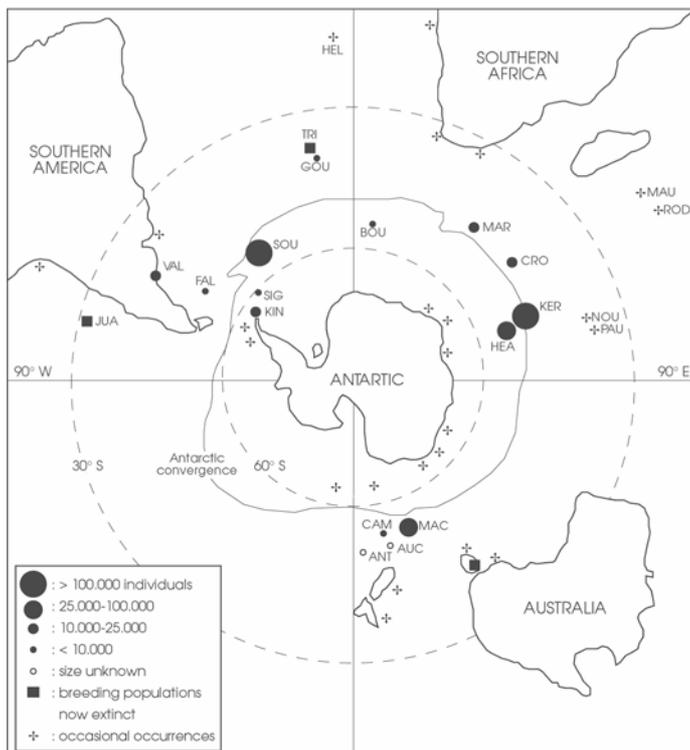


The elephant seals: introduction to the genus

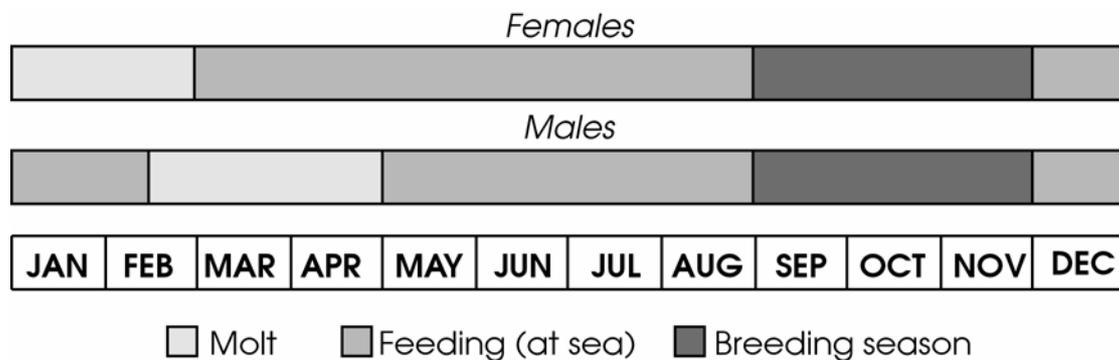
The genus *Mirounga* comprises two species, the southern elephant seal (*M. leonina*) and the northern (*M. angustirostris*). Northern elephant seals breed in California and Baja California. They were hunted almost to extinction during the 19th century, but after the introduction of protection laws in the United States and Mexico the species recovered at fast rate, and it is currently expanding outside its previous breeding range. The two species of the genus are very similar: external appearance, behaviour at sea, movement on land, gross traits of mating system and reproductive behaviour. The first difference is size, with the southern species much larger. In northern elephant seals maximum weight is about 2300 kg for males versus 3700 kg for southern, while females are more similar. On the contrary, secondary sexual traits are more developed in the northern species: the trunk is longer, and the neck and chest shield is more developed. The two species have similar breeding cycle, but they breed at different time of the year (January-February in the northern species, September-November in the southern).



Southern elephant seals have a circumantarctic distribution, with populations grouped in three main stocks (South Georgia, Kerguelen, and Macquarie). The elephant seal population of the Falklands is part of the South Georgia stock, which includes South Georgia, the South Orkney Islands, the South Shetland Islands, Gough Island and the Valdés Peninsula. 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. On the contrary, during the molting season, there is immigration of individuals from the Valdés and emigration to the South Shetlands.

The Southern elephant seal: biology of the species

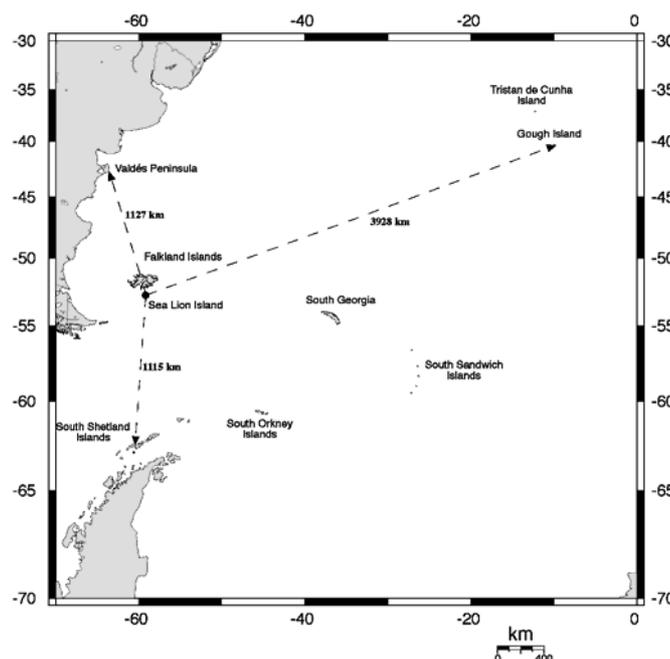
- Southern elephant seals have a mixed life style, with two aquatic phases and two land phases (breeding and molting).



