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Research on elephant seals of Sea Lion Island: demography, socionomy and breeding biology

Preliminary report

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Introduction

We are carrying on a research project about sexual selection and breeding strategies in southern elephant seals (*Mirounga leonina*) using as main research site Sea Lion Island, a small island in the Falklands Island.

During our routine work we have collected a large amount of information about the demography, socionomy and breeding biology of the local population of Sea Lion Island. Due to the complete lack of published information about the elephant seals of the Falklands we think that our data should be useful in a broad sense. This report is a descriptive summary of these general findings.

Methods

Sea Lion Island (52° 26' S - 59° 05' W) has been selected because of it shelters a small isolated population of elephant seals: this represent an ideal situation to collect high resolution data about ecology and behaviour of individual animals.

The work has been carried on by four people (Dr. Filippo Galimberti and three assistant coming from the Dept. Of Animal Biology of the University of Rome and the Dept. Of Environmental Biology of the University of Milan) for the whole length of two elephant seals breeding season: we have actually worked for 84 days (September 4 to November 26 in 1995 and September 2 to November 24 in 1996) doing more than 8000 hours of field work.

All the breeding individuals have been marked: the main breeding males (44 in 1995 and 47 in 1996), all the males 5 years old and older appeared on the beaches for at least few hours, more than 500 females in each year, and all the pups. At the end of each breeding season we have also begun an intensive marking plan of young and subadult males coming to the beaches for molting. The marking has been accomplished by putting cattle tags (Jumbo Rototag - Dalton Supplies Ltd) on the interdigital web of the hind flippers: this is a well established marking methods for elephant seals [Testa & Rothery, 1992; Erickson et al., 1993 b]. To achieve good recognition of the animals during behavioural observations we have also marked the breeding males and most of the breeding females with names and identification numbers painted by hair dye or bleach.

Various techniques have been used to collect general data about the population demography and socionomy:

- daily counts of the animals in the main breeding areas, with recording of sex, age class and size
- daily census of the all the marked animals, with recording of position and breeding status and activity (in particular for newly arrived individuals)
- weakly counts of the animals along the whole perimeter of the island

To gather behavioural data we have carried observation period of standard length (more than two thousand and a half hours) recording:

- all male-male aggressive interactions
- all reproductive interactions and copulations
- rare events like arrival from sea of females, parturitions, departures

To study the structure and function of male vocal behaviour we have recorded male vocalizations using DAT recorders.

Due to the difficulties of direct measurement of very large animals to study size and facial morphology of breeding males we applied a photogrammetric technique.

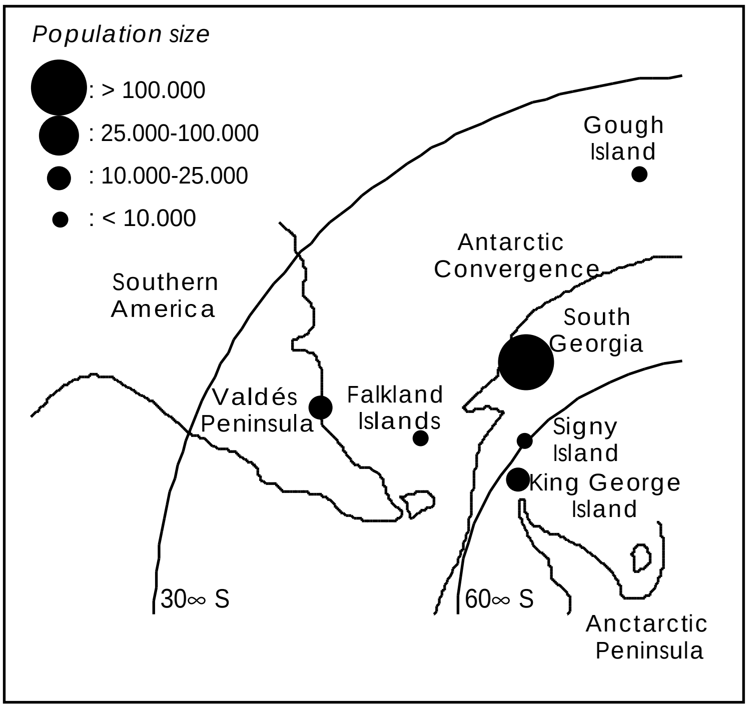
The weighing of pups has been carried on using an apparatus made by an especially designed weighing bag, a 500 kg digital dynamometer (C.A.M.I. Paviglianiti - Trezzano sul Naviglio (MI)- Italy) and a crane (OMCN - Villa di Serio (BG) - Italy).

We have also collected skin samples for DNA analysis from all the breeding males, a large number of females (almost all the females of six harems) and almost all the pups by using earpunch plyers.

Demography of Sea Lion Island population

The South Georgia breeding stock

The elephant seals population of the Falklands is a part of a larger breeding stock which comprises South Georgia, South Orkney Islands, King George Island, Gough Island and the Valdés Peninsula [Laws, 1994; Fig. 1]. The Falklands population could provide a link between the two larger populations of the breeding stock, the South Georgia and Valdés Peninsula ones, but is almost isolated from the other two populations during the breeding season.



Population	Lat.	Long.	Size	Source
Valdés Peninsula	42° - 43° S	63° - 64° W	36400	Falabella et al., 1993
Falkland Islands	51° - 53° S	57° - 62° W	17500	Strange, 1992
King George Is.	62° 16’ S	58° 37’ W	1960	Laws, 1994
Signy Island	60° 43’ S	45° 36’ W	20	Laws, 1994
South Georgia	54° 19’ S	36° 25’ W	357000	McCann, 1985
Gough Island	40° 20’ S	9° 54’ W	105	Bester, 1980

Fig. 1 & Tab. 1 - Position and approximate size of the populations of the South Georgia elephant seals breeding stock

The resight of marked individuals coming from the Valdés Peninsula and from South Georgia are restricted to the molting season [Lewis et al., in press]. During the two breeding season of our study on Sea Lion Island we haven't resighted any animals of other populations, with one exception: at the end of the 1995 breeding season we have resight a male marked in the Valdés Peninsula, but it was a juvenile male in molt.

Number of breeding females

Sea Lion Island seems to be the main breeding site for elephant seals in the Falkland Islands: preliminary data [Mike Bingham, pers. comm.] suggest that Sea Lion is the only conspicuous breeding site of this species in the Falklands, with more than 90% of the breeding females of the whole Falklands. Unfortunately the lack of a proper census of elephant seals along the Falklands coast in recent years hinder a more precise statement. It's quite difficult to determine directly the size of a breeding population of elephant seals (total number of breeding females) because of the pattern of arrival and departure of females during the three months of the breeding season [Erickson et al., 1993 a; Fig. 2].

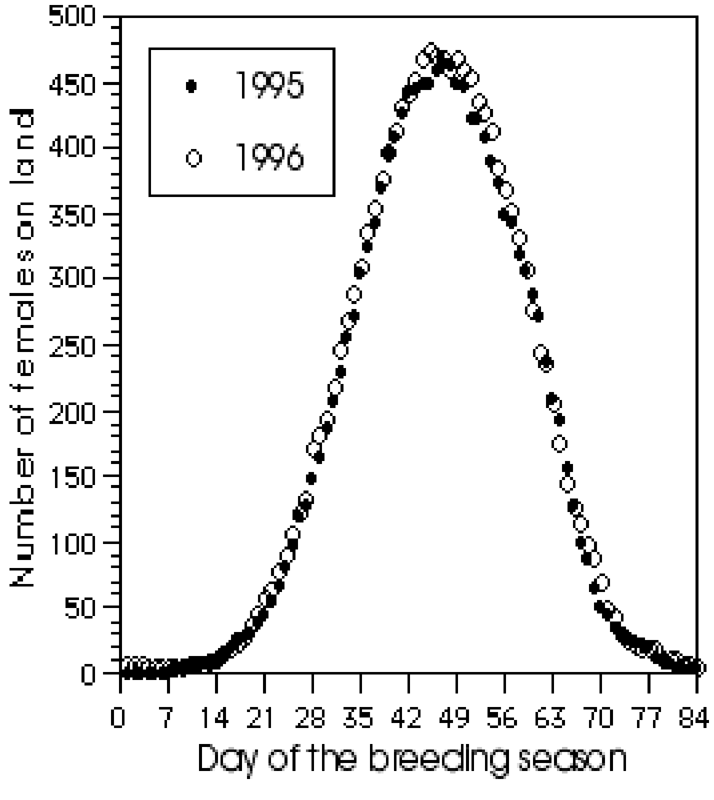


Fig. 2 - Number of females on land counted during daily census of Sea Lion Island breeding beaches during 1995 and 1996 breeding season

On Sea Lion Island the maximum number of females on land was 465 in 1995 and 467 in 1996, and it has been recorded the same day (October 20) in both seasons. This figure should represent about 90% of the number of females actually breeding in the population [McCann, 1985]. Thanks to the intensive tagging plan we can derive a direct estimate of the number of breeding females from the tagging records of females an their pups: the number of breeding females on

Sea Lion has been almost the same during the two breeding season (516 in 1995 and 518 in 1996): this figure agree with the estimate from the maximum number of females observed on the breeding beaches.

From daily counts we have derived a mathematical model of the percentage of females on the breeding beaches in each day of the season: this model is a simple gaussian model [Hindell & Burton, 1988] that fits the data much better than alternative models (eg. quadratic model: VanAarde, 1980 b). We have fitted the model first to 1995 data (r2 = 0.997) with free parameters, and we have checked it with 1996 data using the same set of parameters, with a very good result (r2 = 0.997). The fitted model was:

$$\%\ \text{Females on land} = 250\ \frac{1}{\sqrt{2\Pi}\ e^{-\frac{1}{2}\left(\frac{D-\mathbf{46.73}}{\mathbf{12.31}}\right)^{2}}}$$

We can conclude that the gaussian model is a very good model of the pattern of arrival and departure of females, and this seems a result of general interest because a simple model give a good description of a complex behavioural dynamics. The almost perfect symmetry of the variation of females on land in 1995 and 1996 is a demonstration of the present steady state of the population. The gaussian model is useful because it permits to standardize the irregular counts of females carried on before the beginning of our study, which are difficult to compare directly because they have been done in different moments of the breeding season, sometimes quite far away from the date of peak presence of females on land.

