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DEMOGRAPHY AND BREEDING BIOLOGY OF A SMALL, LOCALIZED POPULATION OF SOUTHERN ELEPHANT SEALS (*MIROUNGA LEONINA*)

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Abstract

Southern elephant seals have been studied in depth in most of their breeding range. One notable exception is the Falkland Islands population. We present data on demography and breeding biology of elephant seals of Sea Lion Island, the main breeding site of this species in the Falklands. Sea Lion Island shelters a small, localized population of southern elephant seals (516 breeding females in 1995 and 518 in 1996). Comparison with the few available census data collected prior to our study suggests that the population has been stable in the short term (1989–1996). Females produced pups at maximum rate and pup mortality was low (2.13%). Breeding sex ratio was strongly unbalanced, with about 14 females per breeding male and 47 females per harem-holding male at peak haul-out. Survival rate between breeding seasons was 67.4% for females and 50% for males. Timing of the breeding season was very similar to that recorded in other populations and was in accordance with clinal variation with latitude. Sex ratio at birth was balanced, and no significant weight dimorphism at weaning between sexes was detected (males: 135.4 kg; females: 132.0 kg). Weaning weight was correlated with size class of the mother.

Key words: southern elephant seal, *Mirounga leonina,* demography, breeding biology, Falkland Islands.

Southern elephant seals (*Mirounga leonina*) have been studied in depth in most of their breeding range (Laws 1994), and data about present status, demography, and breeding biology are available for most populations (Macquarie Island: Hindell and Burton 1987; Iles Crozet and Iles Kerguelen: Gui-

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net *et al.* 1992; Valdés Peninsula: Campagna *et al.* 1993; Marion Island: Bester and Wilkinson 1994; South Georgia: Boyd *et al.* 1996). One notable exception is the Falkland Islands population; no detailed account of its status has been published (Laws 1994).

The elephant seal population of the Falklands is part of a larger stock which includes South Georgia, the South Orkney Islands, King George Island, Gough Island, and the Valdés Peninsula (Laws 1994). The Falklands population could provide a link between the two larger populations of the breeding stock, namely those of South Georgia and the Valdés Peninsula, but it appears to be almost isolated from these two populations during the breeding season (Lewis *et al.* 1996, our observations).

Preliminary information from a survey of the entire Falklands coast (M. Bingham, personal communication), carried out at the end of the elephant seal breeding season, showed very limited signs of breeding. The only breeding site of elephant seals with a large local population is Sea Lion Island (52°26′S, 59°05′W), the southernmost inhabited island of the Falklands. Here we present data on the demography and breeding biology of this population collected during two consecutive breeding seasons.

MATERIALS AND METHODS

Field work was carried out daily by four people from 4 September to 26 November 1995 and from 2 September to 24 November 1996. Our study area was the eastern point of the island. The coast line is composed of three continuous stretches of sandy beach divided by two rocky areas; breeding units occupied only sandy beaches (total length = 7.2 km, estimated from aerial photographs). Females formed large groups (harems), usually with at least one male in attendance. A harem is defined as a group of two or more females; females are considered grouped when their distance apart is less than 10 standard body lengths (SAB) (American Society of Mammalogists 1967). Harems were scattered along the beaches and their spacing was uneven, with long (up to 1 km) stretches of beach with no females. Median harem size was about 30 females at maximum haul-out (1995: median = 31 females, median absolute deviation [MAD] = 22, n = 11 harems; 1996: median = 35, MAD = 17, n = 10).

Almost all breeding seals were individually marked. These included all breeding males (44 in 1995 and 47 in 1996; breeding male = male present in breeding areas for a continuous period of at least two weeks), all males of class SAM2 or older (see below) that were on the beaches for even a few hours, almost all females (>98% in each season), and all pups. Seals were at least double-tagged in the interdigital web of the hindflippers using cattle tags (Jumbo Rototag, Dalton Supplies Ltd, Oxon RG9 5AB, United Kingdom) following Testa and Rothery (1992) and Erickson *et al.* (1993*a*). Most breeding males were marked with three or four tags. The breeding males and most of the breeding females were also marked by painting an identification code on their flanks using hair dye; the marks lasted for the entire breeding season and until the molt. The joint use of tags and paint marks ensured recognition of all breeding animals.

On each of the 84 d of the breeding season, one observer counted the seals while walking along all breeding beaches during low tide. From daily censuses, three kinds of data were obtained: counts of the number of individuals on land by sex and age class, data on the structure of breeding units (number and identity of females and number, status, and position of males near the harem; see below for definition of status), and data on marked males and females (age class, size class, breeding status, and location). To check for presence of breeding individuals outside our main study area we also carried out weekly censuses by walking along the cliff-tops of the entire perimeter of the island; only one pup was born outside our study area during the two breeding seasons.

An accurate estimate of the net production of breeding was obtained by marking all pups with one tag when they were still with their mothers in the harem and then again after weaning.

To gather data on breeding activities we recorded (with at least 24-h precision) arrivals on land, departures to sea, births, copulations, and weanings (departure of the mother and following expulsion from the harem). We collected data during two-hour periods from fixed observation points overlooking one or more harems (a total of 1,258 h of observation in 1995 and 1,294 h of observation in 1996) using all-occurrence sampling (Altmann 1974) with continuous recording of events on log sheets. The majority of observations were carried out between 0600 and 2000 local time, but a limited number of observations were also made during the night using spot lights and night-viewing equipment.

Breeding status of males was defined at two levels, seasonal and daily. We classified males on a seasonal basis as *principal* if they stayed on land for long continuous periods (≥2 wk) and if they gained control of a harem for three or more consecutive days when at least one female was receptive; *secondary,* if they stayed on land for long periods (as for principal males) but never got control of a harem for more than two consecutive days; *tertiary,* if their presence on land during the breeding season was occasional and short-term (<2 wk). On a daily basis males were scored (during daily censuses) by their distance from females as: alpha (within the female group, distance = 0 SBL), beta (a second male within the female group, but with fewer females at his side than near the alpha), peripheral (1–5 SBL from the closest female in the harem), marginal (6–10 SBL), or solitary (>10 SBL). In this population an established alpha male had unrestricted control of the harem and an uncontested access to the females (*e.g.,* the alpha male of the largest harem made about 95% of the copulations in and near a harem of 124 females in 1995 and of 129 females in 1996). By "harem control" by the alpha male we mean both the active control of female movements by herding and the exclusion of other males by direct and conventional competition.

