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The food consumption of Southern elephant seals (*Mirounga leonina*)

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Summary

This study concerns the food consumption of 1 male and 2 female Southern elephant seals at Marineland, Antibes, France. The females' food intake increased for about 3 years after which it stabilized at around 3400 kg/year. The male's annual intake reached a peak of 11.600 kg during his 6th year after which it dropped and stabilized at around 8000 kg/year. Although the animals were allowed to eat as much as they wanted, the food intake fluctuated seasonally. The annual periods with a low food intake correspond with the breeding (after maturity) and moulting seasons in both sexes. After each moult, the animals increased their food consumption to replenish their energy reserves. In relation to their body weight, the animals ate less than the rough estimate normally used for animals in the wild. This could be because, at Marineland, the air and water temperatures are higher, the diet has a higher energy content, and less energy is needed for feeding than in the wild.

Introduction

The Southern elephant seal (*Mirounga leonina*) is the largest pinniped and has a circumpolar distribution in the Southern Ocean. The major breeding population occurs on islands around the Antarctic Convergence (McCann, 1985). Southern elephant seals were hunted so intensely that the numbers had declined to around 600 000 in 1960. After sealing stopped at South Georgia in 1964, numbers increased (Laws, 1979). However, the number of Southern elephant seals on the Kerguelen Islands seems to have decreased during the last decade. The causes for this decline are not known, but diminution of fish numbers due to increased commercial fishing activities could have been of influence (Laws, 1979; Van Aarde, 1980; Pascal, 1985). To determine the annual energy requirement of a population, information is needed on its size and composition, and on the annual food consumption of the animals. This latter is dependent on sex and age. Laws (1956) has studied the stomach contents of a few Southern elephant seals. This small sample showed that cephalopods, taken mostly in pelagic waters, constitute roughly 75% of the diet, and fish (mainly *Notothenia spp*) constitute the remaining 25% of the diet and are taken mostly inshore. Clarke & MacLeod (1982) also found cephalopods in Southern elephant seal stomachs.

More detailed information is needed on the prey species taken in different areas, seasons and years. Very little is known about the amount of food consumed per day, or about food intake changes due to the time of year, the age, the reproductive cycle, and sex-linked food intake differences. This type of data can be derived from food records of animals kept in zoological parks. Marineland in Antibes, France, has kept Southern elephant seals from the Kerguelen Islands since 1972. This paper is about the food consumption of 3 Southern elephant seals at the park. The results may be useful for energetic studies to assess the impact of the world population of Southern elephant seals (which is estimated at 750 000; McCann, 1985) on fish populations. The need of the parameter of food intake in the design of a rational management plan for this seal species has been stressed by Laws (1979), Bonner (1982) and McCann (1985).

Materials and Methods

Study animals

This study concerns the food consumption of 3 Southern elephant seals (*Mirounga leonina*). One female (code: M1MA002) was born on the Kerguelen Islands in October 1971 and arrived at Marineland on 12 January 1972. The male (code: M1MA001) and another female (code: M1MA003) were born on the Kerguelen Islands in October 1975, and arrived at Marineland on 4 March 1976. All 3 animals were bottle-fed for some weeks until they accepted fish. To make the pups start to accept dead fish in a pool, live Trout (*Salmo trutta*) were offered, a technique which was described earlier by Bullier (1954). In the wild, newly weaned 3-week-old pups are deserted by their mothers and fast for 5 to 6 weeks during which they learn to swim near the beaches. A month later they leave the breeding grounds (Carrick *et al.*, 1962a).

Study area

Between 1972 and 1983 the animals were kept in an outdoor pool (19 m × 13 m; 2 m deep) filled with natural sea water from the Mediterranean. In the beginning of 1984 they were transferred to a larger pool (30 m × 15 m; 2.5 m deep). The water temperature varied from 8°C to 25°C, air temperature from −2°C to 35°C. Adjacent to the pool a beach was available where the animals could haul out. Marineland is located 7°3′ East longitude and 43°30′ North latitude.

Food

The animals were fed 2 to 4 times per day on a mixed diet of, on average, 50% Mackerel (*Scomber scombrus*) and 50% Herring (*Clupea harengus*), based on weight. Vitamins were added to the fish, after it had been defrosted. During the last feed of the day the animals were given as much as they wanted to eat. Feeding was stopped as soon as the animals started to play with the food instead of consuming it immediately. This was considered a sign of satiety. Records were kept of the amount and type of food consumed during each feed. These daily food intake data form the basis of the present study.