Year	**Census date**	**Count**	**Peak**	**Source**
1989	10 October	338	460	D. Gray
1990	16 October	444	464	D. Gray
1993	13 October	407	465	D. Gray
1995	20 October	465	465	this study
1996	20 October	465	465	this study

Tab. 2 - The available estimate of the size of Sea Lion Island population

Counts and corrected estimates of the maximum number of females on land, from a gaussian model of the variation of females on land during the breeding season.

By applying a correction from the mathematical model to the old censuses is possible to derive a picture of the dynamic of the population during the last years: the population seems to be almost steady, not increasing and not decreasing (Tab. 2).

The central part of the growth phase of the number of females on the beach is almost linear: by fitting a simple linear model to the number of females during day 21 to 42 of the breeding season (week IV-VI) is possible to get an estimate of the daily increase rate of females on the beaches [Nepomnaschy, 1994], and a similar decrease rate may be estimated from the number of females during day 49 to 70 (week VIII-X). For the 1995 breeding season the fit of the model is very good (increase: r2 = 0.995; decrease: r2 = 0.986): it gives an increase rate of 20.5 females/day (SE = 0.342) during the weeks IV-VI of the breeding season and a decrease rate of 20.6 females/day (SE = 0.571)during the weeks VIII-X: this means that the gaussian curve is almost symmetrical with a slightly faster decrease. The same apply for the 1996 breeding season.

The density of females on Sea Lion Island is quite low (111 females per km of coastline) if compared to the ones recorded in other subantarctic populations (Tab. 3).

Population	Density	Source
South Georgia	175-250	McCann, 1980
Kerguelen	400	Bester & Lenglart, 1982
	520	Van Aarde, 1980 b
Heard	2188	Carrick et al., 1962
Macquarie	1100	Carrick & Ingham, 1960
Valdés Peninsula	62	Baldi et al., 1996

Tab. 3 - Female density in various populations of southern elephant seal *Mirounga leonina*

The table contains the available data about female density (number of females per km of coastline) in elephant seal populations. Sometimes is not clear if the reported value refer to total coastline or just the portion of coastline suitable for elephant seals breeding.

Production and pup mortality

By tagging all the pups when they are yet with their mothers in the harems, and repeat the tagging them after weaning, we have been able to get an exact estimate of the net production of the breeding in each year.

In 1995 the gross production has been 517 pups (516 single birth and one twin birth) and the net production, at the end of the breeding season, has been 505 weanlings, with a preweaning mortality of 1.74% and a total mortality at the end of the breeding season of 2.32%. In 1995 the gross production has been 518 pups (all single birth) with a preweaning mortality of 1.54% and a total mortality at the end of the breeding season of 1.93%. These mortality figures are lower than the ones reported in literature (Tab. 4).

Population	Mortality	n	Source
South Georgia	4.5		McCann, 1985
Heard	5-10		Carrick et al., 1962
Macquarie	5-10		Carrick & Ingham, 1962
	5.8	3106	Hindell & Burton, 1987
Marion Island	6.0		Condy, 1977
Gough Island	4.1	225	Bester, 1980
Vadés Peninsula	3.5	3487	Baldi et al., 1996

Tab. 4 - Preweaning mortality in various populations of southern elephant seal *Mirounga leonina*

The table contains the available data about preweaning mortality (% pups died before weaning) in elephant seal populations; n = sample size.

In the northern elephant seal the very high mortality of pups (10-40%: LeBoeuf & Laws, 1994) is due to trampling and crushing by males during agonistic activities and starvation due to prolonged separation of the pup from the mother by effect of female aggression or male interference [LeBoeuf & Briggs, 1977; Riedman & LeBoeuf, 1982]; the same hold for high density elephant seals populations [Macquarie Island: Carrick & Ingham, 1960; Marion Island: Condy, 1979; South Georgia: McCann, 1982]. On Sea Lion Island we haven't done proper autopsy of dead pups but from visual inspection we haven't derived any indication of crushing by adult individuals. During thousands of hours of observation we have seen many short term separation of pups from the mother due mainly to male interference, but none of these has been definitive. The mortality was due in large part to stillbirths, again in analogy to what observed in the Valdés Peninsula [Baldi et al., 1996]. Sea Lion Island is a low density population characterized by medium sized harems and modest crowding: low mortality could hence be a result of the low level of agonistic activity between males and the low level of female aggression in the harems, in analogy to what happens in the Valdés Peninsula [Baldi et al., 1996]. The good production and low mortality of pups together are strong indicators of the healthy status of this population.

Size of the whole Falklands population

It's quite difficult to have a good estimate of the size of pinnipeds populations, because some of the individual will be at sea at any time. The most useful method to cope with this problem is to estimate the total production of pups and from this figure calculate the effective size of the population using information about age structure of the population, mainly from life tables [Eberhardt et al., 1979]. On the basis of published life tables for elephant seals [McCann, 1985] is possible to determine a 3.5 correction factor to calculate the number of individual of age 1 or older from the number of pups. The whole population of Sea Lion Island should be around 1800 individuals of age 1 or older. Without a proper census of the other breeding sites is not possible to give an estimate of the size of the whole Falklands population, but it should be much lower than the latest one found in literature [Strange, 1992].

Sex ratio

The sex ratio is an important parameter of the demography of a population, in particular for a species with an highly polygynous mating system and a strong tendency to have an highly unbalanced ratio of the adult individuals due to life history constraints [Laws, 1994].

From daily counts of the number of males and females on the breeding beaches we can derive a detailed picture of the variation of sex ratio during the breeding season: the various measurements of the sex ratio are the result of a demographic process (differential mortality of the two sexes) and of a social process (interference due to intermale competition for access to breeding females). The first process result in the adult sex ratio (ASR), which is the number of breeding females per male physiologically capable of reproduction (age 5 or older). On Sea Lion the ASR has a daily variation with a gaussian shape, symmetric to the variation of the number of females on land, and reach a maximum (11.5 females per male in 1995) just before the peak of the breeding season.

The social process is best represented by a series of measure, starting with the breeding sex ratio (BSR), which is the number of females per active breeding male. By active breeding male we mean the males which stay on the breeding beaches for prolonged times actively pursuing access to females. BSR has a daily variation analogous to the one of ASR and also reach a maximum (14.5 females per male in 1995) just before the peak of the season.

A more strict criterion to calculate the sex ratio of breeding females to breeding males is to include in the male just the alpha males, that is to say those males that, having control of an harem, have an unrestricted access to breeding females: this should be the best measure of the real sex ratio of breeding individuals in a polygynous species with an harem defense mating system. On Sea Lion Island the ratio of breeding females to alpha males reaches the maximum (46.9 females per male in 1995) just after the peak of the season (Fig. 3).

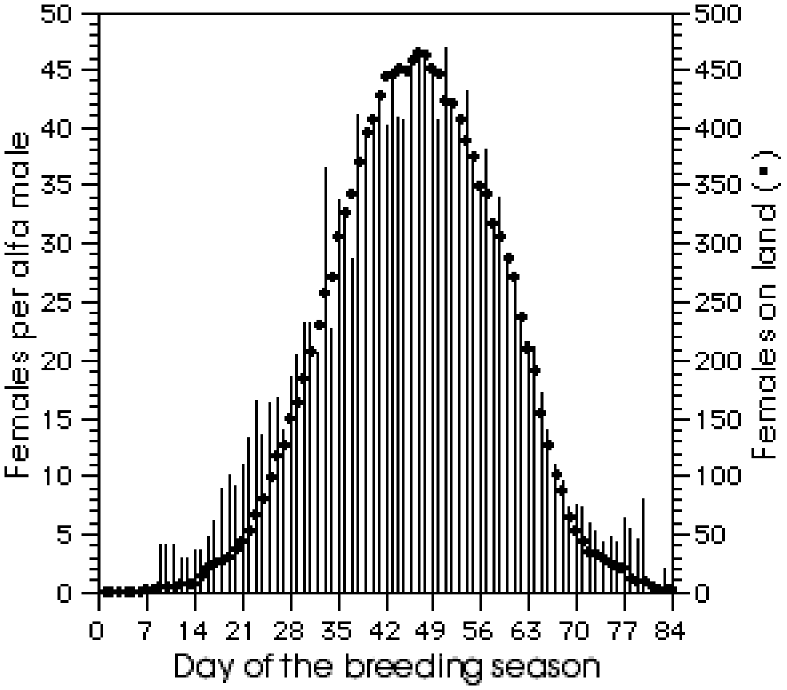


Fig. 3 - Mean daily number of females per alpha male during the 1995 breeding season, along with the number of females on land

Male age structure

We lack direct measurements of male age, but we may put males in age classes by mean of their morphology and external appearance (in particular of the frontal shield and proboscis): this kind of classification has been used successfully in the northern elephant seal [Deutsch et al., 1994] and seems to work quite well in the southern species. We have defined 8 age classes for males elephant seals: yearlings (Y), 1 year old; 2 years (2Y), 2 year old; juveniles (JUV), 3 years old; class 1 subadult (SAM1), 4 years old; class 2 subadult (SAM2), 5 years old; class 3 subadult (SAM3), 6 years old; class 4 subadult (SAM4), 7 years old; adult (8 years old or older).

There is a large variation in the timing of arrival on the breeding beaches of different age classes, and so the age structure of the population on land change a lot during the breeding season. There is a steady increase of the number of active males on land during the first month of the breeding: at the beginning of the fifth week of the season about 80% of the active males are on the beaches, and the daily variation of their number decrease sharply.

