

INFORMATION TO USERS

The most advanced technology has been used to photograph and reproduce this manuscript from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

U·M·I

University Microfilms International
A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
313 761-4700 800 521-0600

Order Number 9033141

**Reproductive behavior and maternal investment of Australian
sea lions**

Higgins, Lesley Vivian, Ph.D.

University of California, Santa Cruz, 1990

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

UNIVERSITY OF CALIFORNIA

SANTA CRUZ

**REPRODUCTIVE BEHAVIOR AND MATERNAL INVESTMENT OF
AUSTRALIAN SEA LIONS**

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

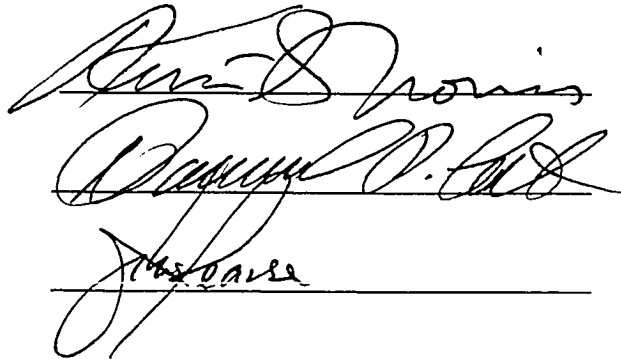
BIOLOGY

by

Lesley Vivian Higgins

June 1990

The dissertation of Lesley Vivian
Higgins is approved:



The image shows three handwritten signatures, each written over a horizontal line. The top signature is 'R. D. Norris', the middle one is 'D. W. P. Hill', and the bottom one is 'J. H. Davis'.

Dean of Graduate Studies and Research

THE UNIVERSITY OF ADELAIDE

BOX 498, G.P.O., ADELAIDE, SOUTH AUSTRALIA 5001

DEPARTMENT OF ANATOMY & HISTOLOGY

Telephone: (08) 228 5998

UNIVAD: AA 89141

Facsimile: (08) 22-40464

Ref:L0744ARA

24th May, 1990

Office of Graduate Studies and Research
University of California. U.S.A.

TO WHOM IT MAY CONCERN

This is to certify that Ms L. Higgins has my approval to include the manuscript titled 'Attacks on pups by male Australian sea lions, Neophoca cinerea, and the effect on pup mortality', which we coauthored, as part of her PhD dissertation.



R. A. Tedman
Lecturer.

Copyright © by
Lesley Vivian Higgins
1990

TABLE OF CONTENTS

	<u>page</u>
LIST OF FIGURES.....	vi
LIST OF TABLES.....	vii
ABSTRACT.....	viii
ACKNOWLEDGEMENTS.....	x
GENERAL INTRODUCTION	
Background.....	1
References.....	3
CH. 1. A NON-SEASONAL 17.7 MONTH BREEDING CYCLE FOR A POPULATION OF AUSTRALIAN SEA LIONS	
Introduction.....	4
Methods.....	7
Results.....	11
Discussion.....	18
Previous estimates of timing of breeding.....	19
Environmental cues.....	22
References.....	25
CH. 2. BREEDING BEHAVIOR OF AUSTRALIAN SEA LIONS	
Introduction.....	28
Methods.....	29
Study area.....	30
Identification of animals.....	30
Results.....	33

	<u>page</u>
Parturition and mating.....	33
Female and pup movements.....	40
Male breeding behavior.....	41
Discussion.....	52
Density of females.....	52
Male territoriality.....	54
References.....	56
CH. 3 ATTACKS ON PUPS BY MALE AUSTRALIAN SEA LIONS AND THE EFFECT ON PUP MORTALITY.....	59
References.....	64
CH. 4 MATERNAL INVESTMENT IN AUSTRALIAN SEA LIONS	
Introduction.....	65
Methods.....	68
Results.....	70
Pup production and weaning.....	71
Females with yearlings.....	74
Attendance cycles.....	74
Pup growth rates.....	85
Discussion.....	93
Time to weaning.....	93
Feeding trips.....	96
Pup growth.....	98
References.....	100

	<u>page</u>
APPENDIX A. Female breeding data for 1986-87, 1988 and 1989-90.....	103
APPENDIX B. Attendance data: means and standard deviations of trips to sea and stays ashore for individual females.....	110
APPENDIX C. Pup growth rate data: y-intercepts and slopes of regression lines for individual pups.....	113
APPENDIX D. Yearling growth curves.....	117

LIST OF FIGURES

	<u>page</u>
CHAPTER 1	
Figure 1. Geographic location of the area of study.....	7
Figure 2. Temporal distribution of births in the study areas.....	12
Figure 3. Timing of breeding seasons from 1973-1990.....	16
CHAPTER 2	
Figure 1. Map of Seal Bay.....	31
Figure 2. Spatial distribution of parturient females.....	35
Figure 3. Territorial attendance of males with and without females present.....	43
Figure 4. Copulatory success of males.....	46
Figure 5. A schematic representation of territorial attendance.....	48
Figure 6. Reproductive success of males as a function of time on territory.....	50
CHAPTER 4	
Figure 1. Departures and returns of females as a function of time of day.....	78
Figure 2. Frequency distribution of time at sea during 1986-87 and 1988.....	80
Figure 3. Frequency distribution of time ashore during 1986-87 and 1988.....	82
Figure 4. Time at sea and ashore of females as a function of pup age.....	86
Figure 5. Growth rates of male and female pups in 1986-87.....	88
Figure 6. Growth rates of male and female pups in 1988.....	90
Figure 7. Growth rates of yearlings from 0-28 months of age.....	94

LIST OF TABLES

	<u>page</u>
CHAPTER 1	
Table i. Birth dates and pupping intervals of females.....	15
CHAPTER 2	
Table 1. Female reproductive data.....	37
CHAPTER 4	
Table 1. Pup production and time to weaning of females who gave birth in 1986-87.....	72
Table 2. Pup production and time to weaning of females who gave birth in 1988.....	73
Table 3. Validation of female attendance cycles.....	77
Table 4. Trips to sea and stays ashore according to month.....	84

REPRODUCTIVE BEHAVIOR AND MATERNAL INVESTMENT OF AUSTRALIAN SEA LIONS

Lesley V. Higgins

ABSTRACT

The breeding cycle, breeding behavior, female attendance cycles and pup growth of Australian sea lions were studied at Kangaroo Island, South Australia, during December to May, 1986-87, April to October, 1988, and November to March 1989-90. Animals were identified using paint, dye and bleach marks during each breeding season and with tags and natural scars between seasons.

Females exhibited a synchronized, non-seasonal breeding cycle that is unique for pinnipeds. Data from 191 births gave 527 and 532 day intervals between the median pupping dates of the three breeding seasons. Sixteen females had a mean pupping interval of 540 ± 12.0 days (17.7 ± 0.4 months). Comparison to the timing of the breeding seasons during a previous study show a seasonal shift of 3-4 months during a 12 year period.

Breeding females were non-gregarious and parturition sites were spread out in the study area. As a consequence, male territories were plastic in space and time. Tenure on territories ranged from almost continuous occupation to less than one day a week depending on whether females were present. Differential reproductive success of males was low. Males usually attended one female at a time and thus practiced serial polygyny to achieve more than one copulation. Attacks on pups by adult territorial males accounted for 19% of pup mortality during two breeding seasons.

Females suckled their pups for 15-18 months until the birth of the next pup, although 23% did not give birth consecutively each breeding season, and continued to suckle their yearlings for up to 23 months. Female attendance cycles consisted of feeding trips of about two days in length and stays ashore of about 1.5 days, and did not change over time. Feeding trips were significantly shorter during the winter months of June and July and may reflect a day length affect. Pup age or sex seemed to have no influence on attendance cycles. Male pups were significantly heavier than female pups and grew faster in 1988, but not in 1986-87. Growth rate data of older pups indicate that there was a reduction in the rate of growth at about one year of age but this was not always related to time of weaning.

ACKNOWLEDGEMENTS

I would like to thank the many people and institutions who made this work possible. A special thanks go to my advisor, Ken Norris, who had faith and confidence in me, even though I proposed to undertake a project in a far-off country without his direct supervision. Appreciation is extended to John Pearce, who as a committee member, provided valuable comments and insights during the writing of the dissertation, and who was always supportive of my work. I greatly valued my relationship with Dan Costa, as my unofficial advisor and collaborator, and especially for the many discussions we had concerning the project, which were instrumental in focusing my thoughts and efforts in the right direction.

Without the contributions of my field assistants there would have been no project. Carolyn Brawner, Luciana Honigman, Sean Hanser, Lelia Gass and Brennen McKenzie were wonderful field assistants and their enthusiasm and appreciation of the sea lions greatly added to my experience at Seal Bay. I particularly benefited from the help of the participants of the University Research Expeditions Program, who contributed their time and money to the project: S. Alexander, G. Anderman, M. Asazawa, A. Brodie, I. Casson, C. Crites, F. Crites, L. Crow, T. DuBow, A. Ehrenseucht, M. Elenbass, M. Fowle, P. Franklin, J. Frechou, R. Frosh, K. Green, J. Hess, L. Johnson, S. Johnson, K. Kalbfleisch, L. Miller, P. J. Pedroni, N. Rose, J. Schain, R. Schilling, M. Soiferman, V. Soudek, L. Wallace, R. Weeks, H. Wentzell and L. Wheeler.

I am grateful to the South Australian National Parks and Wildlife Service for granting permission to work on Kangaroo Island, and providing logistical support. Many NP&WS personnel were involved with the project at various stages and I am especially appreciative of the help of Terry Dennis and Anthony Maguire. Many thanks go to the guides at Seal Bay, who were valuable sources of information on the marked animals and made the work there more fun; with special thanks to Mel, Rob, John, Barry and Prue for helping weigh yearlings. I am indebted to Rod Ashenden for his extensive help with weighing pups and yearlings and for teaching me his approach to the animals.

While in Australia, I was helped tremendously by Pin and Leslie Needham, who basically served as a surrogate family while I was away from home: I can't thank them enough for everything they did for me. On Kangaroo Island, Heather and Philip Buck provided accommodation and some interesting entertainments for my UREP participants.

Financial support was provided by the University Research Expeditions Program, Berkeley, California through their participants. The Institute of Marine Studies, the Biology Board, and the Graduate Division of the University of California at Santa Cruz also gave me some financial support.

Comments on parts of the dissertation by C. Campagna, C. Deutsch, and N. Rose were helpful and greatly appreciated. The friendship and support of my fellow graduate students was also an important factor in my stay at Santa Cruz. Special thanks go to Marie Mc Cullough and Gigi Neighbors in the Marine Sciences office.

Last but not least, the stimulus for the entire project was of course, the sea lions themselves. I will always carry with me a tremendous admiration and

respect for these beautiful animals, for as one of my favorite professors is fond of saying, "the animal is always right", and as human beings we can only attempt to fathom the true nature of their behavior.

Note: The text of this dissertation includes the following manuscript which is in press in the Journal of Mammalogy:
Higgins, L. V. and R. A. Tedman. Effect of attacks by male Australian sea lions Neophoca cinerea on the mortality of pups.

INTRODUCTION

The Australian sea lion, Neophoca cinerea, was first described by Péron when he stayed on Kangaroo Island during the winter of 1802-03. Péron mistakenly gave two names to this species, Otaria cinerea and O. albicollis, because he believed adult males, with their dark brown bodies and distinctive blond manes, were a different species from the grey and cream colored females and juveniles (Wood Jones, 1925). From 1816, Australian sea lions, also known as hair seals, were referred to as Arctocephalus cinereus or A. lobatus, until Grey (1866) named the genus Neophoca (Scheffer, 1958).

Prior to the period of seal exploitation during the last century, Australian sea lions inhabited a much larger range and were more abundant than they are today. They were formerly found around the east coast of Australia, from the coast of Victoria south to the islands of the Bass Strait and northern Tasmania (Walker and Ling, 1981). Today the sea lions inhabit a range beginning at the Page Islands and Kangaroo Island off of the coast of South Australia, and extending west to the islands off of Houtman Abrolhos in Western Australia. Information on their former abundance is not available, but over a 25 year period beginning around 1800, they were collected for skins and meat by explorers and sealers and were almost exterminated (Marlow and King, 1974). Matthew Flinders (1814) describes finding hair seals in coves on the east and north sides of Kangaroo island where they are not found today.

In recent times Australian sea lions have occupied only the south coast of Kangaroo Island, with the greatest numbers occurring at Seal Bay. The population of sea lions at Seal Bay consists of approximately 500 animals on

land, and is the second largest breeding rookery in Australia after the Page islands. This number has remained relatively constant since counts were initiated in 1962 and reflects an underestimate, since many of the sea lions are at sea during censusing.

Until the mid 1950's, the Seal Bay rookery was virtually inaccessible to humans except by boat. At that time a dirt track was cut through the mallee scrub to the coast enabling locals and tourists to view the sea lions at close range. The presence of human visitors at the Seal Bay rookery has resulted in the sea lions becoming habituated to humans. Tourists have been able to walk freely among the sea lions and are largely ignored by them. Nevertheless, by the early 1970's, the rookery was suffering from unregulated human disturbance and in 1972, under the National Parks and Wildlife Act, certain parts of Seal Bay were designated prohibited to people (Robinson and Dennis, 1988). Further concern that increasing numbers of tourists could adversely impact the breeding rookery led to the implementation of a guiding system in 1987. Now all breeding areas are protected and tourism is limited to the main non-breeding beach where contact with the animals is prohibited.

The goal of this study was to clarify and describe the breeding cycle of the sea lions at Seal Bay, to document the breeding behavior of males and females, and to quantify maternal investment in terms of attendance cycles, pup growth rates and time to weaning. The animals at Seal Bay are ideally suited for long term study. Their tolerance of humans makes them easy to mark and identify and this characteristic also enables researchers to monitor their activities at close range without the disturbance caused in other rookeries.

REFERENCES

- Flinders, M. 1814. A voyage to Terra Australis in the years 1801, 1802 and 1803 in H. M. ship Investigator. (London: G. and W. Nicol).
- Grey, J. E. 1866. Notes on the skulls of sea-bears and sea-lions (Otariadae) in the British Museum. *Ann. Mag. Nat. Hist.* 18:228-37.
- Marlow, B. J. and J. E. King. 1974. Sea lions and fur seals of Australia and New Zealand - the growth of knowledge. *Austr. Mammal.* 1:117-135.
- Robinson, A. C. and T. E. Dennis. 1988. The status and management of seal populations in South Australia. In: *Marine Mammals of Australasia, Field Biology and Captive Management*. M. L. Augée, Ed. Royal Zool. Soc. N.S.W., Sydney.
- Scheffer, V B. 1958. *Seals, Sea Lions and Walruses: A review of the Pinnipedia*. Stanford University Press, Stanford. 179 pp.
- Walker, G. E. and J. K. Ling. 1981. Australian sea lions. In: *Handbook of marine mammals*. Academic Press, London, 235 pp.

CHAPTER 1

**A NON-SEASONAL 17.7 MONTH BREEDING CYCLE FOR A
POPULATION OF AUSTRALIAN SEA LIONS**

INTRODUCTION

Timing of reproductive events in mammals is thought to be affected by environmental, social and nutritional factors. Changes in photoperiod, temperature or food availability may induce maturation of reproductive organs and the onset of mating activity. These factors have been termed proximate causes of breeding cycles (Baker, 1938a). Some mammals, however, show an endogenous rhythm of reproduction that is not directly related to light-dark cycles, but evidence for this is limited (Flowerdew, 1987). Ultimate causes of temporal fixation of breeding seasons involve utilizing the optimal time of year for development of food reserves so that neonates can attain an optimal body size for independent survival (Flowerdew, 1987).

In pinnipeds, breeding seasons are typically discrete seasonal events thought to be constrained by physiological and environmental factors (Bartholomew, 1970; Boness, in press). Climatic conditions and food availability may have determined the timing of breeding seasons in the northern and southern hemispheres, as most seals begin breeding in the late spring or early summer in their respective latitudes. Annual light cycles and environmental change become increasingly stable as the equator is approached, and a negative correlation between birth synchrony and latitude has been found to exist in pinnipeds (Boness, in press). This indicates that environmental factors are affecting length of the breeding season at higher

latitudes, whereas there is reduced pressure for synchronized reproduction at lower latitudes.

Australian sea lions, Neophoca cinerea, have been suspected of having a breeding cycle of 17-18 months and this phenomenon poses some profound questions concerning the proximal and ultimate causes of their reproductive cycle (Ling and Walker, 1980). In other species of pinnipeds, females copulate within one month of parturition and give birth 11 months later. After copulation, implantation of the blastocyst is delayed some three months, giving a gestation period of about nine months (Rand, 1955; Craig, 1964; Odell, 1981). The reproductive cycles for most species are not well worked out, however, and some rely on regression lines of pup growth rates to calculate duration of gestation.

Neophoca cinerea is one of three sea lion species found in the southern hemisphere, occupying a range between 27 ° and 38 ° south latitude. These sea lions breed on islands from Houtman Abrolhos to the Recherche Archipelago off Western Australia, and east to the Spencer Gulf region, Kangaroo and Page Islands off South Australia. They were almost exterminated by heavy sealing in the 19th century and occupy a smaller range today than in previous times. Estimated at no more than 5000 individuals, this species is one of the rarest pinnipeds (Walker and Ling, 1981). Males are sexually dimorphic and polygynous and females suckle their pups for one to three years (Marlow, 1975; Walker and Ling, 1981).

Past reports of the breeding season of Neophoca cinerea have been confusing. Before 1976, it was believed to occur from October to December (Wood Jones, 1925; Walker, 1964; King, 1964; Maxwell, 1967; Harrison, 1969;

Stirling, 1972), although it had been reported as extending from September through January by Marlow (1975).

The first indication that breeding was not a regular seasonal event was provided by Ling and Walker (1976, 1977, 1978, 1980) who showed that the population on Kangaroo Island underwent prolonged eight month pupping seasons 15-18 months apart. They report the breeding season of 1973 as beginning in July with most pups born between September and December. In 1975 the breeding season began in February with most births in May and June; in 1976 the season began in mid-July, peaked in October, and extended to April 1977; in 1977-78 pupping was estimated to have begun in December or January and finished in July although one pup was born in October 1978. In 1979, pupping began in June. Consequently, pupping seemed to alternate between spring-summer and fall-winter, but even this did not appear to be fixed. Ling and Walker's (1980) results are unclear, because the ages of the pups born during the season were estimated and the actual timing and number of births were not reported. However, they do report pupping intervals for two tagged females of 17-18 months, but the actual birth dates were unknown, and no behavioral or other reproductive data were collected.

The present study clarifies the reproductive cycle of the Kangaroo Island population as being from 17.4 to 17.7 months and presents data collected on 16 females with 22 birth intervals for three consecutive seasons. Birth dates of an additional 169 females during the two seasons help to describe the distribution of births during the season. Comparisons of the timing of breeding seasons during the Ling and Walker study (1976, 1977, 1980) with the three seasons in this study show that the timing of reproduction is not seasonally regular, but

exhibits a shift of approximately 1-2 weeks earlier each consecutive breeding season.

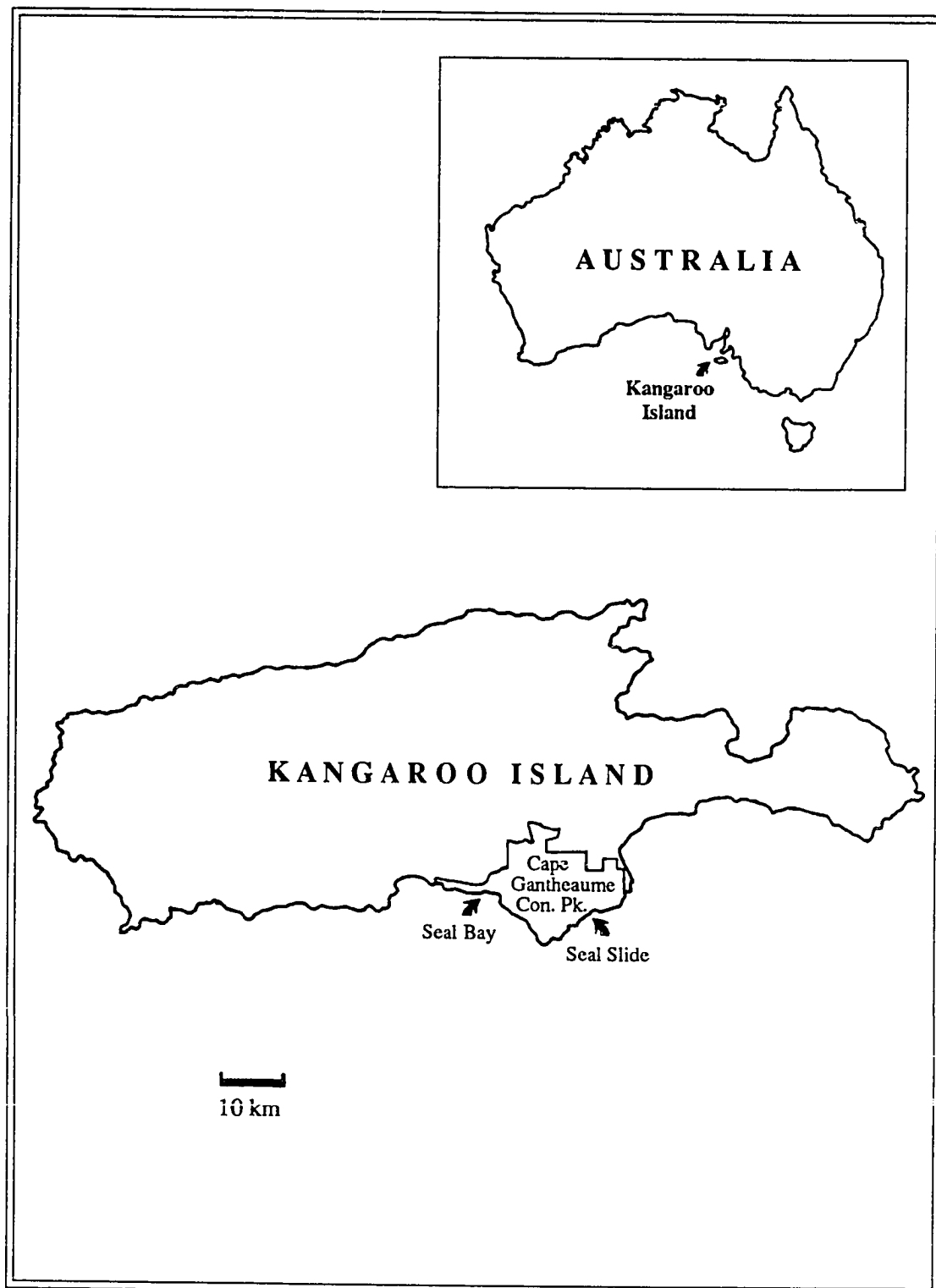
METHODS

The study took place at Seal Bay, Kangaroo Island (36° S, 137° 20' E), South Australia (Figure 1). Kangaroo Island is 50 km wide and 145 km long and is 140 km south-west of Adelaide. There are two breeding colonies on the south side of the island within the Cape Gantheaume Conservation Park. The largest is at Seal Bay, with about 400-500 sea lions, and the other is located at the Seal Slide and is a much smaller colony of about 40-70 sea lions (Robinson and Dennis, 1988).

This study took place during the austral summer season, from December 14 to May 18, 1986-87, the austral winter season, from April 30 to October 30, 1988, and from October 21 to March 30, 1989-90. As 1988 was a leap year, calculations of pupping intervals between 1987 and 1988 were adjusted accordingly. Observations and censuses were conducted daily between the hours of 08:00 and 20:00 during 1986-87 (approximately 6-12 hours per day), between 08:00 to 17:30 during 1988 (approximately 6-10 hours per day), and between 08:30 and 18:30 during 1989-90 (approximately 6-10 hours per day).

Seal Bay is divided into four areas. The Main Beach is a tourist attraction and is the preferred haul-out beach for the sea lions during the non-breeding season. Pup Cove is a steep walled cove on the west side of Seal Bay where roughly 60% of the pups are born although accurate counts were not available due to the terrain. My main study areas at Seal Bay were the Western

Figure 1. Map of Kangaroo Island showing the two rookeries of Seal Bay and the Seal Slide in the Cape Gantheaume Conservation Park.



Prohibited and Eastern Prohibited Areas, which are situated on either side of the Main Beach and account for the remaining 40% of births (see Ch. 2 for details).

Observations were conducted throughout the day to record breeding behavior and to determine movements of marked animals. The Eastern Prohibited Area was checked once or twice a day to record births but not many observations were conducted there. Due to its inaccessibility, Pup Cove was not used as a study site except to monitor the two births of one marked female.

During each breeding season, females were marked immediately after parturition with paint pellets (Nelson Paint Co., Iron Mountain, MI) projected from a wrist mounted sling shot, and later with numbers applied to the pelage with Nyanzol D dye (J. Belmar Inc., North Andover, MA) when they were sleeping. Between seasons, the females were identified by plastic tags applied to the trailing edge of the fore-flippers, natural scars, or by association with their tagged pups from the previous season. Pup adoption was rarely observed and never lasted longer than two weeks. Observations were conducted within 4-20 m of the animals, although due to the non-gregariousness of breeding females and the size of the study area, each animal was not observed continuously during the day.