We classified males into age classes; size was used to recognize gross differences, but finer classification was achieved using external morphology (in particular spread of scars on the frontal shield and neck, appearance of the facial area and development of the proboscis) in order to obtain an estimate of age as independent of size as possible. Eight age classes were recognized: yearlings (Y), estimated age 1 yr; estimated age 2 yr (2Y); juveniles (JUV), estimated age 3 yr; class 1 subadults (SAM1), estimated age 4 yr; class 2 subadults (SAM2), estimated age 5 yr; class 3 subadults (SAM3), estimated age 6 yr; class 4 subadults (SAM4), estimated age 7 yr; and adults (AD), estimated age 8 yr or more. Because we have no data on actual age of males, our age classification is only tentative and has only a descriptive purpose. Internal consistency of our classification is more relevant than agreement with actual ages. To check the consistency of various observers in classification of male age, we chose a random sample of the censuses of the 1996 breeding season (10 censuses of week VII-X, when most males were on land) and compared ages of males. We found a high and significant concordance between classification of male ages in different censuses (Kendall coefficient of concordance: $W = 0.93$ [0.99 when excluding one of the four observers], $P < 0.0001$; we found analogous results for 1995 censuses). For males present in both seasons, age class attributed in 1996 was consistent with that attributed in 1995. This classification system gives a consistent ordering of the ages of breeding males; and we are confident that it has a good relationship with the actual ages of males; a comparable system has been used with good results on northern elephant seals (Deutsch *et al.* 1994).

In the southern elephant seal there is a threefold variation in female size (Fedak *et al.* 1996) which allows a rough classification of females into size classes by visual inspection (Campagna *et al.* 1992). Females ($n = 500$) were classified into five classes by repeated comparison with adjacent individuals (extra-small, 2.0%; small, 10.8%; medium, 35.0%; large, 45.0%; extra-large, 6.2%). To evaluate the accuracy of size classification, we compared the size classes as independently scored by two observers for all the females breeding in an intensively observed harem; concordance among observers was high (*rho* $= 0.97$; $n = 63$ females; $P < 0.0001$). For analysis, extra-small females were pooled with small females, and extra-large with large.

Three indices of male breeding performance were estimated from behavioral data: control of females (mean daily number of females controlled by a male), mating rate (number of copulations with intromission lasting at least one minute per 100 h of observation), and fertilization success (product of the proportion of copulations realized by a male in one harem and the number of females that breed in the harem, summed over all harems in which the male copulates (Le Boeuf 1974, Deutsch *et al.* 1990).

Weanling sex ratio (number of females per male) was estimated by recording the presence or absence of a penile opening in every (marked) individual lying on its back.

The pups were weighed using a weighing bag (a cotton sheet with straps cut out to fully enfold the weanling, held up by two horizontal aluminum poles connected by steel chains and springs to a dynamometer) and a 500-kg digital dynamometer (model DIN-1R/TS—accuracy ±0.5%, C.A.M.I. Paviglianiti, Trezzano sul Naviglio, Italy) connected to a half-ton crane (model GP5/DE, OMCN, Villa di Serio, Italy).

There was large variation in the interval between weaning and weighing of pups (21 ± 9 d, n = 100): to mitigate these differences we corrected the observed weight by the weight lost between weaning and weighing. The weight loss was estimated as the product of the number of days between weaning and weighing and a sex- and week-dependent correction factor of 0.78–1.02 kg lost per day, as presented by Campagna *et al.* (1992) for the Valdés Peninsula population.

Statistics are presented as mean and standard deviation or, more frequently due to the asymmetric distribution of variables, as median and median absolute deviation (MAD, Rousseeuw and Crou 1993). Parameter estimates from models are presented with standard errors (SE) when necessary. Exploratory data analysis, calculation of statistics and tests were performed with SYSTAT version 5.2.1 (Wilkinson *et al.* 1992) and SPSS version 6.1 (Norusis 1994). Randomization tests (10,000 replicates) were performed with RT version 2.0 (Manly 1992).

RESULTS AND DISCUSSION

Demography

Population size—Pinniped population sizes are not easily estimated, as a portion of the population is at sea at any one time. The easiest way to cope with this problem is to estimate the total production of pups and then use this figure to calculate the actual size of the population, using information on the population age structure from life tables (Eberhardt *et al.* 1979). On the basis of published life tables for elephant seals (McCann 1985), we applied a correction factor of 3.5 to calculate the number of individuals of age 1 yr and older from the number of pups (see below). Therefore, the entire population of Sea Lion Island is estimated to be 1,800 seals 1 yr old or older. In the absence of a reliable census of the other breeding sites, an estimate of the whole Falklands population size cannot be obtained. However, given the scarce breeding outside of Sea Lion Island, we think that the population size may be significantly lower than the last previously published estimates (Strange 1992), which suggested a net production of about 5,000 pups.

Number of breeding females—Sea Lion Island seems to be the only conspicuous breeding site for this species in the Falkland Islands, with more than 90% of the breeding females of all the Falklands. It is quite difficult to obtain directly the total number of breeding females in populations of elephant seals because of the pattern of arrival and departure of females during the three-month breeding season (Erickson *et al.* 1993*b*). A first estimate was obtained through our daily counts. On Sea Lion Island the maximum number of females on land was 465 in 1995 and 467 in 1996, recorded on the same date (20 October) in both years. On South Georgia the maximum number of females

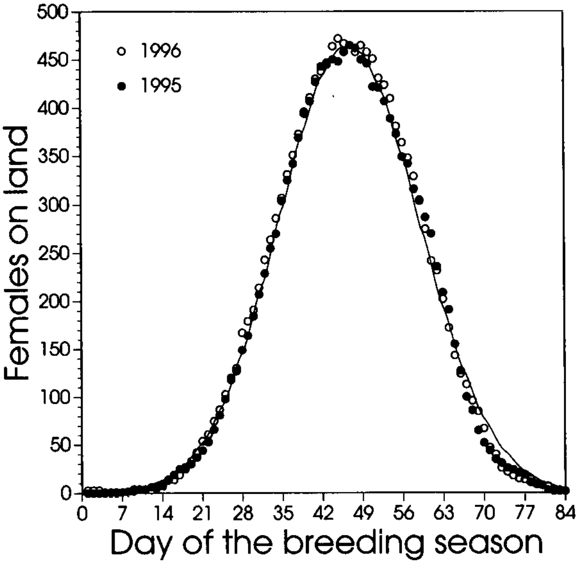

Figure 1. Number of female Southern elephant seals recorded during daily counts at Sea Lion Island breeding beaches in 1995 and 1996. Time of counts defined as number of days from first day of the season (4 September in 1995 and 2 September 1996). A Gaussian model fits these data (see text) as well as data for each breeding season.

on land accounts for 90%–95% of the total number of females actually breeding in the population (McCann 1985).