In some months of 1979 and 1980, Herring and Mackerel were difficult to obtain. Instead Whiting (*Merlangius merlangus*) was given and a reduction in the food consumption resulted. For this reason the records of 1979 and 1980 were omitted in the analysis of the seasonal intake fluctuations. In 1984 the animals were moved into a new pool. This change of environment probably caused the male and female 002 to eat much less than expected in that year. The food records of 1986 were incomplete, so this year was omitted in the analysis.

Results

Age related changes and sexual differences

The male's annual food consumption increased steadily until in his 5th year he ate 6300 kg. Then his food intake increased dramatically to reach a maximum of 11.600 kg in his 6th year (Fig. 1A). After this, his food consumption dropped and stabilized at around 8000 kg/year.

Female 002's annual food consumption increased slightly until her 4th year in which she ate 3500 kg (Fig. 1B). During female 002's fifth year, animals 001 and 003 were introduced to her pool. In that year she only ate 2400 kg. After her fifth year, her intake remained around 3500 kg/year, but was lower during her 8th and 9th year (1979 & 1980). Each year between her 10th and 14th year she gave birth to a full-term pup in April or May. Although she did not suckle her pups, the food intake increased during these reproductive years to a maximum of 4500 kg during her 14th year. After these reproductive years her food intake dropped to around 3200 kg/year.

Female 003's annual food consumption increased until her 3rd year in which she ate 3800 kg (Fig. 1C). After that it dropped for 2 years (1979 & 1980) and stabilized around 3500 kg/year. Although she mated, she never produced offspring.

Seasonal changes

When examining the seasonal changes, the male's food consumption record can be divided into 4 periods. In March of his first year he started to eat fish and no intake pattern could be detected that year. The food consumption increased almost every month of both his second and third year, indicating that the animal was growing (Fig. 2A). The food consumption was relatively less in September and October when moult occurred. No mating was observed in these years. Between the age of 4 and 9 years, when the animal did mate, there were marked seasonal fluctuations in the amount of food consumed per month (Fig. 2B). The animal ate much less than the yearly average between March and July (almost every year he stopped eating completely for about a week in that period), around average in August and September, and much more than average between October and January. In these years the period of sexual activity occurred between March and July. The male was obviously sexually active because his proboscis was erected and made the nose appear bigger, he made lots of noise, and he mated with and bit the females. The moult occurred between July and September, months during which his food intake was relatively low. Between the age of 10 and 13, the male's annual feeding pattern continued to fluctuate, but the extremes occurred in slightly different months (Fig. 2C). He ate less than average between February and April (when he was sexually active) and in September and October (when he moulted). Between November and January he ate much more than the yearly average.

The food consumption record of female 002 can be divided into 3 periods. She started to eat fish in January of her first year. Between the age of 1 and 8 (years without mating) her monthly food intake fluctuated only a little seasonally (Fig. 3A). She ate a little less than average between April and September, and a little more than average between October and February. Moult occurred between July and September. Until the age of 5 she was without a male companion. In 1976 the male was introduced, but he was not sexually mature until 4 years later in 1980 when female 002 was 9 years old. Between her 10th and 14th year of age she gave birth to a pup every year in April or May (Fig. 3B). In these years her monthly food intake showed marked seasonal