Observations by personnel of the National Parks and Wildlife Service provided estimates of the first births of each season for all pupping areas of Seai Bay and were based of size of pups, presence of an umbilicus (which falls off after three days), or evidence of fresh blood or placental material. I estimated the births in the Western Prohibited Area in November and the first

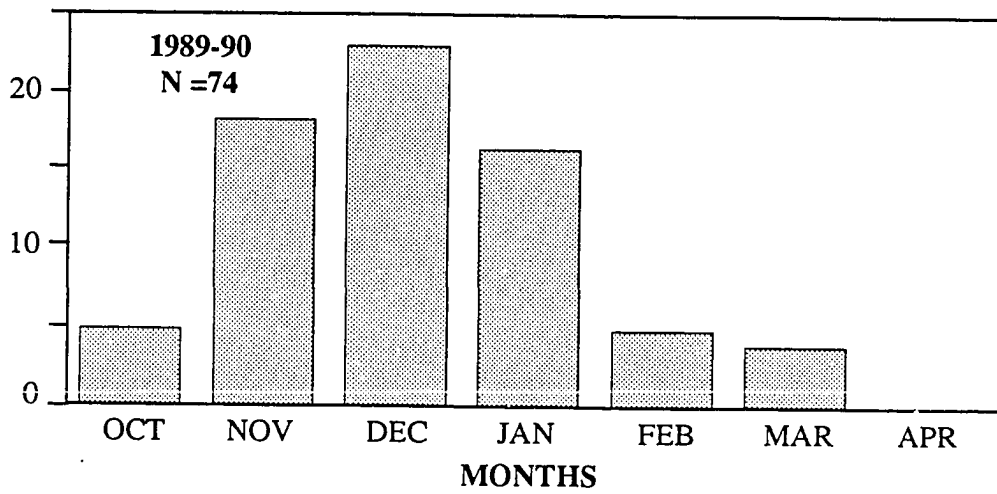
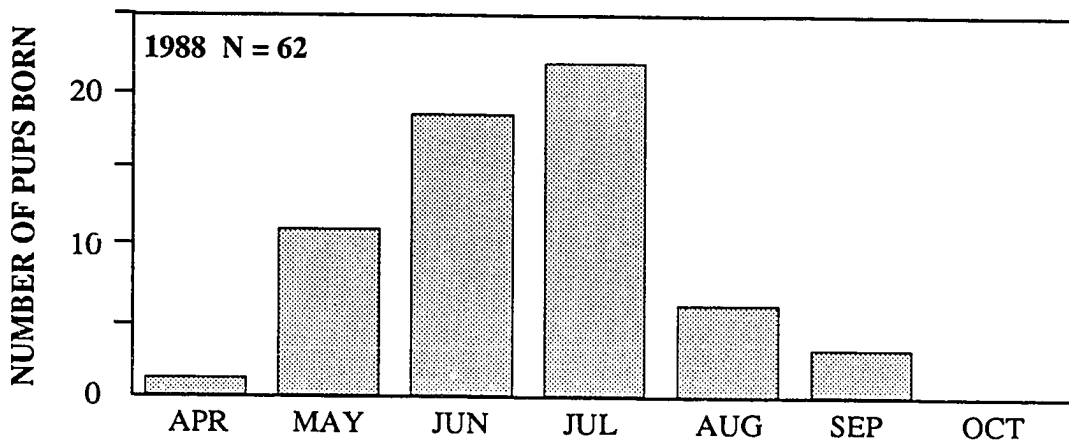
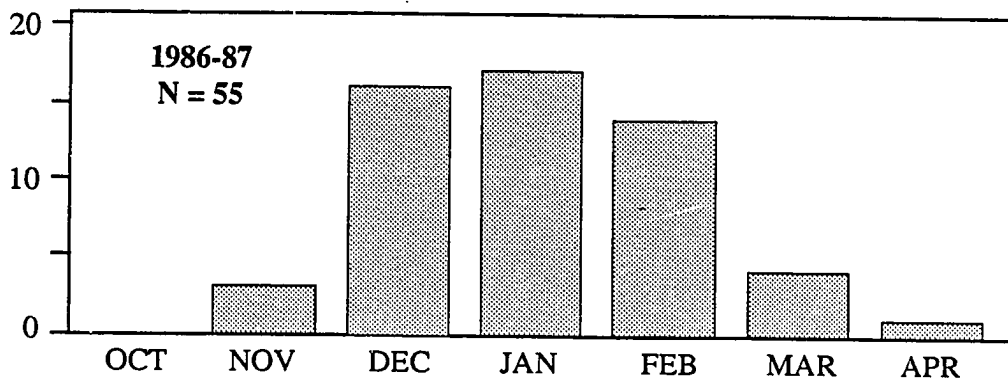
part of December in 1986 based on the size of the pups followed by comparison to known age pups.

RESULTS

At Seal Bay during the breeding season of 1986-87, the first pups were born in mid-November, 1986 (Research Officer T. Dennis, NP&WS, pers. comm.), and the last pup was born on 4 April, 1987. During the season of 1988, the first pup was born on about 8 April, 1988 (T. Dennis, pers. comm.), and the last pup was born on 13 September, 1988. In 1989, the first pups were born in mid-October (Ranger A. Maguire, Cape Gantheaume Conservation Park, pers. comm.), and the last on 14 March. The first births each season were not determined accurately enough for meaningful comparisons between seasons but the intervals between the last birth of each season was 528 days (17.3 months) between 1986-87 and 1988, and 547 days (18.0 months) between 1988 and 1989-90.

During the 1986-87 breeding season, 55 births were recorded in the Western Prohibited and Eastern Prohibited Areas, during 1988 there were 62, and during 1989-90 there were 74. Actual monthly distributions of known births are shown in Figure 2 (see Appendix 1 for details). The increased number of births each year seems to be due to greater numbers of females pupping outside of Pup Cove; the total number of pups censused each year has remained the same (A. Maguire, pers. comm.). In each season births were spread out over a five month period. Median pupping dates provide better indication of the time interval between the two breeding seasons. The median

Figure 2. Temporal distribution of births in the WPA and EPA during the breeding seasons of 1986-87, 1988 and 1989-90.



MONTHS

date of birth during the 1987 season was 21 January, and in 1988 it was 1 July. This gives an interval between the median dates of birth of 527 days (17.3 months). The median date of birth during the 1989-90 season was 15 December, and the interval between the medians of 1988 and 1989-90 was 532 days (17.5 months).

Nine females with recorded births in 1986-87 gave birth again in 1988. In 1989-90, six of the females from the 1986-87 season and an additional seven from the 1988 season gave birth (Table 1). The mean pupping interval of the females between 1986-87 and 1988 was 539 ± 9.4 days, and the mean pupping interval of the females between 1988 and 1989-90 was 541 ± 13.8 days. The combined mean for the three breeding seasons was 540 ± 12.0 days (17.7 months, $n = 22$). These data indicate that females pup evenly throughout the early, middle and late part of the season, and confirm that individual females exhibit the 17-18 month cycle.

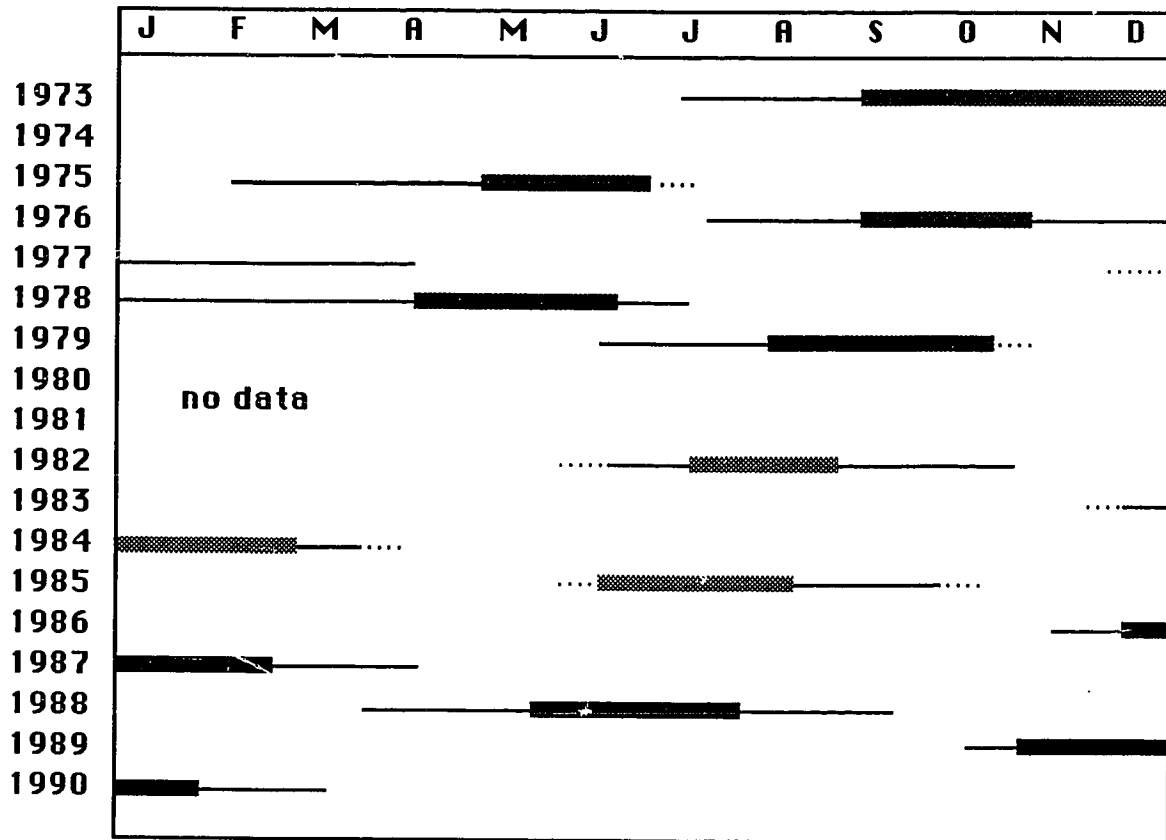
Moulting also occurs on a 17-18 month cycle. During each of the three breeding seasons of the study, females began moulting about four months after the birth of their pups. Juvenile animals moulted throughout the breeding season, and adult males did not begin to moult until nine months after the breeding season (A. Maguire, pers. comm.).

Census data collected at Seal Bay over an 18 year period (Figure 3) confirm that the population has exhibited the 17-18 month cycle since at least 1973. Data from 1973 to 1979 were taken from Ling and Walker (1976, 1977, 1980) and, between 1982 and 1985, the beginning and end of the breeding seasons as well as peak pupping were estimated from monthly censuses

Table 1. Parturition intervals for females identified during the 1986-87, 1988 and 1989-90 breeding seasons.

FEMALE I.D.	PARTURITION DATE		INTERVAL (days)	PARTURITION DATE	
	1986-87	1988		1989-90	INTERVAL (days)
11	19 Dec, 86	31 May, 88	529	6 Dec, 89	554
17	24 Dec, 86	24 Jun, 88	548		
14	11 Jan, 87	21 Jun, 88	527	9 Dec, 89	536
25	18 Jan, 87	6 Jul, 88	535	21 Dec, 89	533
37	20 Jan, 87	21 Jul, 88	548	13 Jan, 90	541
28	29 Jan, 87	10 Jul, 88	528	8 Jan, 90	547
51	6 Feb, 87	8 Aug, 88	549	2 Jan, 90	512
8	12 Feb, 87	11 Aug, 88	546		
60	18 Mar, 87	10 Sep, 88	542		
H		17 May, 88		25 Nov, 89	557
P		14 Jun, 88		4 Dec, 89	538
AD		3 Jul, 88		1 Jan, 90	547
AH		8 Jul, 88		15 Dec, 89	525
C2		13 Jul, 88		17 Jan, 90	553
D2		17 Jul, 88		29 Jan, 90	561
AK		26 Jul, 88		11 Jan, 90	534

Figure 3. Timing of breeding seasons at Seal Bay from 1973 to 1990 by month. Length of breeding season and peak pupping periods are indicated with narrow and wide lines. Data from 1973-1979 are from Ling and Walker (1976, 1977, 1978, 1980). Data from 1982-1985 was provided by Terry Dennis of the South Australian National Parks and Wildlife Service.



_____ Length of pupping season
 Peak pupping
 - Ling and Walker (1973-79)
 - NP&WS (1982-85)
 - This study
 Unconfirmed

provided by the National Parks and Wildlife Service (T. Dennis, in litt).

Uncertainties are noted in the figure since actual birth dates were not recorded.

The 17-18 month breeding cycle can be verified by comparing the timing of the breeding seasons during the 1970's with the timing of later seasons. Given that pupping would occur 1-2 weeks earlier each time (every 1.5 years), in 12 years, the season should occur approximately four months earlier than it would if the interval was precisely 18 months. In 1975 pupping began in February and was concentrated in May and June; in 1986-87 (11.5 years later), pupping began in November and was concentrated between December and February: a shift of three months earlier for the onset of pupping, but 4-5 months earlier for the peak time. Comparison of the 1976 season with the 1988 season gives a three month shift for onset of pupping and 3-4 months for peak pupping. These comparisons are not absolute since the data from the two studies were collected in different ways and estimation of peak pupping periods is subject to interpretation.

DISCUSSION

The sea lions at Seal Bay exhibit a synchronized, non-seasonal breeding cycle. The 17.7 month mean interval for individual females and 17.3 and 17.5 month medians for the three pupping seasons demonstrate that the breeding cycle is not 18 months as indicated by Ling and Walker (1978). The greater precision of the data obtained here indicates that the breeding cycle is out of synch with any seasonal cues, as shown by the one month shift forward in time between the 1986-87 and 1989-90 breeding seasons. Although the

population is synchronized so that virtually all births occur in a five month period, this is not related to season because of the 17.7 month interval for individuals.

Female sea lions in captivity at the Adelaide Zoo were also on a 17-18 month breeding cycle (D. Schultz, Zoo Veterinarian, pers. comm.). The pup intervals of two females over three and four year periods were 499 days, 558 days, and 533 days. One of the females skipped giving birth one year and her three year interval was 1024 days. These females pupped during the early part of the breeding season at Seal Bay, where presumably they were originally captured.

Part of the confusion concerning past information on the breeding season of Neophoca cinerea stems from reports coming from different islands and from different breeding seasons. Also, early findings were based on one year's observations only (Wood Jones, 1925; Stirling, 1972). The most extensive data come from Marlow (1975), who worked on Dangerous reef (34° 49' S, 136° 12' E) during the breeding seasons of 1966 (from 10 July to 13 October), 1967 (from mid-July to mid-October), 1969 (from early November to mid-December), and 1970 (from early October to early December). He reported seeing the first live births in the beginning of October 1966, but was not there long enough to gauge the length of the season. For the years 1967, 1969 and 1970, he did not give the dates of the onset of pupping, but reported that the breeding season was "highly variable and extends for at least two months from mid October to mid December". He also stated that it may last as long as from the beginning of October into January. However, his time on the island was too limited to make any quantitative predictions as to actual length of the pupping

season. Marlow's consecutive seasons of 1969 and 1970 are hard to explain in terms of an 18-month cycle, and unfortunately yearly censuses have not been recorded since his observations.

The long pupping season of eight months reported by Ling and Walker (1980) for some years probably was the result of counting out-of-season births (a solitary female giving birth months before or after the other females). During 1988, one birth was recorded in January at Seal Bay (T. Dennis, pers. comm.) and if this birth had been included in the 1988 breeding season, the pupping season would have been 8-9 months long. These out of season births are probably the result of a shortening or an elimination of the delay of implantation of the blastocyst. Early or out of season births have been reported in other species of pinniped as well (Gentry, 1970; Odell, 1981).

Another possible variable relating to the length of the pupping season is that only 76-85% of females give birth each season (Ling and Walker, 1980; Ch 4). Length of the breeding season might be influenced by the timing of individual females giving birth, and a predominance of early or late breeders could cause a shift in the frequency distribution of births.

An extended reproductive cycle of 17-18 months is problematic when the two components of pregnancy are considered. Pooled copulation data on 42 females from the three seasons gave a mean of 7.0 days post-partum, which is consistent with most otariids studied to date (Ridgeway and Harrison, 1981). In other species of pinnipeds studied, implantation is delayed for about three months, giving a gestation period of about nine months (Rand, 1955; Craig, 1964; Odell, 1981). In Neophoca cinerea, either the time to implantation of blastocyst has lengthened from the postulated three months, or the actual

period of gestation is longer than nine months, or some combination of both. It is most likely that there is a prolonged delay in implantation of eight to nine months. This is not unique in mammals; the weasel, Mustela nivalis, has a delay of about 280 days (Deansley, 1943; Flowerdew, 1987). Delayed development in utero has been shown in some species of non-hibernating bats and appears to be related to food availability at parturition (Flemming, 1971b; Wimsatt, 1975). Studies of reproductive hormone levels relating to blastocyst implantation are underway and will shed light on this question for Neophoca cinerea (N. Gales, pers. comm.).

Ling and Walker (1980) hypothesize that Neophoca cinerea females may cycle again later in the year and are impregnated at that time. Reproductive behavior and copulations between breeding season have not been reported at Seal Bay by the National Parks and Wildlife Service since a guiding system was established in August of 1987. It is also unlikely that the animals are departing to other rookeries to copulate since the marked or tagged males and females of the 1988 breeding season remained at Seal Bay at least through March of 1989 (A. Maguire, pers. comm.). Gentry and Holt (1986) found that when they sequestered female northern fur seals during estrus and prevented them from becoming inseminated, none of the females were pregnant during the next breeding season, indicating that no copulations had occurred out of season.

Another exception to the annual cycle in pinnipeds is the walrus, Odobenus rosmarus, which has a 15-month reproductive cycle, consisting of a four to five month delay of implantation and about 11 months of gestation (Fay, 1981). Consequently, these animals breed every 24 months on average and

the period of parturition is separated from estrus by three months, so that reproductive events occur during the same season each year. Other mammals with a longer than 12 month cycle are the two-toed sloth, Choloepus hoffmanni, which has a variable post-partum estrus resulting in an interbirth interval of 14-18 months with a gestation period of 11.5 months (Zoo records, Eisenberg, 1981); a species of wild cattle, Bos grunniens, with an interval of 13-27 months and gestation period of 8.6 months (Zoo records, Eisenberg, 1981); and the pygmy hippopotamus, Choeropsis liberiensis, with an interval of 16.7 months and a gestation period of 6.5 months (Zoo records, Eisenberg, 1981).

Although it is generally accepted that birds breed according to an annual cycle (Faaborg, 1988), a population of sooty terns, Sterna fuscata, on Ascension Island have been found to breed every 9.5-10.0 months (Ashmole, 1963; Chapin and Wing, 1959). A suggested cause of this breeding cycle is the effect of the lunar cycle (Chapin and Wing, 1959), although this is discounted by Ashmole (1963), who believes the time required for courtship, breeding activity and moulting is important. Although most other populations of sooty terns have annual cycles, there have been some documented with 6-month or non-seasonal breeding cycles (Ashmole, 1963).

As a proximate mechanism, it is difficult to see how seasonal cues could determine reproductive events in Neophoca cinerea. Photoperiod probably does not trigger reproduction since the breeding season shifts and occurs at different times of the year. Likewise, temperature effects would have to be discounted. However individual females exhibit consistent and predictable cycling, which must represent some sort of endogenous rhythm not related to seasonal events. Since moulting seems to be linked to the breeding cycle, it

appears that the whole physiology of the animal is tied to an 17-18 month cycle and not an annual one. Within population synchrony may be maintained by social interactions, such as mating, but how this is accomplished is unknown.

Environmental conditions that cause the need to disperse and migrate between breeding seasons are considered one of the ultimate causes of the short, annual breeding seasons seen in other pinniped species (Bartholomew, 1970). One exception is the Galapagos sea lion (Zalophus californianus wollebaeki), which exhibits a long (4 to 10 month) breeding season with a variable onset of pupping and, like Neophoca cinerea, no migration is thought to occur (Trillmich, 1986). These animals live at the equator where there are little seasonal differences compared to sub-polar and temperate areas, although there are fluctuations in food stocks due to El Niño events that affect pup survival (Gentry and Kooyman, 1986). In Neophoca cinerea, temperate climatic conditions and abundant food availability may have eliminated the need for dispersal and migration. The population at Seal Bay is resident year-round and males and females have no need to adhere to a seasonal time-table to ensure that both sexes are at the same place at the same time to breed. Instead of breeding throughout the year though, as might be expected, the females at Seal Bay are still synchronized to breed over a five month period. Why this non-seasonal synchrony exists is unclear.

The ultimate cause of the 17-18 breeding cycle probably has to do with pup survival. The length of maternal investment is important to the successful rearing of a pinniped neonate. In sea lions this period is variable and seems to be related to maternal nutritional status and seasonal availability of food (Gentry et al., 1986). Little is known about the foraging habits of Neophoca cinerea,

although recent work indicates that nursing females forage along the bottom for fish, cephalopods and crustaceans (Costa, pers. comm.; Higgins, unpublished data). Pups, with their much smaller body mass, may not be able to dive for as long or as deep as older animals and perhaps are limited in their foraging, as well as being at higher risk for shark predation. By prolonging the period of neonate dependence, females could provide extra nutrition to their young as they are making the transition to independence. Unfortunately, the age at which pups begin to forage on their own has not yet been determined and is a subject for further study.

The unique breeding cycle of Neophoca cinerea poses many questions about the ultimate and proximate causes of the timing of reproductive events. Animals like Neophoca cinerea and Sterna fuscata indicate that there is much to learn before our understanding of the factors affecting breeding cycles is complete.

REFERENCES

- Ashmole, N. P. 1963. The biology of the Wideawake or sooty tern Sterna fuscata. *Ibis* 103b:297-364.
- Baker, J. R. 1938a. Evolution of breeding seasons. In: *Evolution: Essays on aspects of evolutionary biology presented to Professor E. S. Goodrich*, pp. 161-77. G. R. de Beer, Ed. Oxford University Press, London.
- Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. *Evolution* 24:546-559.
- Boness, D. J. 1990. Determinants of mating systems in the Otariidae (Pinnipedia). In: *Mechanisms and Evolution of behavior in Pinnipeds*. D. Renouf, Ed. Chapman and Hall, London. In press.
- Chapin, J. P. and L. W. Wing. 1959. The Wideawake calendar, 1958 to 1958. *Auk* 76:153-8.
- Craig, A. M. 1964. Histology of reproduction and the estrus cycle in the female fur seal, Callorhinus ursinus. *J. Fish. Res. Board. Ca.* 21(4): 773-811.
- Deansley, R. 1943. Delayed implantation in the stoat (Mustela mustela). *Nature* 151:365-6.
- Eisenberg, J. F. 1981. *The mammalian radiations*. University of Chicago Press, Chicago. 610 pp.
- Faaborg, J. 1988. *Ornithology: an ecological approach*. Prentice Hall, Englewood Cliffs, N.J. 470 pp.
- Fay, F. H. 1981. Walrus. In: *Handbook of marine mammals, Vol 1*. S. H. Ridgway and R. J. Harrison, Eds. Academic Press, London, 235 pp.
- Flemming, T. H. 1971b. Artibeus jamaicensis: Delayed embryonic development in a Neotropical bat. *Science* 171:402-4.
- Flowerdew, J. R. 1987. *Mammals: Their reproductive biology and population ecology*. Edward Arnold, London. 241 pp.
- Gentry, R. L. 1970. Social behavior of the Steller sea lion. Unpub. Ph. D. Thesis. University of California, Santa Cruz. 113 pp.

- Gentry, R. L. and J. R. Holt. 1986. Attendance behavior of northern fur seals. In: *Fur seals: Maternal strategies on land and at sea*. R. L. Gentry and G. L. Kooyman, Eds. Princeton University Press, Princeton, N. J.
- Gentry, R. L. and G. L. Kooyman. 1986. Introduction. In: *Fur seals: Maternal strategies on land and at sea*. R. L. Gentry and G. L. Kooyman, Eds. Princeton University Press, Princeton, N. J.
- Gentry, R. L., D. P. Costa, J. P. Croxall, J. H. M. David, R. W. Davis, G. L. Kooyman, P. Majluf, T. S. McCann, and F. Trillmich. 1986. Synthesis and conclusions. In: *Fur seals: Maternal strategies on land and at sea*. R. L. Gentry and G. L. Kooyman, Eds. Princeton University Press, Princeton, N. J.
- Harrison, R. J. 1969. Reproduction and reproductive organs. In: *the biology of marine mammals*. H. T. Andersen, Ed. Academic Press, New York and London.
- King, J. E. 1964. *Seals of the world*. British Museum (Natural History), London.
- Ling, J. K. 1980. Sea lions of North Fisherman Island, Western Australia. *Western Aust. Nat.* 14(7):203-204.
- Ling, J. K. and G. E. Walker. 1976. Seal studies in South Australia: Progress report for the year 1975. *South Aust. Nat.* 50:59-68,72.
- Ling, J. K. and G. E. Walker. 1977. Seal studies in South Australia: Progress report for the period January 1976 to March 1977. *South Aust. Nat.* 52:18-30.
- Ling, J. K. and G. E. Walker. 1978. An 18-month breeding cycle in the Australian sea lion? *Search* 9(12):464-465.
- Ling, J. K. and G. E. Walker. 1980. Seal studies in South Australia: Progress report for the period April 1977 to July 1979. *South Aust. Nat.* 58:68-79.
- Marlow, B.J. 1975. The comparative behavior of the Australian sea lions *Neophoca cinerea* and *Phocarctos hookeri*. *Mammalia* 39(2):160-230.
- Maxwell, G. 1967. *Seals of the world*. Houghton Mifflin Co., Boston. 151 pp.
- Odell, D. K. 1981. California sea lion. In: *Handbook of marine mammals*, Vol 1. S. H. Ridgway and R. J. Harrison, Eds. Academic Press, London, 235 pp.