A more exact estimate was obtained from the marking records of females and their pups. The total number of breeding females marked during the two breeding seasons was 516 in 1995 and 518 in 1996. These estimates correlate well with direct counts of females (females on land at peak haul-out = 90% of the total number of breeding females). The two independent estimates are consistent, and the second is considered a very accurate estimate of the real number of females that breed on Sea Lion Island.

A mathematical model of the percentage of females on the breeding beaches in each day of the season was worked out from our daily counts. It is a simple Gaussian model (Hindell and Burton 1988) that fits the data much better than other models (*e.g.*, quadratic model: Van Aarde 1980*b*). We fitted the model first to 1995 data (r^2 = 0.997) with free parameters, and then checked it using 1996 data and the same set of parameters, obtaining a consistent result (r^2 = 0.997). There is an almost perfect symmetry in the variation of the number of females on land in 1995 and 1996 (Fig. 1). We used the Gaussian model to standardize the irregular counts of females carried out prior to our study. These estimates were difficult to compare directly because they had been made in different periods of the breeding season. Since the timing of breeding in our population is almost constant in different years (see below), we may use our model to correct the old counts (data from David Gray,

Table 1. Female density on land (number of females per km of coastline) in various populations of southern elephant seals. It is not always clear (*e.g.*, Carrick *et al.* 1962, Carrick and Ingham 1960) if the reported density refers to total coastline or just the portion of coastline suitable for elephant seal breeding.

Population	Density	Source
Sea Lion Island	111	this study
South Georgia	175–250	McCann 1980
Kerguelen	400	Bester and Lenglart 1982
	520	Van Aarde 1980*a*
Heard	2,188	Carrick *et al.* 1962
Macquarie	1,100	Carrick and Ingham 1960
Valdés Peninsula	62	Baldi *et al.* 1996

personal communication). The population seems to be stable (total number of breeding females: 1989 = 511; 1990 = 516; 1993 = 517), and no significant trend of increase or decrease in the 1989–1996 period is apparent (randomization test for trend: $P_{10,000} > 0.20$). However, current short-term stability is not definitive evidence of stability in the long term, as the small population of Marion Island demonstrates (Bester and Wilkinson 1994). The other small, localized breeding population of elephant seals for which data are available, at Gough Island, is almost stable (Bester 1990).

The density of females on Sea Lion Island was quite low (111 females per km of the coastline suitable for breeding) compared to densities recorded in other subantarctic populations (Table 1). This low level of crowding of females probably results from the small population size and the abundance of sandy beaches with a gentle slope. It is known that these are the preferred breeding habitat for elephant seals (Van Aarde 1980*a,* Boyd *et al.* 1996), probably because of the ease of access and the sand's favorable properties for thermoregulation (Campagna and Lewis 1993).

Production and pup mortality—In 1995 gross production was 517 pups [515 single births and one twin birth; twinning is uncommon in elephant seals (McCann 1985)], and net production at the end of the breeding season was 505 weanlings. Preweaning mortality was 1.74%, and total mortality at the end of the breeding season was 2.32%. In 1996 gross production was 518 pups (all single births), net production was 508 weanlings, preweaning mortality was 1.54%, and total mortality at the end of the breeding season was 1.93%. Mortality rate was homogeneous between years (preweaning: Fisher exact test, $P > 0.80$; total: Fisher exact test, $P > 0.65$), hence overall estimates of mortality can be derived: 1.64% preweaning ($n = 1035$) and 2.13% total.

The mortality was mostly due to still births (1995: 58%, $n = 12$; 1996: 60%, $n = 10$), similar to that in the population of the Valdés Peninsula (Baldi *et al.* 1996). The mortality rates found in our study are lower than those reported for other southern elephant seal populations (Table 2). In the northern elephant seal the high pup mortality (10%–40%; Le Boeuf and Laws 1994) is mainly due to trampling and crushing by the males during their agonistic

Table 2. Preweaning mortality (% pups dead before weaning) in various populations of southern elephant seals; *n* = sample size, when available.

Population	Mortality	*n*	Source
Sea Lion Island	1.64	1,035	this study
South Georgia	4.5		McCann 1985
Heard	5–10		Carrick *et al.* 1962
Macquarie	5–10		Carrick and Ingham 1962
	5.8	3,106	Hindell and Burton 1987
Marion Island	6.0		Condy 1977
Gough Island	4.1	225	Bester 1980
Valdés Peninsula	3.5	3,487	Baldi *et al.* 1996

activities and to starvation through prolonged separation of the pup from the mother because of female aggression or male interference (Le Boeuf and Briggs 1977, Riedman and Le Boeuf 1982). The same events have been reported for high-density southern elephant seal populations (Macquarie Island: Carrick and Ingham 1960; South Georgia: McCann 1982).

We did not perform autopsies on the dead pups of Sea Lion Island. Visual inspection, however, did not offer any indications of crushing by adult individuals. In a sample of 434 male-female interactions, separation of the pup from the mother was recorded in 29% of cases, but separation was always short (mean duration = 5 min, *n* = 87; in only one case was separation longer than 15 min) and in no case definitive. We may conclude that the main sources of mortality observed in crowded populations of elephant seals are of minor importance on Sea Lion Island.

The Sea Lion Island population is a low-density population characterized by medium-sized harems (see Materials and Methods). Low mortality could hence be a result of the low level of agonistic activity between males (unpublished data), the low crowding of females and the low level of female aggression within the harems, as in the Valdés Peninsula population (Baldi *et al.* 1996).

Sex ratio—Variation in the sex ratio during the breeding season was estimated from the daily counts of the number of males and females on the breeding beaches.

Three different estimates of the sex ratio were calculated using daily census data. The first is the sex ratio for mature individuals (MSR), the number of breeding females per male of class SAM2 or older. In our population, SAM2 are the youngest males able to achieve intromission during occasional circumstances in which access to estrous females is not restricted by social constraints. We assume that SAM2 males are physiologically mature, because age at maturity in elephant seals is estimated at 4–6 yr (Laws 1956). On Sea Lion Island, the MSR showed a daily variation of Gaussian shape, symmetric for variation in the number of females on land, and reached a maximum (11.5 females per male in 1995; 9.9 in 1996) just before the peak haul-out of females. The second index is the breeding sex ratio (BSR), the number of females per breeding male (the males which stay on the breeding beaches for prolonged periods actively pursuing access to females). BSR had daily variation analogous to that of MSR and also reached a maximum (14.5 females per male in 1995; 13.0 in 1996) just before the peak haul-out.