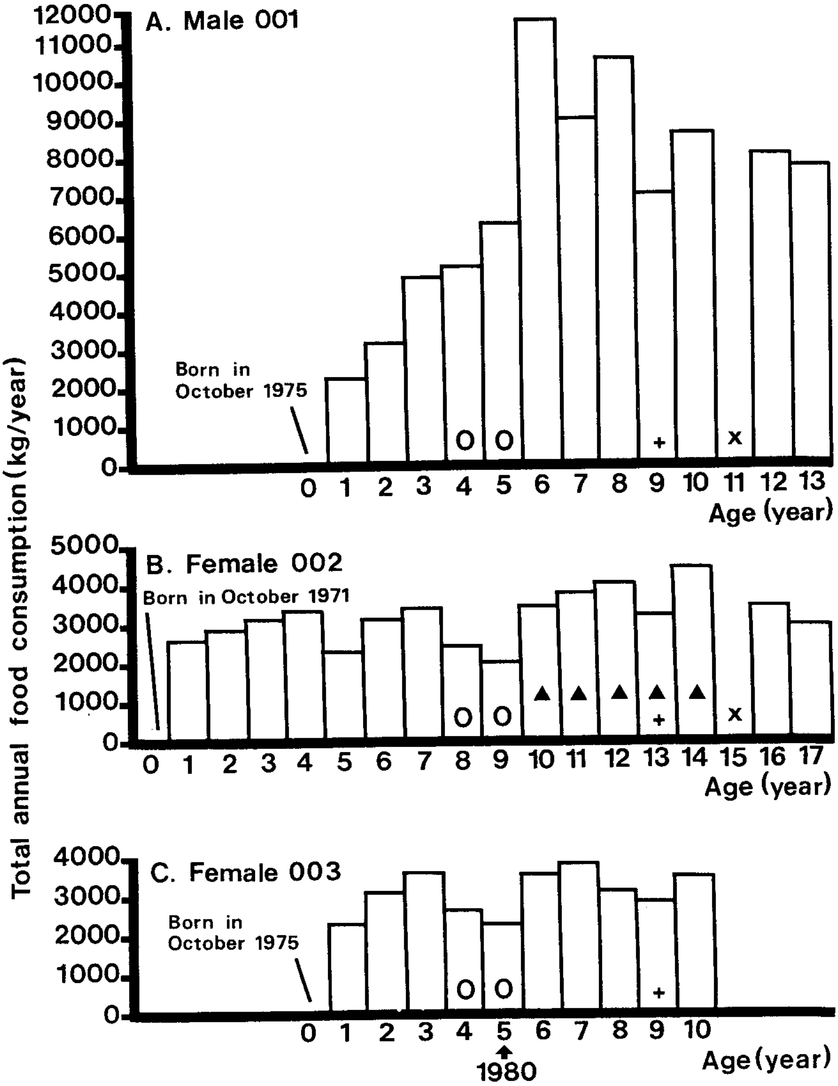

Figure 1. The annual food intake of a male (A) and 2 female (B & C) Southern elephant seals. Age 1 represents the first calendar year after the year of birth. 0 = low intake due to the introduction of a less preferred fish species. + = low intake due to transfer to a new pool. Triangle = a year in which a pup was born. x = a year in which the food records were incomplete and thus omitted.

changes. She ate much less than the yearly average between April and July (almost every year she stopped eating completely for about a week in that period), and much more than average between October and December. After these reproductive years, her food intake hardly fluctuated seasonally at all.

Female 003's food consumption record can be divided into 3 periods. She started to eat fish in March of her first year, and no monthly intake pattern could be detected that year. Both during her second and third year (years without mating) female 003's food intake showed a monthly increase indicating growth (Fig. 4A). Between the age of 4 and 10 years (when the male was sexually mature and mated with her) she ate much less than average between March and July (almost every year she stopped eating completely for about a week in that period), and much more between October and January (Fig. 4B). Sexual activity took place between March and June but she

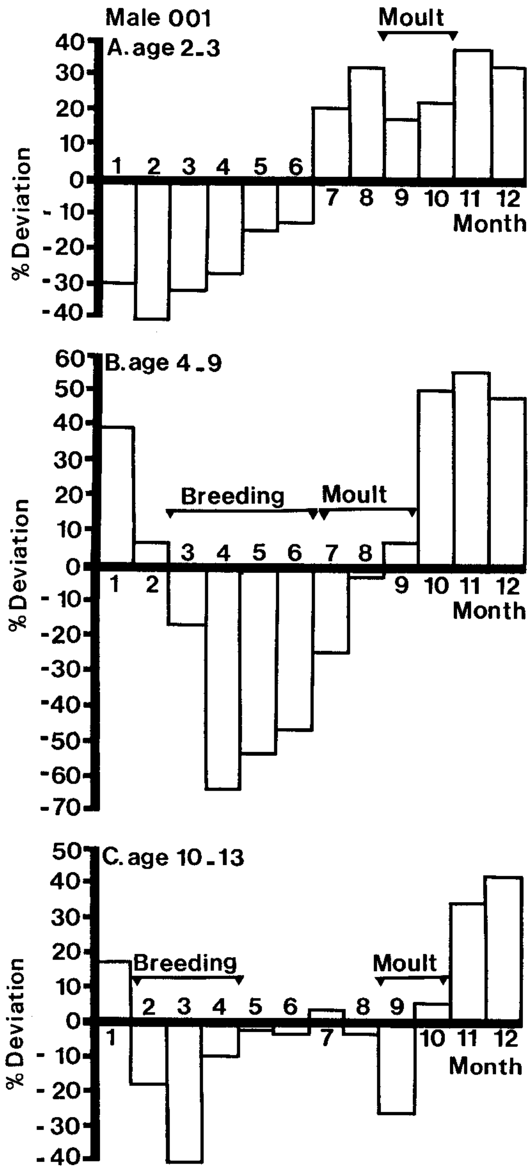

Figure 2. The average deviation (%) from the annual average monthly food consumption of the male Southern elephant seal; A) between age 2 and 3, B) between age 4 and 9, and C) between age 10 and 13.

