE, N. 1979. The androgens in the guinea pig foetus throughout the embryonic development. *Acta Endocrinol.* 100: 301 - 307.

ROBERTS, A.M. 1972. Gravitational separation of x and y spermatozoa. *Nature, Lond.* 238: 223 - 225.

ROBERTS, A.M. 1978. The origins of fluctuations in the human secondary sex ratio. *J. Biosoc. Sci.* 10: 169 - 182.

RUSSELL, W.S. 1976. Effect of twin birth on the growth of cattle. *Anim. Prod.* 22: 167 - 173.

SANDEGREN, F.E. 1976. Agonistic behaviour in the male northern elephant seal. *Behaviour* 57: 136 - 158.

SCAR. 1991. Report of the workshop on southern elephant seals. Monterey, California, USA. 22-23 May 1991. 29pp.

SCHULZE, B.R. 1971. The climate of Marion Island. In: Marion and Prince Edward Islands: Report of the South African Biological & Geological Expedition/ 1965-1966. (eds) E.M. van Zinderen Bakker Snr., J.M. Winterbottom & R.A. Dyer. Balkema, Cape Town. pp. 16 - 31.

SEBER, G.A.F. 1982. The Estimation of Animal Abundance. 2nd edn. Macmillan, New York.

SERGEANT, D.E. 1976. History and present status of populations of harp and hooded seals. *Biol. Conserv.* 10: 95 - 118.

SHAUGHNESSY, P.D. In press. Population estimates of the cape fur seal *Arctocephalus pusillus*. II. From tagging and recapturing. *Investl. Rep. Sea Fish. Inst. S. Afr.*

SIMPSON, M.J.A. & SIMPSON, A.E. 1982. Birth sex ratios and social rank in rhesus monkey mothers. *Nature, Lond.* 300: 440 - 441.

SINIFF, D.B., DeMASTER, D.P., HOFMAN, R.J. & EBERHARDT, L.L. 1977. An analysis of the dynamics of a Weddell seal population. *Ecol. Monogr.* 47: 319 - 335

SKINNER, J.D. & VAN AARDE, R.J. 1983. Observations on the trend of the breeding population of southern elephant seals *Mirounga leonina*, at Marion Island. *J. Appl. Ecol.* 20:

707 - 712.

SMITH, T.G. 1973. Population dynamics of the ringed seal in the Canadian eastern Arctic. *Fish. Res. Board Can. Bull.* No 181.

SMITH, V.R. & STEENKAMP, Marianna 1990. Climate change and its ecological implications at a subantarctic island. *Oecologia* 85: 14 - 24.

SMITHERS, R.H.N. 1983. The Mammals of the Southern African Subregion. University of Pretoria, Pretoria.

SORENSEN, J.H. 1950. Elephant seals of Campbell Island. *Cape Exped. Ser. Bull.* 6: 1 - 31. pp.

STEWART, B.S. 1989. The ecology and population biology of the northern elephant seal, *Mirounga angustirostris* Gill 1866, on the southern california channel islands. PhD thesis, University of California, Los Angeles.

STEWART, R.E.A. & LAVIGNE, D.M. 1984. Energy transfer and female condition in nursing harp seals *Phoca groenlandica. Holarctic Ecology* 7: 182 - 194.

STIRLING, I. 1971. Variation in the sex ratio of newborn Weddell seals during the pupping season. *J. Mammal.* 52: 842 - 844.

TAYLOR, R.H. & TAYLOR, G.A. 1989. Re-assessment of the status of southern elephant seals (*Mirounga leonina*) in New Zealand. *N. Z. Jl Mar. Freshwat. Res.* 23: 201 - 213.

TEMTE, J.L. 1985. Photoperiod and delayed implantation in the northern fur seal (*Callorhinus ursinus*). *J. Reprod. Fert.* 73: 127 - 131.

TESTA, J.W. 1987. Juvenile survival and recruitment in a population of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. *Can. J. Zool.* 65: 2993 - 2997.