A stricter criterion for calculating the ratio for breeding individuals is to consider only the alpha males, the males that have control of a harem and, therefore, almost unrestricted access to breeding females (at least in our study population). This may be the best measurement of the actual sex ratio of breeding individuals in a polygynous species with a harem-defense mating system. On Sea Lion Island, the overall ratio of breeding females to alpha males reached the maximum (46.9 females per male in 1995; 46.7 in 1996) just after the peak in the number of hauled-out females.

The sex ratio between breeding individuals recorded on Sea Lion Island is intermediate between that reported by Campagna and Lewis (1993) for the Valdés Peninsula (females per alpha male = 11) and those reported for most subantarctic populations, for example by McCann (1980) for South Georgia (females per alpha male = 74.2), Van Aarde (1980*b*) for the Kerguelen Islands (102.3) and Carrick *et al.* (1962) for Macquarie Island (277). These data on sex ratio should be interpreted with caution because there may also be great variation in sex ratio within populations.

Male age structure—There was great variation in the timing of arrival of different age classes at the breeding beaches. Consequently, the age structure of the population on land changed throughout the breeding season. The pattern of male arrival depended on age; adult males (median day of arrival = day 9 of the breeding season, $n = 37$ males) and older subadults (SAM4: day 19, $n = 22$) arrived earlier than the younger animals (SAM3: day 25, $n = 20$; SAM2: day 26.5, $n = 12$; Kruskall-Wallis test: $H = 22.27$; df = 3; $P < 0.0001$). A peculiar pattern of this variation in age structure was a decrease in the relative number of fully adult males (AD) in the population, a common feature of most elephant seal populations (Le Boeuf and Laws 1994); at peak haul-out they represented less than 40% of the males active in breeding areas.

The number of breeding males in each age class increased gradually from subadult class 1 males to adult males ($n = 44$ males: SAM1 = 3.6%, SAM2 = 17.9%, SAM3 = 14.3%, SAM4 = 28.6%, AD = 35.7%). This age structure is typical of a highly competitive mating system in which older males tend to have a higher resource-holding potential and tend to keep younger individuals away from breeding areas and females.

Survival—More than half of the breeding females tagged in 1995 were observed again on Sea Lion Island in 1996 (67.4%, $n = 516$). As females of the genus *Mirounga* are known to show fidelity to a breeding site (Le Boeuf and Laws 1994), this is likely to be a good estimate of the actual survival rate of females between breeding seasons. We estimated the rate of tags lost by using double-tagged individuals and applying a binomial model of tag loss (Eberhardt *et al.* 1979). The probability of losing a single tag was 0.164 and the probability of losing two tags was 0.027. Therefore, although the tag loss rate was higher than that recorded for the Marion Island population (Bester and Wilkinson 1994), the lack of identification of marked females would not significantly change the estimate of female survival between breeding seasons. Nevertheless, the estimate of survival was more accurate for breeding males than for females, as we marked most breeding males in 1995 with more tags than females, recorded every scar or natural mark on males, and checked each male for signs of lost tags on flippers. We assumed that males not present during the 1996 breeding season had died, because of the strongly phylopatric nature of the species, because of the lack of evidence that males may skip a breeding season (unpublished data), because of the high quality of our daily resight records, and because of the limited chances of breeding outside Sea Lion Island. Fifty percent of the breeding males marked in 1995 (n = 44) survived until the next breeding season. This survival rate is similar to that recorded by us at the Valdés Peninsula between 1993 and 1994 (48%, n = 52; unpublished data).

Breeding Biology

Timing of the breeding season—Reproduction in elephant seals occurs during a fixed three-month period when females come on land to give birth, suckle their pups and mate. The timing of the breeding of pinnipeds is regulated photoperiodically (Boyd 1991). On Sea Lion Island, the peak presence of females on land was recorded on 20 October in both years. There is a rough clinal variation of the day of maximum number of females hauled out in various populations of southern elephant seals (Campagna *et al.* 1993), and the timing of maximum haul-out on Sea Lion Island is in accordance with this cline (Table 3). Females began to come on land during the second week of September. The first birth was recorded on 11 September 1995 and on 17 September 1996. The last departure of females was on 3 December 1995 and on 27 November 1996; the late departure in 1995 was due to an isolated female with an unusual breeding pattern.

It is rather difficult to make a comparison among populations of the length of the entire breeding season because of intrinsic factors (such as the early arrival of some males and the atypical arrival of a few females at the beginning of the season) and the variability of criteria for calculation (McCann 1980). It is much easier to compare the length of the parturition period. On Sea Lion Island, births were recorded over a 60-d period in 1995 and a 58-d period in 1996. These periods are longer than those reported for the Îles Kerguelen (43 d, Angot 1954) and Îles Crozet (36–51 d, Barrat and Mougin 1978) but similar to the time estimated for South Georgia (60 d) by Laws (1956). On the whole, the length of the birth season seems to be regular both across populations and across seasons in the same population, confirming the strict control of timing of breeding in this species.

Female breeding—The timing of female reproduction in land-breeding pinnipeds is usually very regular (Boyd 1991), and elephant seals are no exception (Campagna *et al.* 1993). The typical female comes on land a few days before parturition, gives birth, suckles the pup for about three weeks, mates once or

Table 3. Geographic location and timing of reproduction in some populations of southern elephant seals, ordered by latitude. Peak is date of peak haul-out of females; Dist. is estimated distance (km) from Antarctic Convergence (−: south, +: north). Punta Delgada represents Valdés Peninsula population; Sea Lion Island represents Falkland Islands population.