never produced offspring. The moult fell immediately afterwards between July and September.

The animals of the present study spent a relatively large amount of time on land during the moult. They usually lay on the beach or in the shallow part of the pool, never seeking the shade provided. Although food was offered *ad libitum*, they reduced their intake significantly.

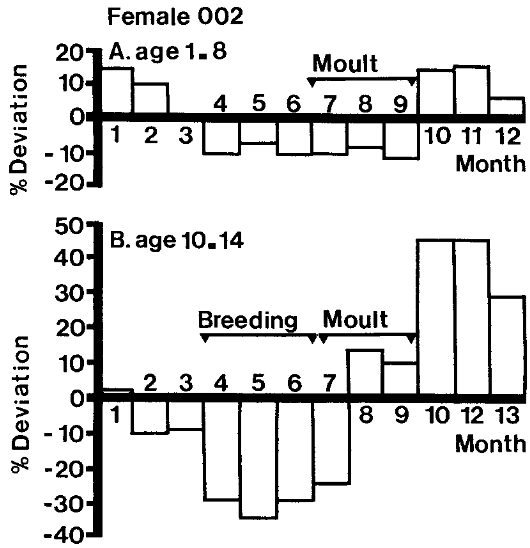

Figure 3. The average deviation (%) from the annual average monthly food consumption of Southern elephant seal female 002; A) between age 1 and 8 (years without mating), B) between age 10 and 14 (years in which she delivered a pup).

Two fish of the same species can have different nutritional or caloric values depending on the season and geographical area in which the fish were caught. The fish fed at Marineland is caught in different quantities and areas, and sometimes stored for several months. Probably, the seasonal or regional changes in caloric value of the fish cancelled each other out over the years, and did not lead to an artifical annual fluctuation in food consumption.

Discussion and conclusions

Influence of age and sex on annual food intake

Until the age of 2, the annual food consumption of all 3 animals increased similarly. After this age the male's food intake continued to increase strongly until he was 6 years old. Female 002's food intake increased until she was 4 years old and female 003's until she was 3 years old. After these years, the females were neither growing nor lactating, and their food consumption stabilized, except during female 002's reproductive years. These food intake patterns seem to correspond with the growth pattern of wild Southern elephant seals. There is little difference in body size between males and females until the age of 3 years (Carrick *et al.*, 1962b). After their third year the males continue to grow much faster than the females (Laws, 1953; Ling & Bryden, 1981). This difference in growth between males and females is thought to be linked to the age of maturation.

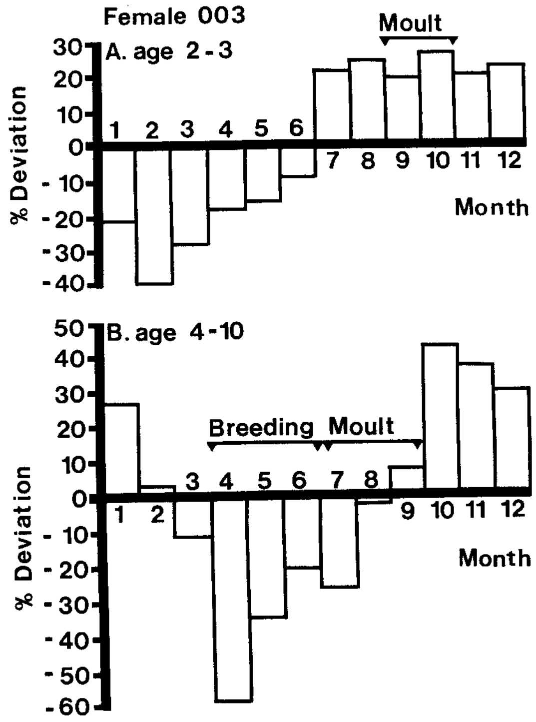

Figure 4. The average deviation (%) from the annual average monthly food consumption of Southern elephant seal female 003; A) between age 2 and 3 (years without mating), B) between age 4 and 10 (years in which she mated, but produced no pup).