THOMAS, J.A. & DeMASTER, D.P. 1983. Parameters affecting survival of Weddell seal pups (*Leptonychotes weddelli*) to weaning. *Can. J. Zool.* 61: 2078 - 2083.

TIERNEY, T.J. 1977. The southern elephant seal, *Mirounga leonina* (L.), in the Vestfold Hills, Antarctica. *Aust. Wildl. Res.* 4: 13 - 24.

TRILLMICH, F. 1986. Maternal investment and sex allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. *Behav. Ecol. Sociobiol.* 19: 157 - 164.

TRIVERS, R.L. 1972. Parental investment and sexual selection. In: Sexual Selection and the Descent of Man. (ed.) B. Campbell. Heinemann, London. pp. 137 - 179.

TRIVERS, R.L. & WILLARD, D.E. 1973. Natural selection of parental ability to vary sex ratios of offspring. *Science* 179: 90 - 92.

VAN AARDE, R.J. 1980a. Fluctuations in the population of southern elephant seals *Mirounga leonina* at Kerguelen Island. *S. Afr. J. Zool.* 15: 99 - 106.

VAN AARDE, R.J. 1980b. Harem structure of the southern elephant seal *Mirounga leonina* at Kerguelen Island. *Rev. Ecol. (Terre Vie)* 34: 31 - 44.

VERGANI, D.F., LEWIS, M.N. & STANGANELLI, Z.B. 1987. Observations on the haulout patterns and trends of the breeding populations of southern elephant seal at Peninsula Valdes (Patagonia) and Stranger Point (25 de Mayo - King George Is.). *SC-CAMLR-VI/BG/36*: 1 - 9.

VERME, L.J. 1989. Maternal investment in white-tailed deer. *J. Mammal.* 70: 438 - 442.

VERME, L.J. & OZOGA, J.J. 1981. Influence of temporal relationships during oestrous on deer sex ratio. *J. Wildl. Mgmt.* 45: 710 - 715.

VERWOERD, W.J. 1971. Geology. In: Marion and Prince Edward Islands: Report of the

South African Biological & Geological Expedition/ 1965-1966. (eds) E.M. van Zinderen Bakker Snr., J.M. Winterbottom & R.A. Dyer. Balkema, Cape Town. pp. 40 - 62.

WILKINSON, I.S. & BESTER, M.N. 1990a. Continued population increase in fur seals *Arctocephalus tropicalis* and *A. gazella* at the Prince Edward Islands. *S. Afr. J. Antarct. Res.* 20: 58 - 63.

WILKINSON, I.S. & BESTER, M.N. 1990b. Duration of post-weaning fast and local dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. *J. Zool., Lond.* 222: 591 - 600.

WITTENBERGER, J.F. 1981. Animal Social Behavior. Duxbury press, Boston.

WOLFF, J.O. 1988. Maternal investment and sex ratio adjustment in American bison calves. *Behav. Ecol. Sociobiol.* 23: 127 - 133.

YORK, Anne E. 1983. Average age at first reproduction of the northern fur seal (*Callorhinus ursinus*). *Can. J. Fish. Aquat. Sci.* 40: 121 - 127.

ZAR, J.H. 1984. Biostatistical Analysis. 2nd edn. Prentice-Hall, Englewood Cliffs, New Jersey.