Population	Lat.	Long.	Dist.	Peak	Source
King George 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
Macquarie Is.	54°29′S	157°00′E	+160	16–10	Carrick *et al.* 1962
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
Campbell Is.	52°33′S	169°09′E	+800	16–10	Sorensen 1950
Sea Lion Island	52°26′S	59°05′W	+630	20–10	this study
Kerguelen	49°21′S	70°12′E	0	15–10	Van Aarde 1980*a*
Marion Is.	46°55′S	37°45′E	+290	17–10	Condy 1979
Crozet	46°25′S	51°45′E	+320	16–10	Barrat and Mougin 1978
Punta Delgada	42°46′S	63°38′W	+1,550	02–10	unpublished data

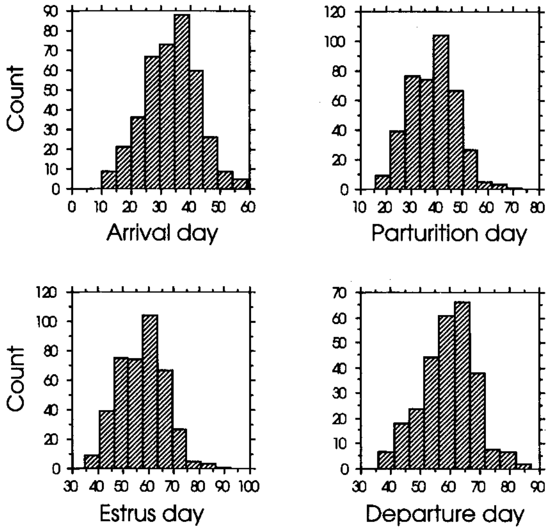

Figure 2. Distribution of days of occurrence of various breeding events for female elephant seals breeding on Sea Lion Island during 1996. Arrivals: *n* = 394 females; parturitions: *n* = 406; estrus: *n* = 404; departures: *n* = 275.

more during a couple of days, and finally returns to sea. Median arrival date was 5 October in both 1995 (MAD = 7 d, *n* = 223) and 1996 (MAD = 6 d, *n* = 394). Parturition was also very regular, and the median date was 12 October in 1995 (MAD = 7 d, *n* = 137) and 10 October in 1996 (MAD = 6 d, *n* = 406). The departure date was more irregular, showing a median on 6 November in 1995 (MAD = 6 d, *n* = 107) and 1 November in 1996 (MAD = 6 d, *n* = 275). As a consequence of the regular timing of parturition and the predictable interval between parturition and estrus, the distribution of days of estrus was very similar in the two years, the median date being 28 October in 1995 (MAD = 6 d, *n* = 298) and 29 October in 1996 (MAD = 6 d, *n* = 404). This regularity probably has a significant effect on male breeding, as the distribution of females in estrus is very predictable both in space and time (Fig. 2). The total time spent on land (arrival to departure) was very similar among females (CV = 0.122, *n* = 212 in 1995 and 0.151, *n* = 414 in 1996) showing a median of 27 d (MAD = 2 d) in both years. The interval between parturition and the beginning of estrus (first non-protested copulation) was also regular (CV = 0.123, *n* = 116 in 1995 and 0.321, *n* = 238 in 1996) with a median of 20 d (MAD = 2 d) in both years. This regularity is expected to promote synchronization in female mating and the predictability of the distribution of fertile periods over the breeding season. The timing of reproduction in our study area was almost the same as that reported for the Valdés Peninsula (Baldi *et al.* 1996) and South Georgia (McCann 1980, Boyd *et al.* 1996). The main difference between the populations was the day the season started, while internal timing was almost identical.

Female phenotype and timing of reproduction—Preliminary evidence suggests that the timing of reproduction partly depends on some aspects of the female phenotype, particularly size. Small females tended to arrive earlier than large females (median arrival day = 29 *vs.* 34, $n = 49$ and 163, respectively), with medium females closer to large ones (33, $n = 156$). In spite of the large variation within each class (CV > 0.2 in each class), the difference is significant (Kruskal-Wallis test: $H = 11.785$, df = 2, $P = 0.0028$). Small females also tended to give birth earlier than large females (median parturition day = 34 *vs.* 40, $n = 51$ and 163, respectively), and the difference is again statistically significant (Kruskal-Wallis test: $H = 15.022$, df = 2, $P = 0.0005$). This variation in the timing of breeding of females of different age classes suggests a variation in breeding strategies based on phenotypic differences. Large females are expected to have greater fat reserves (Campagna *et al.* 1992) and hence be able to stay on land and suckle their pups for a longer period. Small and medium females spent a lower median number of days on land than large females (27 d *vs.* 29 d, $n = 184$ and 151, respectively), and the relative variation was similar (CV = 0.118 and 0.106); the difference between large and pooled small and medium is significant (Mann-Whitney test: $U = 18303$; $n = 151, 184$; $P < 0.0001$). Small and medium females spent a lower median number of days suckling their pups than large females (21 d *vs.* 23 d, $n =$ 151 and 186, respectively); the relative variation is again similar (CV = 0.083 and 0.092) and the difference between large and pooled small and medium is also significant ($U = 18{,}910$; $n = 151, 186$; $P < 0.0001$). Large females seem to be able to stay on land longer and to suckle their pups for more days than smaller females. The absolute value of the difference in timing is small, but suckling is a heavy cost for the mother (Deutsch *et al.* 1994), as the energy transfer rate between mother and pup is very high (Costa *et al.* 1986). Therefore, even one additional day of suckling may have a significant impact on the female's energy consumption and the weaning weight of the pup.

Sex ratio at weaning—As the preweaning mortality on Sea Lion Island was very low, the weaning sex ratio can be considered a good indicator of sex ratio at birth (Campagna *et al.* 1992). Moreover, there is no indication of differential preweaning mortality between sexes (Lewis 1989, Le Boeuf and Laws 1994). In our study area, the sex ratio was slightly biased toward males (0.86 females per male in 1995, $n = 439$; 0.84 in 1996, $n = 453$), although the difference from an equal sex ratio was not significant in either year (1995: $\chi^2 = 2.48$, df = 1, $P > 0.10$; 1996: $\chi^2 = 3.36$, df = 1, $P = 0.07$). A slight bias toward males at birth is common in the majority of elephant seal populations, ranging from 0.82 in South Georgia (Laws 1953) to 0.89 in the Kerguelen (Pascal 1979) and 0.90 on Heard Island (Carrick and Ingham 1962), although an almost balanced sex ratio may sometimes be found (Kerguelen 0.99, Angot 1954).

Classical theory of evolution of breeding effort (Trivers and Willard 1973) predicts an adaptive variation of sex ratio in offspring of mothers with different phenotype. We compared sex ratio at birth of Sea Lion females classified by size and found small, non-significant differences between size classes (small: 58.7 % males; medium: 52.9%; large: 54.0%; $\chi^2 = 0.467$, df = 2, $P > 0.75$).