- Rand, R. W. 1955. Reproduction in the female Cape fur seal Arctocephalus pusillus (Schreber). Proc. Zool. Soc. London 124(4):717-740.
- Ridgway, S. H. and R. J. Harrison. 1981. Handbook of marine mammals, Vol 1. Academic Press, London, 235 pp.
- Robinson, A. C. and T. E. Dennis. 1988. The status and management of seal populations in South Australia. In: Marine Mammals of Australasia, Field Biology and Captive Management. M. L. Augée, Ed. Royal Zool. Soc. N.S.W. , Sydney.
- Stirling, I. 1972. Observations on the Australian sea lion, Neophoca cinerea (Peron). Aust. J. Zool. 20:271-9.
- Trillmich, F. 1986. Attendance behavior of Galapagos sea lions. In: Fur seals: Maternal strategies on land and at sea. R. L. Gentry and G. L. Kooyman, Eds. Princeton University Press, Princeton, N. J.
- Walker, E. P. 1968. Mammals of the World, Vol. 2. Johns Hopkins Press, Baltimore. 1500 pp.
- Walker, G. E. and J. K. Ling. 1981. Australian sea lions. In: Handbook of marine mammals, Vol 1. Academic Press, London, 235 pp.
- Wimsatt, W. A. 1975. Some comparative aspects of implantation. Biology of Reproduction 12:1-40.
- Wood Jones, F. 1925. The mammals of Australia, Part 3. Govt. Printer, Adelaide. 158 pp.

CHAPTER 2

BREEDING BEHAVIOR OF AUSTRALIAN SEA LIONS

INTRODUCTION

The evolution of pinniped polygyny is thought to be shaped by the environmental constraints of island breeding and the gregariousness of parturient females (Bartholomew, 1970; Boness, in press). Sexual selection for size is favored when a few males are able to monopolize breeding females and perform most of the copulations (Darwin, 1871). Differential reproductive success in males due to sexual dimorphism has been demonstrated in northern fur seals, Callorhinus ursinus, (Bartholomew and Hoel, 1953), Steller sea lions, Eumetopias jubatus, (Gentry, 1970), northern elephant seals, Mirounga angustirostris, (Le Boeuf, 1974), grey seals, Halichoerus grypus, (Andersen and Fedak, 1985) and California sea lions, Zalophus californianus, (Peterson and Bartholomew, 1967). In pinnipeds, male agonistic behavior can result in a small number of males having access to the breeding females either by territorial or female defense (Boness, in press). In a population of Australian sea lions, Neophoca cinerea, pupping events spread out in time and space appear to have prevented the degree of polygyny that would be expected based on the degree of sexual dimorphism in this species.

Neophoca cinerea is one of three sea lion species found in the southern hemisphere. They are sparsely distributed on offshore islands from Houtman Abrolhos, Western Australia, to the Page Islands, South Australia. Estimated at no more than 5000 individuals, the Australian sea lion is one of the rarest and

least studied pinnipeds (Walker and Ling, 1981). Adult males weigh up to 300 kg (Walker and Ling, 1981) and are chocolate brown with distinctive blond hair on the top of the head and the back of the neck. Adult females weigh 63-96 kg (Walker and Ling, 1980; Costa and Higgins, unpub. data) and are medium grey to brown on the back with a cream underbelly. The most detailed behavioral descriptions of parturition, post-partum and mating behavior of Neophoca cinerea have been provided by Marlow (1975), who worked at Dangerous Reef, South Australia. Ling and Walker (1976, 1977, 1980) conducted a population study on Kangaroo Island that provided the first evidence of a non-seasonal breeding cycle.

The aim of this study was to quantify the mating behavior of individual sea lions and to investigate the relationship between male and female breeding strategies using individually marked animals. The life history parameters of the population on Kangaroo Island, South Australia are unusual compared to other pinnipeds in that the breeding season occurs in a non-seasonal cycle with an average period of 17.7 months (Ch. 1). This study focuses on how the prolonged breeding season and non-gregariousness of females effects the breeding behavior and success of males. Males appear to alter their territorial behavior to maximize their access to females.

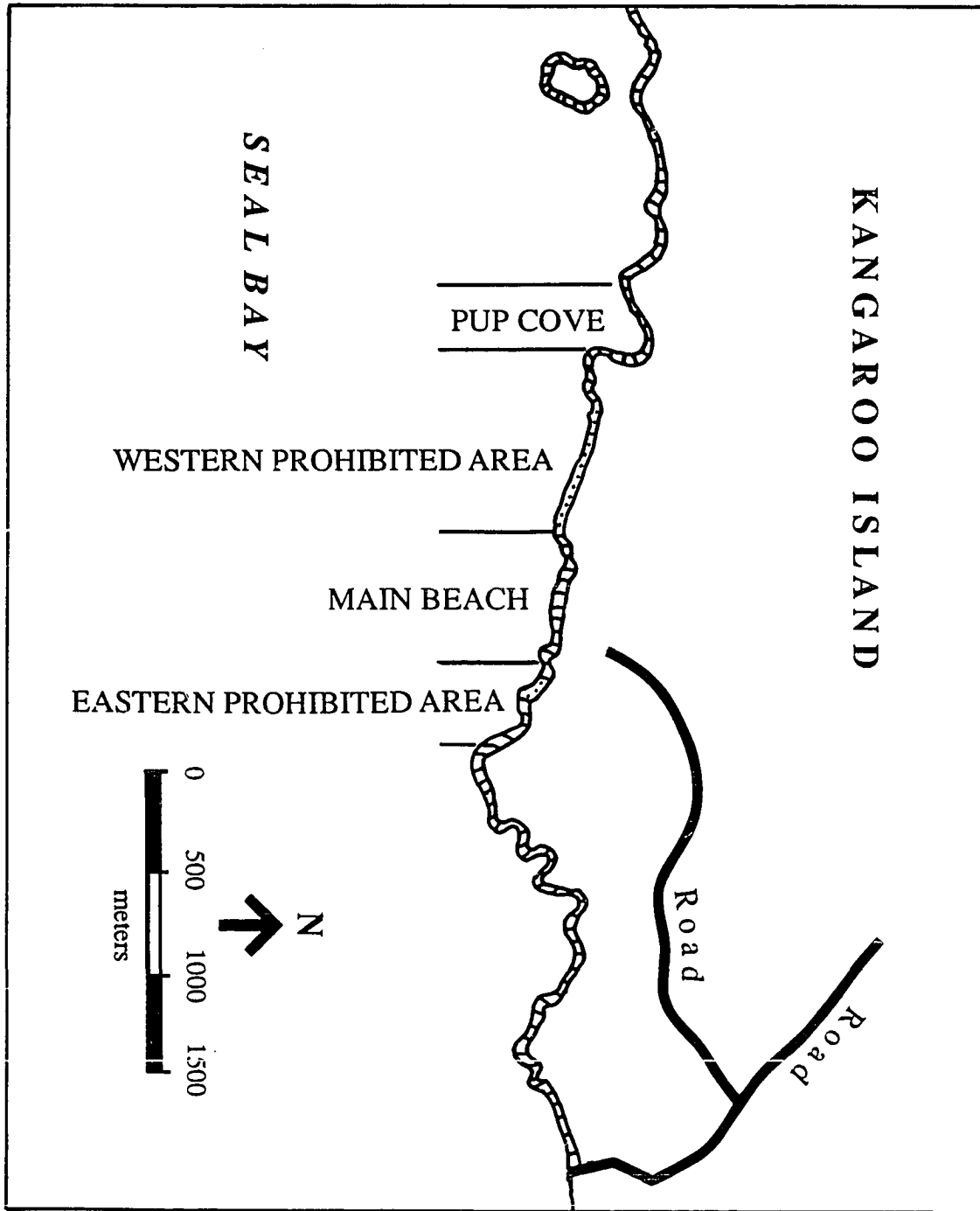
METHODS

The study took place at Seal Bay, Kangaroo Island, South Australia (36° S, $137^{\circ} 20'$ E), during the austral summer from 14 December to 18 May, 1986-87 and during the austral winter from 30 April to 30 October, 1988. Seal Bay is

divided into four areas (Figure 1). The Main Beach is the preferred haul-out area for sea lions and is a local tourist attraction. It is 587 m long and about 20 m wide and is composed of a gently sloping, sandy beach. The Main Beach is not used for pupping, although about once every breeding season one female gives birth there. Behind the Main Beach is a vegetated sand dune area extending about 200 m inland. The sea lions move into this area during cold weather in the winter and sometimes during cool nights in the summer. Pup Cove is a steep walled (75 m deep and about 200 m long), boulder strewn cove on the west side of Seal Bay and roughly 60% of the pups are born there. Pup Cove is nearly inaccessible and only about 50% of pups could be seen from the rim at any one time. The Western Prohibited Area (WPA) is situated between Pup Cove and the Main Beach and measures 908 m long and about 15 m wide and is comprised of sandy and pebble beaches interspersed with platforms of weathered beachrock. The Eastern Prohibited Area (EPA) is composed of two coves, only one of which is used by a small number of breeding females. This cove measures 110 m long and 80 m wide.

Each breeding season, about 60 females and 40 males were marked initially with paint pellets (Nelson Paint Co., Iron Mountain, MI), and later with numbers or letters applied to the pelage with Nyanzol D dye (J. Belmar Inc., North Andover, MA) from a squeeze bottle when they were sleeping. Females were marked either just before or immediately after parturition. Fourteen females were identified both seasons using plastic tags (Nasco West, Modesto, CA) applied to the trailing edge of the fore-flipper, natural scars or by their association with their tagged pup from the previous season. Pups were marked

Figure 1. Map of Seal Bay showing the locations of the breeding areas and the Main Beach.



at about 10 days of age on the pelage with Wellite cream bleach (Wella Corp., Englewood, NJ) mixed with hydrogen peroxide.

The research team of one to five people was present at Seal Bay on a daily basis during peak pupping (January-March, 1987 and June-August, 1988) and at least six days a week during the first and last months of each breeding season. Field work was begun at 08:00 and terminated at 20:00 in 1986-87 and 17:30 in 1988. Within these time periods, observations and censuses were conducted for approximately 6-12 hours a day in summer, and 6-10 hours a day in winter. Since the size of the study area and low density of females precluded continual observation of more than a few animals at a time, male and female movements in the rookery were monitored 2-3 times a day by inspection of all breeding areas. For about two months each season, Pup Cove was also checked once a day. Behavioral observations were made approximately 5-20 meters from the animals and occurred primarily in the WPA.

Data for both the summer and winter breeding seasons were pooled unless otherwise indicated. Numerical results are given as mean \pm one standard deviation. Statistical tests were performed using Statview 512+ statistical software (Abacus Concepts, Inc.).

RESULTS

Parturition and Mating--With one exception (T. Dennis, pers. comm.), pups were born during a five month period each breeding season at Seal Bay. During 1986-87, pupping began in mid-November (actual date unknown) and continued to 4 April. In 1988, pupping began 25 April and continued to 13

September. In the WPA in 1986-87, 85 % of the pups were born during the three month period of December to February ($n = 55$), and in 1988, 84 % of the pups were born during May to July ($n = 62$). Virtually all pupping took place in the prohibited areas and Pup Cove, the exception being a female who gave birth to a premature pup on the Main Beach in 1988. Fourteen females were identified both breeding seasons, nine of which gave birth each time (see Appendix 1 for details).

Breeding females were spread out in the WPA, with 18 different pupping sites in the 0.9 km long area, many of which the females used sequentially (Figure 2). Overall, the density of females was extremely low and, during peak season, there were only 0.13 females/100 m². There were some preferred parturition sites, however, and the highest density recorded was 0.39 females/100 m². In 1986-87, only two females pupped in the EPA, while in 1988 14 females were concentrated in one area giving a density of 5 females/100 m². Female density in Pup Cove was not measured, but appeared to be higher than in the other breeding areas. Although tides were higher during winter, all the females in the WPA gave birth near or on the beach as they did in the summer, except for one who pupped in the vegetated dune areas above the beach (Figure 2).

In the breeding areas, females spent about two days on a pupping site before giving birth (Table 1). Pregnant females were usually seen on the Main Beach before moving into the breeding areas to give birth. However, in 1988, 5 of 9 tagged females were not seen at Seal Bay until 0-3 days prior to parturition. Seven out of nine females identified both seasons gave birth within four meters of where they had given birth the previous season.

Figure 2. Spatial distribution of parturition sites in the Western Prohibited Area during 1986-87 and 1988.

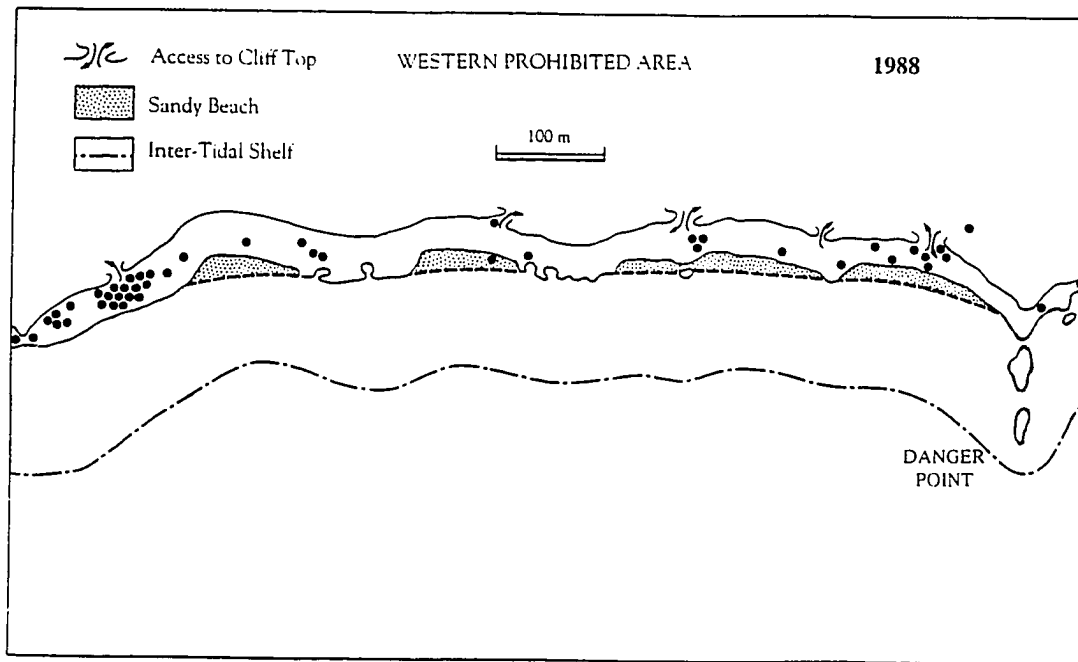
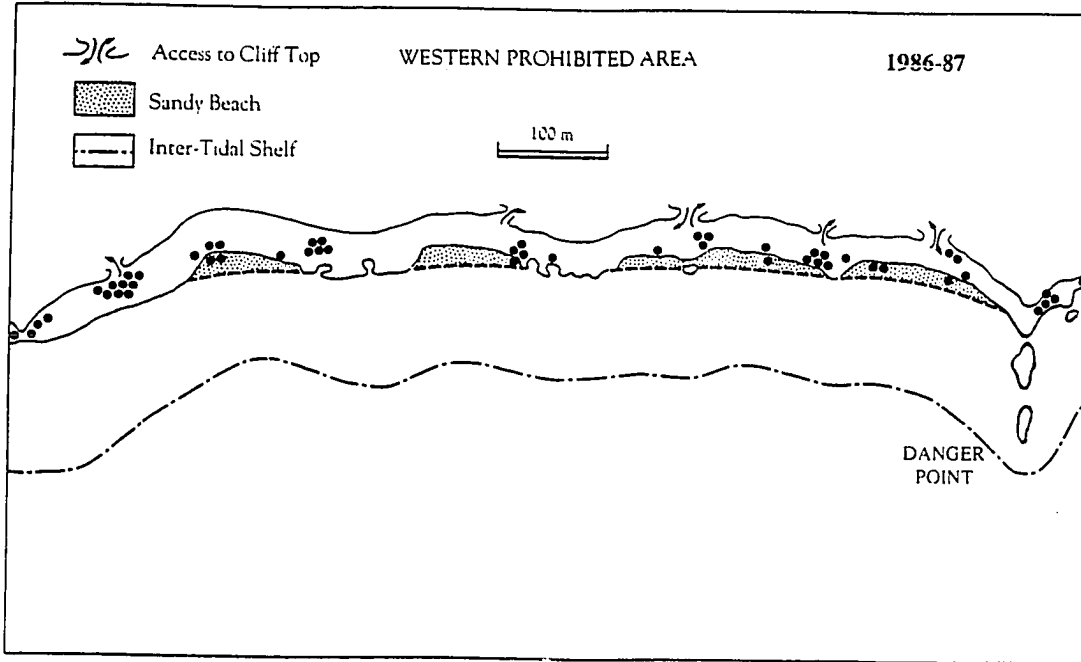


Table 1. Female reproductive data (in days).

	Arrival to Parturition	Parturition to Copulation	Parturition to First Trip	Copulation to First Trip
$\bar{X} \pm \text{S.D.}$	1.9 \pm 1.1	7.0 \pm 1.4	10.0 \pm 1.8	2.9 \pm 2.5
N	73	27	96	27
Range	(0-5)	(4-10)	(4-15)	(-2.5-11)

Births took 12-79 minutes once the females were noticed to be in labor, although one birth took at least 2.5 hours. Pups were born either head or tail first and the female immediately mouthed it or picked it up. Lethargic pups were seen to be bitten and dropped more often than active pups. Mother and pup smelled and vocalized to each other and this behavior was presumably important for establishing mutual recognition (Marlow, 1975). One female was separated from her pup at birth, and neither recognized the other when they were reunited two days later. Females whose pups died stayed in the area for about a week, although this varied from 1-12 days. Females whose pups were severely injured as a result of male attacks (see Ch. 3) largely ignored them if the pups were unable to move and vocalize fully.

The most-used pupping locations were characterized by the presence of rock falls or ledges which formed holes and crevices. Pups would seek out these holes when the females were at sea and would remain hidden until their mother's return. These pup holes ranged in size from barely larger than the pup itself to being large enough to hold three pups. The pup holes were used by 95% of the pups studied, when the pups were primarily between 0-60 days of age. At this age, pups were susceptible to male attacks (see Ch. 3), and the approach and vocalization of territorial males would cause the pups to retreat into their holes.

A total of 34 copulations were observed during the two breeding seasons. The time interval from parturition to oestrus (observed copulations) was about seven days (Table 1). Virtually all of the females copulated prior to departing on their first foraging trip. The two exceptions involved unusual

circumstances; one was a female who continued suckling her yearling after the birth of the pup and the other female had been separated from her pup at birth.

Four females were observed copulating twice (each with the same male), and the duration of estrus was estimated to last 12-24 hours. During the summer breeding season, 10% of copulations occurred in shallow water, whereas in the winter all the copulations took place on land. Copulations were initiated by the males and involved an initial period of mouthing on the females' neck and abdomen. Copulations lasted 10-25 min ($\bar{x} = 16.6 \pm 4.3$ min, $n = 21$). Females exhibited lordosis during copulations and would bite the males neck during intromission. In 74% of observed cases the female terminated the copulation by agitated struggling and vocalizing. During copulations the pups moved away from the females, or the females would move away from the pups. Occasionally mother-pup separations occurred when the female could not relocate the pup.

The sex ratio of pups born in 1986-87 was 20 males:30 females, and in 1988 it was 31 males:25 females. The combined sex ratio for the two seasons is not significantly different from 1:1 (One sample binomial, $Z = 0.4$, $n = 106$, $p > .05$).

Out of 110 female-pup pairs observed regularly, there were 14 cases (13%) of females suckling pups other than their own. Only two of the cases (2%) involved females adopting pups for more than one day: one female suckled two pups for one week until the real mother of one of the pups moved it away; and the other female (whose own pup had died) took turns suckling a pup with the pup's real mother for two weeks, until they moved away. The other cases involved females suckling strange pups for periods of a few minutes up to

a few hours. In general, when pups attempted to steal milk from females, which occurred rarely since most pups were afraid of strange females, they were almost always repulsed after a few seconds of attempted suckling.

Female and pup movements--Except during copulations, females stayed at the parturition site in constant attendance to the pup before departing on their first foraging trip 10 days later (Table 1), although on hot days they sometimes left their pups and went into the water. After about 30 days, females moved their pups away from the parturition site (1986-87: $\bar{x} = 30.9 \pm 11.7$ days, $n = 34$; 1988: $\bar{x} = 30.0 \pm 10.7$ days, $n = 42$). These initial movements varied in distance from 5-313 m (1986-87: $\bar{x} = 107.2 \pm 86.5$ m; 1988: $\bar{x} = 100.4 \pm 71.9$ m) and were usually achieved by walking rather than swimming. In the winter, when pups were about 2-3 weeks old, some of the females took their pups up into the dune areas or onto the hillsides abutting the pupping areas. The pups stayed there and did not move away until the female moved them to a new location.

During each breeding season, females moved pups several times, almost always in an easterly direction towards the Main Beach (for the EPA females, it was either east to the second cove or west to the Main Beach). In 1986-87, 79% of females were on the Main Beach with their pups just over two months after parturition ($\bar{x} = 64.3 \pm 22.5$ days, $n = 27$). In 1988, 62% of females didn't take their pups to the Main Beach until they were almost three months old ($\bar{x} = 85.2 \pm 28.9$ days, $n = 26$). The remaining females had not moved their pups from the breeding areas by the time the study had ended.

When pups were older and no longer hiding in pup holes, they would congregate in areas that are away from humans and adult sea lions, such as

Danger Point rocks and a vegetated area behind the Main Beach. In these areas, the pups are able to swim and play without coming into contact with many adult animals.

Females did not exhibit the "nanny" behavior of protecting pups who were not their own that has been described in previously undocumented sources (Nowak and Paradiso, 1983). There were no "nursery" groups of pups that were being looked after by one female while the other mothers were at sea. In fact, females would approach pups in response to pup distress vocalizations, but invariably would bite the pups upon discovering that they were not their own.

Male breeding behavior--Males utilized 24 different territories in the WPA. The EPA held only three territories since the terrain caused females to be more concentrated there. Territories were plastic in size and in the amount of time spent on them, but individual males did exhibit site fidelity. Average size of territories was 440 m² and ranged from 9-1266 m². Some territories were used sequentially by as many as five males during the length of the breeding season. Territories were not scent marked, and since territorial boundaries were flexible, there were no ritualized boundary displays as in other otariids (Peterson and Bartholomew, 1967; Peterson, 1968; Gentry, 1970; Gisiner, 1985).

Tenure on territories was dependent on whether females were present and ranged from a few days a week to almost continuous occupation. Males did not stay on their territories continuously, but took breaks and were seen in the non-breeding areas of the Main Beach and the second EPA cove. Those males with long term occupation were observed to leave their territories for 1-3

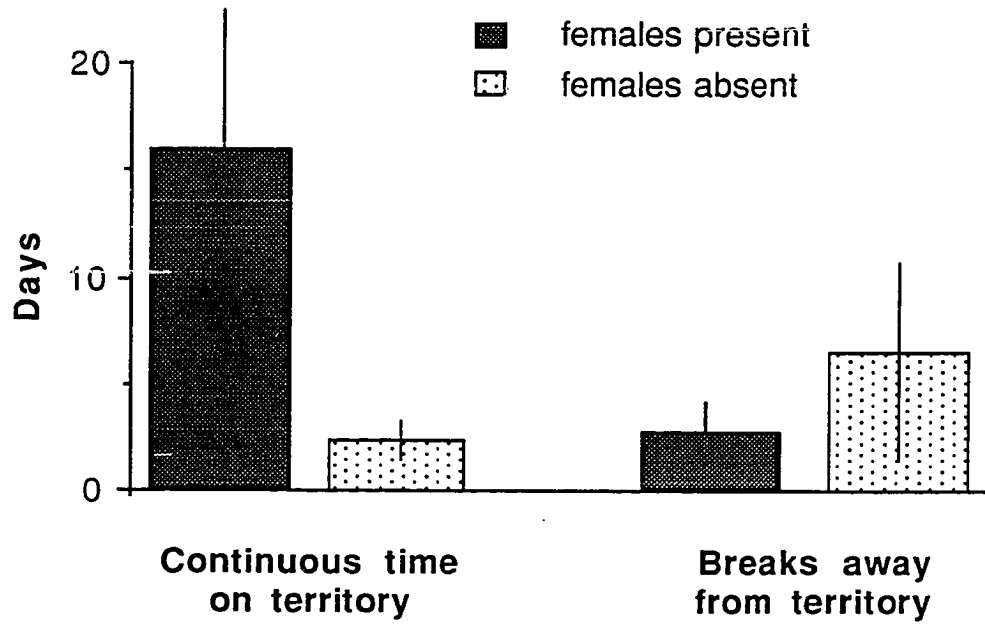
days every 3-4 weeks, presumably to feed since they defecated upon their return. At the end of the breeding season when the females and pups had moved to the Main Beach, some of the males were still seen on their territories a few days a week.

Figure 3 shows territorial attendance during 1986-87 and 1988 of males who spent at least 25 total days on their territories. Males with pregnant or near-estrus females on their territories stayed 16.0 ± 7.1 days continuously (range = 6-32 days, n = 23), while males without females stayed only 2.4 ± 1.0 days (range = 1-5 days, n = 23). The breaks males took from territorial attendance were also influenced by female presence. If pregnant or near-estrus females were on the territory, males left the rookery for only 2.7 ± 1.4 days (range=1-7 days, n =22), whereas if no females were present, males were gone 6.5 ± 5.5 days (range = 1-24 days, n = 22).