APPENDIX I

THE RELATIONSHIP BETWEEN RELATIVE AGE, BODY SIZE AND SOCIAL STATUS

Determination of age, size and social status

Adult females are bitten on the neck by males during copulation (Laws 1953, Carrick *et al.* 1962b), consequently, as cows get older the numbers of scars on their neck increase. A female giving birth to her first pup usually bears a single set of four scars (Carrick *et al.* 1962b). Her coat is smooth and the skin on the face and neck unwrinkled. A multiparous cow will have more scar sets on her neck and the skin on her neck and face is rougher in appearance than the primiparous female. As the cows age these scars increase in number to such an extent that they form large scar patches on the neck (Figure 36), often linked by a scarred area on the top of the neck, producing a lighter coloured "yolk" (Laws 1953). A further effect of ageing is the progressive greying of the face to give a "mask" effect (Figure 37). For the purpose of the study, cows were divided into three, relative age classes. Age class 1 consisted of all apparently primiparous (first time breeding) cows, *i.e.* those with a single set of neck scars, and smooth unwrinkled skin. Age class 2 included multiparous cows that possessed more than the single set of neck scars and a rougher skin appearance, while age class 3 cows were those possessing large scar patches on either side of the neck and a facial "mask".

As it was not possible to accurately measure cows during the study, they were divided subjectively into those that were "obviously large" and those which were "obviously small". Those that remained were classed as "medium" in size. Cows of "medium" size will be considered in this appendix, but in the main body of the dissertation only the "large" and "small" categories will be used in comparisons, given the highly subjective nature of the classification.

Cow-cow interactions were observed at the study beach on a daily basis each breeding season. In each encounter between cows their identities and reproductive condition (pregnant/parturient) were noted. Both the initiator of the encounter and the victor were

Figure 36. Large scar patches seen on the neck of a multiparous southern elephant seal cow, resulting from bites by bulls during copulation.

Figure 37. Southern elephant seal cow exhibiting greying of the face producing a "mask like effect. This is a characteristic feature of older cows.

recorded. The contest either resulted in no clear victory (in which case it was not included in the cow's total number of interactions), or in one cow displacing the other. In some cases this displacement involved a clear retreat from the victor, or more usually only involved a slight change in position (Bartholomew & Collias 1962, McCann 1982, Ribic 1984).

The percentage of encounters in which a cow, after the birth of her pup, was dominant, was recorded. These percentages were ranked for each of the three seasons and those cows in the top fifty percent were classed as high ranking, while those in the bottom half were classified as low ranking. A dominance matrix could not be drawn up as all the cows, in a given year, were not present on the beach concurrently (See Chapter 3), and therefore certain confrontations were impossible. Had all the cows been present at the same time, large numbers of interactions would have had to be recorded (630 possible dyads with 35 cows on the beach) to produce a meaningful matrix.

To allow comment on whether level of aggression and dominance status changes after the birth of the pup, pregnant and *post-partum* cows were compared. The percentage of encounters that were initiated and won by pregnant and *post-partum* cows were recorded for all those females involved in more than ten interactions (it was felt that any fewer may result in a bias toward higher proportions than was a reality). These proportions were transformed using an arcsine transformation (Zar 1984) and the subsequent values used to determine mean and standard deviations of each category, before being transformed back to the original percentages. Comparisons between categories of female were made using Student's "*t*" test (Zar 1984) on the transformed values.

The three maternal variables (age, size and social status) were correlated to look for inter-relationships using a partial correlation procedure (Zar 1984) to remove the effects of the third variable in the comparison. In addition to the cross-sectional data above, the relationships were investigated among individual cows which were present in the study in more than one season (*i.e.* longitudinal data).

Age, size and social status, and their interrelationships

The numbers of cows in each of the three age categories for each season are shown in Figure 38. In all three seasons the primiparous (age class 1) group made up the smallest proportion, while the younger multiparous (age class 2) cows accounted for the highest proportion of the breeding cows.

The percentage of encounters initiated by pregnant cows was lower than by *post-partum* cows (t_{132}=3,00; P<0,01; Table 40), and the percentage of encounters in which pregnant cows dominated was also lower than in those that had given birth (t_{132}=2,76; P<0,01; Table 40).

Table 40. A comparison between the percentage of encounters initiated and/or dominated by pregnant and *post-partum* southern elephant seal cows at Trypot beach, Marion Island for the years 1986 to 1988. Values are means ± 1S.D. and sample sizes (n) are given in parenthesis.