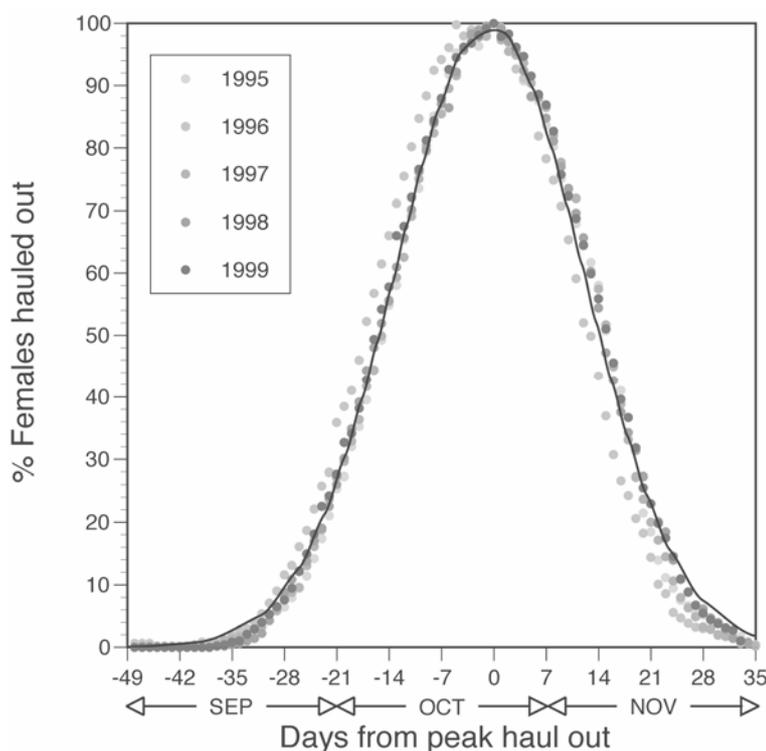
- When not on land, elephant seals show a nearly continuous pattern of long and deep dives, feeding mainly on squids. Feeding areas are usually very far away (up to a few thousands km) from the breeding sites. Elephant seals are able to deep dive up to 1200 m, while the mean depth is 500 m. They spend under water a mean of 23 minutes per dive, but up to more than 100 minutes. This exceptional diving capability is the result of a series of specialized adaptations to aquatic life, including the reduction of metabolic rate.
- They feed during the aquatic phases of the yearly cycle but fast during the land ones. The combination of fasting and concentrated breeding effort implies for both males and females a large weight loss, around 32 % for females and even more for males.
- Growth of males is a two phases process, with a notable growth spur just after puberty. Maturation in males is very long: puberty is reached when they are about five years old, but true maturity is reached only many years later. They usually are not able to get control of an harem until they are nine years old or older.
- Pre-breeding mortality of males is high, hence just a small percentage of each male cohort reaches full maturity and starts breeding.
- Breeding is strongly colonial. Females concentrate in large groups, of up to many hundreds individuals, and this produces a polygynous mating system.
- Reproduction is concentrated in a three months breeding season (September to November, with some variation between populations). Most of the females breed in a small part of the season, and 88% of matings occurs in a three weeks period.
- The mating system of elephant seals is the purest form of harem defense polygyny. Males compete between themselves using both conventional competition and direct fights. One male, called *harem holder* or *harem master*, has an almost complete control of each female group or *harem*, and most dominant males are in charge of the largest harems.

The elephant seals of Sea Lion Island: the population

The population of Sea Lion Island is small and localized. Of the 20.3 km of perimeter of the island, only the eastern sandy beaches (approx. 7.2 km) are occupied by breeding elephant seals. In the rest of the islands only isolated breeding females or very small groups are found. The island is almost isolated from the other elephant seals populations during the breeding season. The movements of individuals between the populations of the South Georgia stock are concentrated in the molt season, and during the breeding we never saw on Sea Lion Island a breeding individual marked in other populations. During the molt animals marked on Sea Lion Islands were observed in various places (see map).