The pattern of arrival of males depends on their age: the first male who come to land are adult ones, or subadult of the older classes. Then there is a steady increase of subadult of the younger classes. During the last part of the season there is a rapid increase of younger animals: the most of them are 4 years old or younger, coming to beaches for molting. They not participate to the breeding activities and they tend to be spatially segregated from the breeding ares. The most peculiar pattern of this variation is the decrease of the relative number of adult males in the population: at peak breeding they represent less than 40% of the active males on land (Fig. 4).

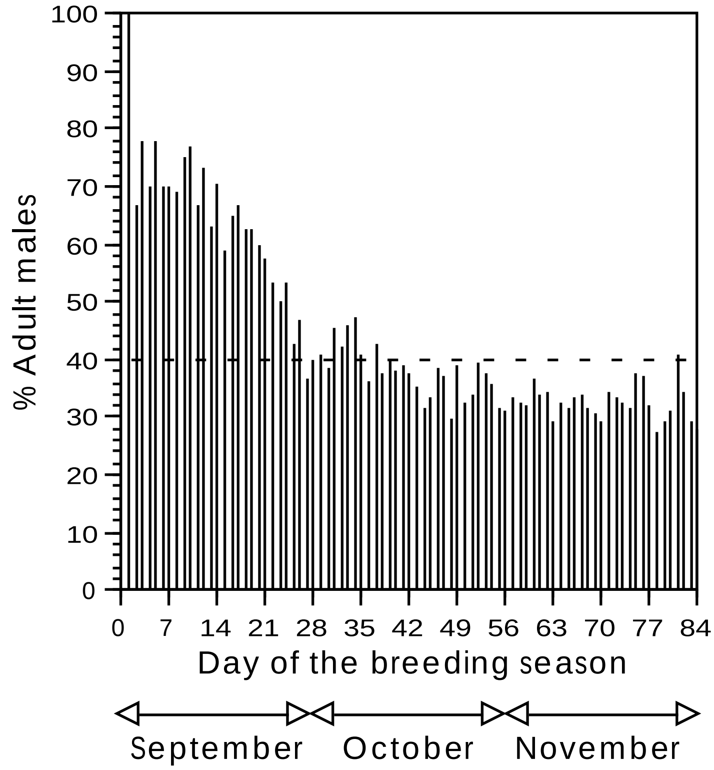


Fig. 4 - Daily percentage of adult males in the breeding population during the 1995 breeding season

The age structure of the breeding males has, as expected, an inverted pyramid shape: the most of the breeding males are adult ones, and then there is a decrease in the number of males going towards the younger age classes. Except from a reduction in the adult age classes, the age structure of breeding males is quite similar to the one recorded in the Valdés Peninsula population during 1993 and 1994 breeding season. This age structure is typical of an highly competitive mating system, in which older males tend to have an higher resource holding potential, and tend to keep younger individuals away from the breeding areas and from females.

Survival

67.4% (n = 516) of the breeding females tagged in 1995 have been observed on Sea Lion in 1996. Due to the fidelity to breeding site show by females of this species this should be considered a good estimate of the effective survival rate of females between breeding seasons. This estimate is obviously a crude one because it pool together females of different age class and doesn't take into account the tag loss rate. We have estimated tags loss rate by using double tagged individuals and applying a binomial model of tag loss [Eberhardt et al., 1979]; this procedure assume that the loss of each tag is an independent event and the probability of losing both tags is the square of the probability of losing one tag [Erickson et al., 1993 b]. the probability of lose a single tag is 0.164 and the probability of lose two tags is 0.027: the chance to lose two tags is low and so the lost of marked females should not change very much our estimate of survival of females between breeding seasons.

The estimate of survival of breeding males is better than the one for females because we have put three and sometimes four tags on breeding males in 1995 , and the small number of breeding males permits a very good check of each individual for sign of lost tags in the flippers: so we feel sure of the correct identification of returned breeding males.

50% (n = 44) of the breeding males survived until the next breeding season. This survival rate is similar to the one recorded in the Valdés Peninsula between 1993 and 1994 (48% - n = 52). A preliminary analysis revealed that he survival of breeding males is not correlated with their breeding effort: for 1995 breeding males (n = 44) a logistic regression analysis revealed no relationship between survival and three components of breeding success, number of females controlled during the season (R2 = 0.0209; LL = 0.6386; Chi-square = 1.277; p = 0.2584), mating per 100 hours (R2 = 0.0087; LL = 0.2650; Chi-square = 0.5299; p = 0.4664), number of females fertilized (R2 = 0.0076; LL = 0.2304; Chi-square = 0.4608; p = 0.4973).

Socionomy of Sea Lion Island population

Introduction

The social system of elephant seals populations is shaped by two factor: land breeding during a short breeding season and strong tendency of females to aggregate when on land. These two factors are common in land breeding pinnipeds and result in an high level of polygyny [Bartholomew, 1970]. Two additional factors should be considered when dealing with elephant seals: the low mobility of females on land and enormous sexual dimorphism [LeBoeuf & Laws, 1994 b]. All these factors result is a mating system based on harem formation: females aggregate in large groups, each one defended by a single male (the alpha male or harem master) with exclusive (or almost exclusive) access to breeding females of the harem. This mating system permits the achievement of the highest level of polygyny recorded in mammals [LeBoeuf & Reiter, 1988]

The stability of harems in both space and time is the result of the strong tendency of females to aggregate and of the reduction of movements after parturition. The grouping of females is an autocatalitic process: the increase in size of an harem make it much more visible and more attractive for females, and that favor the increase in size.

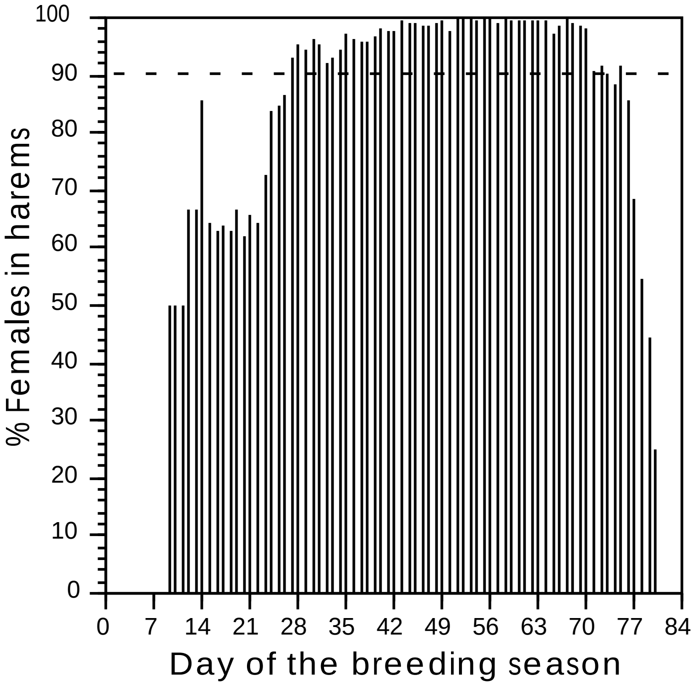


Fig. 5 - Percentage of females grouped in harems during the 1995 breeding season

The graph depicts the percentage of harem female (both pregnant and with pup) each day of breeding season. During the central phase of the season more than 90% of the females are found inside harems, e this figure rise close 100% in most of the days.

The percentage of females in harems is higher than 90% for the most of the breeding season (Fig. 5), and isolated pupping is very unusual (a single case in 1996, with death of the pup). So breeding in an harem is an almost obliged component of female breeding strategies in this species. The structure of the mating systems depends on local demography, which defines the basal level of polygyny, and on the intensity and result of intermale competition, which defines the realized level of polygyny. We call the sum of demographic and social factors is socionomy of the population.

Stability of the social system

There is a low change of the breeding males system across breeding seasons. 66.0 % (n = 47) of the breeding males of the 1996 breeding season have been marked as resident males in 1995; 34.0 % of the breeding males have been breeding males during the previous season. This is a much higher rate of return than the one recorded in the Valdés Peninsula (40.0 % and 15.0 % respectively - n = 60 males). The difference between the return rate of the two populations is significant (Fisher Exact Test: p = 0.0111 including all the resident males of the previous season, breeding and non breeding; and p = 0.0370 including only the males already breeding in the previous season). Sea Lion Island is a small island who shelter a small local population of elephant seals; preliminary data show that there is very few breeding of elephant seals in the rest of the Falklands: so breeding males should have less opportunity to roam around than in the Valdés or in other large populations. This reduction in opportunities should determine a greater stability of the social system. This low level of change of males could be one of the reason of the higher stability and lower aggressive interaction rate we have observed on Sea Lion if compared to Punta Delgada (Valdés Peninsula): the interaction rate at Punta Delgada (8.6 interactions/hour - n = 3176 interactions - in 1993 and 9.5 interactions/hour - n = 5157 interactions - in 1994) is about two times the one recorded on Sea Lion (4.3 interactions/hour - n = 5419 interactions - in 1995).

Spatial distribution of harems

On Sea Lion Island the settlement of females is uneven and the distribution of harem is irregular: all the breeding activities happen on the sandy beaches at the eastern tip of the island (Fig. 6). The same preference for sandy beaches has been recorded in the Valdés Peninsula and has been correlated with thermoregulatory behaviour: the climate of the Valdés Peninsula implies a huge thermal stress for breeding animals and sand facilitate thermoregulation by flippering [Campagna & Lewis, 1993]. The climate of Sea Lion Island render less likely the thermoregulation hypothesis: the restriction of breeding to sandy beaches could depend upon the easy of access, because their modest slope facilitate the haul-out of pregnant females [Bester, 1980].