	Pregnant (n=25)	*Post-partum* (n=109)
Initiated encounter*	18,9 ± 9,8%	34,6 ± 6,2%
Dominated encounter*	30,0 ± 10,2%	48,1 ± 8,5%

* = Significantly different at P<0,05.

The relationships between the individual variables are shown in Figures 39, 40 and 41. Positive partial correlations were obtained for comparisons of age versus size (r_{134}=0,358; P<0,001), age versus dominance (r_{133}=0,292; P<0,001) and for size and dominance (r_{133}=0,386; P<0,001).

Twelve of the seventeen cows that gave birth at Trypot beach for more than one of the years of the study showed a gradual move toward increased relative age, body size and social status. Three of the cows apparently displayed a decline in relative body size with increasing age, and three changed status from high to low ranking individuals in successive seasons (one of these also displayed a reduction in relative body size.

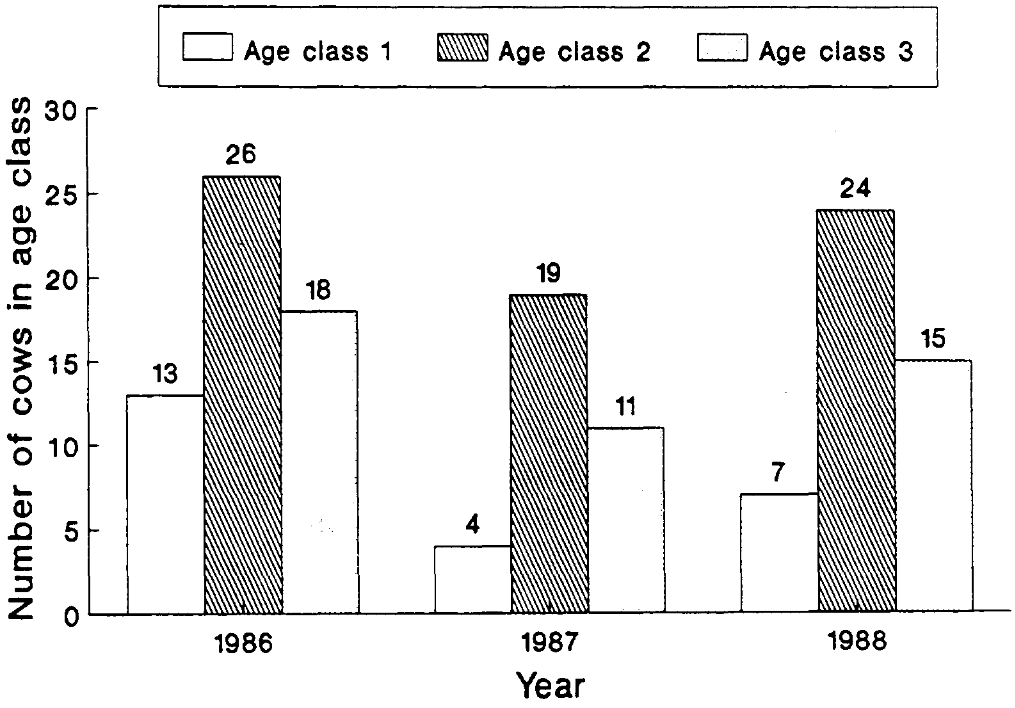

Figure 38. Numbers of southern elephant seal cows in each of three relative age classes during the breeding season at Trypot beach, Marion Island, between 1986 and 1988.