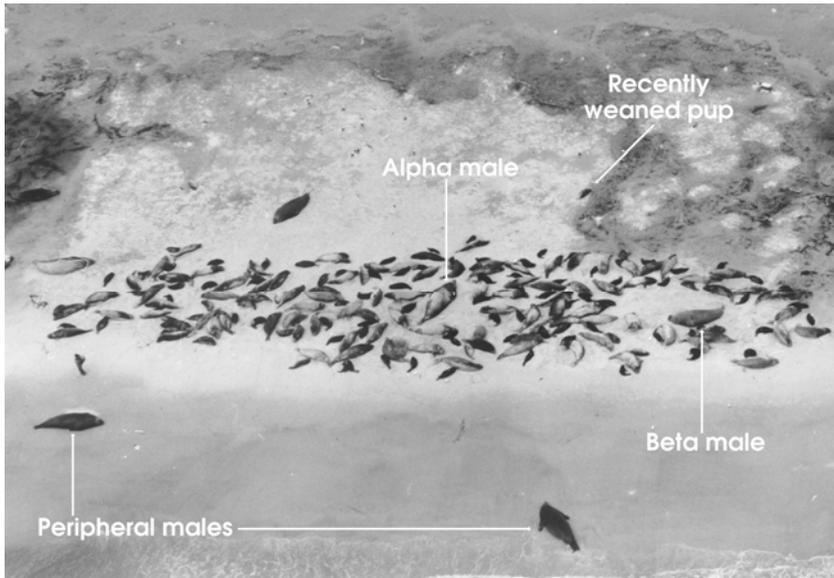


Females have a predictable pattern of presence on land during the breeding season. On Sea Lion Island, females begin to haul out during the second week of September; almost all the females have already gone back to sea by the third week of November. A typical female stays on land for 27 days: after a mean of 5 days spent on land she gives birth; then she suckles the pup for a mean of 20 days before coming into estrus; then she copulates for a mean of 2 days, while carrying on the lactation; at the end, she weans the pup (after a mean of 23 days of suckling), leaves the harem and goes back to sea.



The number of breeding females at peak haul out (19-20th of October) is about 480 females, that means an estimate for the entire population of 1800 seals one year old or older. Mean net productivity is about 520 pups, with very low pup mortality ($< 4\%$), among the lowest recorded for this species. Sex ratio at birth is almost balanced, with a slight prevalence of males. Estimated survival for breeding individuals is quite high, with 67-78% for females and about fifty percent for males. After an increase in number during the 1970s and early 1980s the population was almost stable from 1989 onward, with some annual fluctuation and a maximum increase of 7% from 1996 to 1997.

The elephant seals of Sea Lion Islands: the social structure



More than 90% of females breed in harems and isolated pupping is very rare. Females density is low, with 111 females per km of coastline suitable for breeding, and harems are small, with a median size from 31 to 35 females and a maximum of 125 females at peak haul out. Usually only the harem holder or *alpha* male is found among the females and males that are not able to get control of an harem (called *peripheral* males) roam

around the groups of females trying to get some copulations when the harem holder is busy or not paying attention. In some case also a *beta* male (a male in touch with females but subordinates to the alpha) is present in large harems. The ratio of breeding females to alpha males reaches the maximum just after the peak in the number of hauled out females, with 46-47 females per male. This may give an idea of the high level of polygyny of this species/population.

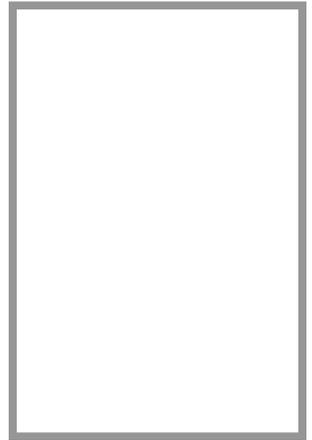
Fidelity to breeding site of individual females across seasons is high, with one third of females that came back to exactly the same harem for breeding. On Sea Lion Island all the breeding activities happen on the sandy beaches at the eastern tip of the island, where we usually have from 9 to 12 harems. Each harem usually starts around the third week of September and persists for about 55 days, with larger harems tending to begin earlier in the season.

To evaluate the role of male spatial strategies, and the effect of harem size and shape on efficiency of harem control we are mapping individuals and harems using a GPS system. To map position of individuals, we simply approach the resting individuals from the back and gather its position. To map harems we use mobile differential and walk around the harem trying to stay as much close to the peripheral females as possible. More recently we also started to map position of weaned pups after their expulsion from harems. The final goal is to develop a mathematical model of dispersion of pups during the land phase before the first feeding trip to sea.



Marking: long term study of individuals

One of the main goal of the research is to collect information on a large sample of breeding individuals of known age and with fully known life history. This requires safe individual recognition through the use of artificial marking. Long term marking is accomplished by tagging. Each breeding season we apply nylon cattle tags to the hind flippers of all the breeding males, the vast majority of breeding females (usually more than 98%) and all pups. Males and females are tagged in an opportunistic way, in most cases as soon as they arrive on land. Pups are tagged a first time shortly after birth, when they are with their mother, and a second time after weaning. Between seasons tag loss rates are very low for both males and females.



To improve the quality of long term marking of pups, we implemented an electronic identification system based on passive transponders. The system consists in a portable sensing device which transmits a radio-frequency signal to a specially designed implantable tag, which responds with another radio message containing its ID code. Transponders are packaged in disposable needles, pre-sterilized and ready-to-use, and are implanted with a special applicator. They are implanted between the tail and the begin of the right hind flipper. The harassment of the animal is very short. No detrimental effect of the implantation was detected. The main advantage of passive transponders is the reduction of the risk of tag failure, while their obvious disadvantages are cost (about twenty times the cost of a plastic tag), and the need to get close to the animal and use a sensing device to read the code.