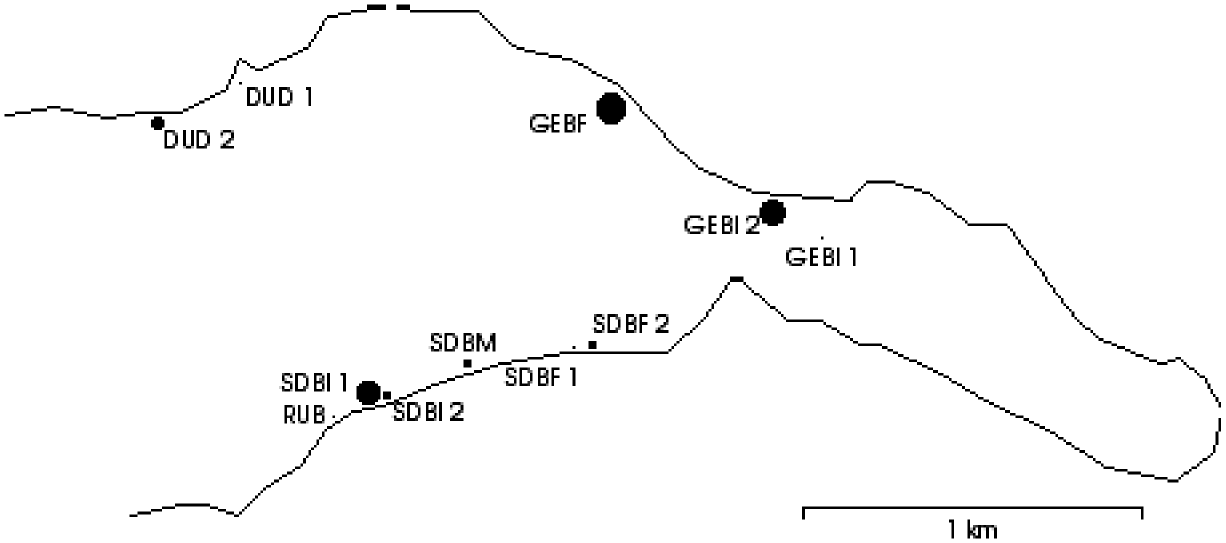


Fig. 6 - Sketch map of the harems on Sea Lion Island

The map depicts the spatial distribution of harems on Sea Lion Island during 1995 breeding season (derived from 1:50000 Falkland Islands map sheet 29; positions calculated at peak breeding with a commercial GPS system). The size of each dots is proportional to the number of females in the harem at peek breeding.

The distribution of harems show a little variation between breeding season on large scale, apart from two aspect : creation of small new harems in previously unused areas and hundred meters scale variation of the initial site of the harem . The fidelity of individual females to pupping sites is very high on large scale but may be quite low on a finer one: in elephant seals there is a strong relationship between prepartum movements and male interference [Carricks et al., 1962; Bester, 1980] and so the settlement of females depends non only on preferences at arrival but also on interaction with males in arrival phase.

We have tried to measure fidelity on individual females by examining their settlement for parturition at three levels: breeding zone (a side of the island, on or more kilometer long, separated form other zones by large part of coast unsuitable for elephant seals breeding), breeding area (a beach or well defined part of a beach, well connected with other areas of the same zone), and harem. Movements of both males and females (before parturition) are limited between breeding zones but quite common between breeding areas and harems. Fidelity is high at zone level: 71.3% (n = 348) of females tagged in 1995 have come back to the same zone for breeding; fidelity decrease at area level, with 42.0% of females breeding in the same area in both seasons; fidelity is also quite low at harem level, with 38.6% of females breeding in the same harem, 55.0% of females breeding in another harem already present in the previous season and 5.8% of females breeding in new harems (Fig. 7).

Fidelity to breeding site of individual females across seasons is high on kilometer scale but quite low at hundred meter scale: any case it's quite remarkable that more than 1/3 of females came back to exactly the same harem for breeding.

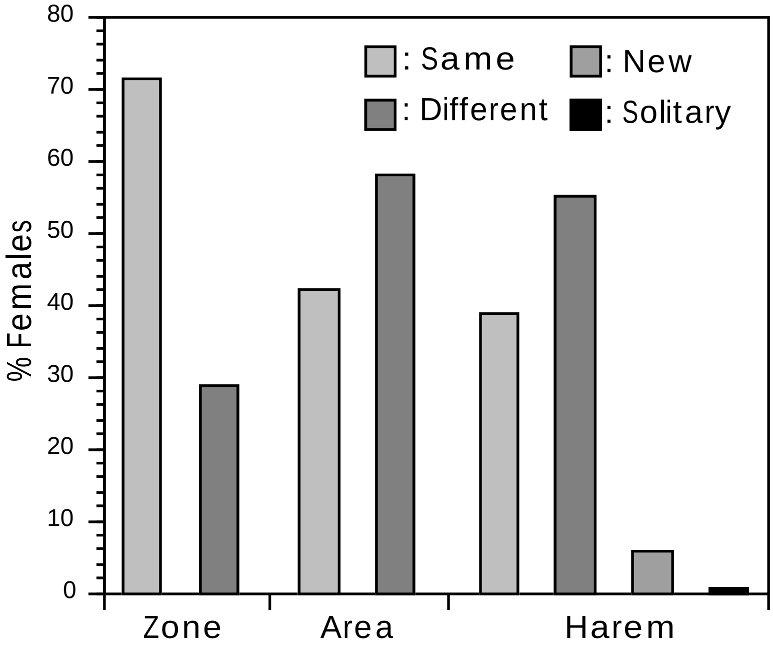


Fig. 7 - Fidelity of females to breeding site at various scale

The graph depicts the percentage of females tagged in 1995 that came back to the same or a different zone, area and harem in 1996. In 1996 some females have settled in 1996 in harems not present in 1995, and two of them have been solitary for the most of their permanence on land.

Timing of harems formation

Different harems have different timing of formation and disappearance. The median day of formation has been day 20 (23-09) of the breeding season in 1995 (MAD = 6 days; n = 10) and day 23 (24-09) in 1996 (MAD = 6 days; n = 11), but on of the harems has begun as late as day 40 in 1995 and day 35 in 1996, almost at mid season.

There is less variation in harem disappearance: the median day of end has been day 75 (17-11) of the breeding season in 1995 (MAD = 4 days) and day 73 (13-11) in 1996 (MAD = 3 days). Late forming harems tend to disappear at about the same time of early forming ones. The result is a variation in lifetime of harems: the median lifetime of harems has been 53 days (MAD = 4.5) in 1995 and 57 days (MAD = 4.0) into 1996. These figures are smaller than the one recorded in the Valdès Peninsula in 1994 (median = 63 days; MAD = 4; n = 11): this result agree with a general impression of a more concentrated breeding season on Sea Lion.

There is a general relationship between the date of formation of an harem and its size (Fig. 8), with an early beginning for larger harems (1995: rho = 0.742; n = 11; p = 0.0261 - 1996: rho = 0.703; n = 10; p = 0.0262), but this relationship is not an absolute one, and also late forming harem may achieve a mid range size (eg. a late forming harem in 1995 has grown up to 54 females at peak breeding).

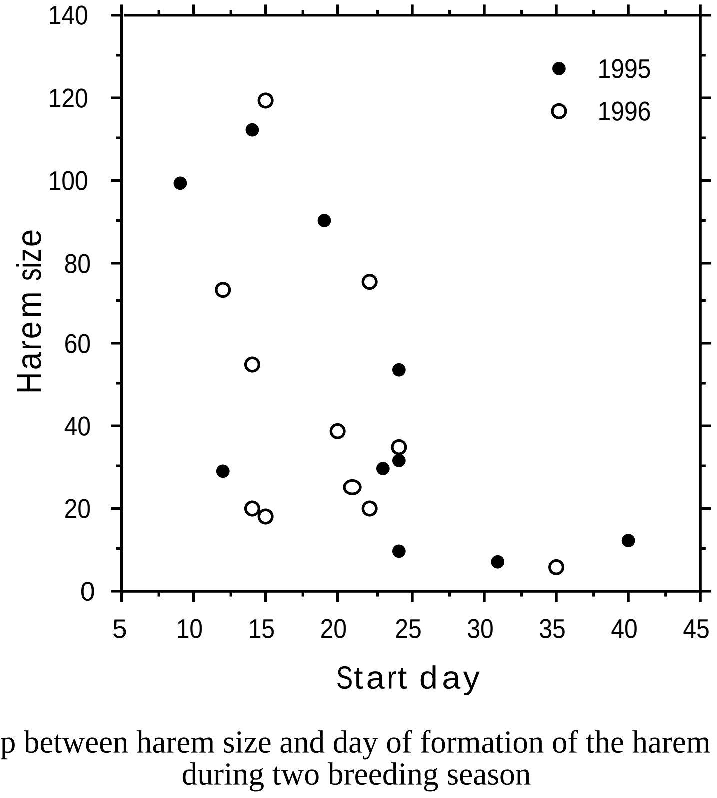


Fig. 8 - Relationship between harem size and day of formation of the harem on Sea Lion Island during two breeding season

The variation in the timing of different harems has a deep effect on male mating strategies: males excluded from the control of harems at the beginning of the season have additional opportunity to get control of late harems. These means that the most powerful males will get control of the early harems, which are usually but not always the larger ones, but later in the season new opportunities will be available for less powerful males. Sometimes late harems will grow up to a large size giving a good breeding opportunity to secondary males; in at least one case a late harem has become larger than an early adjacent one (75 females vs 55 females). This process reduce the strength of the link between male phenotypic qualities and access to females, reducing the opportunity for sexual selection to operate.

Harem size

The single most important component of socionomy is harem size, which measures the tendency of females to breed in an aggregated social system. We define harem size as the maximum number of females counted in an harem during the daily census; it represent about 90% of the number of females that actually breed in the harem.