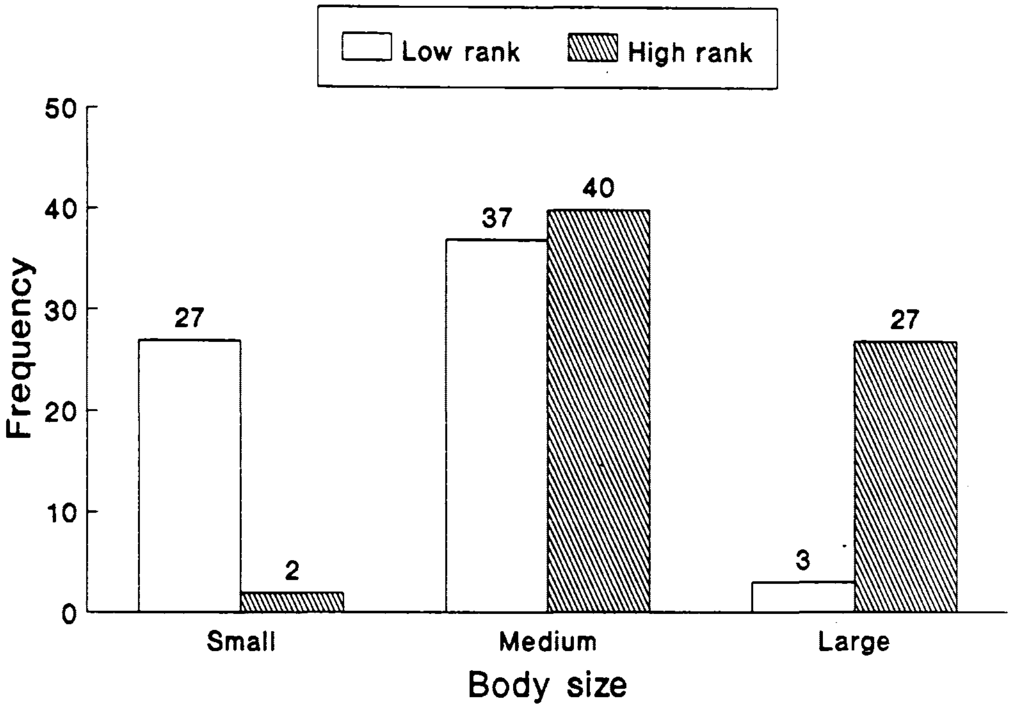

Figure 39. The relationship between body size and social rank of southern elephant seal cows at Trypot beach, Marion Island between, 1986 and 1988.