To recognize individuals during social interactions, we mark all breeding males and as much females as possible (usually 70-85%), by painting an identification code on their back and/or flanks using commercial black hair dye. We understand very well that our intensive marking of animals may reduce the wilderness feeling of visitors of the island. Unfortunately, artificial marking is the single most important method of any research focused on the ecology and behaviour of individual animals. Moreover, the collection of detailed data about individuals is the only way



to get good estimates of demography and population dynamics of wild populations, that in turn are the most valuable tool for population forecasting and conservation.

Observation of behaviour: male competition

The core of the research project is the collection of behavioural data. From 1995, when we started our project, to 2000, we carried on a total of 7154 hours of behavioural observations. During each observation period we carefully collect on log sheets information on agonistic interactions between males, mating attempts and copulations, movements of males and females, and maternal behaviour.

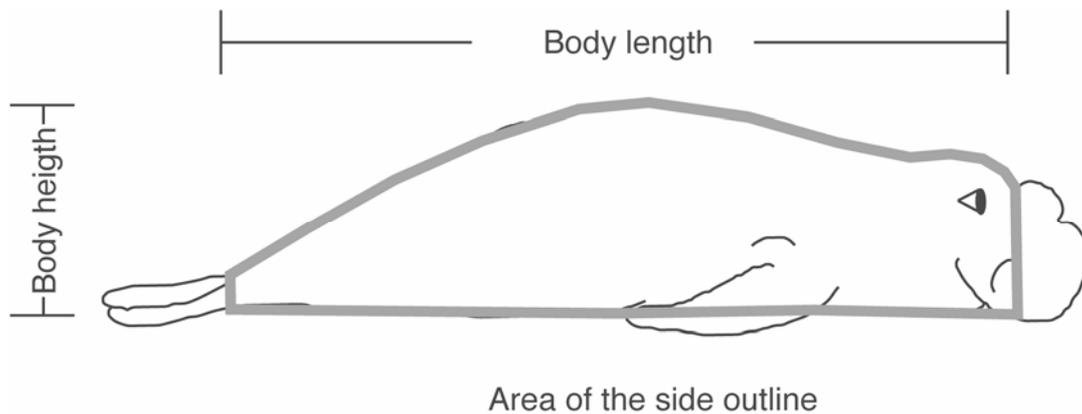


The core of our study of behaviour is the variation of male tactics of competition and breeding. The most impressive component of male behaviour is fighting. To get control of an harem, and thus be able to reproduce, a male should defeat all the other males of the area. Then, to maintain this, he needs to constantly keep other males away from females of the harem, by enforcing his status using vocal and visual displays.

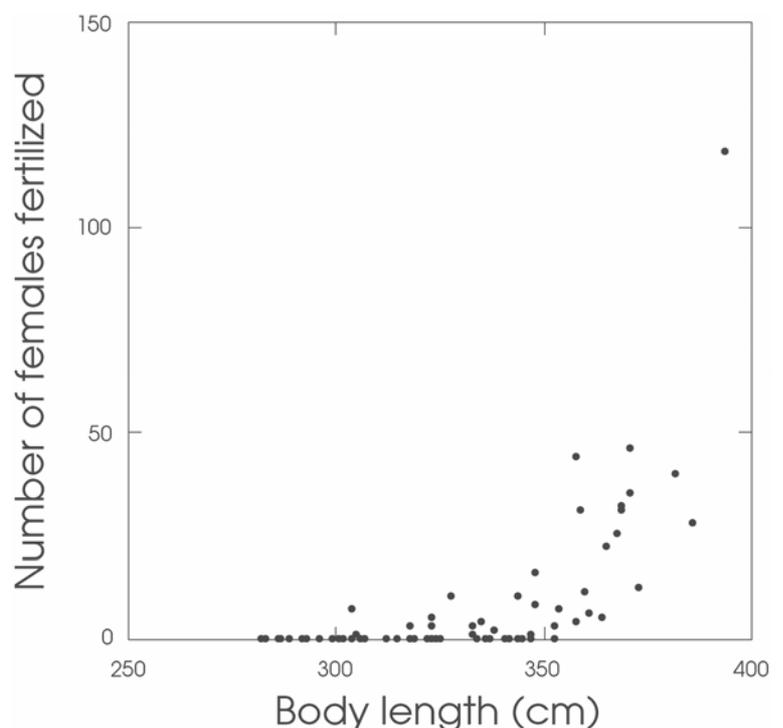
Male agonistic behaviour comprises two components, conventional assessment and direct aggression: both are very important in establishment and maintenance of dominance relationships. Assessment through visual and acoustic threats is more frequent than direct aggression and it is used to settle the most of the contests, especially between males with large differences in resource holding potential (size, age, experience). Aggression through direct interaction with physical contact and long all out fight, although less frequent, is of crucial importance in the initial phase of settlement of dominance relationships between males with almost equal RHP. The result of this intense competition is a huge skew in mating: a few males get control of an harem, and may fertilize more than one hundred females each breeding season, while the most of the other males don't copulate at all. Hence the variation in competitive abilities results in a large variation of breeding success, and this drives an intense sexual selection. By doing thousands of hours of observation of agonistic and breeding behaviour, and by videotaping fights, we hope to be able to determine which components of male phenotype build up a successful fighter and mate.