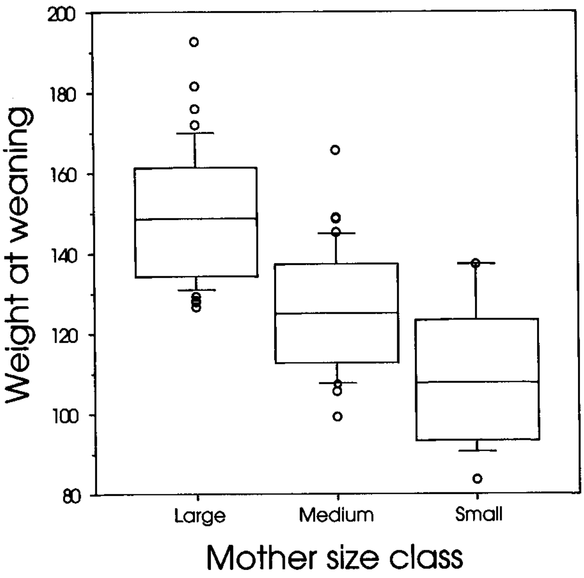

Figure 3. Distribution of weight at weaning by size class of mother of sample of pups of the 1996 breeding season (n = 100 weanlings).

This is rough, preliminary evidence against adaptive variation of sex ratio at birth according to capability of maternal investment. Previously published data are contradictory; Le Boeuf *et al.* (1989) reported no adaptive shift in parental investment in *Mirounga angustirostris,* while for *M. leonina* there is variation between studies (Campagna *et al.* 1992, Arnbom *et al.* 1994).

Weight at weaning—The distribution of weights was almost normal (g_1 = 0.003, g_2 = −0.220), as usually found for morphometric variables, with a mean weight of 133.6 kg (SD = 22.0 kg, CV = 0.165). There was a modest sexual dimorphism at weaning in favor of males (males: 135.4 ± 21.6 kg; females: 132.0 ± 23.3 kg), but the difference was not statistically significant (t = −0.688, df = 89, P = 0.4931). Weight at weaning was partly related to the duration of suckling: the number of days between birth and weaning was positively correlated to weanling weight (r = 0.3564, n = 77, P = 0.0016). The weights recorded on Sea Lion Island were similar to those reported for the Valdés Peninsula (Campagna *et al.* 1992) and higher than those reported for South Georgia (McCann *et al.* 1989, Fedak *et al.* 1994). For the Valdés Peninsula population, Campagna *et al.* (1992) reported a proportional increase in weaning weight with an increase in female size (measured by a three-size-class system as in our study).

In our population there was a clear relationship between mother's size and weight at weaning (Fig. 3); mean corrected weanling weight rose from 109.2 kg (SD = 17.1, n = 15) for small mothers to 125.1 kg (SD = 15.3, n = 36) for medium-sized mothers, to 149.1 kg (SD = 15.9, n = 44) for large mothers. These weights by size class are very similar to those found at Valdés. The difference in weaning weight among size classes is highly significant both for the whole comparison (ANOVA: F = 43.7; df = 292; $P < 0.0001$) and for all pairwise comparisons (Scheffé test for unplanned comparisons: small *vs.* medium $P = 0.0068$; small *vs.* large $P < 0.0001$; medium *vs.* large $P < 0.0001$). Our results confirm that the total breeding effort of females depends on their size.

Male breeding—As shown above, there was large variation among age classes in the median day of arrival on land of males. Large variation was also found in total time spent on land. The first males came on land at the very beginning of the breeding season during the first week of September, before the haul-out of the first female. Some of the breeding males stayed on land for the entire breeding season, fasting for as much as three months, while others were on land for just a small part of the season.

We considered total presence (number of days in which a male was on land) and active presence or tenure (number of days in which a male was on land and involved in competition for access to females). In a sample of 91 resident breeding males in the 1995 and 1996 breeding seasons, the median number of days spent on land was 55 (MAD = 14 d, CV = 0.298), yet the number of days in which the males were active in breeding was only 15, with a MAD of 12 d (CV = 0.893). The variability for the active portion suggests that only a few males were able to sustain a large breeding effort throughout most of the breeding season. The variation of active presence is symmetrical with the variation of total presence, and the correlation between the two is high ($rho = 0.768$, $n = 91$, $P < 0.0001$).

According to the predictions of an age-specific tuning of the breeding effort based on life history theories (Roff 1992), a large variation in presence on land is expected among male age categories. The total presence on land was greater for adult males than for subadult males (Kruskall-Wallis test: $H = 31.818$, df = 3, $P < 0.0001$), but the difference was not large and only modest variation among subadult classes was revealed. There was much larger variation in active presence among age categories. In this case, there was a gradual increase in the number of days spent on land from subadult class 2 to subadult class 4 and a steep increase between SAM4 and adult males (Kruskall-Wallis test: $H = 59.514$, $K = 3$, $P < 0.0001$). The effect of aging on presence on land is revealed by a comparison of the number of days spent on land by males breeding on Sea Lion Island in 1995 and again in 1996; 87.1% ($n = 31$) of the males that returned stayed on land longer in 1996, and that percentage becomes 94.7 ($n = 19$) if we consider only males who were subadults in 1995. For subadult males, the mean increase in presence on land in the second season was 17.6 d. This result confirms an increase in the breeding effort as males get older (Fig. 4).

Another correlate of length of presence on land was the seasonal breeding status of males. Principal males, which controlled females during the breeding season, spent more days on land than secondary males (median = 73 *vs.* 49 d, $n = 23$ and 68) and the difference was very significant (Mann-Whitney test: $U = 1{,}364.5$; $n = 23, 68$; $P < 0.0001$). Our result is similar to that obtained at Valdés Peninsula (Campagna *et al.* 1993) and is supported by

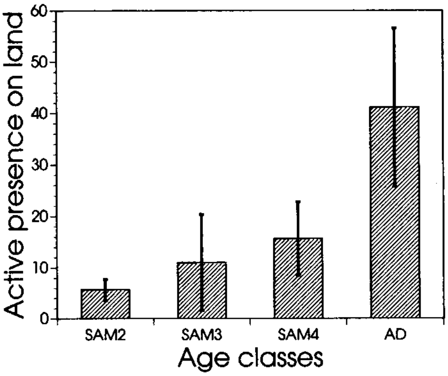

Figure 4. Active presence on land (median and range) of various age classes of male elephant seals (adult males and three classes of subadult males) on Sea Lion Island during 1995 breeding season. Active presence defined as number of days in which a male is not only on land but also in active breeding state.

anecdotal evidence from other populations (McCann 1981). The role of time spent on land is clarified by examining its relationship with breeding performance. The number of days spent on land has a strong positive correlation with level of control of breeding females ($rho = 0.586$, $n = 91$ males, $P < 0.0001$), with mating rate ($rho = 0.638$, $n = 91$, $P = 0.0002$), and with estimated fertilization success ($rho = 0.641$, $n = 91$, $P < 0.0001$). Length of presence on land therefore seems an important component of male breeding performance. In our study area we confirmed that older males with higher status tended to arrive on land earlier and to stay longer, gaining large breeding benefits from their long tenure.