Population	**BSR**	**Harem size**	**Source**
Iles Crozet	18.3	45.4	Barrat & Mougin,1978
Gough Island	3.1	10.7	Bester, 1980
Heard Island	12.2	45	Gibbney, 1957
Iles Kerguelen	11.4	55.7 (r = 180)	Angot, 1954
	11.4	-	Pascal, 1979
	15.2	102.3 (r = 1345)	Van Aarde, 1980
King George Island	-	63 (m = 190)	Vergani, 1985
Macquarie Island	11	277 (m = 1000)	Carrick et al., 1962
	12.8	-	Hindell & Burton, 1987
Marion Island	11	15.3	Condy, 1977
Signy Island	2	12	Laws, 1960
South Georgia	13	24-52	Laws, 1953; Laws,1960
	9.2	74.2 (r = 224)	McCann, 1980
Valdés Peninsula	7.5	11 (r = 120)	Campagna & Lewis, 1992
Punta Delgada	-	47 (r = 144)	Nepomnaschy, 1994

Tab. 5 - Breeding sex ratio and harem size in various populations of southern elephant seal *Mirounga leonina*

The table contains the available data about breeding sex ratio (BRS) and harem size (mean or median) in elephant seal populations; when available also maximum harem size (m) and range of harem size (r) are reported. For the Valdés Peninsula two values are reported: the first one regards the whole population and the second one a small piece of coast around Punta Delgada, which the area of highest density in the Peninsula.

On Sea Lion median harem size was similar in 1995 (31; MAD = 22; n = 11) and in 1996 (35; MAD = 17; n = 10). The harem size recorded at Sea Lion is smaller than the ones recorded at Punta Delgada - Valdés Peninsula (med. = 47), and also much smaller than the mean harem size reported for South Georgia by McCann (1980) (mean = 74.2) and the majority of other population of southern elephant seals (Tab. 5; Fig. 9), but is larger than the median harem size of 11 females calculated for the whole Valdés Peninsula population [Campagna & Lewis, 1993]. The intraseasonal variation of the harem size is large (1995: range = 7-112; 1996: range = 6-119): this is the first indicator of the huge variation in breeding performance between the males who are able to maintain control of a harem.

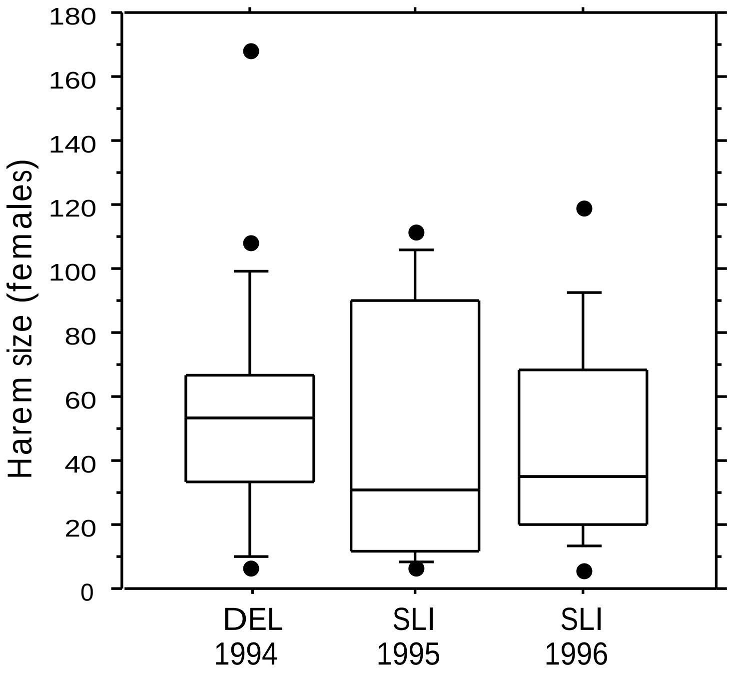


Fig. 9 - Boxplots of harem size during 1994 breeding season at Punta Delgada (Valdés Peninsula) and on Sea Lion Island (Falkland Islands)

This variation in size of harems is on the main source of variance in mating success, and hence of potential for sexual selection. The variability of harem size is slightly larger on Sea Lion than at Punta Delgada (CV = 0.777 vs 0.685), but the difference is not statistically significant.

Social and behavioural effects of harems structure

The first correlate of harem structure should be the level of competition: the mating system elephant seals is an overcompetitive one, with the most of the breeding males excluded from direct control of females. These peripheral males usually assemble around the larger harems, and so we expect a positive relationship between competition pressure and harem size. In fact an index of potential level of competition calculated from the daily number of secondary males associated to each harems has a strong correlation with harem size (rho = 0.838; n = 21; p = 0.0002 - Fig. 10). This relationship is almost linear (82% of variance explained by the linear component) and similar to the one found for the Punta Delgada population (rho = 0.870; n = 24; $p < 0.0001$). The linearity of this relationship is important because it implies a gradual increase in costs of defense with the increase of benefits due to access to a larger number of breeding females.

The competitive interaction rate (interactions per observation period) has a wide variation between harems, with median values ranging from 1 to 18. There is a strong positive relationship between median interaction rate and harem size (rho = 0.889; n = 11 harems; p =

0.0049), but the relationship is not linear: for harems up to about 60 females of size the interaction rate is low and grows slowly, while for larger harem the increase in interaction rate with size of the harem is sharp. This two speed process implies an increase of cost of defense more than proportional for very large harems: only large, adult, experienced males are able to manage this level of competition pressure.

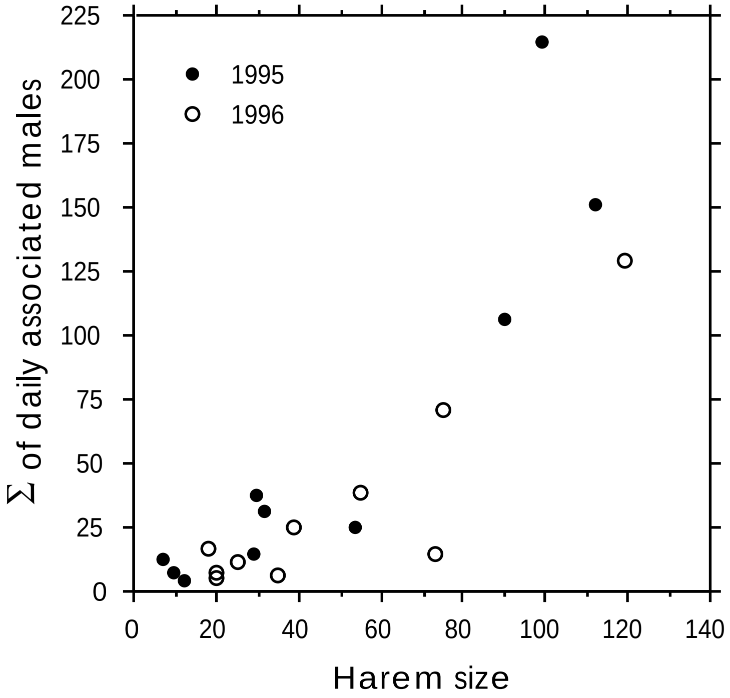


Fig. 10 - Competition pressure and harem size on Sea Lion Island

The graph depicts the relationship between and index of competition pressure, the sum of the daily number of male associated to an harem, and harem size for two breeding season, 1995 and 1996.

Basic aspects of breeding biology

Timing of the breeding season

Reproduction in elephant seals happens during a fixed three months period during which females comes to land to give birth, suck their pup and mate. Timing of breeding in Pinnipeds is regulated by photoperiodic control [Boyd, 1991] and this implies both a strict succession of events during the season and a clinal variation of the beginning of the season related to the geographic position of the population.

Population	Lat.	Long.	Dist.	Peak	Source
Peninsula Valdés	42° - 43° S	63° - 64° W		02-10	unpublished data
Falkland Islands	51° - 53° S	57° - 62° W		20-10	this study
King Goerge Is.	62° 16’ S	58° 37’ W	- 460	25-10	Muller-Schwarze et al., 1978
Signy Island	60° 43’ S	45° 36’ W	- 400	22-10	Laws, 1956 b
South Georgia	54° 19’ S	36° 25’ W	- 240	25-10	McCann, 1985
Heard Island	53° 00’ S	73° 30’ E	- 320	18-10	Carrick et al., 1962 b
Kerguelen	49° 21’ S	70° 12’ E	0	15-10	Van Aarde, 1980 a
Macquarie Is.	54° 29’ S	157° 00’ E	+ 160	16-10	Carrick et al., 1962 b
Marion Is.	46° 55’ S	37° 45’ E	+ 290	17-10	Condy, 1979
Crozet	46° 25’ S	51° 45’ E	+ 320	16-10	Barrat & Mougin, 1978
Campbell Is.	52° 33’ S	169° 09’ E	+ 800	16-10	Sorensen, 1950

Tab. 6 - Geographical position and timing of reproduction in some populations of southern elephant seal Mirounga leonina

The table present the available information about date of peak breeding in various elephant seals population; Dist. Is the estimated distance from Antarctic Convergence (-: south, +: north).

Peak presence of females on land has been recorded on October 20 in both seasons. There is a clinal variation of the day of peek breeding in the various population of elephant seals: the timing of the breeding on Sea Lion seems in good accordance with this cline [Campagna & Lewis, 1993; Tab. 6].

On Sea Lion Island females begin to come to land during the second week of September; in 1996 we have recorded an early arrival of two females: they have been on the beach for a few days before disappearing for a while and come again later to give birth. We have recorded the first birth on September 11 in 1995 and September 17 in 1996. The last departure of females was on December 3 in 1995 and November 27 in 1996: the very late departure in 1995 was due to a isolated female with an unusual breeding pattern (the same female has come back in 1996 and has shown a more standard timing of the breeding).