Body size: measurement problems and evolutionary role

The most amazing fact about elephant seals is the huge difference in size and morphology between males and females. Males may weight up to four tons while maximum recorded weight for females is around 700 kgs. Males are provided by a proboscis, enlarged canine teeth and a stiff dermal shield in the chest. All these characters may be the result of evolution by sexual selection: larger males may be much more effective in fighting and larger canine teeth could be used to give deeper bites. Moreover, females may prefer to mate with males with larger proboscis. Due to the huge size, direct measurement of elephant seals is not easy. Moreover, the most puzzling character, the trunk, should be measured while inflated and with the animal behaving naturally to provide meaning full data. Hence, we used indirect photogrammetric methods to measure length of the body and dimension of the proboscis and canines: by taking pictures of the animal with a calibrated surveying pole in view we are able to achieve a good precision in measurement without any direct manipulation of the animal. The area of the side outline as measured from picture is a very good indicator of weight: the estimated weight of the largest males on Sea Lion Island is over 4 tons.



Body size is a very important component of male success in competition. Body length is positively correlated to fighting success and to estimated number of females fertilized (see graph), although the relationship is not linear. Smaller males, usually subadults, have a very low success. Among adult males, the largest ones are the most successful, get top ranks in dominance hierarchies, and achieve the control of the biggest harems. Occasionally smaller adult males are able to get an harem, but this is always a small and marginal one.

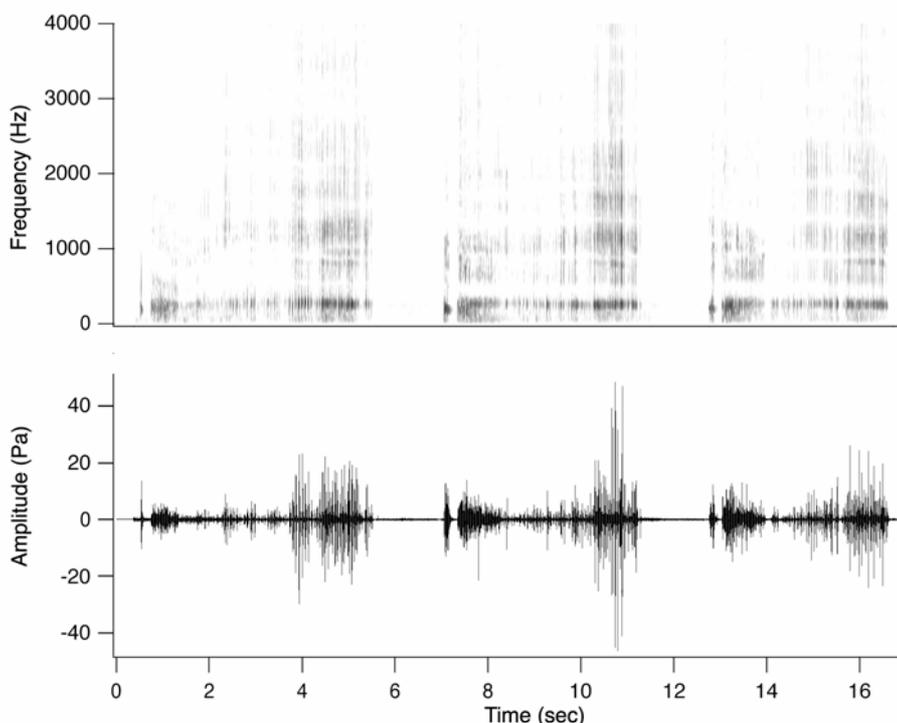


Sound recording: the study of acoustic communication

Agonistic interactions between males relies a lot on vocal communication: most of the interactions is infact solved by the only use of vocalizations. The study of acoustic communication is hence one of the main target of our research project. We have begun recording elephant seals sounds, starting with adult males and then taking records of younger males, females and pups for comparison. Due to the environmental noise caused by heavy winds we developed a recording protocol in which the people carrying on the recording is the stimulus that evokes the vocalization. This way we are able to get excellent quality recordings from a large number of males in a short period of time, when environmental condition are at best.



Spectrographic analysis of sounds revealed a very constancy of vocalization of each male and a large variation between males: hence vocalizations may permit recognition between individuals, and this had preliminary confirmation by playback tests. The acoustic parameters of sound are very well correlated with age: hence aggressive vocalizations