On the Kerguelen Islands, males reach sexual maturity at 3 years, and they become harem bulls at 5–7 years of age (Angot, 1954). However, the age at which sexual maturity is reached depends on the sexual composition of a population. In non-hunted wild populations, most males become sexually mature around the age of 6, but do not breed until they are almost 10 years old. In populations in which the breeding males are hunted, the males mature 2 to 3 years earlier probably because of the lack of competition (Carrick *et al.*, 1962b). Since the male in the present study had no rivals he matured at an early age, around his 4th or 5th year. At around that time he went through a growth spurt, probably regulated partially by testosterone. At the Stuttgart Zoo, also in a situation without male competition, a pair of Southern elephant seals first mated when the male was only 5 years old and the female 4 (Neugebauer, 1967).

It is thought that at about the age of 4 the body size and body composition of males and females start to differ and sexual dimorphism becomes clear (Fig. 5) (Carrick *et al.*, 1962b). Males produce more muscle than females (Bryden, 1972), the head becomes broader, the large canine teeth erupt, and the proboscis starts to develop (Carrick *et al.*, 1962b). Around that age the food intake of the males and females in the present study started to differ. Sexual differences in food intake after maturation have also been observed in other sexually dimorphic pinnipeds such as Grey seals (*Halichoerus grypus*), Steller sea lions (*Eumetopias jubatus*) and South African fur seals (*Arctocephalus pusillus*) (Kastelein *et al.*, 1990, a, b & c).

If the females of the present study had been lactating, their annual food intake would probably have been higher. Pups weigh around 40 kg at birth and gain around 160 kg in the 23 day long suckling period (Laws, 1953). The mothers may lose up to 240 kg in that period (Bryden, 1969), which must be replenished after weaning. Lactation in Grey seals causes a 15% increase in the mother's annual food consumption (Kastelein *et al.*, 1990b).

Seasonal changes

The seasonal changes in food intake seem to be mainly influenced by 2 events: breeding and moult.

A. Seasonal food intake changes due to breeding

Males

The marked seasonal fluctuations in the male's food intake start in the year that copulation was first observed. This suggests that the decrease in the male's food consumption between March and July during his 4th to 9th year, was related to reproduction. In the wild, male Southern elephant seals start to come ashore in late August, a few weeks before gravid females haul out to give birth. Breeding bulls generally arrive earlier than bachelors (Carrick *et al.*, 1962b). Bulls are polygamous, but there is no physically defined territory. Breeding bulls station themselves near small groups of cows, when they arrive. Such a group then forms the nucleus of a harem. The bulls eat almost nothing during the reproductive period and try to mate with every female in their surroundings that is in oestrus (Ling & Bryden, 1981). During mating the bull typically grips the cow by the neck and this may leave tooth-marks on her neck (Carrick *et al.*, 1962b; McCann, 1981). For the breeding bulls, the breeding season is very long, since births, followed by females coming into oestrus, occur over a period of 2 months. During the breeding season the male in the present study usually stopped eating completely for a week.

Because the annual periods with the lowest food intake only partially overlap with the warmest months of the year (Fig. 7), the decrease in food consumption cannot be fully accounted for as a thermoregulatory adaptation. Because the male in the present study was given as much food as he wanted, it

Figure 5. A mature Southern elephant seal bull surrounded by mature females. Note the obvious sexual dimorphism. (Photo: W. N. Bonner, courtesy of the British Antarctic Survey).

seems plausible that the reduction in appetite between March and July was caused at least partly by endogenous factors. Griffiths (1985) observed that the testes of male elephant seals in the wild (= southern hemisphere) are quiescent from December to July inclusive. This corresponds to June to January in the northern hemisphere, the period in which the male of the present study eats much more than average. Griffiths (1985) found that as daylength increased, the gonadotrophin production by the pituitary gland increased, which initiated the onset of spermatogenesis. He reports that the first sperm reached the epididymis in September and the production was already reduced by November. This would be from March to May in the northern hemisphere, the period in which the food intake of the male in the present study was extremely low.