Males engaged in fights primarily when females were present but also when no females were present. Fights lasted from 1-30 minutes and sometimes involved more than two males. Fighting behavior mainly involved chest-to-chest pushing, lunges at the neck and fore-flippers, and bites to the neck or back with the object of displacing the other male onto his back. During fights there was a specific male "I surrender" vocalization which served to minimize injuries by signaling the attacking male to desist so that the defeated male could retreat without sustaining more bites. This high pitched vocalization was similar to that of females and juveniles when in agonistic situations.

The greatest number of females a male attended at one time was four, although most males were observed with just one female at a time. Because not all of the copulations were observed, a copulation was attributed to a

Figure 3. Mean territorial attendance of 23 breeding males who spent 25-80 total days in the breeding rookery. Vertical lines indicate one standard deviation.



particular male if that male was observed attending the female throughout her presumed estrus period. Fifty-seven percent (51/90) of the males observed were categorized as breeding males since they were observed or inferred to have copulated. Fifty-one percent (26/51) of these males achieved just one copulation. The highest number of copulations attributed to a male was seven (Figure 4).

Males were not entrenched on their territories and would attempt to change them if no females were present. Forty-five percent of the breeding males changed territories, and 65% of those were seen attending females at the new site. Some of the males tried out a new site, only to return to the old one if unsuccessful. Males were more successful at defending their territories than in their attempts to take over new ones. Figure 5 is a schematic representation of territorial attendance. The male represented changed to a territory about 300 m away, after which he then returned to the original territory. He was never with more than two females at one time, but was assumed to have copulated with six of seven females on his two territories over the 60 day period.

There was a positive correlation between the amount of time males spent in the breeding rookery and the number of copulations they achieved (Figure 6; $r = 0.78$, $p < 0.001$). Thirty-six percent of the males studied spent 25 or more total days on territory and in this group, 88% achieved at least one copulation. Thirty-two percent of the males spent 5-25 days on territory and 69% of these "part-time" territory holders achieved copulations. Thirty-two percent of the males did not have territories at all (less than five days in the rookery overall), but were seen in the rookery periodically and spent most of their time in the non-breeding areas. Only 10% of these males copulated. One of these

Figure 4. Presumed copulatory success of 90 males during the 1986-87 and 1988 breeding seasons.

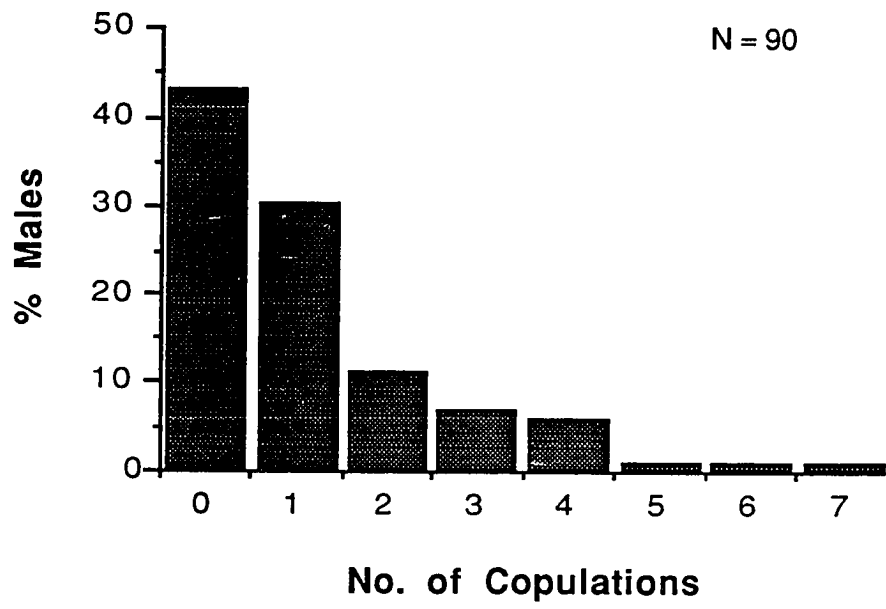


Figure 5. Territorial attendance of one male during a 60 day period. Blank spaces indicate breaks. Arrow indicates territory change. Female symbols represent females who gave birth on the territories.

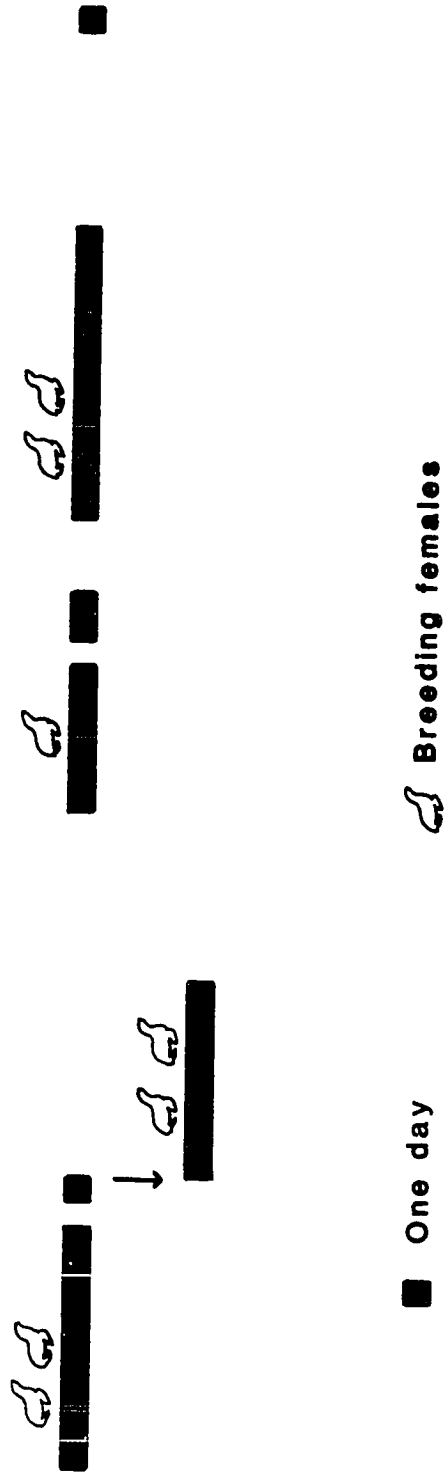
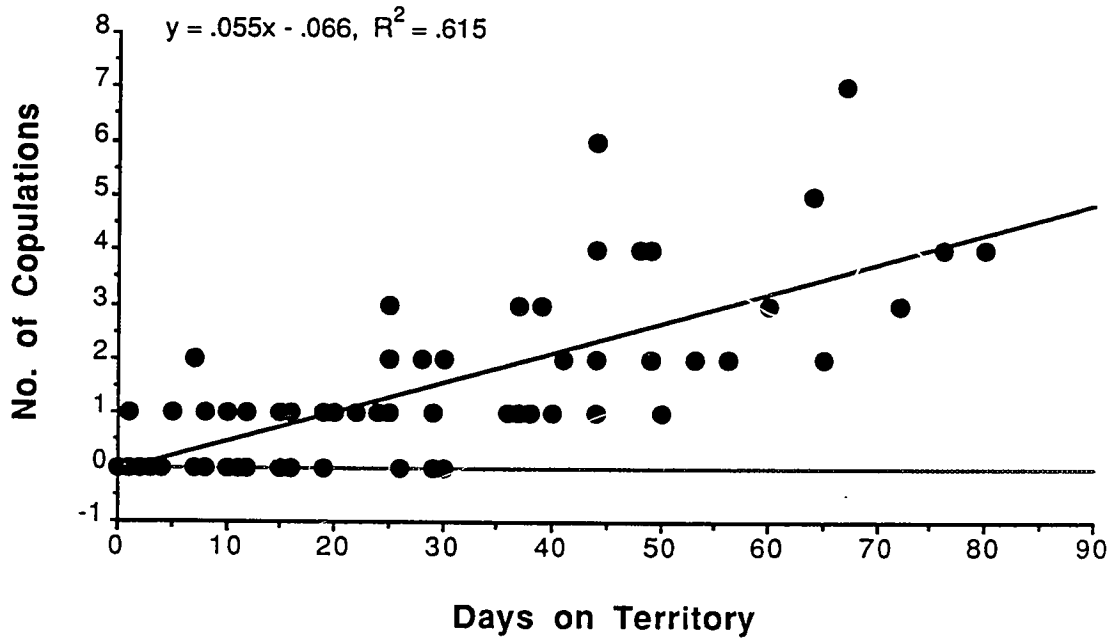


Figure 6. Reproductive success of males vs. the total time spent in the breeding rookery.



"transient" males was observed copulating during the first season, but was territorial the second season and was seen attending four females.

DISCUSSION

The degree of sexual dimorphism present in this species would indicate a highly polygynous breeding system. Instead, the differential reproductive success of males at Seal Bay was low and a high proportion of them had access to at least one female during each breeding season. The female sea lions were non-gregarious when breeding and thus did not form the dense aggregations seen in many species of pinnipeds (Bartholomew and Hoel, 1953; Le Boeuf, 1974; Fay, 1981; Campagna and Le Boeuf, 1988). In otariid species, high densities range from 150 females/100 m² in northern fur seal females (Francis, 1987) to 80 females/100 m² in California sea lions (Francis, 1987) and Steller sea lions (Gentry, 1970). The low density of females at Seal Bay is probably a result of the reduction the species suffered during the early 19th century (Marlow and King, 1974), when many of them were killed for food and skins. The ancestral breeding rookeries were probably more crowded and males would have had access to more females during the breeding season. In recent times, density at other rookeries appears to have been higher than at Seal Bay. On Dangerous Reef, Marlow (1975) describes breeding males attending as many as four females at a time, and the numbers and density of sea lions on the Pages (35° 47' S, 138° 17' E) during the 1986-87 and 1988 breeding seasons was higher than at Seal Bay (Robinson and Dennis, 1988).

Because of low female density, the most successful Neophoca cinerea males were unable to monopolize large groups of females and achieved relatively low reproductive success compared to California sea lions with 14-25 females per male (Peterson and Bartholomew, 1967) and Steller sea lions with a mean of 10 females per male (Gentry, 1970). In addition, many Neophoca cinerea males who might have been excluded from breeding were able to copulate at least once. This also occurs in a population of southern elephant seals Mirounga leonina, where the low density of females results in a high proportion of males having access to breeding females (Honigman, 1988).

Neophoca cinerea females gave birth in areas where their pups could hide and these "pup holes" could be a limiting resource influencing the distribution of breeding females. The tendency of pups to remain in holes when they are young may be an adaptive response to the aggressive behavior of males, which contributes to pup mortality (Ch. 3). Whether females actively chose areas to breed based on the presence of pup holes is unknown, although the areas with the highest density of females did contain the highest density of pup holes. The overall low number of pups and their tendency to remain hidden for long periods of time precluded pups from forming pods on the rookery while the females were at sea, as occurs in northern fur seals (Bartholomew and Hoel, 1953) and Steller sea lions (Gentry, 1970).

Why females moved their pups out of the breeding areas is unclear. Certainly, the presence of humans on the Main Beach was not a deterrent to the sea lions using it as a resting area and pups became habituated rapidly. Access to the Main Beach and the Eastern Prohibited Area is probably expedited since there is no inter-tidal shelf such as the one fronting the Western

Prohibited Area. The phenomenon of females moving pups is not unusual. In Steller sea lions (Sandegren, 1970; Higgins, 1984) and California sea lions (Heath, 1989) females begin moving pups at 4-6 weeks of age to different parts of the rookery.

Male breeding behavior was a combination of territoriality and female defense which resulted in a system combining elements of both types of breeding strategies. Pre or post-partum females greatly influenced the amount of time males spent on territories, although males also stayed on territories and would defend them when there were no females present. The length of the pupping season at Seal Bay was sufficiently long that males were unable to remain on territory the entire time, and territorial tenure seemed to be influenced by fasting ability.

Males did not hold "harems" in the breeding rookery as has been described previously for this species (Wood Jones, 1925; Marlow, 1975). Indeed, what might have been called a harem at Seal Bay, upon closer examination, turned out to be a collection of juvenile males and non-reproductive females. Since females were spread out in the breeding rookery, males could not control or herd females as was described by Marlow (1975) on Dangerous Reef (34° 49' S, 136° 12' E), and as occurs in Southern sea lions, Otaria byronia (Campagna and Le Boeuf, 1988), and in northern fur seals (Bartholomew and Hoel, 1953).

Changing territories was one strategy to increase reproductive success and resulted in the males having access to females sequentially. This form of serial polygyny was advantageous, since females virtually always copulated prior to departing on their first foraging trips (Table 1) and males who

monopolized females from the time of birth were assured of copulations. The transient behavior of some males may be an alternative breeding strategy and could also serve to familiarize males with the pupping sites on the rookery and prepare them to become territorial in subsequent seasons.

It appears that Australian sea lion breeding behavior is plastic and, as such, reflects an ability on the males' part to adapt to the breeding behavior of the females. By holding loosely defined territories and changing them as the situation arises, males maximize their reproductive success. Why the females exhibit such low densities at Sea Bay is unclear although the availability of pup holes may influence female spacing. This population provides an example of an alternate breeding situation for sea lions and illustrates the need to study different populations to uncover the variability in a species behavior.

REFERENCES

- Anderson, S S. and M. A. Fedak. 1985. Grey seal males: energetic and behavioral links between size and sexual success. *Animal Behavior*, 33:829-838.
- Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. *Evolution* 24:546-559.
- Bartholomew, G. A. and P. G. Hoel. 1953. Reproductive behavior of the Alaska fur seal, Callorhinus ursinus. *J. Mammalogy*, 34:417-436.
- Boness, D. J. Determinants of mating systems in the Otariidae (Pinnipedia). In: *Mechanism and evolution of behavior in Pinnipeds*. D. Renouf, Ed. Chapman and Hall, London. In press.
- Campagna, C. and B. J. Le Boeuf. 1988. Reproductive behavior of southern sea lions. *Behavior* 104:233-261.
- Darwin, C. 1871. *The Decent of Man, and Selection in Relationship to Sex*. Princeton University Press (1981), Princeton, N.J.
- Fay, F. H. 1981. Walrus. In: *Handbook of marine mammals*, Vol 1. S. H. Ridgway and R. J. Harrison, Eds. Academic Press, London, 235 pp.
- Francis, J. M. 1987. Interfemale aggression and spacing in the northern fur seal Callorhinus ursinus and the California sea lion Zalophus californianus. Ph. D. Dissertation, University of California, Santa Cruz. 155 pp.
- Gentry, R. L. 1970. Social behavior of the Steller sea lion. Ph. D. Dissertation, University of California, Santa Cruz. 113 pp.
- Gisiner, R. C. 1985. Male territorial and reproductive behavior in the Steller sea lion, Eumetopias jubatus. Ph. D. Dissertation, University of California, Santa Cruz. 146 pp.
- Heath, C. 1989. The behavioral ecology of the California sea lion, Zalophus californianus. Ph. D. Dissertation, University of California, Santa Cruz. 252 pp.
- Higgins, L. V. 1984. Maternal behavior and attendance patterns of the Steller sea lion in California. M.S. Thesis, University of California, Santa Cruz. 37 pp.

- Honigman, L. 1988. Mating strategies in southern elephant seals, *Mirounga leonina*. M.S. Thesis, University of California, Santa Cruz. 52 pp.
- Le Boeuf, B. J. 1974. Male-male competition and reproductive success in elephant seals. *American Zoologist*, 14:163-176.
- Ling, J. K. and G. E. Walker. 1976. Seal studies in South Australia: Progress report for the year 1975. *South Australian Naturalist*. 50:59-68,72.
- Ling, J. K. and G. E. Walker. 1977. Seal studies in South Australia: Progress report for the period January 1976 to March 1977. *South Australian Naturalist*. 52:18-30.
- Ling, J. K. and G. E. Walker. 1980. Seal studies in South Australia: Progress report for the period April 1977 to July 1979. *South Australian Naturalist*. 58:68-79.
- Marlow, B.J. 1975. The comparative behavior of the Australian sea lions *Neophoca cinerea* and *Phocarctos hookeri*. *Mammalia*, 39(2):160-230.
- Marlow, B. J. and J. E. King. 1974. Sea lions and fur seals of Australia and New Zealand - the growth of knowledge. *Austr. Mammal.* 1:117-135.
- Nowak, R. M. and J. L. Paradiso. 1983. *Walker's Mammals of the World*. 4th ed. Vol. II. The Johns Hopkins Press, Baltimore. 1362 pp.
- Peterson, R. S. 1968. Social behavior in pinnipeds with particular reference to the northern fur seal. In: *The behavior and physiology of pinnipeds*. R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice and R. J. Schusterman, Eds. Appleton-Century-Crofts, New York.
- Peterson, R. S. and G. A. Bartholomew. 1967. The natural history and behavior of the California sea lion. *Am. Soc. Mammal. Spec. Pub. No. 1*.
- Robinson, A. C. and T. E. Dennis. 1988. The status and management of seal populations in South Australia. In: *Marine Mammals of Australasia, Field Biology and Captive Management*. M. L. Augée, Ed. Royal Zool. Soc. N.S.W., Sydney.
- Sandegren, F. E. 1970. Breeding and maternal behavior of the Steller sea lion *Eumetopias jubatus* in Alaska. M.S. Thesis, University of Alaska. 135 pp.
- Walker, G. E. and J. K. Ling. 1980. Body weights and dimensions of adult female Australian sea lions, *Neophoca cinerea*. *Journal of Mammalogy*, 61:164-65.

- Walker, G. E. and J. K. Ling. 1981. Australian sea lion-Neophoca cinerea.
In: Handbook of Marine Mammals, Vol. 1: The walrus, sea lions, fur seals
and sea otter. S. H. Ridgway and R. J. Harrison, Eds. Academic
Press, London. pp 99-118.
- Wood Jones, F. 1925. The mammals of Australia, Part 3. Govt. Printer,
Adelaide. 158 pp.

CHAPTER 3

**EFFECT OF ATTACKS BY MALE AUSTRALIAN SEA LIONS,
NEOPHOCA CINEREA, ON MORTALITY OF PUPS**

Aggressive behavior among males often is found in species exhibiting sexual dimorphism in size (Trivers, 1985). In pinnipeds this behavior appears to be related to a clumped distribution of females during the breeding season (Bartholomew, 1970; Campagna and Le Boeuf, 1988; Gentry, 1970; Le Boeuf, 1974). Although aggression usually is directed towards other males, females and pups are targets in the northern fur seal, Callorhinus ursinus (Bartholomew and Hoel, 1953), southern elephant seal, Mirounga leonina (Carrick et al., 1962), southern sea lion, Otaria byronia (Campagna et al., 1988), and northern elephant seal, Mirounga angustirostris (B. J. Le Boeuf, pers. comm.). However, observations of aggression directed towards pups and the consequences thereof are rare and difficult to quantify. Herein we provide evidence that this behavior is a major cause of pup mortality in Australian sea lions (Neophoca cinerea).

Australian sea lions are sexually dimorphic, polygynous, and are described as extremely aggressive and prone to attack and injure young pups (Marlow, 1975). Adult males weigh a maximum of 300 kg, females 60-100 kg, and newborn pups only 7-8 kg (Walker and Ling, 1981). During the breeding season, territorial males attend females from a few days before birth until approximately 10 days postpartum when females depart to sea to forage. Copulations occur during this interval (Ch. 3; Marlow, 1975). Herein, we document eight attacks (four of which were fatal) on six pups. The pups were

examined subsequently for injuries, and necropsies were performed on three of the pups.

This study was conducted at Seal Bay, Kangaroo Island, South Australia during the breeding seasons of 1986-87 (14 December-18 May) and 1988 (30 April-26 September). During each 5-month breeding season, females were marked immediately after parturition with paint pellets (Nelson Paint Co., Iron Mountain, Michigan) projected from a slingshot, and later with numbers applied to the pelage with Nyanzol D dye (J. Belmar Inc., North Andover, Massachusetts) when they were sleeping. Known-age pups of marked females were marked with bleached numbers when they were between the ages of 1-12 days. Males were marked with paint pellets and dye after their acquisition of a territory. Observations took place 6-12 h every day during peak pupping (January-March, 1987 and June-August, 1988), and about 4-8 h 6 days a week during the first and last months of each breeding season. Records were kept of adult breeding behavior, pup behavior, and growth rates. Dead pups were weighed and frozen for later necropsy, which included investigation for subcutaneous and deep bruising, external lacerations, internal injuries and skeletal damage.

Six of eight observed attacks were by six different territorial males. Five of these males were attending pregnant or near-estrus females. The two unobserved attacks were assumed to have been by adult males because of the depth of the wounds and the proximity of aggressive territorial males. The pups (four males, two females), were <2 months old and ranged in age from 7-57 days. All attacks appeared to be without provocation, although in two cases the males were threatening other males immediately before to the attacks. Four of

the pups were with their mothers and stationary before the attacks, while the other two pups were alone and moving towards the male. After the attacks, males returned to their usual position on the territory.

When females were ashore, they were aggressive in protecting their pups, but could not always prevent males from approaching. Although females were observed to throw strange pups 1-2 m when the pups approached too closely, no injuries were seen as a result. Subadult and juvenile males occasionally sequestered older pups and engaged in biting, mounting and holding them under water, but they did not show the aggression of adult males.

Canine teeth of adult males have a height (above alveolus) of 26-38 mm and a maximum crown diameter of 11-17 mm (R. A. Tedman, in litt). These canines are capable of inflicting large wounds, and injuries sustained by pups while being shaken often were extensive. In addition to receiving bites, pups were thrown 2-4 m and received fractures and dislocations if they landed on a rocky surface instead of sand.

When the four dead pups were examined, one was found to have puncture wounds (bite wounds 1-2 cm deep) on either side of the midline dorsally and in the mid-lateral area of the lower thoracic and upper lumbar regions. In the left hind limb, the proximal tibiofibular junction was fractured and the ankle joint possibly dislocated. This pup died 10 days after the attack. Another pup, which was attacked twice and died minutes after the second attack, suffered bruises to subcutaneous tissue and jaw muscles of the right side of the head and to the right panniculus carnosus muscle of the lower thoracic region. The capsule of the left knee joint was lacerated. On the right side, there was marked tearing of latissimus dorsi and serratus muscles. Wrist

bones of the right fore-flipper were exposed and possibly fractured. There was a 4 cm laceration to the liver with consequent pooling of blood in the abdominal region. The third pup also was attacked twice, sustaining a laceration of the left cerebellar hemisphere and a fractured occipital bone. These injuries resulted in intracranial bleeding and death 4 days later. The fourth pup died 1 day after being attacked, and no external injuries were found although the pup was extremely lethargic before to death. No necropsy was performed.

The two pups that survived attacks also were examined. One sustained a 7-cm long laceration on the left flank (2-cm deep) that severed the obliquus abdominus externus. This pup was partially immobilized for several weeks, but the wound was almost healed 78 days later. The other pup had received four puncture wounds on the rear dorsum (1-2 cm deep), but was otherwise unaffected.

The six pups attacked represented 5% of the pups studied ($n=116$) and the four deaths accounted for 19% of pup mortality ($n= 21$) over the two seasons. Other causes of death were starvation due to rejection because the female was still suckling the previous season's pup (19%); starvation due to the female's death or her failure to return to the rookery (14%); starvation due to separation of mother and pup (10%); drowning due to high water conditions (10%); and unknown (pup found dead without injuries but with no weight loss, 28%).

Attacks on pups by males were not the major cause of death as reported by Marlow (1975), but was third after starvation and unknown factors. Deaths caused by unknown factors could have been due to illness or disease, or in some cases to attacks by males because in one observed attack no externally

visible signs were evident. Because not all pups were examined for cause of death in this study, the percentage of pups killed by bulls may be an underestimate.

Unlike some mammals, Australian sea lion males do not appear to kill pups as part of a reproductive strategy (Campagna et al., 1988; Hrdy, 1979; Packer and Pusey, 1983). In this study, males did not kill pups outright and our observations indicate that the death of the pup was not the intended outcome. Misdirected aggression is the most likely explanation for the aggressive behavior of Australian sea lion males towards pups. At Seal Bay, the density of breeding females is so low that each breeding male usually has access to only one female at a time and not much time is spent fighting. However, aggressive behavior among males is intense when it occurs, and males have been seen biting, shaking, and attempting to lift each other off the ground (Ch. 3). Pups are seen perhaps as a threat to territorial males. At <2 months of age pups are too slow to avoid being attacked, and are generally too small to survive the injuries that in an adult animal would be minor.