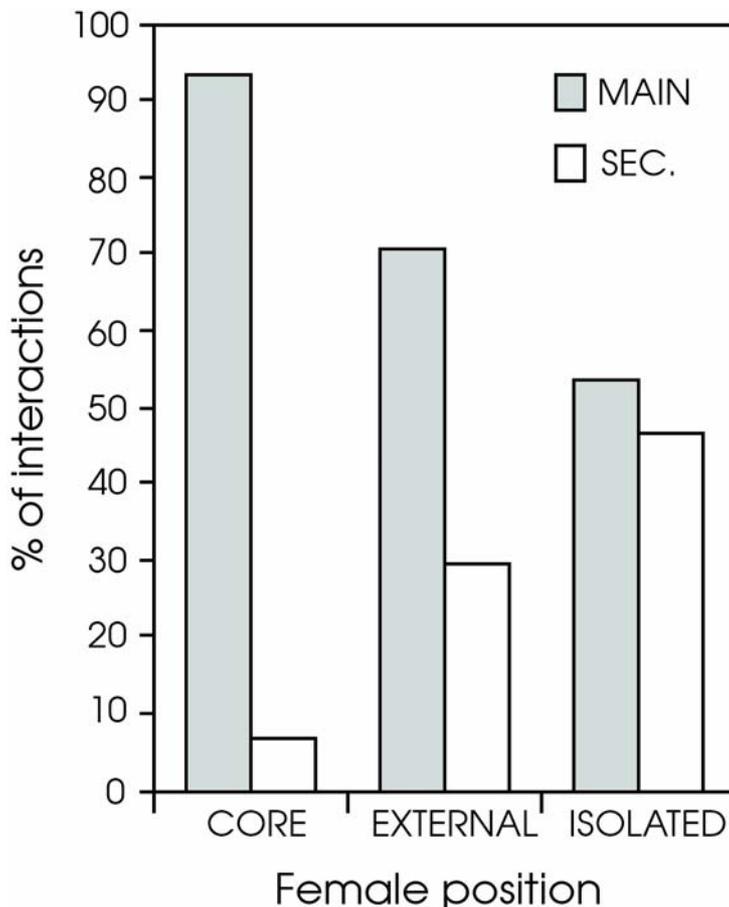
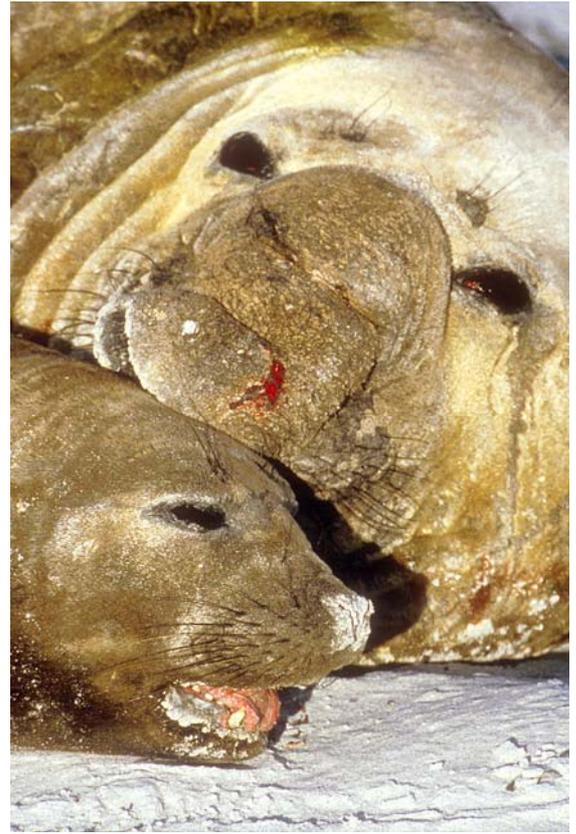
could be used by males to get information about the power of their contestants at the beginning of agonistic interactions.

Moreover the analysis of vocalizations of Sea Lion Island males revealed the presence of a small number of well defined vocalization typologies. The comparison with recordings of the Valdes Peninsula revealed the presence of sounds peculiar of each population. As in the northern elephant seals, the variation between

populations is so wide that we may talk about actual vocal dialects. The hypothesis of a widespread presence of dialects will be tested in the near future by extending the comparison to other populations of southern elephant seals.

Observation of behaviour: mating and harassment of females

Southern elephant seal males are much larger than females, they have enlarged canines, and they are much more agile on land. Hence, females have a small probability of escape from approaching males and may suffer intense sexual molestation. Most males have limited access to females due to the despotic mating system, and their libido is high. Therefore, male molestation may be potentially a serious source of damage for female. On Sea Lion Island, females are approached by males at high frequency, mostly when out of oestrus. The harassment level is negatively related to the ratio of breeding females to breeding males, and females breeding at the peak of the season suffer a lower level of harassment. The main short-term cost of harassment is disruption of the females' activity schedule, although suckling bouts are rarely interrupted by male harassment. On the contrary, long-term effects of harassment seem very limited, with very rare cases of serious physical damage.



Females of large harems are harassed less, and their likelihood to interact with secondary males is lower. Moreover, core harem females suffer less molestation by peripheral males than external females (see graph). Isolated females suffer more herding episodes, and are approached more frequently by secondary males, than harem female.

Females adopt behaviours that reduce the costs of male molestation. They synchronize their breeding activities to reduce harassment risk, and they rarely breed alone to reduce the likelihood of encounters with subadult males. They also show a clear preference for larger harems, that guarantee a lower harassment risk: movements between arrival on land and parturition are mostly from smaller to larger harems, and the likelihood of abandonment of pups is lower for large harems.