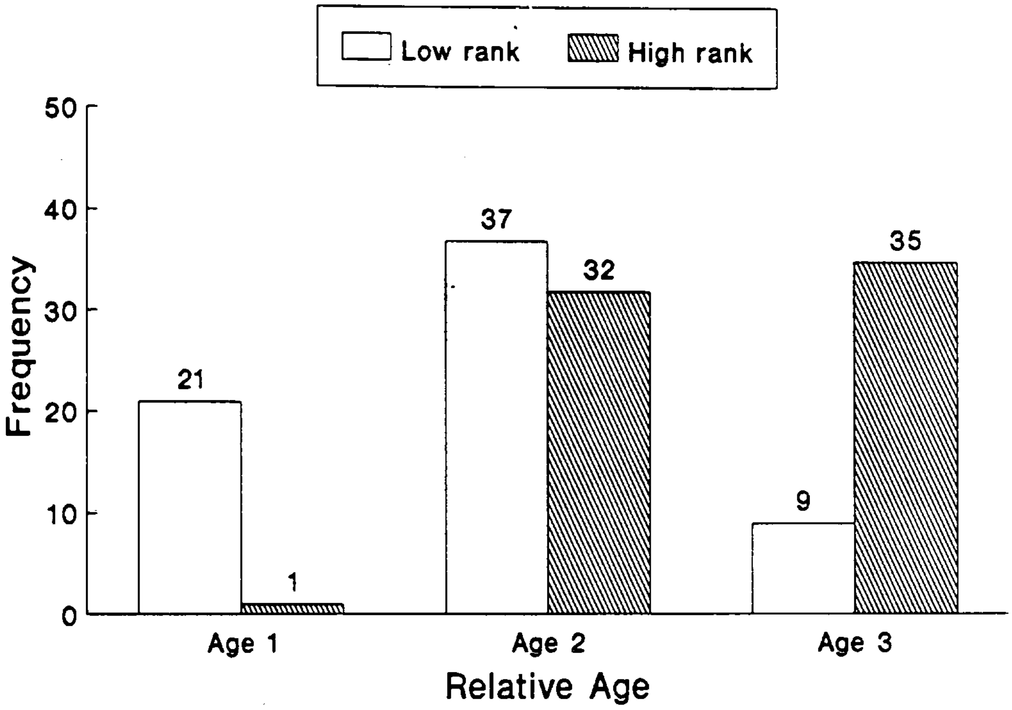

Figure 40. The relationship between relative age and social rank of southern elephant seal cows at Trypot beach, Marion Island between, 1986 and 1988.

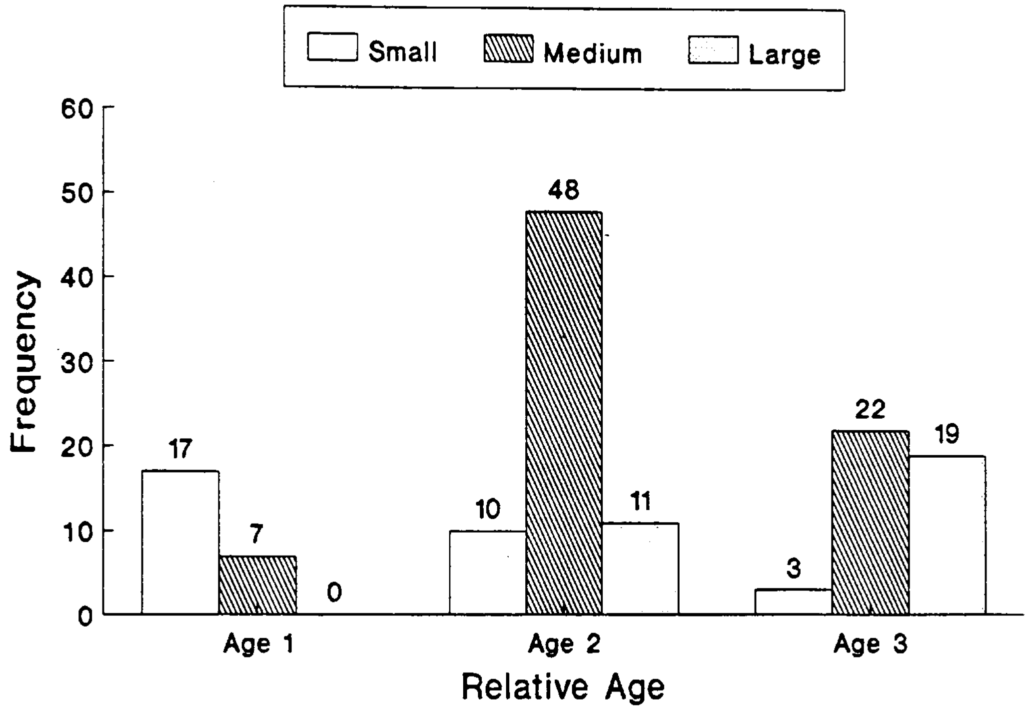

Figure 41. The relationship between relative age and body size of southern elephant seal cows at Trypot beach, Marion Island between, 1986 and 1988.

It is clear that the maternal variables of age, size and social status are related. The older a cow is, the larger she is, and the more dominant she is. However, given the limitations of the broad categories included in the present analysis, the partial correlation coefficients show that size is a more important correlate of social status than is age.

APPENDIX II

The maximum numbers of bulls, cows and pups that were present in the main study area at Marion Island during the breeding seasons from 1974 to 1989 are shown in the table below.

Year	Bulls	Cows	Pups
1974	18	391	406
1975	14	319	317
1976	25	283	301
1977	17	253	260
1980	11	228	239
1981	17	219	243
1982	5	194	205
1983	14	180	199
1984	9	166	192
1985	9	200	200
1986	9	170	183
1987	16	157	177
1988	12	169	177
1989	15	170	184