Conclusion

Within the context of the current research on elephant seal biology, the demography and the breeding biology of the small population of elephant seals of Sea Lion Island are particularly interesting. From a theoretical point of view, they may help us to understand the causes of the current decline that affects the majority of the large populations of elephant seals around the world. The Sea Lion Island population offers the opportunity to analyze the dynamics of the demographic, behavioral, and ecological parameters that affect the breeding biology of a population unit without the disturbing effects of unknown relationships with other populations. In fact, the elephant seal population of Sea Lion Island appears to be fairly isolated during the breeding season from the larger populations of the South Georgia stock; no individual marked in the Valdés Peninsula or in South Georgia has ever been resighted at Sea Lion Island during the breeding season. This is a preliminary but strong indication of absence of gene flow with the rest of the stock (DNA fingerprinting studies are currently in development). Another advantage of the study of a small and almost closed population is that it allows us to track every breeding individual within and through breeding seasons in a very detailed fashion, thus permitting the study of life history and breeding parameters at the individual level.

Moreover, the population of Sea Lion Island seems to represent what is left of the formerly large population of the Falkland Islands, and there is sufficient evidence that breeding of elephant seals in the rest of the Falklands is very scarce. Therefore, the future status of the Sea Lion Island population could have a significant role in the conservation of the entire Falklands and South Georgia stock. Predicting the future of mammalian populations requires long-time series of demographic and life history parameters. For example, the short-term stability of the effective size of our seal population may be confirmed for the long term only when long time series of number of breeding females, pup mortality rate, and adult survival rate are available. One of the goals of our long-term study of this population is to obtain this kind of evidence.

Comparison of behavioral measurements in several populations shows the strong effect of the breeding situation on individual strategies, and this seems to hold for southern elephant seals (unpublished data). Detailed knowledge of the demography, social behavior, and breeding biology is the first step toward a reliable description of the individual strategies and the evaluation of their effect on individual fitness. The baseline data we present in this paper set a reference point for our long-term research program on the breeding strategies of both male and female elephant seals.

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LITERATURE CITED

ALTMANN, J. 1974. Observational study of behaviour: Sampling methods. Behaviour 49:227–267.

AMERICAN SOCIETY OF MAMMALOGISTS. 1967. Standard measurements of seals. Journal of Mammalogy 48:459–462.

ANGOT, M. 1954. Observations sur le mammiféres marins de l'Archipel de Kerguelen. Mammalia 18:1–111.

ARNBOM, T. A., M. A. FEDAK AND P. ROTHERY. 1994. Offspring sex ratio in relation to female size in southern elephant seals, *Mirounga leonina.* Behavioural Ecology and Sociobiology 35:373–378.

BALDI, R., C. CAMPAGNA, S. PEDRAZA AND B. J. LE BOEUF. 1996. Social effects of space availability of southern elephant seals in Patagonia. Animal Behaviour 51:717–724.

BARRAT, A., AND J. L. MOUGIN. 1978. L'eléphant de mer *Mirounga leonina* de l'île de la Possession, archipel Crozet (46°25'S, 51°45'E). Mammalia 42:143–174.

BESTER, M. N. 1980. The southern elephant seal *Mirounga leonina* at Gough Island. South African Journal of Zoology 15:235–239.

BESTER, M. N. 1990. Population trends of subantarctic fur seals and southern elephant seals at Gough Island. South African Journal of Antarctic Research 20:9–12.

BESTER, M. N., AND P. Y. LENGLART. 1982. An analysis of the southern elephant seal *Mirounga leonina* breeding population at Kerguelen. South African Journal of Antarctic Research 12:11–16.

BESTER, M. N., AND I. S. WILKINSON. 1994. Population ecology of southern elephant seals at Marion Island. Pages 85–97 *in* B. J. Le Boeuf and R. M. Laws, eds. Elephant seals. Population ecology, behavior, and physiology. University of California Press, Berkeley, CA.

BOYD, I. L. 1991. Environmental and physiological factors controlling the reproductive cycle of pinnipeds. Canadian Journal of Zoology 69:1135–1148.

BOYD, I. L., T. R. WALKER AND J. PONCET. 1996. Status of southern elephant seals at South Georgia. Antarctic Science 8:237–244.

CAMPAGNA, C., AND M. LEWIS. 1993. Growth and distribution of a southern elephant seal colony. Marine Mammal Science 8:387–396.

CAMPAGNA, C., B. J. LE BOEUF, M. LEWIS AND C. BISIOLI. 1992. Equal investment in male and female offspring in southern elephant seals. Journal of Zoology, London 226:551–561.

CAMPAGNA, C., M. LEWIS AND R. BALDI. 1993. Breeding biology of southern elephant seals in Patagonia. Marine Mammal Science 9:34–47.

CARRICK, R., AND S. E. INGHAM. 1960. Ecological studies of the southern elephant seal, *Mirounga leonina* (L.), at Macquarie Island and Heard Island. Mammalia 34:325–342.

CARRICK, R., AND S. E. INGHAM. 1962. Studies on the southern elephant seal, *Mirounga leonina* (L.). V. Population dynamics and utilisation. C.S.I.R.O. Wildlife Research 7:198–206.

CARRICK, R., S. E. CSORDAS, S. E. INGHAM AND K. KEITH. 1962. Studies on the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. C.S.I.R.O. Wildlife Research 7:119–160.

CONDY, P. R. 1977. The ecology of the southern elephant seal *Mirounga leonina* (Linnaeus 1758), at Marion Island. Ph.D. thesis, University of Pretoria, Pretoria, South Africa. 146 pp.

CONDY, P. R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* at Marion Island. South Africa Journal of Zoology 14:95–102.

COSTA, D. P., B. J. LE BOEUF, C. L. ORTIZ AND A. C. HUNTLEY. 1986. The energetics of lactation in the northern elephant seal, *Mirounga angustirostris.* Journal of Zoology, London 209:21–33.

DEUTSCH, C. J., M. P. HALEY AND B. J. LE BOEUF. 1990. Reproductive effort of male northern elephant seals: Estimates from mass loss. Canadian Journal of Zoology 68:2580–2593.

DEUTSCH, C. J., D. E. CROCKER, D. P. COSTA AND B. J. LE BOEUF. 1994. Sex- and age-related variation in reproductive effort of northern elephant seals. Pages 169–210 *in* B. J. Le Boeuf and R. M. Laws, eds. Elephant seals. Population ecology, behavior, and physiology. University of California Press, Berkeley, CA.