REFERENCES

- Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. *Evolution*, 24:546-559.
- Bartholomew, G. A., and P. G. Hoel. 1953. Reproductive behavior of the Alaska fur seal, Callorhinus ursinus. *Journal of Mammalogy*, 34:417-436.
- Campagna, C. B., and B. J. Le Boeuf. 1988. Reproductive behaviour of southern sea lions. *Behaviour*, 104:233-261.
- Campagna, C. B., B. J. Le Boeuf, and H. L. Cappozzo. 1988. Pup abduction and infanticide in southern sea lions. *Behaviour*, 107:44-60.
- Carrick, R., S. E. Csordas, S. E. Ingham, and K. Keith. 1962. Studies on the southern elephant seal, Mirounga leonina (L.). Commonwealth Scientific and Industrial Research Organization Wildlife Research, 7:119-197.
- Gentry, R. L. 1970. Social behavior of the Steller sea lion. Ph. D. Dissertation. University of California, Santa Cruz, 113 pp.
- Hrdy, S. B. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, 1:13-40.
- Le Boeuf, B. J. 1974. Male-male competition and reproductive success in elephant seals. *American Zoologist*, 14:163-176.
- Marlow, B. J. 1975. The comparative behavior of the Australian sea lions Neophoca cinerea and Phocarcos hookeri. *Mammalia*, 39:160-230.
- Packer, C., and A. E. Pusey. 1983. Adaptations of female lions to infanticide by incoming males. *American Naturalist*, 121:716-728.
- Trivers, R. 1985. *Social evolution*. Benjamin/Cummings Publishing Company, Inc. Menlo Park, California, 462 pp.
- Walker, G. E. and J. K. Ling. 1981. Australian sea lions. Pp. 99-118, in *Handbook of marine mammals* (S. H. Ridgway and R. J. Harrison, eds.). Academic Press, London, England, 235 pp.

CHAPTER 4
MATERNAL INVESTMENT IN AUSTRALIAN SEA LIONS

INTRODUCTION

Maternal investment in pinnipeds is constrained by ecological and physiological consequences of reproducing on land and feeding at sea (Bonner, 1984). Pinniped pups require sufficient nourishment to build up their body stores during the lactation period to ensure their survival at sea after weaning. Almost all female pinnipeds, except the walrus, Odobenus rosmarus (Fay, 1981), reproduce on an annual cycle, and weaning occurs sometime before the next breeding season. The actual length of lactation (or time to weaning) in pinnipeds is difficult to measure, and only a few individuals have been studied for the entire time (Oftedal, et al., 1987). Lactation is more energy intensive than gestation, thus making the length of the lactation period an important component of maternal investment especially since (Millar, 1977).

Female foraging pattern and pup growth rate are also components of maternal investment in otariids and represent some of the energetic costs of reproduction (Gentry and Kooyman, 1986). Measurements of these parameters can provide a basis for comparing maternal investment in the different species of otariid. This study quantifies length of lactation, pup growth and female foraging patterns in an unusual population of Australian sea lions, Neophoca cinerea, that reproduce on a non-seasonal 17-18 month cycle, have a five month pupping season and are non-migratory (Ch. 1).

There are two different strategies employed by the two families of pinnipeds (Bonner, 1984). In phocids, the period of post-partum maternal investment is limited, and ranges from just four days in the hooded seal, Cystophora cristata (Bowen et al., 1985) to 60 days in the ringed seal, Phoca hispida (McLaren, 1958). In otariids, the lactation period can be prolonged, and ranges from 125 days in the northern fur seal, Callorhinus ursinus, (Gentry and Holt, 1986) to about 730 days in the Galapagos fur seal, Arctocephalus galapagoensis, (Trillmich, 1979). The length of the lactation period is thought to be determined by stability of the breeding habitat in phocids and by environmental effects related to latitude in otariids (Gentry et al., 1986; Oftedal et al., 1987). Otariids near the poles generally have shorter lactation periods than those closer to the equator, presumably because food is plentiful but only available seasonally in high latitudes (Gentry et al., 1986).

The timing of the maternal attendance pattern is an important part of the otariid reproductive strategy and varies among species. Unlike phocid females, otariid females leave their pups on shore every few days while they forage at sea during the nursing period. These attendance cycles are variable between and within species and range from less than one day at sea in the Steller sea lion, Eumetopias jubatus, to 9 days at sea in the northern fur seal (Oftedal, et al., 1987). It has been suggested that the temporal patterning and duration of foraging at sea, and the subsequent time spent ashore nursing, are related to distance to the foraging grounds, food availability, latitude, female body mass, and possibly pup sex (Gentry et al., 1986; Costa, 1990).

Although growth rate is an indirect measure of maternal investment it represents the energy investment of the female in her pup through lactation

(Oftedal, et al. 1987). Sexual investment theory suggests that in polygynous, sexually dimorphic species, where large adult size confers an advantage in reproductive success, male offspring would be expected to receive a greater amount of parental investment than daughters (Trivers and Willard, 1973; Maynard Smith, 1980; Charnov, 1982). Male otariid pups are heavier at birth, grow faster (Mattlin, 1981; Doidge et al., 1984; Trillmich, 1986b; Trillmich, 1986c) and consume more milk than female pups (Costa and Gentry, 1986; Trillmich, 1986; Oftedal et al., 1987b). As a sexually dimorphic species in which males are approximately three times larger than females (Walker and Ling, 1981), Neophoca cinerea females would be expected to deliver greater investment to male pups. If attendance cycles reflect foraging effort, and male pups drink more milk, then the amount of time females are ashore or at sea might also be related to differential pup growth.

Neophoca cinerea is one of the least studied otariids. Although the Kangaroo Island population in South Australia has become habituated to humans and individuals are easily approachable, there are few quantified data on pregnancy rate, length of lactation, attendance cycles and growth rates of pups (Ling and Walker, 1975, 1977 and 1980). Previous data on the length of the nursing period are limited and were collected without knowledge of the precise timing or length of the breeding cycle. Stirling (1972) estimated that females suckle pups for two or more years, and Marlow (1975) observed females with older pups he estimated to be 18 months old. Marlow (1975) has suggested that Neophoca cinerea pups may have slower growth and development than other otariid pups and that this is related to the aggressive nature of the adult animals and the resulting timidity of pups. With maternal

care extending over 17 months, a rapid development in mass and physical abilities may not be necessary and a slower growth rate and development might in fact be the result. However, in six species of otariids, growth rates relative to maternal mass for the first few months are similar even though birth weight and length of nursing period are markedly different. (Gentry, et al., 1986). The possibility of an unusually slow pup growth rate was tested in Neophoca cinerea using growth measurements of pups during two consecutive breeding seasons.

This study will show that Australian sea lion pups are not weaned until the start of the next breeding season some 15-18 months after birth. Females who did not give birth in consecutive seasons continued to suckle their pups for up to 39 months. Attendance cycles were comparable to those of other otariids. Time at sea was not correlated with pup growth rate or pup sex but did show a seasonal affect. Pups exhibited the same rate of growth as other otariid pups and were significantly heavier than female pups.

METHODS

The study took place at Seal Bay, Kangaroo Island, South Australia, during the austral summer from 14 December 18 to May, 1986-87, during the austral winter from 30 April to 30 October, 1988 and during the austral summer from 24 November 30 to March, 1989-90. Data on pup production and time to weaning were collected over the course of all three breeding seasons, and data on female attendance cycles and pup growth rates were collected during 1986-87 and 1988. In between breeding seasons, sightings of tagged females and

pups on the Main Beach were recorded by personnel of the National Parks and Wildlife Service working at Seal Bay. See chapter 2 for details of the study areas, female and pup marking and observational effort.

Attendance data were collected only on females who pupped in the Western Prohibited Area (Ch. 2). Since behavioral observations were not possible at night, females who were present two consecutive days were assumed to have spent the night on the rookery. Those who were absent on consecutive days were assumed to have been absent all night. For calculation of at-sea and on-land intervals, arrivals and departures occurring at night were all assumed to have occurred at 1:00 AM. During the day, unobserved arrivals and departures were recorded as the median time between censuses, which was usually within a few hours. Attendance cycles from females whose pups died were not included in the sample. At the end of the season, females with older pups were difficult to find because of their tendency to move into the extensive sand dune/scrub areas behind the Main Beach. Attendance cycles from these females were discarded if it was uncertain whether they were on feeding trips or concealed in the bushes.

Seven females in 1988 were captured with a hoop net and restrained so that radio transmitters (148-149 MHz; Advanced Telemetry Systems, Bethel, Minnesota) could be attached to the pelage with a fast drying epoxy resin (Evercoat "tenset" marine epoxy). Prior to release the females were tagged with plastic Flexi-tags (Nasco West, Modesto, CA) applied to the fore-flippers to aid in future identification. Arrivals and departures were monitored 24 hours a day with a Telonics Inc. TR-2 scanning telemetry receiver (Telonics Inc., Mesa, Arizona) interfaced with an Esterline-Angus event recorder.

During the two breeding seasons, growth rates of 76 pups were measured; 34 pups in 1986-87, and 42 pups in 1988. Pups were not weighed until the mother's first foraging trip, when the pups were about 10 days old. Approximately every 2-3 weeks thereafter, each pup was captured, placed in a duffel bag, and weighed with a spring scale accurate to the nearest 50 gm (Salton, Adelaide, S.A.). Pups were only captured when their mothers were absent on foraging trips so that disturbance was minimized. When all of the pups born in the study areas were 4-8 weeks old, they were tagged on the fore-flippers with jumbo roto tags (1986-87) and Dalton size 1 Supertags (1986-87 and 1988) (Dalton Supplies Australia, Woolgoolga, N.S.W.). Between the 1986-87 and 1988 breeding season, pups were weighed by National Parks and Wildlife Service personnel on an opportunistic basis approximately every two months. One and a half year old pups are referred to as "yearlings" in this study.

Numerical results are given as mean \pm one standard deviation. Statistical tests were performed using Statview 512+ statistical software (Abacus Concepts, Inc.).

RESULTS

Pregnancy rate and weaning--Fourteen females from the 1986-87 breeding season were identified again during 1988. In 1989-90, seven of these females and an additional 11 females from the 1988 breeding season were re-identified. In 15 of 22 births, females gave birth within five meters of where they

had given birth the previous season. Of those who did not, only two showed a location shift of more than 150 m (one to the Main Beach and the other to Pup Cove).

Three out of the 13 females re-identified in 1988 did not give birth during the breeding season (Table 1). In 1989-90, 4 of 18 females did not give birth that year (Table 2). Combining the data gave 7 of 31 (22.6%) incidences where females did not pup in sequential breeding seasons. Of these seven females; four who had not given birth (57%) were still suckling yearlings, one had weaned her yearling at 18.8 months and the remaining two had lost their pups during the previous breeding season. One of the females (#18) did not give birth for two consecutive seasons, and suckled her yearling throughout the 1989-90 breeding season when it was more than three years old (Table 1). These females did not appear to be pregnant at the beginning of the breeding seasons, indicating they had not been fertilized in the previous breeding season or had aborted a fetus. They spent most of their time ashore on the Main Beach, or in the sand dunes, although they occasionally spent time in the breeding areas. In between foraging trips, those with yearlings met up with them at the same locations on the rookery to nurse.

Time to weaning was determined using observations of 18 females and their yearlings (Table 1 and 2). The remaining 13 females in the table, for which weaning was not determined, had either lost their pups the previous breeding season, or there were insufficient data available. In eight of the 18 cases, time to weaning was determined accurately by direct observation over the course of several months. These times ranged from 15.5-19.4 months and all but one of the females gave birth to new pups. In the remaining cases, the yearlings were

Table 1. Pup production and time to weaning for females who gave birth during the 1986-87 breeding season and were re-identified in 1988.

FEMALE I.D.	BIRTH 1988?	WEANING OF YEARLING	COMMENTS
3	Pregnant	Less than 16 mo	Female disappears prior to giving birth and not seen again
4	?	At least 21 mo	Yearling suckling during 1988 breeding season
8	yes	?	Yearling not seen
11	Yes	At least 30 mo	Pup died at birth, yearling continues to suckle
12	No	At least 23 mo	Yearling suckling during 1988 breeding season
14	Yes	17.5 mo	Weaned at birth of new pup
17	Yes	18 mo	Weaned 4 days prior to birth of new pup, pup dies after 7 days
18	No	At least 39 mo	Yearling still suckling during 1989-90 breeding season
25	Yes	17 mo	Weaned 18 days prior to birth of new pup
28	Yes	?	Yearling not seen
37	Yes	?	Yearling not seen
39	No	At least 18 mo	Yearling suckling during 1988 breeding season
51	Yes	15.5 mo	Weaned 76 days prior to birth of new pup
60	Yes	?	Yearling not seen

Table 2. Pup production and time to weaning for females who gave birth during the 1988 breeding season and were re-identified in 1989-90.

FEMALE I.D.	BIRTH 1989-90?	WEANING OF YEARLING	COMMENTS
11	Yes	—	1988 pup dead
14	Yes	16.4 mo	Weaned 37 days prior to birth of new pup
17	No	—	1988 pup died 7 days after birth
25	Yes	At least 11 mo	Yearling not suckling during 1989-90 breeding season
28	Yes	?	Yearling not suckling during 1989-90 breeding season
37	Yes	?	Yearling not seen
51	Yes	16.2 mo	Weaned 18 days prior to birth of new pup
D	Yes	—	1988 pup died after birth
F	No	18.8 mo	
H	Yes	At least 15 mo	Yearling not seen
K	No	Not weaned as of 23 mo	Yearling suckling during 1989-90 breeding season
P	Yes	?	Yearling not seen
U	No	—	1988 pup died after birth
AD	Yes	?	Yearling not seen
AH	Yes	Not weaned as of 21 mo	Pup died after birth, yearling continues to suckle
AK	Yes	—	1988 pup died 21 days after birth
C2	Yes	?	1988 pup starved to death at 11.5 months
D2	Yes	19.4	Yearling weaned 14 days after birth of new pup

not weaned by the end of the breeding season and sightings of them between seasons were patchy, resulting in a probable underestimate of time to weaning. These times ranged from less than 16 months to at least 39 months for female #18. In all of the cases in which the yearlings was still suckling after 18 months, the female either did not give birth to a new pup or the new pup had died within three days of birth and the yearling continued to suckle.

Over the course of the study there were eight cases out of 149 births (5.4%) when females did not wean their yearlings, and the yearlings followed the females into the breeding area prior to pupping. Of these eight females, five failed to wean the yearling and either rejected the new pup, or else allowed both to suckle. In only one case did the both the pup and the yearling survive; in all others the pup starved to death due to being pushed away from the teats by its older sibling. The other three females weaned their yearlings between 0-14 days after the birth of the new pup. Weaning seemed to be contingent on the female aggressively rejecting the yearling and also on how persistent the yearling was at suckling. The weaned yearlings remained in the area for several days although the females would not allow them near their pups. An additional female was observed to suckle a yearling for brief periods on rare occasions when her pup was absent, but the three of them were never seen together.

Attendance cycles--During the 1986-87 breeding season 517 attendance cycles of 38 females were recorded, and during 1988, 522 cycles of 36 females were recorded. This represents an average of 14 trips to sea and stays ashore for each female (see Appendix 2 for details). The higher number of trips

recorded in 1988 represent additional attendance data that were available through radio telemetry. The mean lengths (in hours) of trips and stays for each female were used in calculations since there were an unequal number of attendance cycles for each female.

Not all of the females went to sea immediately after leaving their pups. Starting when the pups were about one month of age, some of the females spent 1-3 hours on the Main Beach prior to or after a foraging trip. By the time pups were about four months of age, females spent even less of their time ashore with their pups. At this age, pups were very active and spent much of their time playing together. The amount of time females were actually with their pups when ashore was not quantified due to the low density of females and personnel limitations.

Radio telemetry data on seven females during 1988 were used to validate attendance cycle data collected by visual observation (table 3). Overall, visual observations of time at sea were overestimated by 3.4% and visual observations of time on shore were underestimated by 9.7%. The greatest error was in estimates of on-shore duration. The combined results from the seven females were not significantly different when the visual observations were compared with the radio telemetry data (At sea t-test: $t = -1.4$, $P > 0.05$; On-shore t-test: $t = 1.64$, $P > 0.05$), although there were large differences in two of the females.

Females exhibited a diurnal cycle with respect to their departures and returns to Seal Bay (Figure 1). Continuous data collected from the seven radio-tagged females gave a total of 189 departures and returns during the period of late July to late September. Although female movements occurred at all times

of the day, significantly more females returned during the early morning hours and departed during the afternoon and early evening than other times of the day (Chi-square test, $\chi^2 = 73.3$, $df = 10$, $P < 0.001$).

During both breeding seasons, the initial trips to sea were significantly shorter than all other trips to sea combined. In 1986-87, the mean of the first trips to sea was 43.2 ± 16.9 hours (t-test; $df = 37$, $t = -2.0$, $P < 0.05$). In 1988, the mean of the first trips to sea was 32.4 ± 14.9 hours (t-test; $df = 29$, $t = -3.4$, $P < 0.01$). First stays on land (after the first trip to sea) were not significantly different from subsequent stays on land (1986-87 t-test; $df = 38$, $t = 1.5$, $P > 0.05$; 1988 t-test; $df = 28$, $t = 1.6$, $P > 0.05$).

Foraging trips and stays ashore for females during 1986-87 and 1988 were quite variable with trips to sea ranging from 14-72 hours and stays ashore ranging from 8-78 hours (Figures 2 and 3; see Appendix 2 for details). In 1986-87 feeding trips averaged just over two days in length ($\bar{x} = 49.3 \pm 11.0$ hours, $n = 36$ females), and stays ashore averaged just under 1.5 days ($\bar{x} = 34.1 \pm 6.7$ hours, $n = 36$ females). On average, feeding trips in 1988 were significantly shorter ($\bar{x} = 40.9 \pm 8.2$ hours, $n = 34$ females) than in 1986-87 (t-test, $t = 3.58$, $P < 0.001$). However, stays ashore in 1988 ($\bar{x} = 32.2 \pm 6.5$ hours, $n = 34$ females) did not differ significantly from 1986-87 (t-test, $t = 1.2$, $P > 0.05$). First trips to sea were also significantly longer in 1986-87 ($\bar{x} = 43.2 \pm 16.8$ hours, $n = 40$), than during 1988 ($\bar{x} = 32.4 \pm 14.9$ hours, $n = 38$; t-test; $t = 3.002$, $P < 0.05$).

To determine if attendance cycles were influenced by time of year, the data were analyzed according to month with first trips to sea excluded to avoid bias in those months with the highest number of births (table 4). Overall, in June and July females took foraging trips that were approximately 28% shorter

Table 3. Comparison of female attendance cycles collected visually to attendance cycles recorded by radio telemetry. Data are presented in hours (mean \pm one standard deviation).

FEMALE I.D.	AT		SEA		stays	ON SHORE		% ERROR
	trips	Radio	Visual	% ERROR		Radio	Visual	
14	n = 10	46.3 \pm 5.1	48.0 \pm 8.7	+3.5	n = 11	42.8 \pm 17.3	38.2 \pm 12.8	-12.0
E	n = 6	36.8 \pm 11.8	34.2 \pm 10.0	-7.6	n = 6	36.8 \pm 11.9	37.8 \pm 12.0	+2.6
K	n = 3	33.1 \pm 13.9	40.0 \pm 13.9	+17.3	n = 3	35.9 \pm 13.7	32.0 \pm 13.9	-12.1
P	n = 8	64.5 \pm 7.8	67.8 \pm 5.6	+4.9	n = 9	37.7 \pm 7.9	34.1 \pm 7.5	-10.6
AD	n = 9	39.8 \pm 10.1	37.9 \pm 9.9	-5.0	n = 10	41.0 \pm 22.2	43.3 \pm 19.9	+5.3
C2	n = 12	44.8 \pm 13.3	51.8 \pm 20.4	+13.5	n = 11	32.1 \pm 11.4	22.6 \pm 12.1	-42.0
V2	n = 12	40.3 \pm 9.1	39.7 \pm 9.4	-1.5	n = 10	46.5 \pm 24.4	47.0 \pm 25.2	+1.1
			\bar{x} =	+3.4			\bar{x} =	-9.7

Figure 1. Radio telemetry data of departures and returns of females with pups as a function of time of day during the 1988 breeding season.

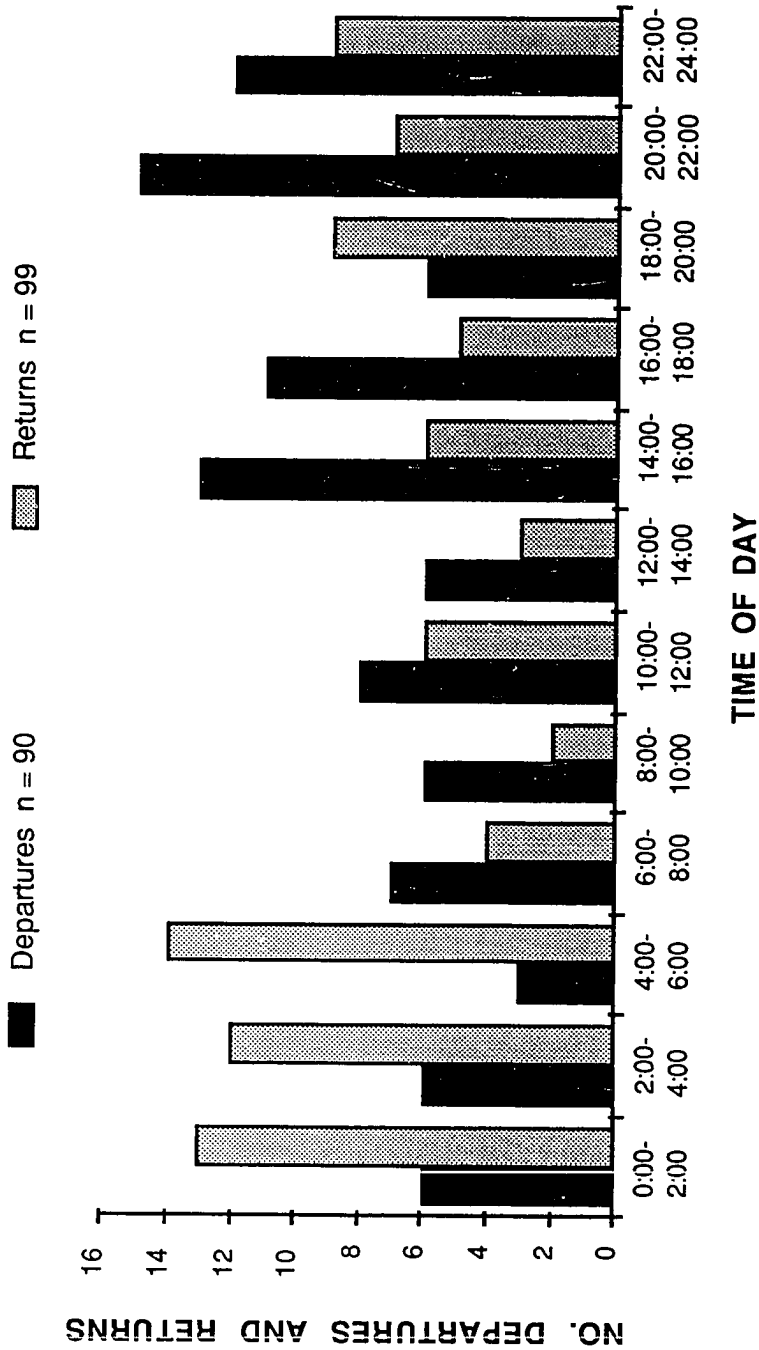


Figure 2. Frequency distribution of mean time at sea of females with pups during the 1986-87 and 1988 breeding seasons.

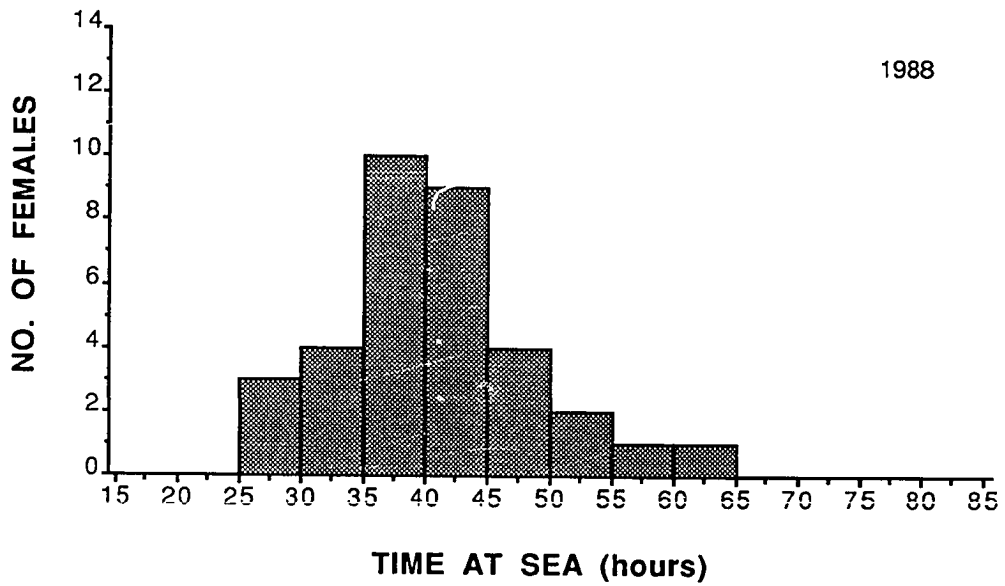
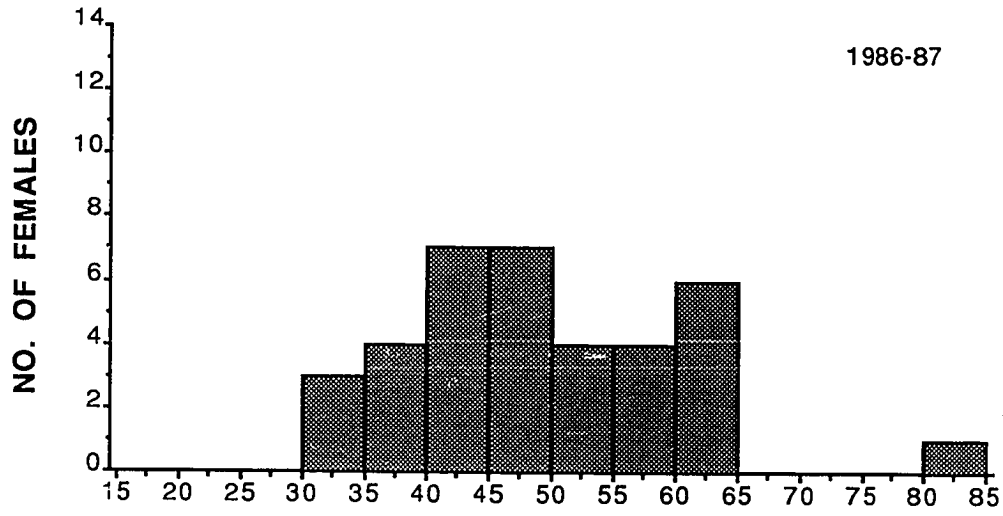


Figure 3. Frequency distribution of mean time ashore of females with pups during the 1986-87 and 1988 breeding seasons.