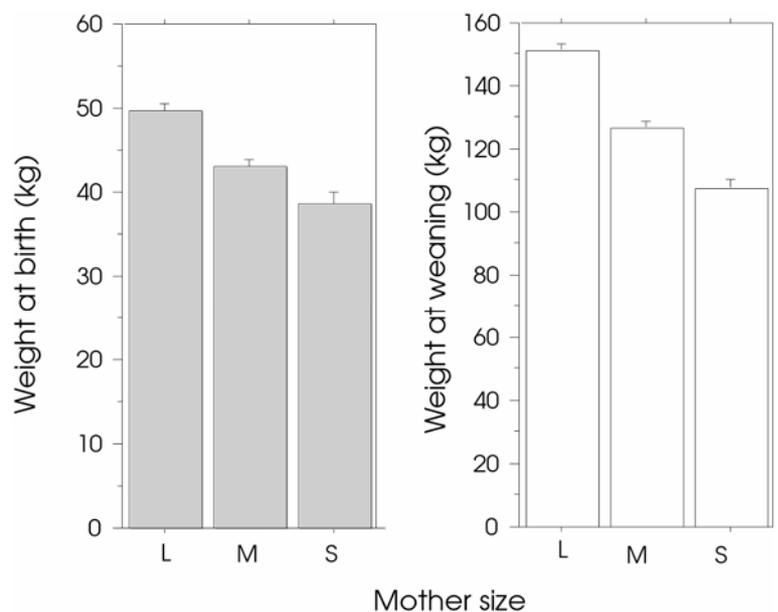
Handling of pups and weanlings: parental investment



A core aspect of the study of breeding strategies is parental investment, which in elephant seals is completely on the side of the mother. The most relevant indices of female parental investment are structural measure of the pups, and in particular: weight at birth, weight at weaning, total pre-weaning growth, and growth rate. To measure these parameters we carried on an intense weighing plan in 1998 and 1999. We sampled 179 pups at birth and 347 at weanings; 113 of the pups weighed at birth were weighed again at weaning. Pups are weighed using a simple canvas bag and a digital dynamometer held up by two people. Weanlings are weighed using a customized weighing bag and the same dynamometer used for pups, held up by an aluminum tripod. In all cases, pups are restrained by hand and handling time is short. Weighing of pups never resulted in physical damage of pup or abandonment by the mother, also weighing of weanlings also never had any detrimental effect.

The preliminary analysis of weighing data lead us to the conclusion that:

- mean weight at birth is about 46 kg, with males significantly heavier (49 vs 43 kg) and slightly longer (132 vs 128 cm) than females
- the difference between the sexes almost disappear by weaning, when females weigh about 133 kg and males about 139
- there is a huge individual variability of weaning weight, from 65 to 210 kg
- pups of bigger mothers are heavier and longer at birth, and they are also heavier at weaning (see graph); weaned pups of small mother weigh a mean of 107 kg at weaning, versus 151 kg for pups of large mothers
- mother size is the single most significant correlate of parental investment, and there is also a smaller effect of the mother experience, with older females being better able to suckle the pup

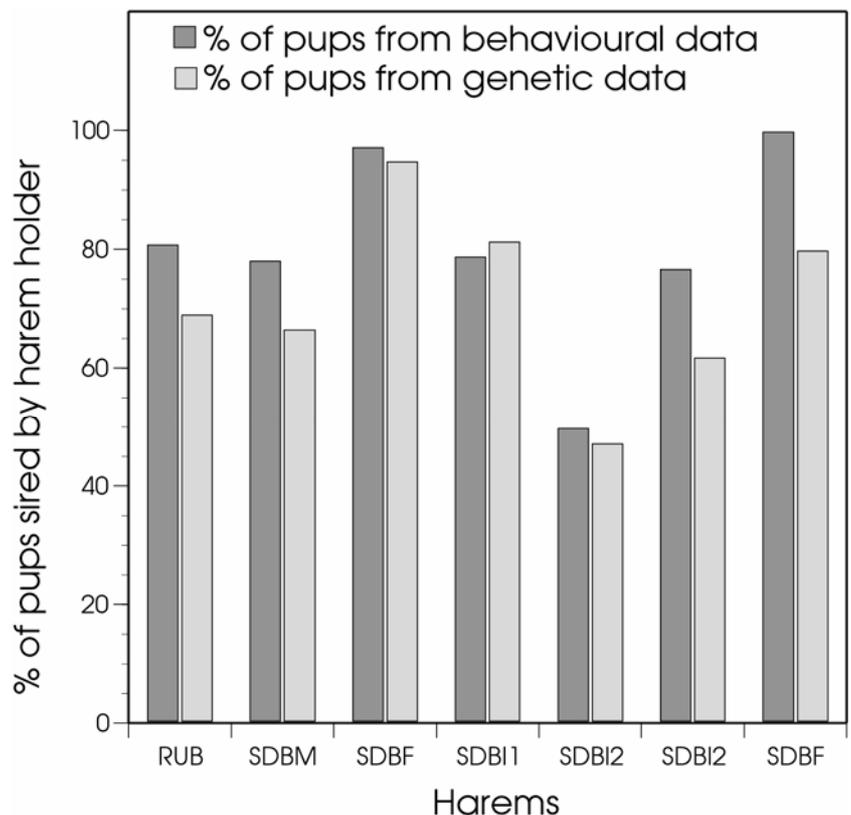


Skin sampling: genetics of paternity and population structure

The main goals of the genetic part of the project are to determine paternity and to compare the genetic structure of Sea Lion Island population to the ones of South Georgia and the Valdés Peninsula. The determination of genetic paternity is used to evaluate the relationships between observational measures of mating success and true reproductive success, while the comparison between populations is important to determine the pattern of gene flow between these populations and may have a significant impact on conservation issues.