After the breeding season, Southern elephant seal bulls leave their breeding grounds in a generally emaciated condition. Bulls live longer (on average 18 years) than the females which live for 10 to 13 years (Laws, 1953; Carrick & Ingram, 1962). This is just the opposite to Grey seals in which the females live longer than the males (35 versus 25 years) (Hewer, 1964). In Grey seals this difference in life expectancy was thought to be due to the stress of fighting and starvation to the males during the mating season. This may not be true, because the breeding strategy of Southern elephant seal bulls seems similar to that of the Grey seal bulls.

Seasonal food intake changes related to the male's reproductive strategy are also found in other pinnipeds. Reproductive males of Steller sea lions (Kastelein *et al.*, 1990a), South African fur seals (Kastelein *et al.*, 1990c), California sea lions (*Zalophus californianus*) (Schusterman & Gentry, 1971), Northern fur seals (*Callorhinus ursinus*) (Spotte & Adams, 1979), Atlantic Harp seals (*Pagophilus groenlandicus*) (Sergeant, 1973), Grey seals, (Kastelein *et al.* 1990b), and Northern elephant seals (*Mirounga angustirostris*) (Ortiz *et al.*, 1984) also reduce their food intake during the breeding period when they haul out and spend most of their time defending their territories or mating.

Females

In the wild, most female Southern elephant seals reach maturity at between 2 and 4 years of age (Angot, 1954; Ling & Bryden, 1981; McCann, 1985) and at some locations between 3 and 6 years (Carrick *et al.*, 1962b). Cows then produce 1 pup every year, but sometimes miss a pregnancy after 6 or 7 pups (Laws, 1953). At the Kerguelen Islands, females produce a maximum of 6 pups (Angot, 1954). Female 002 in the present study did not become pregnant until the age of 9. This was because the male was not introduced until she was 5 years old and he only became sexually mature 4 years later.

In the wild, gravid cows haul out about 5 days before their pup is born. Most births are in September and October, the peak is in mid-October. Lactation continues for 3 weeks after birth, and mating occurs just before weaning. Thus the cows stay ashore and fast for 4 to 5 weeks each breeding season (Carrick *et al.*, 1962a; Ling & Bryden, 1981). Bryden (1968) noticed seasonal changes in the body weight of female Southern elephant seals in the wild due to breeding and moult. During lactation females loose 200 to 240 kg. Laws (1953) reports of an even greater weight loss of 320 kg after a lactation period of 23 days. Ulmer (1962) also noted seasonal food intake fluctuations in a female Southern elephant seal at the Philadelphia Zoo. During the colder months she ate on average 27 kg or fish a day, and during the warm season only 13.5 kg/day.

The food intake of female 002 did not fluctuate seasonally until her first pup was delivered when she was 10 years old. Female 003 showed marked seasonal food intake changes, whereas she did not produce pups. The observations on both females suggests that the presence of a sexually active male influences endogenous factors (steroids) that induce ovulation in a female and make her appetite fluctuate. Induced ovulation has also been suggested for Harbour seals, *Phoca vitulina* (Bigg, 1973).

Comparison between males and females

After the breeding season, both sexes are expected to replenish energy reserves by a drastic increase in food consumption. Males fast for longer than females, and use more energy for locomotion while mating and defending their harem. Females spend a shorter period on land, but use extra energy for lactation. The period of sexual activity of the male in the present study was longer than that of both females. Laws (1953) expected the males to lose relatively less weight than the females due to different hauling out habits. Bryden (1969) expected seasonal fluctuations in condition to be less marked in immature and non-breeding animals, which do not suffer the severe breeding weight loss but have brief haul-out fasts several times during the winter. In some other phocid species the females use relatively more energy during the breeding season than the males. Sergeant (1973) measured the thickness of the fat layer on Harp seals (*Phoca groenlandica*) during several seasons. In this species the blubber layer of reproducing females increased to 80 mm just before delivery and decreased to 20 mm just after weaning of the pup. In adult males, the blubber layer only changes from 60 to 40 mm. Similar sexual differences in weight loss were observed in Grey seals by Fedak & Anderson (1987). Northern elephant seal cows lose 42% of their body weight during lactation (15% loss of lean body mass and 58% loss of adipose tissue). Milk production accounted for 60% of the energy expenditure (Costa *et al.*, 1986).

A sexual difference in food intake in Southern elephant seals has not resulted in relative differences in stomach size. Bryden (1971) reports that the weight of the stomachs of both males and females is 0.54% of total body weight.