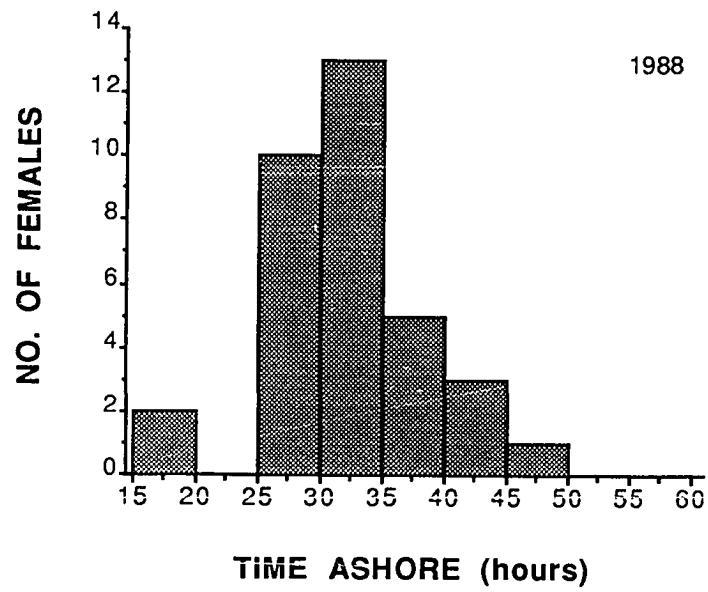
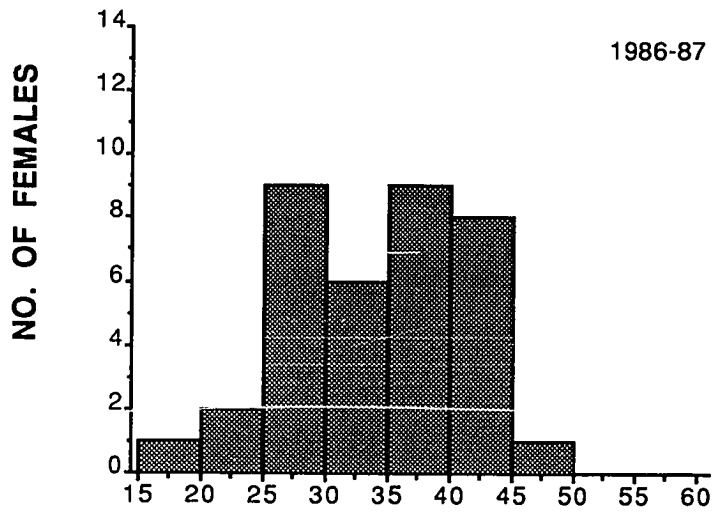


TABLE 4. Trips to sea and stays ashore (in hours) according to month during 1987 and 1988. First trips to sea are excluded.

MONTH	N females	AT SEA		ASHORE	
		$\bar{x} \pm \text{s.d.}$	\bar{x} # trips	$\bar{x} \pm \text{s.d.}$	\bar{x} # trips
1987					
JANUARY	12	46.8 \pm 13.5	6.0	36.7 \pm 12.9	5.8
FEBRUARY	33	49.9 \pm 12.8	4.9	33.6 \pm 10.5	4.9
MARCH	33	50.4 \pm 13.8	4.5	33.9 \pm 10.8	5.0
APRIL	24	50.7 \pm 10.6	2.8	35.5 \pm 8.1	2.7
1988					
JUNE	8	34.8 \pm 9.2	6.0	36.4 \pm 8.5	5.9
JULY	26	34.6 \pm 9.1	6.1	32.3 \pm 11.6	6.1
AUGUST	29	43.1 \pm 11.7	5.6	32.1 \pm 11.0	6.1
SEPTEMBER	29	48.3 \pm 11.4	3.5	29.4 \pm 8.8	3.9

than in the other months, which represents an inter-annual variation not observed in 1986-87. There was a significant difference between the foraging trips in June and all the other months except August, which by itself was not significantly different from any of the months. Trips in July were significantly different from February, April and September, but not January, March or August (ANOVA, $F = 2.8$, $P < 0.05$). There was no significant variation in time ashore as a function of month (ANOVA, $F = 1.2$, $P > 0.05$).

Pup age appeared to have no effect on the duration of feeding trips or stays ashore after the first week. Figure 4 shows foraging trip and on-shore duration as a function of pup age grouped by week. There was an initial increase in feeding trip duration due to the shorter first trips to sea, but then trip duration remains essentially constant.

Pup sex also had no effect on length of trips to sea or stays ashore. The combined data for both seasons gave mean trip durations of 45.6 ± 8.9 hours for mothers of female pups, and 44.6 ± 11.9 hours for mothers of male pups (t-test: $t = 0.38$, $P = 0.702$). Combined data for stays ashore gave a mean of 34.9 ± 6.1 hours for mothers of female pups, and 32.0 ± 6.9 hours for mothers of male pups (t-test: $t = 1.91$, $P = .060$).

Pup growth rates--Growth rates of male and female pups in 1986-87 and in 1988 are shown in Figures 5 and 6. Pup weights were regressed individually and the slopes and y-intercepts compared between male and female pups (see Appendix 3 for individual pup data). During both breeding seasons, male pups were significantly heavier than female pups (1986-87 y-intercept: male pups = 9.43 ± 1.8 kg, female pups = 8.00 ± 1.5 kg, t-test, $t = 2.53$, $P < 0.01$, $df = 32$; 1988

Figure 4. Duration of at sea and on shore periods as a function of pup age during the 1986-87 and 1988 breeding seasons. Vertical lines indicate one standard deviation.

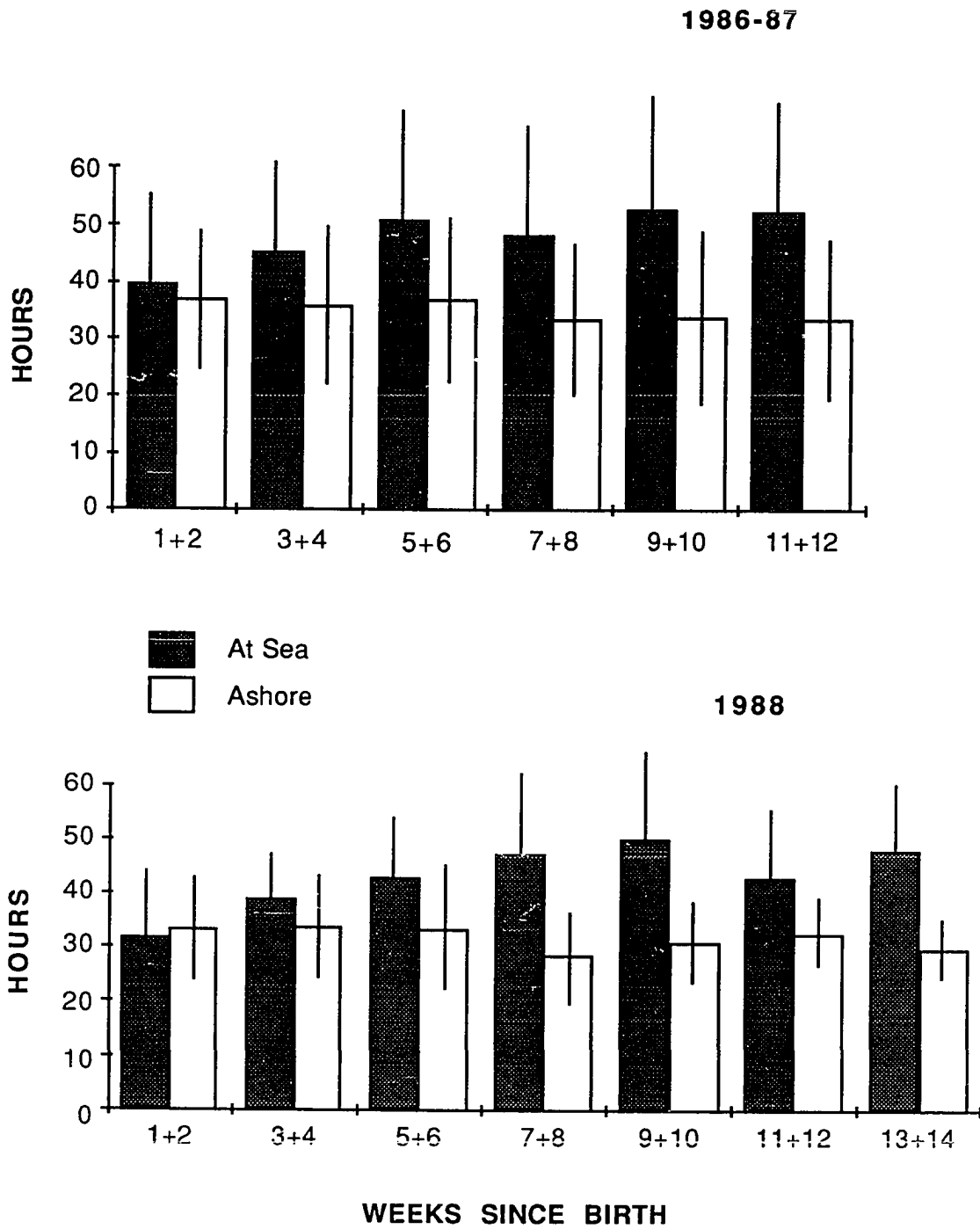


Figure 5. Growth rates of male and female pups weighed during the 1986-87 breeding season.

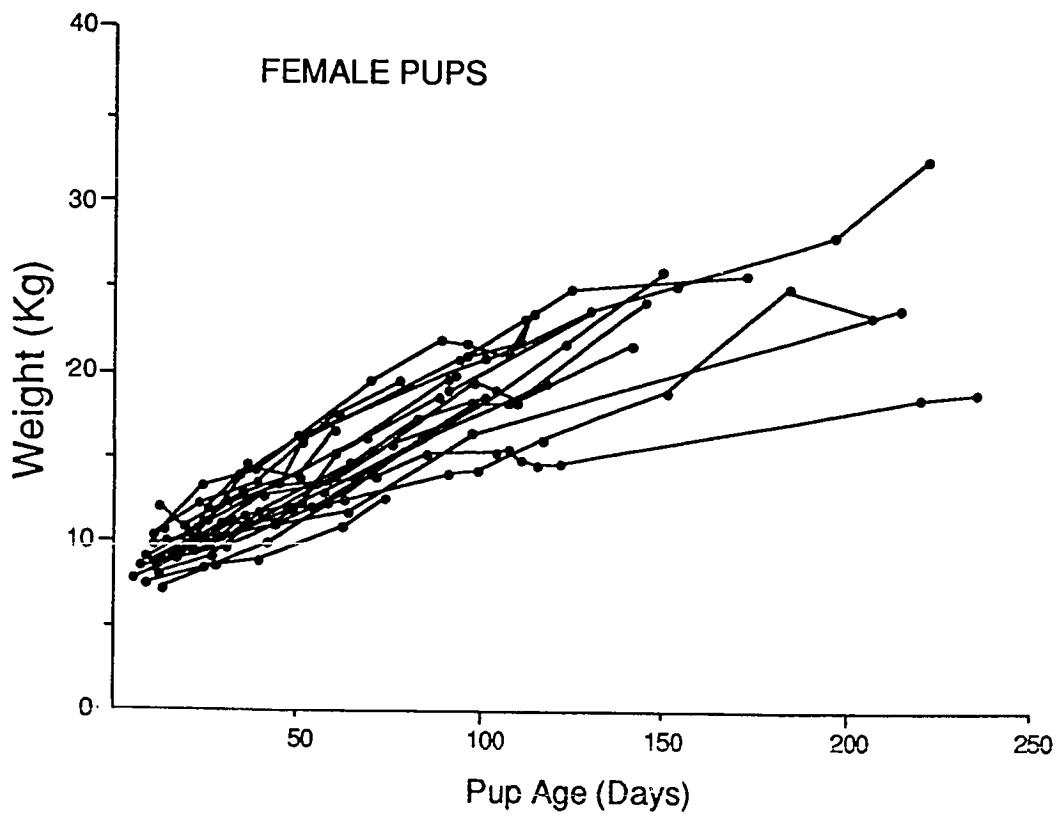
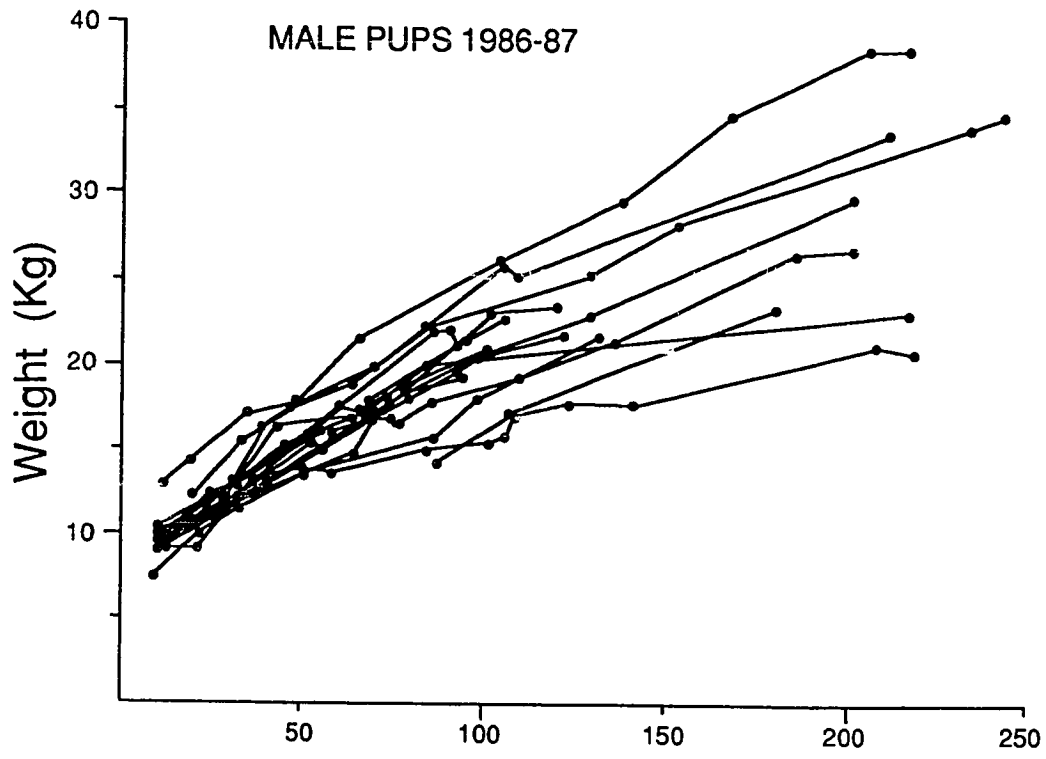
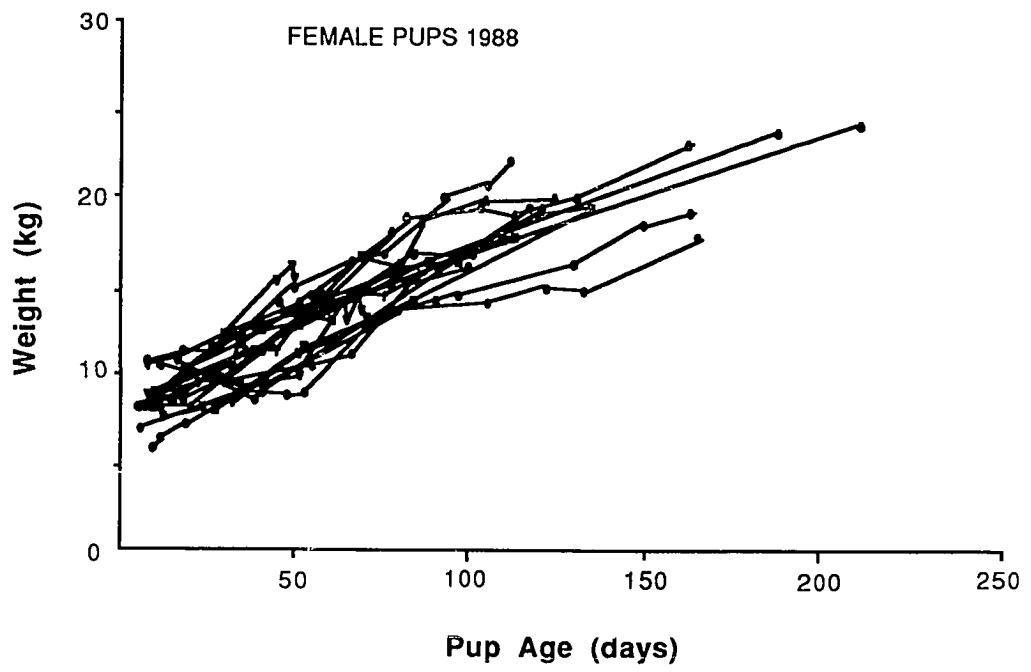
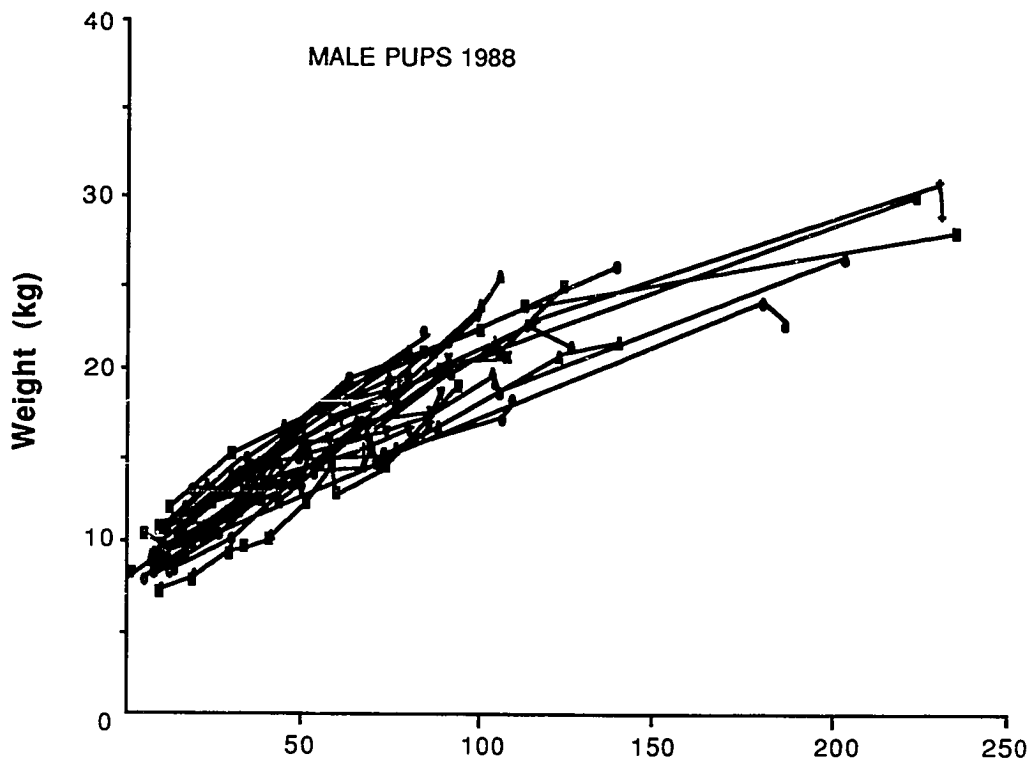


Figure 6. Growth rates of male and female pups weighed during the 1988 breeding season.



y-intercept: males = 8.81 ± 1.8 kg, females = 7.44 ± 1.4 kg, t-test, $t = 2.74$, $P < 0.01$, $df = 40$). There was no difference in the y-intercepts when the two seasons were compared (t-test, $t = -1.64$, $P > 0.05$, $df = 74$).

During the study, four birth weights were recorded when the mother and pup became separated or the pup died soon after birth. Three were male pups with weights of 7.1, 7.2 and 7.7 kg., and one female pup weighed 8.3 kg. Ling and Walker (1977) recorded birth weights of two female pups of 7.9 and 7.7 kg. Because of the unusual circumstances of some of these pups, they may not represent average birth weights.

During the 1986-87 breeding season, male pups gained a mean of 0.109 ± 0.03 kg/day ($n = 15$) and female pups gained 0.105 ± 0.02 kg/day ($n = 19$) with no significant differences between them (t-test, $t = 0.40$, $P > 0.05$). In 1988 male pups grew faster than female pups, gaining a mean of 0.118 ± 0.03 kg/day ($n = 23$), compared to the female pup mean of 0.100 ± 0.02 kg/day ($n = 19$) (t-test, $t = 2.14$, $P < 0.05$). However, there were no differences in growth rates when the two seasons were compared (t-test, $t = -1.18$, $P > 0.05$, $df = 76$), nor was there a difference when the male pups of each season were compared (t-test, $t = -1.56$, $P > 0.05$, $df = 36$).

Thirteen pups were weighed on succeeding days to determine daily weight loss during the female's absence. The mean weight loss for both male and female pups was 0.66 ± 0.03 kg/day (range = 0.35-1.05 kg/day, mean age = 67 days). Daily weight gains were recorded for only two pups, but showed remarkable 1.1 and 1.8 kg gain over a one day period.

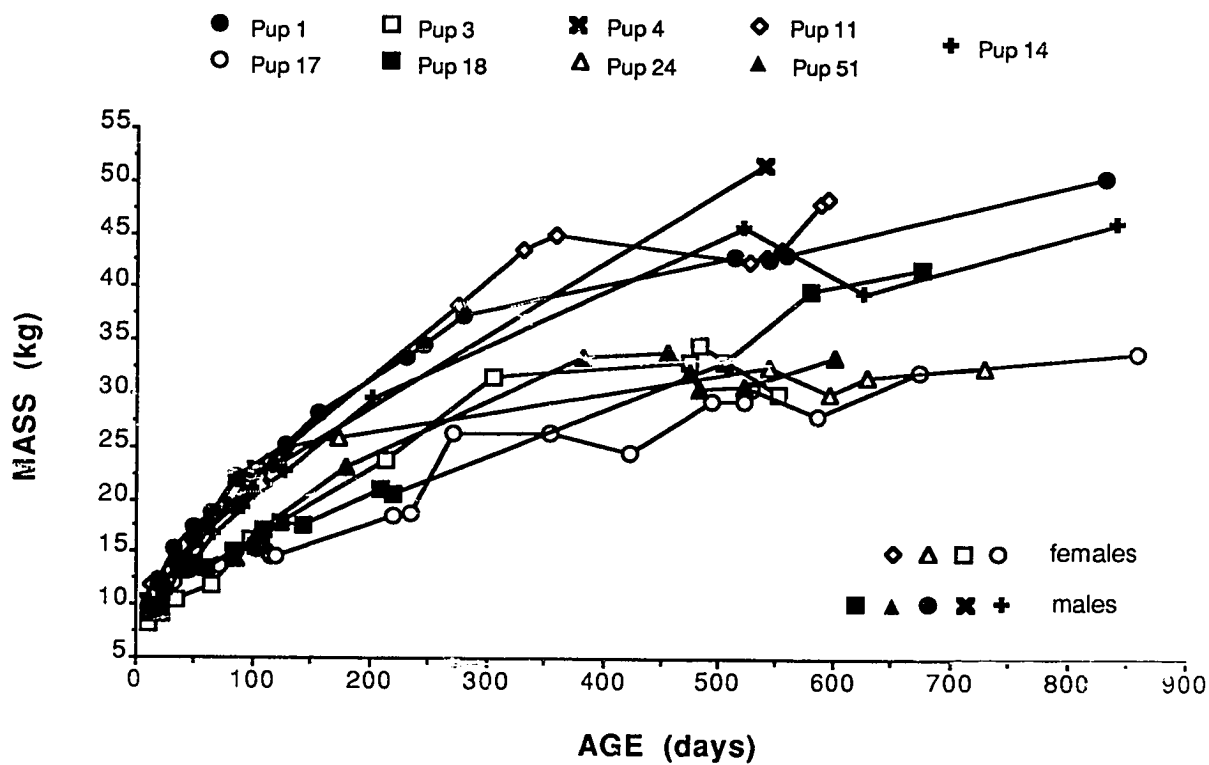
No correlations between female attendance behavior and pup weight were found. The amount of time females spent ashore between parturition and departing on their first foraging trips was not correlated to pup weight ($r = 0.07$, $N = 47$). Nor were there any correlations between pup growth rates and the percent of time females spent on shore ($r = -0.03$, $N = 57$).