EBERHARDT, L. L., D. G. CHAPMAN AND J. R. GILBERT. 1979. A review of marine mammal census methods. Wildlife Monographs 63:1–46.

ERICKSON, A. W., M. N. BESTER AND R. M. LAWS. 1993*a.* Marking techniques. Pages 89–118 *in* R. M. Laws. Antarctic seals. Research methods and techniques. Cambridge University Press, Cambridge.

ERICKSON, A. W., D. B. SINIFF AND J. HARWOOD. 1993*b.* Estimation of population sizes. Pages 29–45 *in* R. M. Laws. Antarctic seals. Research methods and techniques. Cambridge University Press, Cambridge.

FEDAK, M. A., T. A. ARNBOM, B. J. MCCONNELL, C. CHAMBERS, I. L. BOYD, J. HARWOOD AND T. S. MCCANN. 1994. Expenditure, investment, and acquisition of energy in southern elephant seals. Pages 354–373 *in* B. J. LeBoeuf and R. M. Laws, eds. Elephant seals. Population ecology, behavior, and physiology. University of California Press, Berkeley, CA.

FEDAK, M. A., T. ARNBOM AND I. L. BOYD. 1996. The relationship between the size of southern elephant seal mothers, the growth of their pups, and the use of maternal energy, fat, and protein during lactation. Physiological Zoology 69:887–911.

GUINET, C., P. JOUVENTIN AND H. WEIMERSKIRCH. 1992. Population changes and movements of southern elephant seals on Crozet and Kerguelen Archipelagos in the last decades. Polar Biology 12:349–356.

HINDELL, M. A., AND H. R. BURTON. 1987. Past and present status of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. Journal of Zoology, London 213:365–380.

HINDELL, H. A., AND H. R. BURTON. 1988. Seasonal haul-out patterns of southern elephant seals (*Mirounga leonina* Linn.) at Macquarie Island. Journal of Mammalogy 69:81–88.

LAWS, R. M. 1953. The elephant seal (*Mirounga leonina* Linn.). I. Growth and age. Scientific Reports of the Falkland Islands Dependencies Survey 8:1–62.

LAWS, R. M. 1956. The elephant seal (*Mirounga leonina* Linn.). III. The physiology of reproduction. Scientific Reports of the Falkland Islands Dependencies Survey 15: 1–66.

LAWS, R. M. 1994. History and present status of southern elephant seal populations. Pages 49–65 *in* B. J. Le Boeuf and R. M. Laws, eds. Elephant seals. Population ecology, behavior, and physiology. University of California Press, Berkeley, CA.

LE BOEUF, B. J. 1974. Male-male competition and reproductive success in elephant seals. American Zoologist 14:163–176.

LE BOEUF, B. J., AND K. T. BRIGGS. 1977. The cost of living in a seal harem. Mammalia 41:167–195.

LE BOEUF, B. J., AND R. H. LAWS. 1994. Elephant seals: An introduction to the genus. Pages 1–26 *in* B. J. Le Boeuf and R. M. Laws, eds. Elephant seals. Population ecology, behavior, and physiology. University of California Press, Berkeley, CA.

LE BOEUF, B. J., R. CONDIT AND J. REITER. 1989. Parental investment and secondary sex ratio in northern elephant seals. Behavioural Ecology and Sociobiology 25: 109–117.

LEWIS, M. 1989. Dinámica de la población del elefante marino del sur, *Mirounga leonina,* en la Península Valdés. Ph.D. thesis. Universidad Nacional de La Plata, Argentina. 107 pp.

LEWIS, M., C. CAMPAGNA AND F. QUINTANA. 1996. Site fidelity and dispersion of southern elephant seals from Patagonia. Marine Mammal Science 12:138–147.

MANLY, B. F. J. 1992. RT: A program for randomization testing. University of Otago, Otago, New Zealand.

MCCANN, T. S. 1980. Population structure and social organization of southern elephant seal, *Mirounga leonina* (L.). Biological Journal of the Linnean Society 14:133–150.

MCCANN, T. S. 1981. Aggression and sexual activity of male southern elephant seals, *Mirounga leonina.* Journal of Zoology, London 195:295–310.

MCCANN, T. S. 1982. Aggressive and maternal activities of female southern elephant seals (*Mirounga leonina*). Animal Behaviour 30:268–276.

MCCANN, T. S. 1985. Size, status and demography of southern elephant seal (*Mirounga leonina*) populations. Pages 1–17 *in* Ling, J. K. and M. M. Bryden, eds. Studies of sea mammals in South Latitudes. South Australia Museum, Northfield.

MCCANN, T. S., M. A. FEDAK AND J. HARWOOD. 1989. Parental investment in southern elephant seals, *Mirounga leonina.* Behavioural Ecology and Sociobiology 25:81–87.

MULLER-SCHWARZE, D., E. C. WALTZ, W. TRIVELPIECE AND N. J. VOLKMAN. 1978. Breeding status of southern elephant seals at King George Island. Antarctic Journal of the United States 13:157–158.

NORUSIS, M. J. 1994. SPSS 6.1 Base system user's guide. SPSS Inc., Chicago, IL.

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

RIEDMAN, M. L., AND B. J. LE BOEUF. 1982. Mother-pup separation and adoption in northern elephant seals. Behavioural Ecology and Sociobiology 11:203–215.

ROFF, D. A. 1992. The evolution of life histories: Theory and analysis. Chapman and Hall, London.

ROUSSEEUW, P. J., AND C. CROUX. 1993. Alternatives to the median absolute deviation. Journal of the American Statistical Association 88:1273–1283.

SORENSEN, J. H. 1950. Elephant seals of Campbell Island. Cape Expedition Series Bulletin 6:1–31.

STRANGE, I. 1992. Wildlife of the Falkland Islands. Harper Collins Publishers, London.

TESTA, J. W., AND P. ROTHERY. 1992. Effectiveness of various cattle ear tags as markers for Weddell seals. Marine Mammal Science 8:344–353.

TRIVERS, R. L., AND D. E. WILLARD. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92.

VAN AARDE, R. J. 1980*a*. Fluctuations in the population of southern elephant seals *Mirounga leonina* at Kerguelen Island. South African Journal of Zoology 15:99–106.

VAN AARDE, R. J. 1980*b*. Harem structure of the southern elephant seal *Mirounga leonina* at Kerguelen Island. Revue Ecologique 34:31–44.

WILKINSON, L., M. A. HILL AND E. VANG. 1992. SYSTAT. Systat, Inc., Evanston, IL.

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