In 1996 we began the collection of skin samples from breeding adults and weanlings to get the material for DNA analysis. Small skin samples (few millimeters of diameter) are taken from the hind flippers of breeding males, females and pups using ear notchers, an almost pain free procedure. Every season we collect samples from about a half of breeding females, all pups and all breeding males. In all, we collected 4626 skin samples from 3393 individuals. Respectively we sampled 815 adult females, 413 males and 2165 weanlings. DNA is extracted from tissue samples using standard procedures, it is amplified using the polymerase chain reaction (PCR), and the PCR product is visualised using fluorescent imaging. Paternity can be determined by the direct comparison of the genotypes of mother and offspring with that of putative fathers.

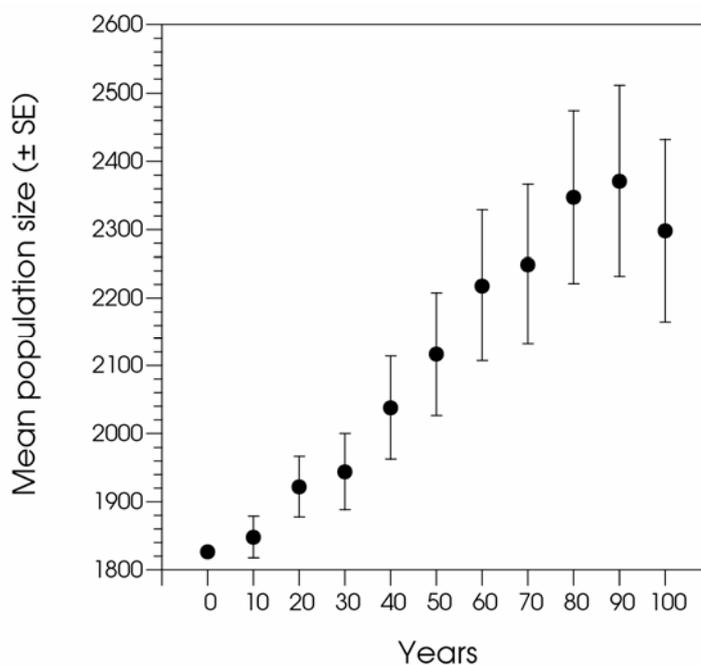
The results obtained with behavioural and DNA analysis show that the mating system of the Sea Lion Island population is strongly polygynous, with only very few males mating and even less achieving an high reproductive success. Genetic results are well in agreement with behavioural estimate of reproductive success. The number of pups sired as estimated from the observed distribution of matings is only slightly different from the number of pups calculated from DNA markers comparison. This means that the observed distribution of matings is representative of the actual number of pups sired by different males. In each harem, the harem holder get the majority of the paternities, regardless of the harem size. This means that harem holders are able to effectively manage the very complex social situation in which breeding happens, successfully stopping the continuous attempts of peripheral males to mate.



The future of the population and research perspectives

Long term viability of the population

Accurate long-term series of demographic data are available for most populations of southern elephant seals. However, research on the elephant seals of the Falkland Islands began only recently, and information for an accurate forecasting of the future of this population is scarce. We used extensive computer simulations to carry out a first analysis of the status of the population (see the graph of the estimated population size in the following hundred years). The most important factor affecting the risk of extinction of the population is the variability of the mortality rates, in



particular of the adult classes. Although the population does not appear to be at immediate risk of extinction, its small size and isolation make it necessary to accurately monitor the population trends and to acquire additional information.

In particular:

- 1) more accurate age-specific schedules of mortality and fecundity are urgently needed; therefore, the mark-recapture study should be continued
- 2) the information collected on SLI should be complemented by a global assessment of the breeding status of the SES in the entire Falklands archipelago
- 3) long distance movement patterns should be urgently studied, by tracking seals at sea: this will permit the identification of foraging areas, which are at the moment completely unknown

The future of the research

We plan to carry on the fundamental parts of our research in the long term: we need to get information about phenotype and breeding success for a large number of years to get the large samples required for a detailed analysis of the action of selection on individual life histories. Sea Lion Island was selected at the beginning of the study because it shelters a small and localized population of elephant seals, and this represents an ideal situation to collect high resolution data about ecology and behaviour of individual animals. Our field work fully confirmed these expectations. Now, our first goal is to carry on the routine work of marking, censusing and observation that permits us to collect detailed information about breeding of marked individuals. On the other side, we plan to experiment and develop new techniques that should improve our understanding of the population and of individual reproduction. In particular, we are currently looking for new funding sources to start the deployment of satellite tags to study movements at sea.