Growth rate of nine pups from the 1986-87 cohort were obtained until they were 1.5-2.3 years old (Figure 7). During the first year, these pups gained a mean of 0.084 ± 0.023 kg/day. The growth curve appears to become asymptotic at 300-400 days of age, and between 12 and 28 months, the growth rate declined to only 0.019 ± 0.043 kg/day (see Appendix 4 for individual regressions of these pups). Pups #4, #11 and #18 were still suckling during the measurement period, and the remaining pups were weaned at around 15.5-18 months of age (Table 1).

DISCUSSION

This study demonstrates that the period of post-partum maternal investment lasts at least 15-18 months in Neophoca cinerea, and extends longer than that for about one third of the females, with a maximum of up to 39 months. Time to weaning appears to be dependant upon whether females give birth the next breeding season, although in a few cases females continued to suckle yearlings to the detriment of the the new pup. These observations suggest that 15 months is the minimum amount of time needed for pups to grow and develop to the stage where they can survive on their own. The observation of the pup that starved to death at 11.5 months (Pup C2, Table 2) supports this

Figure 7. Growth rates of male and female pups up to 28 months of age. First weights recorded during the 1986-87 breeding season.



conclusion, and indicates that at one year pups are still dependant on their mothers for survival. A prolonged dependance may be possible because the population is resident and the mother is always accessible. This also occurs in the non-migratory Galapagos fur seal, which exhibit a long dependency period of up to three years (Trillmich, 1986a). In species such as the sub-polar fur seals (Arctocephalus gazella and Callorhinus ursinus), however, the females migrate to other areas and the pups are weaned after a four month nursing period (Gentry and Holt, 1986; Doidge and Croxall, 1989).

Attendance cycle data indicate that while feeding trips to sea were variable, they did not increase in length as has been found in some other species of otariids (Boness et al., 1985; David and Rand, 1986; Gentry and Holt, 1986; Trillmich, 1986b; Higgins, et al. , 1988). Initial trips to sea were shorter than all other trips, indicating that female time at sea was limited by pup fasting ability. The time females spent ashore remained fairly constant and is consistent with attendance cycles of other otariids (David and Rand, 1986; Gentry and Holt, 1986; Trillmich, 1986a; Higgins et al., 1988). Conditions at sea are probably variable although little is known about foraging locations and prey consumption, and exactly what factors are responsible for the large variation in attendance. The sea lions are known to eat fish (species unknown), cephalopods, and crustaceans, but actual amounts and proportions of prey items have not been quantified (Walker and Ling, 1981; Higgins, unpub. data).

The seasonal differences in time at sea are difficult to explain in the absence of more information on diet and foraging location. However, June, July and August are winter months in the southern hemisphere and have the shortest day lengths of the year. The finding that the shortest foraging trips

occurred in June supports the suggestion that day length influences time at sea. Differences in time at sea may reflect foraging success due to the increased availability of night-time prey, which would allow females to spend less time at sea. For example, crustaceans are one of the known prey items of Australian sea lions, and many species are known to be active at night (Herrnkind, 1983). More information on diet is needed to better understand what affects female foraging patterns.

Pup sex bias in female attendance patterns were not found. Similarly, Trillmich (1986) did not find a correlation between female attendance cycle and pup sex in Galapagos sea lions, whereas significant differences were found in only one of six data sets in Steller sea lions (Higgins, et al., 1988). It would seem that attendance cycles are sufficiently variable as to prevent them from being a reliable measurement of post-partum maternal investment.

The rate at which pups gain weight would also be expected to correlated with female attendance behavior, but the data collected in this study failed to show this. Doidge and Croxall (1989) found that high weaning weight was associated with female time ashore in Antarctic fur seals, and that duration of time at sea was not. Since the Neophoca cinerea pups were not weaned while attendance data were being collected, this may not be a valid comparison, but it does show that time on land may be more important to pup development than time at sea. Pups are adapted to undergo periods of fasting involving rapid weight loss and equally rapid weight gain, and it would appear that milk composition and volume ingested are probably the most important variables. Time on land may be related to pup suckling ability and the time required for the production and consumption of an adequate supply of milk. Pups probably

increase their rate of milk ingestion as they get older, although suckling data are needed to confirm this.

Male pups were heavier than female pups as expected, but the male pups exhibited higher growth rates in 1988 only. Although the absolute mass at all ages was greater for male pups in 1986-87, there was no difference in growth rates. Male pups may be larger than female pups as a result of higher birth weights rather than higher growth rates. However, an equal growth rate does not fit the pattern seen in some other species of sexually dimorphic pinniped (Mattlin, 1981; Doidge et al., 1984; Trillmich, 1986c; Anderson and Fedak, 1987). One exception are grey seal pups, Halichoerus grypus, in which males were significantly heavier than females, but did not grow at a faster rate (Kovacs and Lavigne (1986).

Growth rates of Neophoca cinerea pups fall within the range for other otariids. Based on a birth weight of 7.7 kg (mean of 6 birth weights), and a growth rate of 0.11 kg/day, pups doubled their mass in about 70 days. This result is consistent with doubling times of other species of otariids, although it is faster than northern fur seals (87 days) and slower than Steller sea lions (47 days) (Gentry et al., 1986; Higgins, et al., 1988). Pup birth mass as a function of maternal mass is also consistent with findings from other otariid species (Costa, 1990b). It is interesting that Neophoca cinerea pups do not grow at a significantly slower rate than other otariids, given that the breeding cycle is 17-18 month long. It is possible that, unlike phocids, growth rate is an inflexible trait in otariids that cannot be varied as time to weaning appears to be (Costa, 1990b).

It was not possible to discover when pups began to forage on their own and how much they relied on mother's milk during the second year of life. The observation that pups are not weaned until they are 15-18 months old indicates that there is a nutritional or developmental necessity for pups to still be dependant on their mothers at that age. Pup size may preclude pups from successfully exploiting the foraging areas until they are older, or perhaps there is a learning component to foraging that takes time to develop. Further research to determine the foraging strategies of yearlings may help to shed some light on these questions.

REFERENCES

- Anderson, S. S. and M. A. Fedak. 1987. Grey seal, Halichoerus grypus, energetics: females invest more in male offspring. *J. Zool. Lond.* 211:667-679.
- Boness, D., L. Dabek, K. Ono and O. Oftedal. 1985.. Female attendance behavior in California sea lions. In: Abstracts of the sixth biennial conference on the biology of marine mammals. Vancouver, B. C.
- Bonner, W. N. 1984. Lactation strategies in pinnipeds: Problems for a marine mammalian group. *Symp. Zoology. Soc. Lond.* 51:253-272.
- Bowen, W. D., O. T. Oftedal and D. J. Boness. 1985. Birth to weaning in 4 days: remarkable growth in the hooded seal, Cystophora cristata. *Canadian J. Zool.* 63:2841-2846.
- Charnov, E. L. 1982. The theory of sex allocation. Princeton University Press, Princeton, N. J.
- Costa, D. P. 1990b. Reproductive and foraging energetics of pinnipeds: implications for life history patterns. In: Mechanism and evolution of behavior in Pinnipeds. D. Renouf, Ed. Chapman and Hall, London. In press.
- David, J. H. M. and R. W. Rand. 1986. Attendance behavior of female South African fur seals. In: Fur seals: maternal strategies on land and at sea. R. L. Gentry and G. L. Kooyman, eds. Princeton University Press, Princeton. pp. 126-141.
- Doidge, D. W. and J. P. Croxall. 1989. Factors affecting weaning weight in Antarctic fur seals Arctocephalus gazella at South Georgia. *Polar Biology* 9:155-160.
- Doidge, D. W., J. P. Croxall and C. Ricketts. 1984. Growth rates of Antarctic fur seal Arctocephalus gazella pups at South Georgia. *J. Zool. Lond.* 203:87-93.
- Fay, F. H. 1981. Walrus. In: Handbook of marine mammals, Vol 1. S. H. Ridgway and R. J. Harrison, Eds. Academic Press, London, 235 pp.
- Gentry, R. L. and J. R. Holt. 1986. Attendance behavior of northern fur seals. In: Fur seals: maternal strategies on land and at sea. R. L. Gentry and G. L. Kooyman, eds. Princeton University Press, Princeton. pp. 41-60.

- Gentry, R. L. and G. L. Kooyman. 1986. Introduction. In: Fur seals: maternal strategies on land and at sea. R. L. Gentry and G. L. Kooyman, eds. Princeton University Press, Princeton. pp. 41-60.
- Gentry, R. L., Costa, D. P., Croxall, J. P., David, J. H. M., Davis, R. W., Kooyman, G. L., Majluf, P., McCann, T. S., and F. Trillmich. 1986. Synthesis and conclusions. In: Fur seals: maternal strategies on land and at sea. R. L. Gentry and G. L. Kooyman, eds. Princeton University Press, Princeton. pp. 220-278.
- Herrnkind, W. F. 1983. Movement patterns and orientation. In: The biology of the Crustacea, Vol. 7: Behavior and Ecology. F. J. Vernberg and W. B. Vernberg, Eds; D. E. Bliss, General Ed. Academic Press, New York, N. Y.
- Higgins, L. V., D. P. Costa, A. C. Huntley and B. J. Le Boeuf. 1988. Behavioral and physiological measurements of maternal investment in the Steller sea lion, Eumetopias jubatus. Marine Mammal Science 4:44-58.
- Kovacs, K. M. and D. M. Lavigne. 1986. Growth of grey seal (Halichoerus grypus) neonates: differential maternal investment in the sexes. Canadian Journal of Zoology 64:1937-1943.
- Ling, J. K. and G. E. Walker. 1976. Seal studies in South Australia: Progress report for the year 1975. South Australian Naturalist. 50:59-68,72.
- Ling, J. K. and G. E. Walker. 1977. Seal studies in South Australia: Progress report for the period January 1976 to March 1977. South Australian Naturalist 52:18-30.
- Ling, J. K. and G. E. Walker. 1980. Seal studies in South Australia: Progress report for the period April 1977 to July 1979. South Australian Naturalist 58:68-79.
- Marlow, B.J. 1975. The comparative behavior of the Australian sea lions Neophoca cinerea and Phocarctos hookeri. Mammalia, 39(2):160-230.
- Mattlin, R. H. 1981. Pup growth of the New Zealand fur seal Arctocephalus forsteri on the Open Bay Islands, New Zealand. J. Zool. Lond. 193:305-314.
- Maynard Smith, J. 1980. A new theory of sexual investment. Behav. Ecol. Sociobiol. 7:247-251.
- Millar, J. S. 1977. Adaptive features of mammalian reproduction. Evolution 31:370-386.

- McLaren, I. A. 1958. The biology of the ringed seal (Phoca groenlandica Schreber) in the Eastern Canadian Arctic. Bull. Fish. Res. Board. Canada 118:1-97.
- Oftedal, O. T., D. J. Boness and R. A. Tedman. 1987. The behavior, physiology, and anatomy of lactation in the pinnipedia. Current Mammalogy, vol 1, pp 175-245.
- Oftedal, O. T., S. J. Iverson and D. J. Boness. 1987b. Milk and energy intakes of California sea lion (Zalophus californianus) pups in relation to sex, growth and predicted maintenance requirements. Physiol. Zool. 60:560-575.
- Payne, M. R. 1979. Growth in the Antarctic fur seal Arctocephalus gazella. J. Zool. Lond. 187:1-20.
- Stirling, I. 1972. Observations on the Australian sea lion, Neophoca cinerea (Peron). Australian J. Zool. 20:271-9.
- Trillmich, F. 1979. Galapagos sea lions and fur seals. Not. Galapagos, 29:814.
- Trillmich, F. 1986a. Attendance behavior of Galapagos fur seals. In: Fur seals: maternal strategies on land and at sea. R. L. Gentry and G. L. Kooyman, eds. Princeton University Press, Princeton. pp. 168-185.
- Trillmich, F. 1986b. Attendance behavior of Galapagos sea lions. In: Fur seals: maternal strategies on land and at sea. R. L. Gentry and G. L. Kooyman, eds. Princeton University Press, Princeton. pp. 198-208.
- Trillmich, F. 1986c. Maternal investment and sex-allocation in the Galapagos fur seal, Arctocephalus galapagoensis. Behav. Ecol. Sociobiol. 19:157-164.
- Trivers, R. L. and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90-92.
- Walker, G. E. and J. K. Ling, 1981. Australian sea lion-Neophoca cinerea. In: Handbook of Marine Mammals, Vol. 1: The walrus, sea lions, fur seals and sea otter. S. H. Ridgway and R. J. Harrison, Eds. Academic Press, London. pp 99-118.

APPENDIX A

Female reproductive data

4

FEMALE REPRODUCTIVE DATA 1986-87

FEMALE	BIRTH DATE	LOC	PUP SEX	DAYS TO BIRTH	DATE COP	BIRTH TO COP	1ST TRIP TO SEA	BIRTH TO 1ST TRIP
RP	NOV	WPA	?					
SP	NOV	WPA	F					
DP	DEC	WPA	M					
P11	DEC	WPA	M					
30	DEC	WPA	F					
31	DEC	WPA	F					
32	DEC	WPA	?					
33	DEC	WPA	?					
XX	DEC	EPA	?					
1	14-DEC	WPA	M				24-DEC	10
2	7-JAN	WPA	F	2	12-JAN	6.5	16-JAN	9
3	14-JAN	WPA	F	2	21-JAN	7	24-JAN	10
4	9-JAN	WPA	M	2	17-JAN	8	18-JAN	9
5	5-FEB	WPA	M	2			17-FEB	12
6	11-MAR	WPA	F	3			26-MAR	15
7	16-FEB	WPA	F	0			28-FEB	12
8	12-FEB	WPA	M	1			22-FEB	10
9	25-DEC	WPA	M	4			3-JAN	9
10	16-DEC	EPA	F	1			26-DEC	10
11	19-DEC	WPA	F	3			28-DEC	9
12	NOV	WPA	F					
XXX	JAN	EPA	?					
14	11-JAN	WPA	M	3			22-JAN	11
15	27-JAN	WPA	M	3	4-FEB	8	6-FEB	10
16	22-DEC	WPA	M	1			1-JAN	10
17	24-DEC	WPA	F	2	30-DEC	6	2-JAN	9
18	26-DEC	WPA	M	1			5-JAN	10
19	26-DEC	WPA	F	1	3-JAN	8.5	1-JAN	6
20	28-DEC	WPA	M	2			7-JAN	10.5
22	28-JAN	WPA	F	1			10-FEB	13
23	15-JAN	WPA	M	3			26-JAN	11
24	9-FEB	WPA	F	1			19-FEB	10
25	18-JAN	PC	?					
28	29-JAN	WPA	F	0			6-FEB	8
36	20-JAN	WPA	F	0			31-JAN	11.5
37	20-JAN	WPA	F	0			29-JAN	9
38	21-JAN	WPA	F	0			31-JAN	10
39	21-JAN	WPA	F	0			31-JAN	10.5
40	22-JAN	WPA	M	1			1-FEB	10
41	25-JAN	WPA	F	3	1-FEB	7	3-FEB	9
43	28-JAN	WPA	M	2			1-FEB	4
44	30-JAN	WPA	F	2			12-FEB	13
45	2-FEB	WPA	M	4			12-FEB	10.5
46	1-FEB	WPA	M	1	8-FEB	7.5	11-FEB	10
47	4-FEB	WPA	F	1	12-FEB	8	16-FEB	12
48	4-FEB	WPA	F	1			16-FEB	12
49	5-FEB	WPA	F	2.5	10-FEB	5.5	16-FEB	11
51	6-FEB	WPA	M	0			16-FEB	9.5

FEMALE	BIRTH DATE	LOC	PUP SEX	DAYS TO BIRTH	DATE COP	BIRTH TO COP	1ST TRIP TO SEA	BIRTH TO 1ST TRIP
52	9-FEB	WPA	?	2			19-FEB	9.5
53	10-FEB	WPA	M				20-FEB	10.5
AX	15-FEB	WPA	M	2				
55	20-FEB	WPA	F	2	25-FEB	5	28-FEB	7.5
59	18-MAR	WPA	F				28-MAR	10
60	18-MAR	WPA	F				27-MAR	9
61	17-MAR	WPA	F				23-MAR	9
62	4-APR	WPA	F		10-APR	6.5	14-APR	10

FEMALE REPRODUCTIVE DATA 1988

FEMALE	BIRTH DATE	LOC	PUP SEX	DAYS TO BIRTH	DATE COP	BIRTH TO COP	1ST TRIP TO SEA	BIRTH TO 1ST TRIP
A	25-APR	WPA	M				8-MAY	
C	11-MAY	WPA	F	1			18-MAY	7
D	12-MAY	WPA	F	1	19-MAY	7	21-MAY	9
E	15-MAY	WPA	F	2				
F	16-MAY	WPA	F	1	22-MAY	6	26-MAY	10
G	17-MAY	WPA	F	1			30-MAY	13
H	17-MAY	WPA	F	3.5				
I	21-MAY	WPA	?	2			31-MAY	10
J	24-MAY	EPA	F					
K	26-MAY	WPA	M	0	31-MAY	5	1-JUN	6
L	31-MAY	WPA	M				9-JUN	9
11	31-MAY	MB	M					
AS	JUN	EPA	?					
AT	JUN	EPA	?					
M	2-JUN	EPA	?					
N	10-JUN	WPA	M	2			20-JUN	10
O	11-JUN	WPA	M	3			19-JUN	8
P	14-JUN	WPA	F	3			24-JUN	10
Q	15-JUN	EPA	F				23-JUN	8
R	17-JUN	EPA	F				28-JUN	11
S	19-JUN	EPA	M				29-JUN	10
T	19-JUN	EPA	M				30-JUN	11
B	21-JUN	WPA	F	4			3-JUL	12
14	21-JUN	WPA	M	2			29-JUN	8
U	23-JUN	WPA	M	2	3-JUL	10	1-JUL	8
17	24-JUN	WPA	M	5	1-JUL	7	9-JUL	15
V	25-JUN	WPA	M	3			6-JUL	11
W	25-JUN	WPA	M	2			5-JUL	10
X	26-JUN	EPA	F				8-JUL	12
Y	28-JUN	WPA	F	2			9-JUL	11
Z	30-JUN	WPA	M	4			10-JUL	10
AA	1-JUL	WPA	F	1			13-JUL	12
AB	1-JUL	EPA	M				10-JUL	9
AD	3-JUL	WPA	M	2			15-JUL	12
AC	4-JUL	EPA	F		12-JUL	8	16-JUL	12
25	6-JUL	PC	M				17-JUL	11
AE	7-JUL	WPA	F	3			16-JUL	9
AF	7-JUL	EPA	?					
AG	9-JUL	WPA	M	1			16-JUL	7
AH	8-JUL	WPA	F	1			20-JUL	12
28	10-JUL	WPA	F	3			19-JUL	9
B2	13-JUL	WPA	M		20-JUL	7	22-JUL	9
C2	13-JUL	WPA	M	2			23-JUL	10
D2	14-JUL	WPA	M				26-JUL	12
I2	17-JUL	WPA	M	2	26-JUL	9	29-JUL	12
V2	17-JUL	WPA	M	3	26-JUL	9	29-JUL	12
W2	19-JUL	WPA	F	2	24-JUL	5	26-JUL	7

FEMALE	BIRTH DATE	LOC	PUP SEX	DAYS TO BIRTH	DATE COP	BIRTH TO COP	1ST TRIP TO SEA	BIRTH TO 1ST TRIP
U2	17-JUL	EPA	?				25-JUL	8
37	21-JUL	WPA	F	3			29-JUL	8
AI	21-JUL	WPA	M	3			29-JUL	8
AJ	23-JUL	WPA	M		29-JUL	6	2-AUG	9
AK	26-JUL	WPA	F		3-AUG	8	6-AUG	11
AL	30-JUL	WPA	M		7-AUG	7	9-AUG	10
51	5-AUG	WPA	M	3			14-AUG	9
8	11-AUG	WPA	M	2			21-AUG	10
AR	13-AUG	WPA	F	1			23-AUG	10
AM	19-AUG	WPA	M				30-AUG	11
AN	21-AUG	WPA	F		25-AUG	4	5-SEP	15
AO	24-AUG	EPA	M					
AP	8-SEP	WPA	M	2			18-SEP	10
60	10-SEP	WPA	F	0			19-SEP	9
AQ	13-SEP	WPA	F		19-SEP	6	22-SEP	9

FEMALE REPRODUCTIVE DATA 1989-90

FEMALE	BIRTH DATE	LOC	PUP SEX	DAYS TO BIRTH	DATE COP	BIRTH TO COP	1ST TRIP TO SEA	BIRTH TO 1ST TRIP
154	18-21 OCT	WPA	M					
159	19-21 OCT	WPA	?					
163	21-28 OCT	WPA	F					
164	26-30 OCT	WPA	F					
166	4-NOV	WPA	F					
165	5-NOV	WPA	M					
168	5-NOV	WPA	M					
157	12-NOV	WPA	F					
158	12-16 NOV	WPA	F					
153	14-18 NOV	EPA	?					
SK	16-17 NOV	WPA	F					
162	17-21 NOV	EPA	M				29-NOV	
167	16-18 NOV	WPA	F				26-NOV	
161	16-NOV	WPA	F				25-NOV	9
152	18-22 NOV	EPA	?		27-NOV		28-NOV	
155	20-22 NOV	WPA	M				2-DEC	
156	20-22 NOV	WPA	M				2-DEC	
170	7-14 NOV	EPA	?					
101	25-NOV	WPA	F				4-DEC	9
102	23-NOV	WPA	F		30-NOV	5	5-DEC	12
103	26-NOV	EPA	M				8-DEC	12
169	30-NOV	EPA	?				10-DEC	10
105	30-NOV	EPA	M	5			7-DEC	7
106	1-DEC	EPA	F				11-DEC	10
107	1-DEC	EPA	F				10-DEC	9
P	4-DEC	WPA	M	2			14-DEC	10
11	6-DEC	WPA	F	2			16-DEC	10
12	LATE OCT	PC	F					
104	8-DEC	WPA	F	1			23-DEC	15
108	8-DEC	WPA	M				18-DEC	10
14	9-DEC	WPA	F	2			20-DEC	11
109	9-DEC	WPA	F	2			16-DEC	7
110	11-DEC	WPA	F	2			22-DEC	11
116	10-DEC	WPA	M	1	17-DEC	6	21-DEC	11
AH	15-DEC	WPA	?	2	17-DEC	7		
113	15-DEC	WPA	M	3			24-DEC	9
115	15-DEC	WPA	F				22-DEC	7
117	15-DEC	WPA	F	2	21-DEC	6	25-DEC	10
118	17-DEC	WPA	M	7	21-DEC	4	26-DEC	9
119	18-DEC	WPA	M	2	25-DEC	7	28-DEC	10
120	17-DEC	EPA	F	2				
121	19-DEC	WPA	F	2			27-DEC	8
122	21-DEC	EPA	F				29-DEC	8
25	21-DEC	WPA	M	3			30-DEC	9
123	23-DEC	WPA	F		29-DEC	6	5-JAN	13
124	21-DEC	EPA	M	0			31-DEC	10
126	23-DEC	WPA	M		1-JAN	9	3-JAN	11

FEMALE	BIRTH DATE	LOC	PUP SEX	DAYS TO BIRTH	DATE COP	BIRTH TO COP	1ST TRIP TO SEA	BIRTH TO 1ST TRIP
127	21-DEC	EPA	M				31-DEC	10
134	30-DEC	WPA	M				9-JAN	10
AD	1-JAN	WPA	F	3	9-JAN	8	11-JAN	10
51	2-JAN	WPA	F	1			12-JAN	10
129	4-JAN	WPA	M	2			12-JAN	8
130	6-JAN	WPA	F	0			14-JAN	8
131	6-JAN	WPA	F				17-JAN	11
132	7-JAN	WPA	M				16-JAN	9
133	8-JAN	EPA	F		14-JAN	6	17-JAN	9
28	8-JAN	WPA	F	2			17-JAN	9
AK	11-JAN	WPA	F	2			21-JAN	10
135	11-JAN	WPA	F		18-JAN	7	20-JAN	9
136	14-JAN	WPA	M		20-JAN	6	26-JAN	12
37	13-JAN	WPA	M	0			21-JAN	8
138	16-JAN	WPA	M	2			25-JAN	9
C2	17-JAN	WPA	M	1	24-JAN	7	26-JAN	9
139	25-JAN	WPA	M	1			2-FEB	8
140	27-JAN	WPA	F				6-FEB	10
171	30-JAN	WPA	M					
D2	29-JAN	WPA	F				7-FEB	9
141	1-FEB	WPA	F		8-FEB	7	12-FEB	11
142	6-FEB	WPA	M	2			17-FEB	11
143	13-FEB	EPA	F				20-FEB	7
144	16-FEB	WPA	M	4			27-FEB	11
145	18-FEB	WPA	F	2	24-FEB	6	27-FEB	9
146	1-MAR	WPA	M	1	6-MAR	5	9-MAR	8
147	5-MAR	EPA	?				16-MAR	11
148	7-MAR	WPA	?					
149	14-MAR	WPA	?				24-MAR	10

APPENDIX B

Summarized attendance data

Means and standard deviations of trips to sea and stays ashore for each female. Number of cycles for each female do not necessarily represent total number during study period, since some may not have been included due to insufficient data.