Female breeding

The timing of female reproduction in land breeding pinnipeds is usually very regular, and elephants are non exception. The typical female come to land a few days before parturition, then give birth, suck the pup for about three weeks, mate one or more time during a couple of days, and then come back to sea.

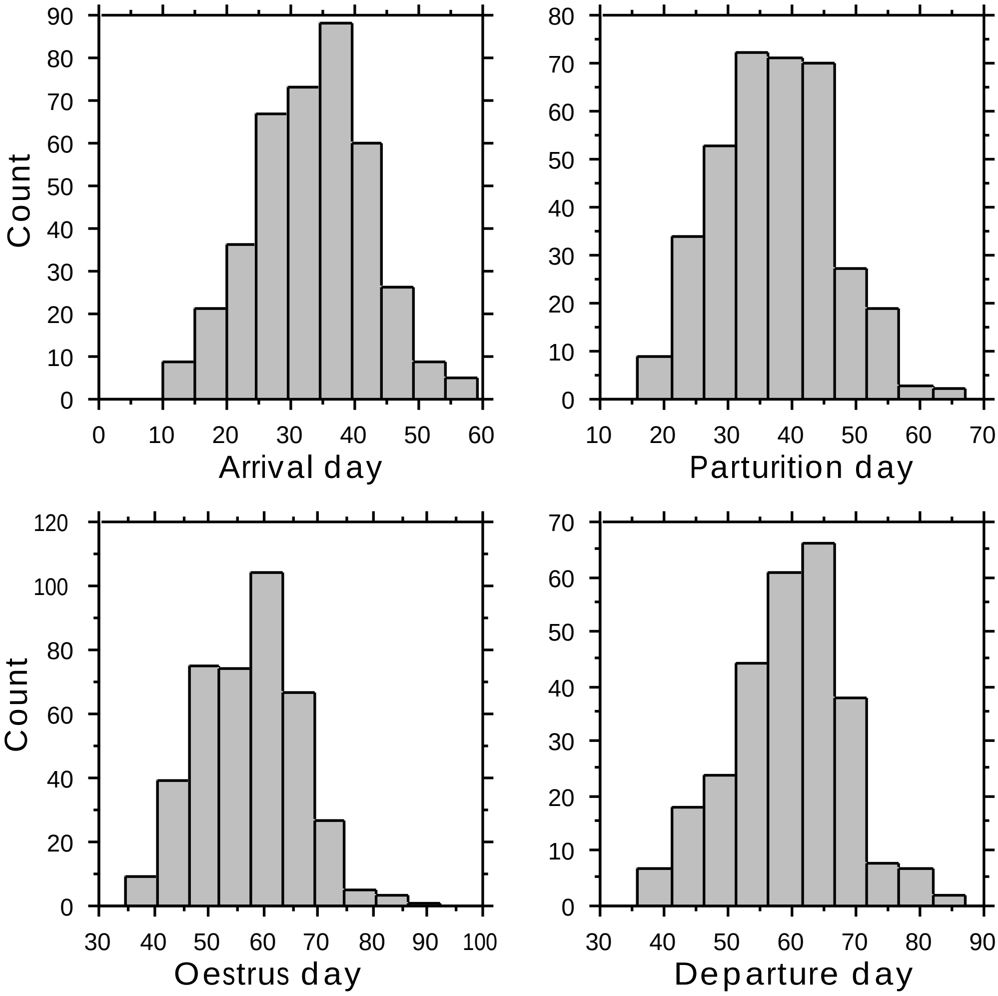


Fig. 11 - Distribution of day (calculated from the beginning of the breeding season) of various breeding events of samples of female elephant seals *Mirounga leonina*

The timing of breeding is very similar across seasons. Median arrival date was October 5 in both 1995 (MAD = 7 days; n = 223 females) and in 1996 (MAD = 6 days; n = 394 females). Parturition is almost as regular as arrival, and median date was October 12 in 1995 (MAD = 7 days; n = 137) and October 10 in 1996 (MAD = 6 days; n = 406). More variable was departure date, with a median on November 6 in 1995 (MAD = 6 days; n = 107) on November 1 in 1996 (MAD = 6 days; n = 275): this difference confirm our impression of a delay in the end of the 1995 breeding season due to the unusual late arrival of few females, who have been on land until the first days of December. Due to the regular timing of parturition and the well defined delay between parturition and oestrus the distribution of days on oestrus is very similar across breeding seasons, with a median date on October 28 in 1995 (MAD = 6 days; n = 298) and on October 29 in 1996 (MAD = 6 days; n = 404). This regularity has a should have a deep effect on male breeding: the distribution of oestrus females is not only quite predictable in space but also very predictable in time.

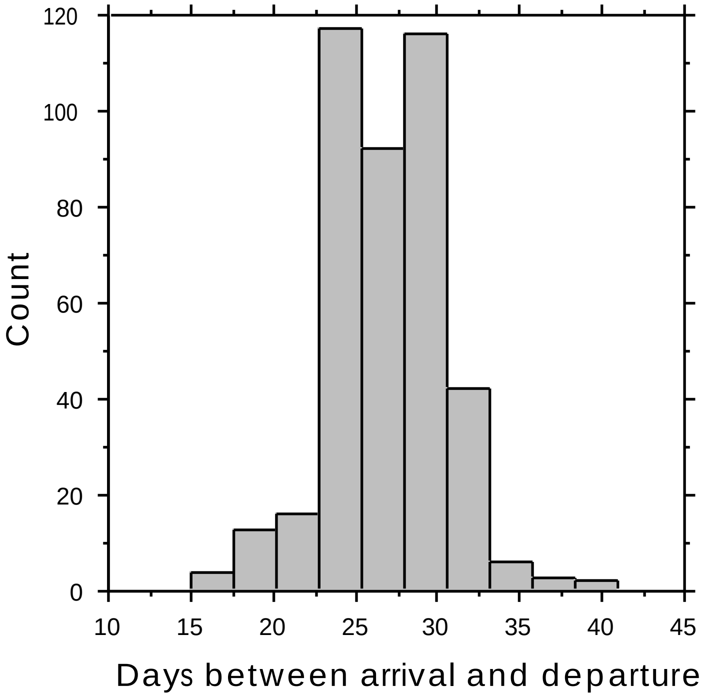


Fig. 12 - Distribution of the number of days between arrival and departure of female elephant seals *Mirounga leonina* (n = 411 females)

The timing between breeding events for each female is also quite regular, except from the delay between arrival and parturition. The number of day before parturition has a median value of 5 days (MAD = 2 days) in both 1995 (n = 204) and 1996 (n = 395), but the variation of this parameter is large (up to CV = 4.446 in 1996).

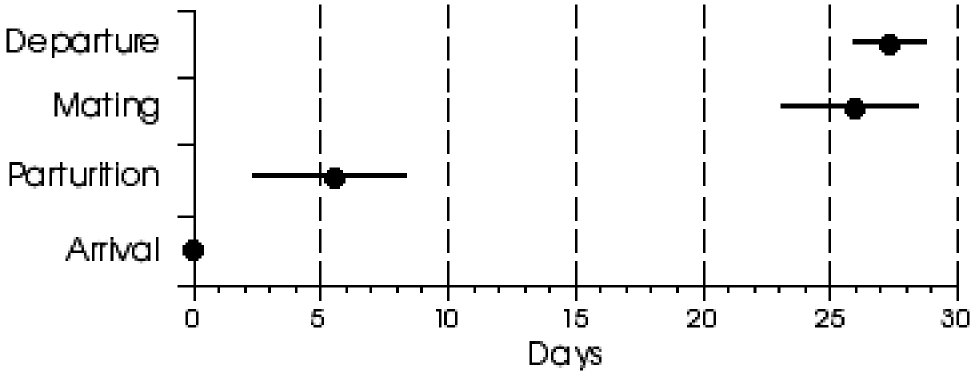


Fig. 13 - Diagram of the timing of female breeding in southern elephant seal
The diagram depicts median (point) and MAD (lines) of the number of days between breeding events for a large sample of females of the 1995 breeding season

On the contrary the total time spent on land (arrival to departure - Fig. 12) is very similar between females (CV = 0.122 - n = 212 in 1995 and 0.151 - n = 414 in 1996) with a median value of 27 days (MAD = 2 days) in both years. Also the interval between parturition and beginning of oestrus (first non protested mating) is regular (CV = 0.123 - n = 116 in 1995 and 0.321 - n = 238 in 1996) with a median value of 20 days (MAD = 2 days) in both years. This regularity of interval between parturition and oestrus has an important effect on the mating system, promoting synchronization of female mating, and has also a practical value because it let us derive an estimate of oestrus by the observed date of parturition.

The figures we have calculated for the timing of reproduction on Sea Lion are in accordance with the ones calculated for the Valdés Peninsula [Baldi et al., 1996]. The main difference between the two population is the concentration of the breeding season in a slightly shorter interval on Sea Lion Island.

• *Female phenotype and timing of reproduction*

There are preliminary evidences that the timing of reproduction depends in part from aspects of female phenotype, size in particular. We have divided female in many different size classes, and by repeated comparison and cross observer judgment we have been to achieve a coherent classification of female size. For analysis we lumped size subclasses in three main ones (small, medium, large), in analogy with other studies on elephant seals [Campagna et al., 1992]. One female who had an unusually long presence on land, due to the adoption of an already weaned pup, has been excluded from the analysis.

Small females tend to arrive earlier than large females (median arrival day = 29 vs 34), with medium ones close to the large ones (33); notwithstanding the large variation inside each classes (CV > 0.2) the difference is significant (Kruskal-Wallis Test: H = 11.785; df = 2; p = 0.0028). Small females tend also to give birth earlier than large females (median parturition day = 34 vs 40), and again the difference is statistically significant (Kruskal-Wallis Test: H = 15.022; df = 2; p = 0.0005 - Fig. 14).