The size difference between male and female Southern elephant seal is thought to be greater than in any other mammal (Bonner, 1989). There are at least 2 explanations for this large sexual dimorphism in Southern elephant seals both of which could be valid. The males could be selected for their strength to defend a harem, and/or for their ability to accrue energy reserves which permits mating in good condition for longer.

B. Seasonal food intake changes due to moult

The moult in Southern elephant seals involves the loss of large patches of cornified epidermis and old hairs (Ling & Thomas, 1967; Ling, 1968). Many pinnipeds grow a fresh coat before a long period in the ocean (Ling, 1970). In the wild, Southern elephant seals haul out on the subantarctic islands to moult (Laws, 1953) and feed at a reduced rate or fast altogether (Ling & Bryden, 1981). The increase in skin temperature caused by hauling out may increase the rate of moult (Ling, 1970). Like other seals, Southern elephant seals moult annually at varying times according to location, age, sex and reproductive condition (Ling & Bryden, 1981). Angot (1954) reports that date of onset of the moult of Southern elephant seals at Kergeulen Islands varies. The moult lasts for about 8 weeks. On average bulls moult a few days longer than females (Carrick *et al.*, 1962b). Burton (1985) reports that 6 to 10 year old bulls at the Vestfold Hills, Antarctica, moult between the beginning of February and the end of April. On the northern hemisphere this would be between the beginning of August and the end of October. This corresponds with the moult and the period of low food intake of the male of the present study.

In the present study the moulting of all 3 animals also varied in timing and duration between individuals and between years. In the wild, Southern elephant seals spend much of their time ashore during the moult and therefore cannot feed. The animals of the present study also spent a relatively large amount of time on land to moult, and reduced their food intake significantly. The factors regulating the moult seem not only to prohibit the animals from spending much time in the water, but also seem to influence their appetite. In the wild this would make the period of fasting more bearable for the animals.

In the wild, especially immature Southern elephant seals sometimes have a winter haul-out. Some stay ashore for several weeks and often appear to be asleep, while others frequently go on journeys. It is not known whether they feed on such trips (Carrick *et al.*, 1962a). This phenomenon is not reflected in the food consumption of the animals at Marineland. However, due to the irregularity of this haul-out observed in the wild, it may have gone unnoticed, and not effected the appetite much.

The present study shows that in Southern elephant seals, body fat plays an important role as an energy supply besides temperature regulation (Bryden, 1964; Irving, 1969), streamlining of the body, protection of the body from shocks, and improvement of buoyancy. Compared with other pinnipeds, Southern elephant seals spend long periods of their lives on land during which they fast and have to depend on their energy reserves (Carrick *et al.*, 1962b; Ling & Bryden, 1981). Although blubber provides most of the energy needed, some energy in fasting seals comes from protein metabolism (Ortiz, 1987). This system has the advantage that it does not reduce the thermal insulation.

Factors influencing the timing of breeding and moult

The 3 Southern elephant seals in the present study were kept in the northern hemisphere, which means that they experience the opposite annual cycle of photo-periods to that which they would in their natural habitat. As a result, the breeding and moult cycles are shifted by approximately 6 months. A similar 6 month shift is seen in other Southern elephant seals kept in the northern hemisphere. Pups are born in April (Klös, 1966 & 1979) and May (Neugebauer, 1967) and the mating season is between April and August (Neugebauer, 1967). At Philadelphia Zoo, male Southern elephant seals start to moult in June and it is complete by early August (Ulmer, 1962).

In the wild, the timing of the breeding season varies at different breeding grounds (McCann, 1985), and could be controlled by annually re-occurring seasonal differences in food availability. Carrick *et al.*, (1962a) report that the moment of weaning anticipates the summer rise of zooplankton in surface waters which increases the pup's chances of survival. The moment of implantation of the blastocyst is thought to be determined by the daylength. During moult, many biological processes in the body change. Ling (1970) noted that moulting is coordinated with

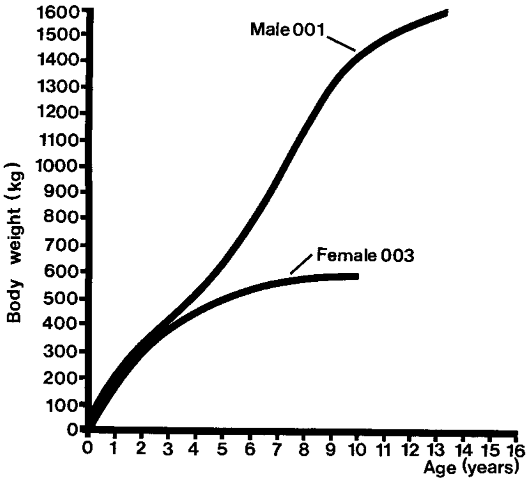

Figure 6. The body weight of the male and female 003 Southern elephant seals in the present study in relation to age (using the age-body length curve from Laws (1953), the post-mortem weights of the 2 full-grown animals in the present study and published birth weights).