SUMMARIZED ATTENDANCE DATA 1986-87
Including first trips

FEMALE I.D.	AT SEA			ASHORE		
	No. TRIPS analyzed	MEAN (hours)	S.D.	No. STAYS analyzed	MEAN (hours)	S.D.
1	23	36.6	10.6	21	26.3	12.2
2	15	61.2	20.9	16	35.6	10.1
3	20	47.4	12.1	20	36.7	11.6
4	14	48.6	12.2	15	38.8	11.5
5	12	41.5	12.8	11	38.1	8.9
7	9	40.1	19.2	9	31.5	12.3
8	9	40.9	9.1	7	27.8	14.0
9	19	58.3	18.0	19	30.6	13.8
10	21	56.9	23.0	21	37.5	14.3
11	15	63.5	13.5	15	44.1	10.9
14	19	34.8	15.3	19	38.4	13.0
15	12	63.8	11.8	12	41.3	9.5
16	23	43.3	13.9	23	40.6	15.6
17	23	52.8	21.5	24	36.2	18.0
18	17	63.9	10.7	19	27.1	7.7
19	21	44.5	8.1	21	27.2	7.2
20	17	31.8	12.1	20	44.0	11.3
22	12	46.8	30.4	11	24.6	8.0
23	11	82.0	7.1	11	37.1	10.9
24	11	53.7	14.4	11	33.1	9.6
28	7	46.5	9.5	9	29.5	7.8
36	14	56.5	18.0	14	28.6	8.1
37	18	52.9	14.5	20	40.5	15.3
38	9	61.9	11.1	11	45.3	11.7
39	10	56.7	11.0	11	31.4	9.3
40	11	41.1	10.0	11	31.7	13.2
41	10	42.0	16.0	11	41.6	12.5
44	3	36.4	8.4	3	40.1	15.2
45	15	31.6	13.5	14	22.8	14.1
46	10	60.2	17.0	10	39.2	10.8
47	12	38.3	12.3	10	41.0	22.3
48	7	39.7	12.4	8	28.3	13.5
49	16	47.7	11.5	16	27.3	9.6
51	11	45.7	20.7	11	19.8	10.9
53	12	54.8	14.9	13	28.0	7.8
55	7	36.0	13.9	8	34.5	10.0
59	4	43.1	5.9	4	28.9	12.9
60	8	49.9	4.3	8	42.0	9.2

SUMMARIZED ATTENDANCE DATA 1988
Including first trips

FEMALE I.D.	AT SEA			ASHORE		
	No. TRIPS analyzed	MEAN (hours)	S.D.	No. STAYS analyzed	MEAN (hours)	S.D.
E	14	41.2	16.8	14	31.3	11.6
F	37	32.3	11.6	37	25.1	12.5
G	5	42.0	11.4	4	42.0	12.0
H	34	35.4	12.7	34	32.3	11.6
K	42	35.6	15.6	43	25.0	10.3
L	17	49.9	4.4	15	28.3	9.0
N	27	34.8	15.4	25	33.9	10.1
O	19	42.4	15.1	20	35.3	15.4
P	23	56.0	15.2	22	39.5	7.8
W	17	25.8	18.7	15	25.1	11.6
Y	14	52.9	5.9	15	41.6	10.2
Z	20	42.8	12.9	21	26.0	11.1
AA	10	42.5	11.4	10	39.2	16.5
AD	16	37.5	11.4	17	36.7	19.5
AE	12	39.2	10.2	12	35.9	8.8
AG	14	49.9	14.2	15	30.2	10.0
AH	14	35.3	16.6	14	30.7	14.2
AI	10	42.5	22.7	10	19.7	15.4
AK	4	48.0	0.0	3	48.0	0.0
AL	10	48.5	18.3	9	31.6	9.1
AM	7	29.2	9.5	6	32.0	9.8
AN	4	34.0	10.6	4	32.0	5.4
AP	1	24.0		1	48.0	
AR	7	33.6	12.3	7	31.5	9.8
B2	12	50.9	19.7	12	29.1	13.3
C2	17	44.5	17.4	17	32.7	9.9
D2	7	63.4	11.4	7	34.3	14.6
I2	13	37.9	15.7	13	33.1	14.3
V2	16	41.2	9.8	16	44.8	19.7
W2	15	41.0	25.7	16	28.3	10.2
8	7	26.8	10.8	6	29.8	13.7
14	25	38.3	11.7	24	33.4	17.2
28	8	39.2	12.5	8	28.5	10.5
37	14	42.1	12.6	13	29.3	10.2
51	9	39.0	4.9	9	17.1	7.7
60	1	48.0		1	24.0	

APPENDIX C

Pup growth rate data

Based on linear regressions of each pup. Weights measured during 0-8 months of age

PUP GROWTH DATA 1986-87

PUP I.D.	SEX	N	AGE (days)	Y-INTERCEPT	SLOPE (KG/DAY)	R ²
1	M	9	20-245	12.56	0.094	0.98
4	M	8	10-121	9.33	0.130	0.96
5	M	6	12-101	8.66	0.130	0.98
8	M	8	10-94	7.61	0.140	0.98
9	M	6	10-218	12.20	0.056	0.77
14	M	8	11-202	8.70	0.109	0.98
15	M	12	10-201	9.27	0.091	0.98
16	M	9	10-212	10.46	0.120	0.94
18	M	13	11-219	10.05	0.054	0.85
20	M	10	11-216	12.20	0.127	0.98
23	M	6	11-122	8.52	0.114	0.98
40	M	4	10-56	8.53	0.137	0.96
45	M	10	10-138	8.64	0.135	1.00
46	M	7	9-133	7.49	0.106	0.98
51	M	3	85-180	6.88	0.091	1.00
2	F	10	12-221	11.22	0.096	0.96
3	F	6	10-214	7.93	0.075	0.98
7	F	9	6-118	7.07	0.103	0.98
10	F	7	19-113	8.50	0.127	0.98
11	F	7	13-114	9.45	0.118	0.96
17	F	13	10-235	10.83	0.036	0.74
22	F	5	12-74	6.43	0.077	0.96
24	F	8	11-173	10.40	0.102	0.94
28	F	7	8-142	7.10	0.105	0.96
36	F	7	12-145	6.40	0.121	0.98
37	F	10	9-208	6.42	0.087	0.96
38	F	2	10-32	7.76	0.109	1.00
39	F	7	11-150	6.84	0.121	0.98
41	F	4	9-93	7.92	0.127	1.00
48	F	2	92-130	7.76	0.121	1.00
49	F	6	11-101	7.33	0.133	0.98
59	F	7	18-88	7.33	0.102	0.98
60	F	6	19-60	8.21	0.135	0.86
61	F	7	15-89	7.08	0.125	0.94

PUP GROWTH DATA 1988

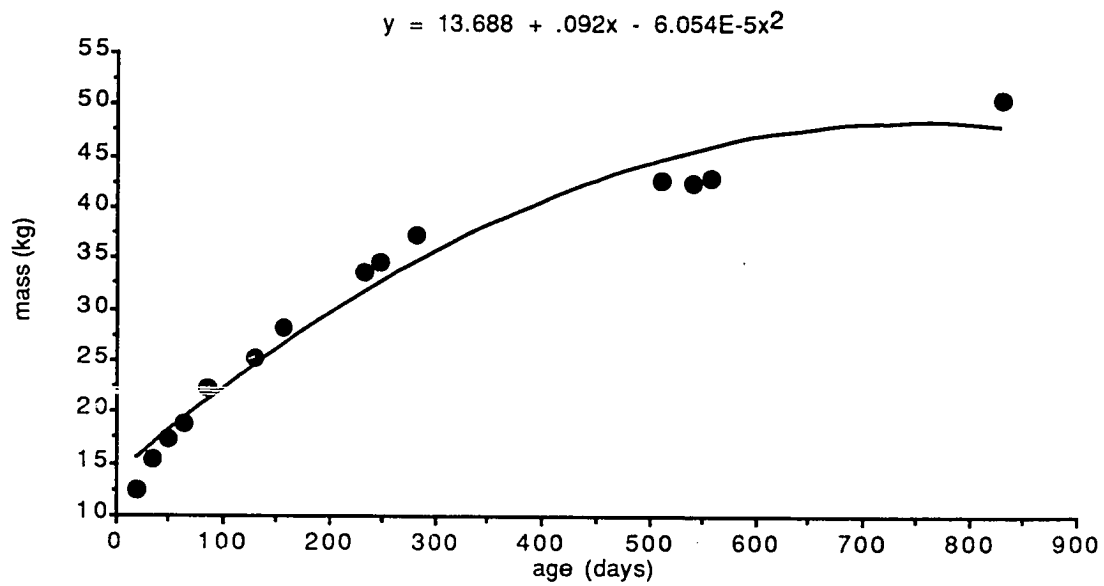
PUP I.D.	SEX	N	AGE (days)	Y-INTERCEPT	SLOPE (KG/DAY)	R ²
K	M	7	6-138	8.70	0.136	0.94
L	M	3	9-30	7.15	0.062	1.00
N	M	7	10-124	9.70	0.117	0.99
O	M	7	8-139	8.14	0.097	1.00
S	M	3	19-80	9.93	0.139	0.98
Z	M	11	8-230	11.31	0.085	0.95
B2	M	5	18-107	9.97	0.110	0.96
C2	M	8	10-109	9.38	0.082	0.92
D2	M	7	12-223	9.05	0.098	0.98
I2	M	6	12-105	9.17	0.148	0.99
V2	M	10	14-203	10.38	0.083	0.97
AB	M	3	12-84	9.53	0.150	1.00
AD	M	9	13-234	12.95	0.083	0.89
AG	M	10	10-94	5.30	0.138	0.96
AI	M	6	37-99	5.63	0.172	0.96
AL	M	8	2-89	8.75	0.112	0.94
AM	M	10	11-187	8.88	0.080	0.97
AO	M	5	13-66	5.88	0.163	0.99
AP	M	5	6-51	9.18	0.138	0.97
8	M	10	10-80	9.64	0.132	0.96
14	M	10	9-126	8.28	0.118	0.96
25	M	3	61-98	6.60	0.173	0.98
51	M	8	9-86	9.10	0.091	0.97
E	F	7	7-166	6.98	0.066	0.96
F	F	13	10-164	5.51	0.088	0.97
G	F	6	13-135	5.70	0.101	0.99
H	F	10	11-163	9.17	0.090	0.95
P	F	8	10-135	8.27	0.086	0.99
Q	F	3	28-84	4.95	0.114	0.97
R	F	4	17-117	6.40	0.104	0.82
X	F	3	12-89	7.65	0.100	1.00
Y	F	7	12-124	6.49	0.121	0.96
W2	F	9	12-211	9.76	0.071	0.99
AA	F	9	7-121	7.47	0.100	0.97
AC	F	2	53-81	6.75	0.118	1.00
AE	F	10	10-113	8.23	0.091	0.92
AH	F	4	21-61	9.12	0.072	0.86
AN	F	10	9-70	7.42	0.089	0.81

PUP I.D.	SEX	N	AGE (days)	Y-INTERCEPT	SLOPE (KG/DAY)	R²
AR	F	7	6-78	6.30	0.139	0.96
28	F	10	9-112	8.96	0.114	0.98
37	F	9	8-100	7.47	0.080	0.89
60	F	6	9-50	8.77	0.142	0.96

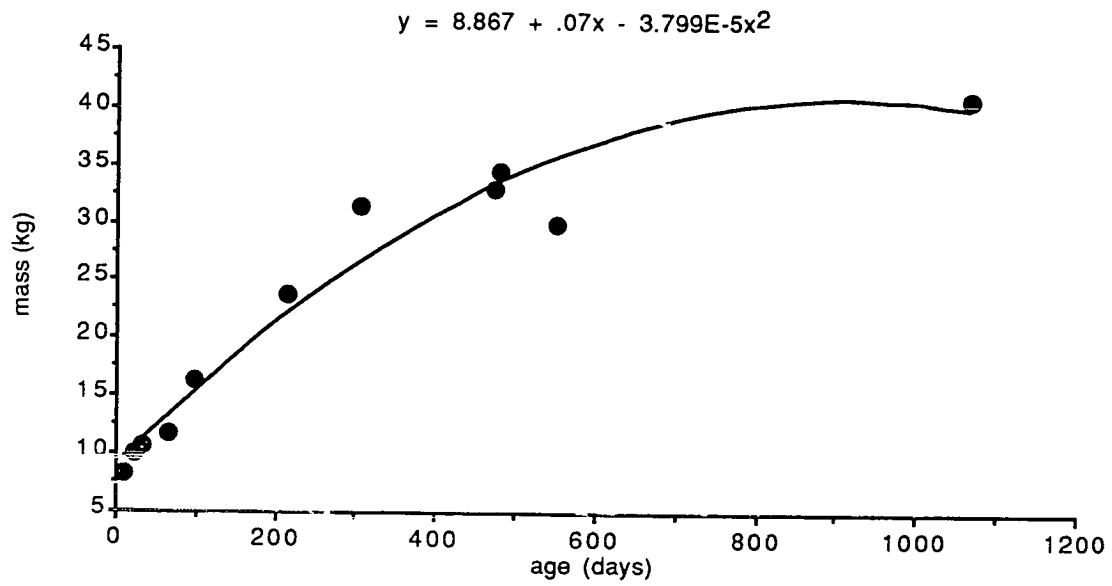
APPENDIX D

Yearling growth curves

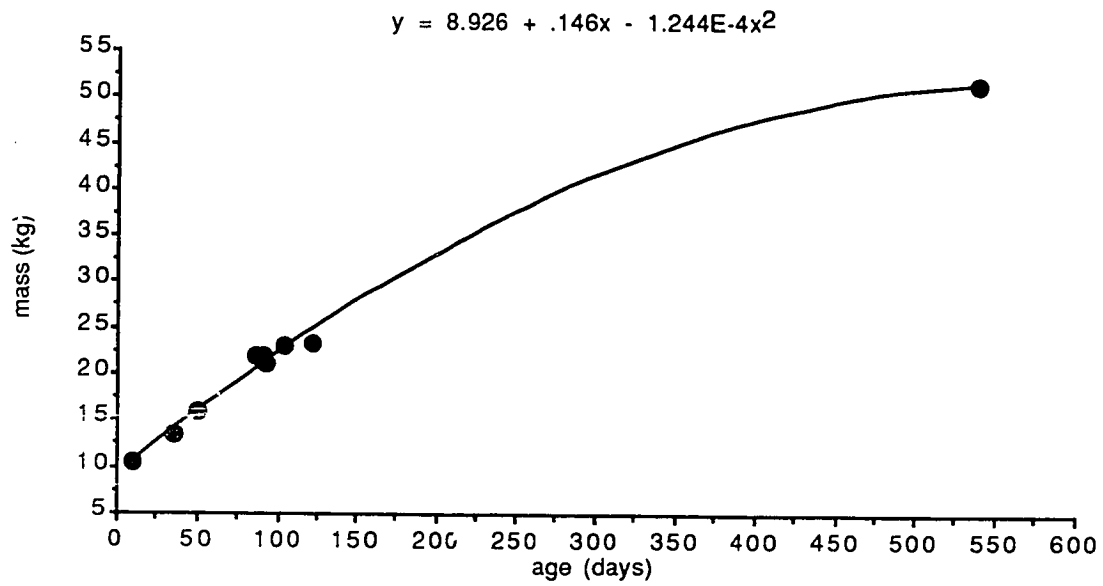
PUP 1 - MALE



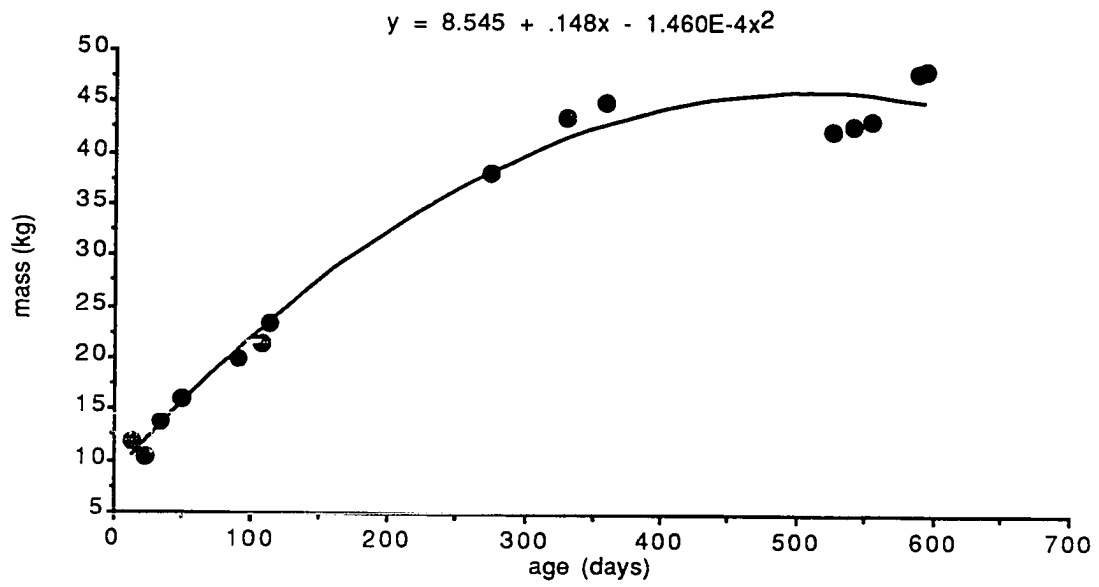
PUP 3 - FEMALE



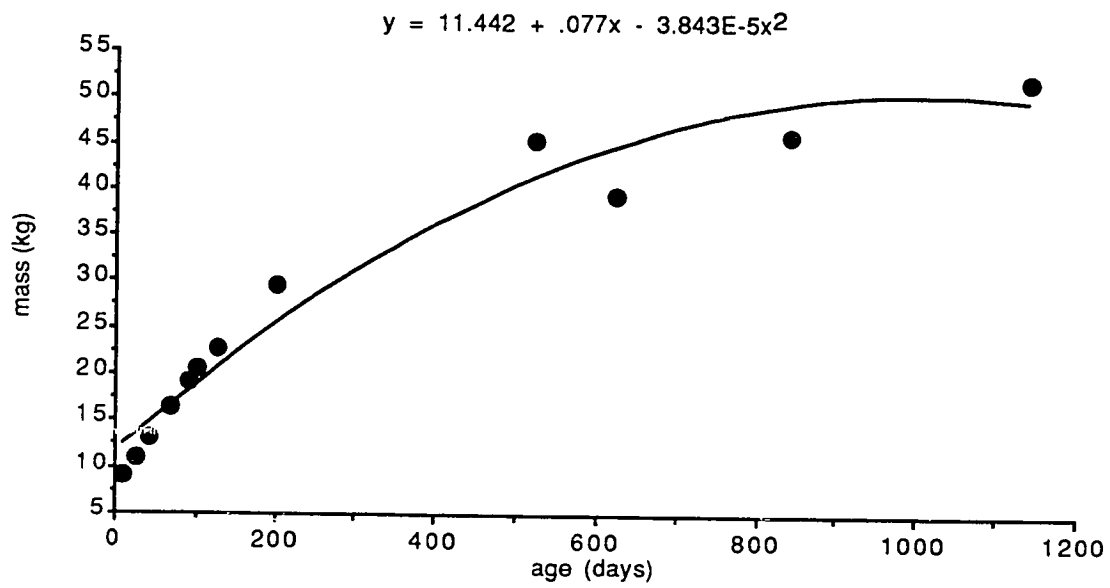
PUP 4 - MALE



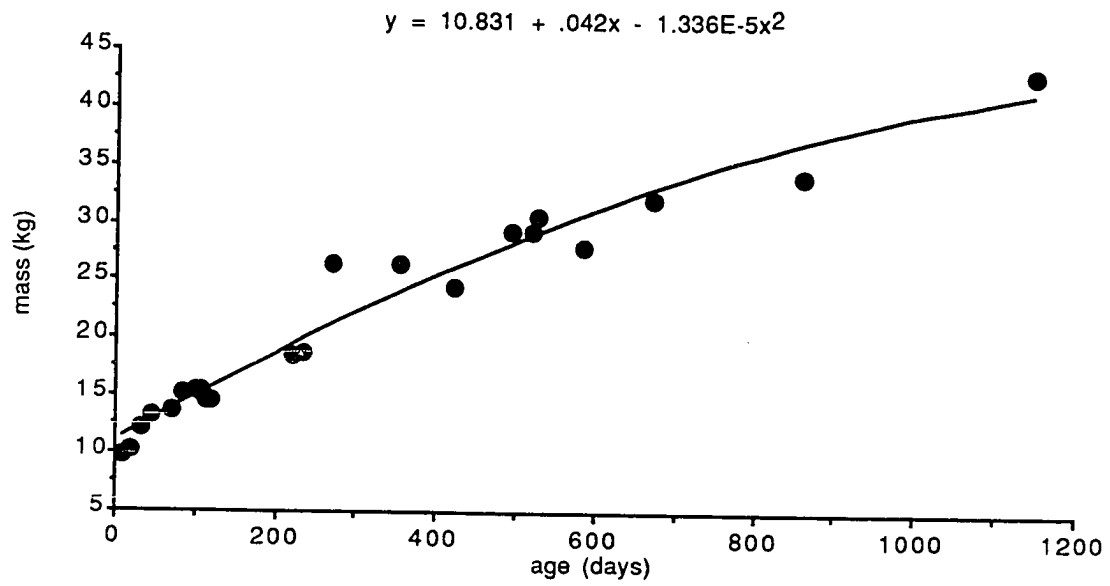
PUP 11 - FEMALE



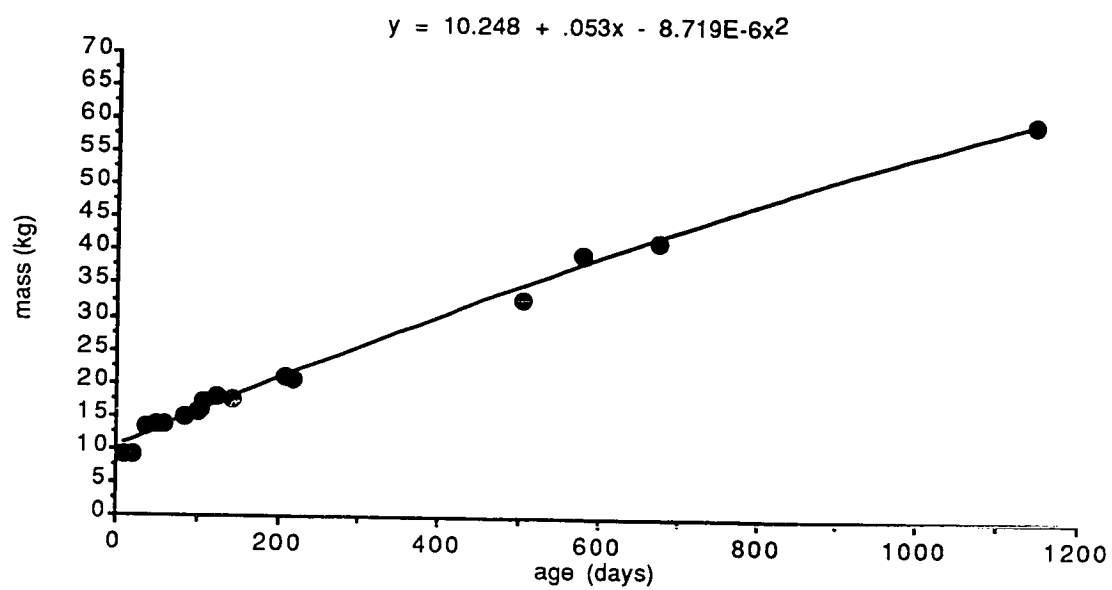
PUP 14 - MALE



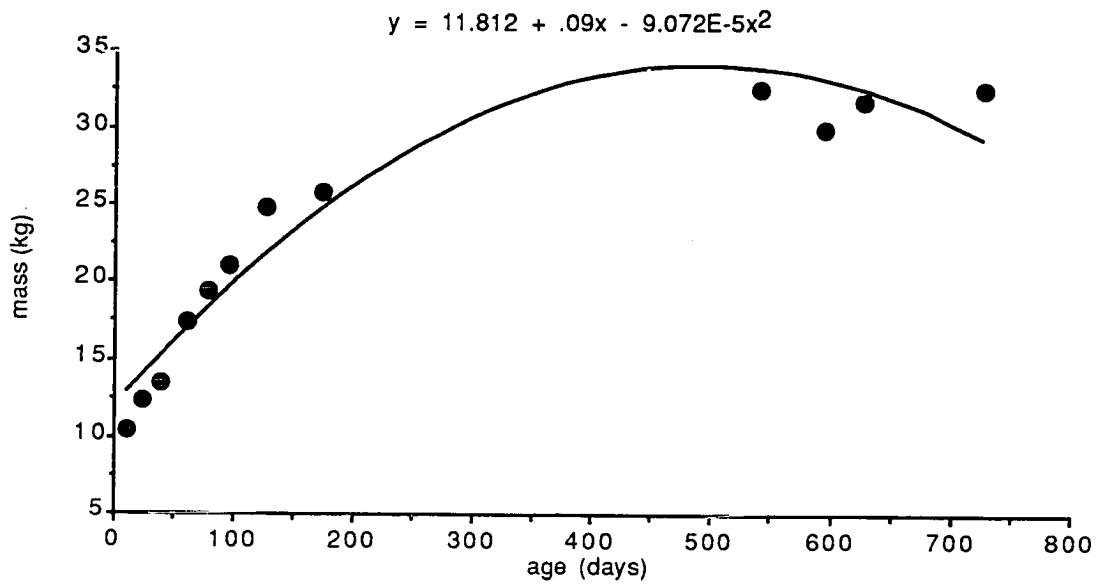
PUP 17 - FEMALE



PUP 18 - MALE



PUP 24 - FEMALE



PUP 51 - MALE