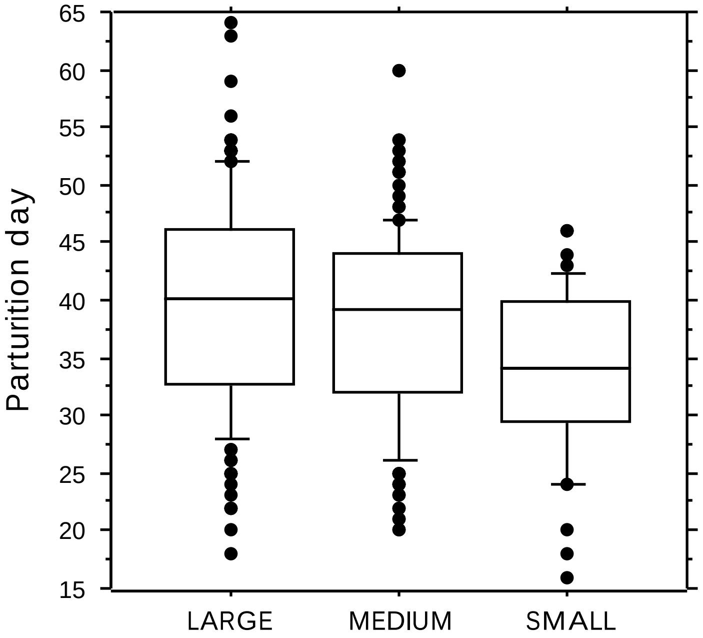


Fig. 14 - Distribution of parturition day by size class of female elephant seals during the 1996 breeding season

The most important factor of timing of breeding from a functional point of view are time spent on land,which, for fasting animals, will be correlated to total energy expenditure during the breeding season, and the number of days of suckling of the pup, which should be a rough measure of breeding effort, or, at least, an important component of it.

Small and medium female spent a median number of days on land lower than large ones (27 days vs 29 days), and the relative variation is similar for all classes; the difference between large and pooled small and medium is significant (U = 18303; n = 151, 184; p<0.0001).

Small and medium female spent a lower median number of days suckling the pup than large ones (21 days vs 23 days); the relative variation is again similar for all classes (CV = 0.07-0.09); the difference between large and pooled small and medium is again significant (U = 18910; n = 151, 186; p < 0.0001 - Fig. 15).

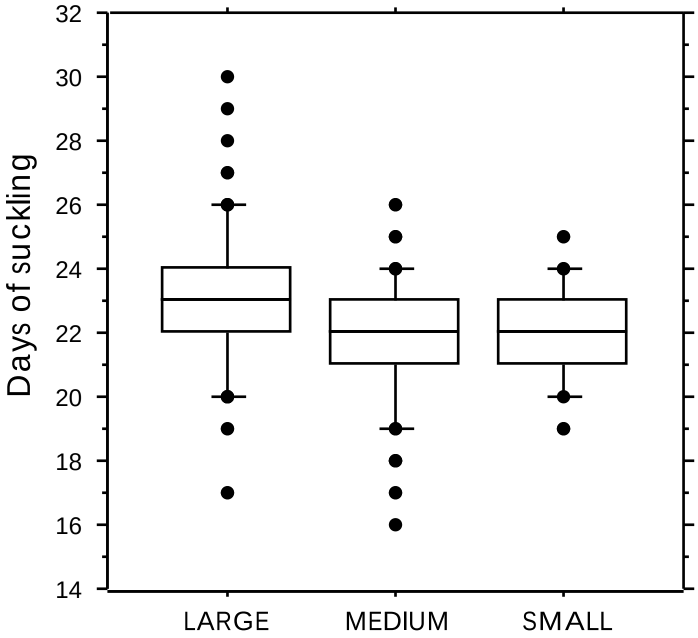


Fig. 15 - Distribution of the number of days of suckling by size class of female elephant seals during the 1996 breeding season

Large females seems to able to stay on land longer and to suckle the pup for more days than smaller ones. Due to the heavy cost of suckling the pup [Deutsch et al., 1994], and the high energy transfer rate between mother and pup achieved in elephant seals [Costa et al., 1986], also one day more of suckling may have an impact on female energy consumption and weaning weight of the pup. The indirect determination of female size suggest us to consider these results very preliminary, although suggestive.

- *Sex ratio at weaning*

Due to the low preweaning mortality and the low chance of differential mortality between sexes until weaning the weaning sex ratio is a very good indicator of sex ratio at birth. In both years of our study we have found a sex ratio slightly biased toward males (0.86 females per male in 1995 - n = 439, and 0.84 in 1996 - n = 453), but the difference from an equal sex ratio is non significant in both years (1995: Chi-square = 2.48; df = 1; p > 0.10 - 1996: Chi-square = 3.36; df = 1; p = 0.07). The slight bias toward males at birth is common to the majority of elephant seals population, with values ranging from 0.82 on South Georgia [Laws, 1953 b] to 0.90 on Heard Island [Carrick & Ingham, 1962 b]. In all cases the deviation from parity is non significant despite the large sample sizes.

• *Weight at weaning*

During the 1996 breeding season we have carried on a plan of measurements of body weight of the weanlings, with two main target:

◊ gather a preliminary estimate of the weight at weaning time for pups of two sexes, to see how it compares with the one recorded in adjacent populations and to check for presence of sexual dimorphism at weaning

◊ apply the weighing technique to a sample of pups to verify the feasibility of an intensive weighing plan of whole cohorts of pups, a prerequisite for a detailed study of female breeding strategies.

Due to a large variation in the interval between weaning and weighing of different pups we have corrected the observed weight by the weight lost between weaning and weighing. We have estimated the loss by the product of the number of days between weaning and weighing and a sex and week dependent correction factor ranging from 0.78 to 1.02 kg lost per day [Campagna et al., 1992].

The distribution of weights is almost normal ($g1 = 0.003$; $g2 = -0.220$), as usually found for morphometric variables, with a mean weight of 133.6 kg (SD = 22.0 kg; CV = 0.165).

There is a modest sexual dimorphism at weaning in favor of males (Males: 135.4 ± 21.6; Females: 132.0 ± 23.3), but the difference is not statistically significant ($t = -0.688$; $df = 89$; $p = 0.4931$).

The weights recorded on Sea Lion are similar to the ones reported for the Valdés Peninsula and somehow larger than the ones reported for South Georgia (Tab. 7). The results about weanling weights agree with the general picture of an healthy population of elephant seals.

Population	**Weight**	**Weight (MM)**	**Weight (FF)**	**Source**
South Georgia		119 ± 15 (23)	112 ± 21 (24)	McCann et al., 1989
	121 ± 25 (30)	124 ± 28 (14)	117 ± 23 (16)	Fedak et al., 1994
Macquarie	134			Bryden, 1969
Vadés Peninsula		131.5 ± 22.4 (52)	131.4 ± 18.3 (38)	Campagna et al., 1992

Tab. 7 - Weanligs weight in various populations of southern elephant seal *Mirounga leonina*

Weight at weaning is in part related to the number of the duration of suckling: the number of days between birth and weaning has a positive correlation to weanlings weight ($r = 0.3564$; $n = 77$; $p = 0.0016$).

Male breeding

The number of days a male spent on land is an important part of his breeding effort because males fast while on land, and so staying on land implies large energetic cost and requires large energetic reserves. The first males come on land at the very beginning of the breeding season, during the first week of September, before the haoul-out of the first female. Some of the breeding males stay on land for the whole breeding season, fasting for as much as three months.

The timing of breeding in males is much less regular than the one of females. There is a very large variation in the arrival date and number of days that different males spent on land, and this variation is related to age class and breeding status of the male.

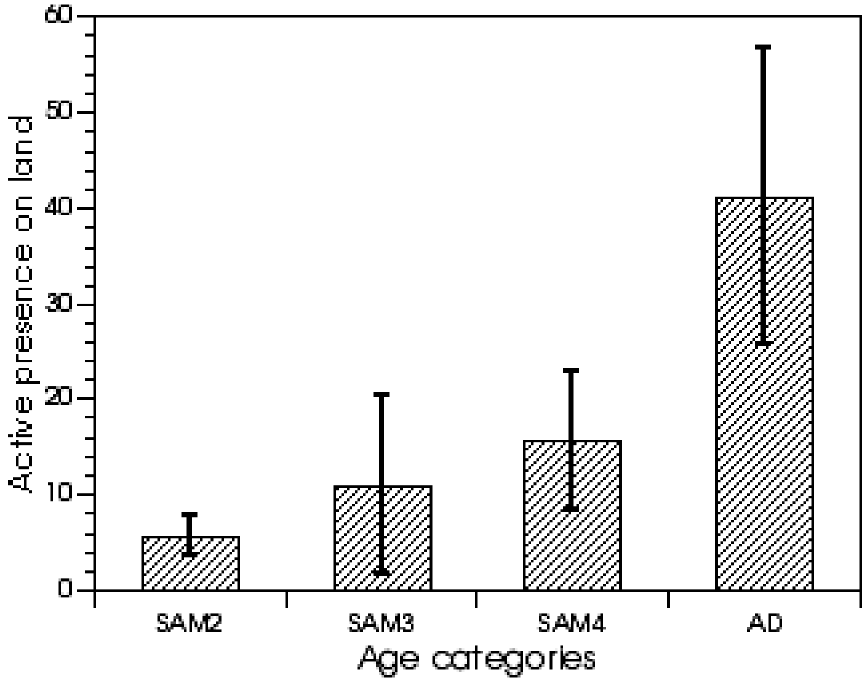


Fig.16 - Active presence on land of different age classes of male elephant seals *Mirounga leonina*

The graph depicts the median and rage of active presence on land; by active presence we mean the number of days in which a male is non only on land but also in active breeding state.

In a sample of 91 breeding males of the 1995 and 1996 breeding season the median number of days spent on land was 55 days (MAD = 14 days; CV = 0.298); if we consider the number of days in which the male is active in breeding the median goes down to 15 days with a MAD of 12 days (CV = 0.893): this large increase of the variability means that just a few males are able to sustain a large breeding effort for the most of the breeding season. There is a large positive and significant correlation between total and active permanence on land (rho = 0.768; n = 91; $p < 0.0001$): the main breeding males are also the males that tend to stay on land longer. This relationship is clarified by examining the relationships between number of days on land and measures of the breeding performance: the number of days spent on land has a strong positive correlation to the level of control of breeding females (rho = 0.596; n = 44; $p < 0.0001$), to the mating rate (rho = 0.569; n = 44; p = 0.0002), and to the estimate fertilization success (rho = 0.648; n = 44; $p < 0.0001$). There should be a large variation of permanence on land of different age categories of males, in accordance with life history theories predicting and age specific tuning of breeding effort [Roff, 1992]. The total presence on land is greater for adult males than for subadult (KW = 31.818; df = 3; $p < 0.0001$), but the difference is not so large and there is a modest variation between subadult classes. There is a larger variation between age categories in the active presence (Fig; 16), i.e., in the number of days a male is not only on land but also in active breeding state: in this case there is a gradual increase of the number of days spent on land going from subadult class 2 to subadult class 4 and a step between this class and adult males (KW = 59.514; k = 3; $p < 0.0001$). This result confirm a gradual increase of breeding effort while males get older.

Prospects for the future

The main goals of our research project are:

- to collect intraseasonal data about the action of sexual selection during many breeding seasons, to get the large samples of males needed to apply sophisticated techniques of analysis
- to look for the variation of sexual selection pattern across breeding seasons

To achieve this goals we plan, subject to the renewal of research permits, to carry on the study of male phenotype and mating tactics in 1997 and following years using the same techniques applied during 1995 and 1996 breeding season.

The most of the work on sexual selection have been focused on the behaviour of males, and few information is available about female reaction to and interaction with male mating tactics [Berglund et al., 1993]. In 1996 we have begun to collect detailed data about female mating behaviour and female breeding tactics. We plan to expand this effort, in particular to get a better understanding of costs and benefits for the female related to the mating system and male mating tactics.

The first target of a long term study is to gain a detailed knowledge of individuals: this means to mark animals in ways suitable for long term recognition. We' ll carry on the intensive marking with cattle tags because this method is cheap, unharmful for the animal and, if animals are tagged another time when they lost the original tags, could be quite effective. For the long term marking of the pups we should adopt a more effective way of marking (eg passive transponders). A long term marking plans make possible the estimation of survival rates of different sex and age classes, the building of life tables, and the prediction of the long term dynamics of the population [Laws, 1994]. It will also enable us to study the survival components of individual fitness and to deepen our knowledge of the long term variation of sexual selection pressures [Charlesworth, 1994]. Selection theory is both the most innovative area of darwinian evolutionary theory and the least accepted [Reznick & Travis, 1996]: the improvement of knowledge in this area depends on long term studies of the dynamics of adaptation.

We plan also to carry on the collection of tissue samples for DNA fingerprinting analysis [Hoelzel, 1992]: the main targets of this job are to study the genetical structure of the Sea Lion Island population and define is position between the South Georgia and the Valdés ones [Laws & Sinha, 1993], and to study paternity to evaluate the relationships between copulation success and reproductive success [Burke, 1989].

A few suggestion for conservation

The main goals of our research project have no direct connection to conservation and so it is not our role to give suggestion about the conservation of elephant seals of the Falklands or the management of Sea Lion Island wildlife.

We just wish to emphasize that the first step in conservation is good knowledge of populations, and this means a regular monitoring.

Due to the strong tendency of females to come back to the same place to give birth in consecutive breeding season the accurate census of a small part of the population could be adequate to check the state of the whole population. Sea Lion Island could be used as an indicator of the state of the whole Falklands population. To get an accurate estimate of the pup production we suggest that, in the unlucky case of a stop of our research work, at least three counts of the females on land should be carried on in the easter tip of the island between the 3rd and 4th week of October. From this figure it easy to get a good estimate of the total number of gross production.

It should also be advisable to carry on the resighting of marked individuals, concentrating during the period of peak presence of breeding females.

We feel that the main problem of our present knowledge of the elephant seals of the Falklands is the lack of detailed information about what happens outside Sea Lion, in the rest of the Falklands. This problem could be solved only by a census of the suitable breeding site all around the Falklands, to be carried on at peak breeding.

Literature cited

Baldi,R. & Campagna,C. & Pedraza,S. & LeBoeuf,B.J. **1996**. Social effects of space availability of southern elephant seal in Patagonia. *Anim. Behav.* **51**: 717-724.

Bartholomew,G.A. **1970**. A model for the evolution of pinniped polygyny. *Evolution* **24**: 546-559.

Berglund,A. & Magnhagen,C. & Bisazza,A. & Konig,B. **1993**. Female female competition over reproduction. *Behav. Ecol.* **4**(2): 184-187.

Bester,M.N. **1980**. The southern elephant seal Mirounga leonina at Gough Island. *S. Afr. J. Zool.* **15**: 235-239.

Boyd,I.L. **1991**. Environmental and physiological factors controlling the reproductive cycle of pinnipeds. *Can. J. Zool.* **69**: 1135-1148.

Burke,T. **1989**. DNA fingerprinting and others methods for the study of mating success. *TREE* **4**(5): 139-144.

Carrick,R. & Ingham,S.E. **1960**. Ecological studies of the Southern Elephant seal, Mirounga leonina (L.), at Macquarie Island and Heard Island. *Mammalia* **34**: 325-342.

Charlesworth,B. **1994**. *Evolution in age-structured populations*. Cambridge Un. Press, Cambridge.

Condy,P.R. **1977**. The ecology of the southern elephant seal Mirounga leonina (Linnaeus 1758), at Marion Island. PhD Thesis. University of Pretoria, Pretoria (South Africa).

Condy,P.R. **1979**. Annual cycle of the Southern elephant seal Mirounga leonina at Marion Island. *S. Afr. J. Zool.* **14**: 95-102.

Costa,D.P. & LeBoeuf,B.J. & Ortiz,C.L. & Huntley,A.C. **1986**. The energetics of lactation in the Northern elephant seal, Mirounga angustirostris. *J. Zool. Lond.* **209**: 21-33.

Deutsch,C.J. & Crocker,D.E. & Costa,D.P. & LeBoeuf,B.J. **1994**. Sex- and age-related variation in reproductive effort of Northern Elephant Seals. B.J. LeBoeuf & R.M. Laws - *Elephant seals. Population ecology, behavior, and physiology*. Un. California Press, Berkeley (CA).

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

Erickson,A.W. & Siniff,D.B. & Harwood,J. **1993 a**. Estimation of population sizes. Laws,R.M. - *Antartic seals. Research methods and techniques*. Cambridge Un. Press, Cambridge.

Erickson,A.W. & Bester,M.N. & Laws,R.M. **1993 b**. Marking techniques. Laws,R.M. - *Antartic seals. Research methods and techniques*. Cambridge Un. Press, Cambridge.

Hindell,H.A. & Burton,H.R. **1988**. Seasonal haul-out patterns of southern elephant seal (Mirounga leonina Linn.) at Macquarie Island. *J. Mammal.* **69**: 81-88.

Hoelzel,A.R. (Ed.) **1992**. *Molecular genetic analysis of populations. A practical approach*. Oxford Un. Press, Oxford.

Laws,R.M. & Sinha,A.A. **1993**. Reproduction. R.M. Laws - *Antartic seals. Research methods and techniques*. Cambridge Un. Press, London.

Laws,R.M. **1994**. History and present status of southern elephant seal populations. B.J. LeBoeuf & R.M. Laws - *Elephant seals. Population ecology, behavior and physiology*. Un. California Press, Berkeley (CA).

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

LeBoeuf,B.J. & Laws,R.H. **1994.** Elephant seals: an introduction to the genus. B.J. LeBoeuf & R.M. Laws - *Elephant seals. Population ecology, behavior and physiology*. Un. California Press, Berkeley (CA).

LeBoeuf,B.J. & Reiter,J. **1988**. Lifetime reproductive ruccess in northern elephant seals. Clutton-Brock,T.H - *Reproductive success*. Un. Chicago Press, Chicago & London.

Lewis,M. & Campagna,C. & Quintana,F. **1995**. Site fidelity and dispersion of southern elephant seals from Patagonia. *Mar. Mammal Sci.* **in press**: .

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

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

McCann,T.S. **1985**. Size, status and demography of Souther elephant seal (Mirounga leonina) populations. Ling,J.K. & Bryden,M.M. - *Studies of sea mammals in the South Latitudes*. South Austr. Museum, Sidney.

Nepomnaschy,P.A. **1994**. Estructura de los harenes del elefante marino del sur (Mirounga leonina). Su relacion con aspectos del comportamiento social individual. Degree Thesis. Universitad Nacional De La Patagonia San Juan Bosco, Puerto Madryn (Chubut - Argentina).

Reznick,D. & Travis,J. **1996**. The empirical study of adaptation in natural populations. M.R. Rose & G. V. Lauder - *Adaptation*. Academic Press, London.

Riedman,M.L. & LeBoeuf,B.J. **1982**. Mother-pup separation and adoption in Northern elephant seals. *Behav. Ecol. Sociobiol.* **11**: 203-215.

Roff,D.A **1992**. *The evolution of life histories: theory and analysis*. Chapman and Hall, London.

Testa,J.W. & Rothery,P. **1992**. Effectiveness of various cattle ear tags as markers for Weddel seals. *Mar. Mammal Sci.* **8**(4): 344-353.

VanAarde,R.J. **1980**. Harem structure of the southern elephant seal Mirounga leonina at Kerguelen Island. *Rev. Ecol.* **34**: 31-44.