season by the direct proximate stimulus of light acting through neuro-endocrine pathways. Pelage growth may also be regulated directly by nutritional status and, to some extent, indirectly by temperature and behaviour. Later, Condy (1979) reported that the mean day length appeared to act as an obligatory proximate factor initiating the haul-out to breed and onset of hair growth. He found that in addition temperature and radiation were obligatory factors initiating the haul-out to moult.

The variation in timing of breeding and moult linked to sex and age classes probably has an ecological advantage (Carrick *et al.*, 1962a). The adjustment of the terrestrial phase of Southern elephant seals with respect to time of arrival of the different age and sex classes, prevents crowding which would lead to an increase in intraspecific aggression (Ling, 1969).

Applicability of the results

Two of the animals in the present study were weighed post mortem (the weighing machine rounded off to the nearest 100 kg). The male weighed 1400 kg at the age of 14 years. He was lean at death, and probably weighed around 1600 kg when he was healthy. Female 003 weighed 600 kg at the age of 11 years. She was in a robust condition when she died. A rough age/body weight curve (Fig. 6) of these animals can be constructed using their annual food intake (Fig. 1), Laws' (1953) age/body length curve, and reported birth weights of 27 to 45 kg (Laws, 1953; Klös, 1966 & 1979; Neugebauer, 1967). This graph (Fig. 6) is not applicable for all Southern elephant seals, since several authors have reported large weight and growth rate

Table 1. The estimated body weights and average daily food intake (taken over a year) of the male and female 003 Southern elephant seals at certain ages

Animal	Sex	Age (year)	Estimated body weight (kg)	Daily food consumption (% of body weight)
M1MA001	M	2	300	3.0
M1MA001	M	4	500	2.9
M1MA001	M	6	750	4.3
M1MA001	M	8	1150	2.5
M1MA001	M	10	1400	1.7
M1MA001	M	12	1550	1.4
M1MA003	F	2	300	2.9
M1MA003	F	4	450	1.7
M1MA003	F	6	550	1.8
M1MA003	F	8	575	1.6
M1MA003	F	10	600	1.7

differences in adult animals of both sexes within one population and between populations (Carrick *et al.*, 1962b). Bryden (1972) reports that adult bulls weigh on average 2300 kg, and Laws (1979) estimates that mature males weigh between 2000 and 3000 kg. King (1983) describes adult males of 3600 kg. This suggests that the male in the present study was a relatively small animal. Also for female Southern elephant seals a wide range of weights have been reported. Bryden (1972) reports that adult cows weigh on average 390 kg, and Laws (1979) suggests a weight of between 400 and 900 kg. King (1983) describes cows weighing 900 kg. This suggests that female 003 was a medium-sized animal.

Figure 6 allows the comparison of the body weight estimate of the male and female 003 of the present study with their food consumption at different ages (Table 1). All intake averages are over an entire year and include the seasonal fluctuations. As expected, the data show that growing animals of both sexes need more energy relative to their body weight than full-grown animals. Especially the male ate a lot during his growth spurt around the age of 6 years. Unexpectedly in animals with such a pronounced sexual dimorphism, the adult male needed only about 0.3% less food in proportion to his body weight than adult female 003. Maybe this was due to his more strenuous and longer terrestrial breeding period. In the wild, both the breeding and moult periods are several weeks longer for the males than for the females (Ling, 1970). Condy (1979) calculates that the total annual haulout time of males is 65% longer than that of females.

The only food intake estimate discovered in the literature is from Laws (1960). He estimates the average weight of Southern elephant seals at 500 kg, and later (Laws, 1977) reports that they require 6% of their body weight per day (30 kg/day) for 9–10 months (females fast 2 months, males 3 months; Laws, 1956). On a 12 month basis this would mean a daily food intake of 4.9% for females and 4.5% for males. When male 001 was estimated to weigh 500 kg (at the age of 4), he was eating around 3% of his body weight per day. When female 003 was estimated to

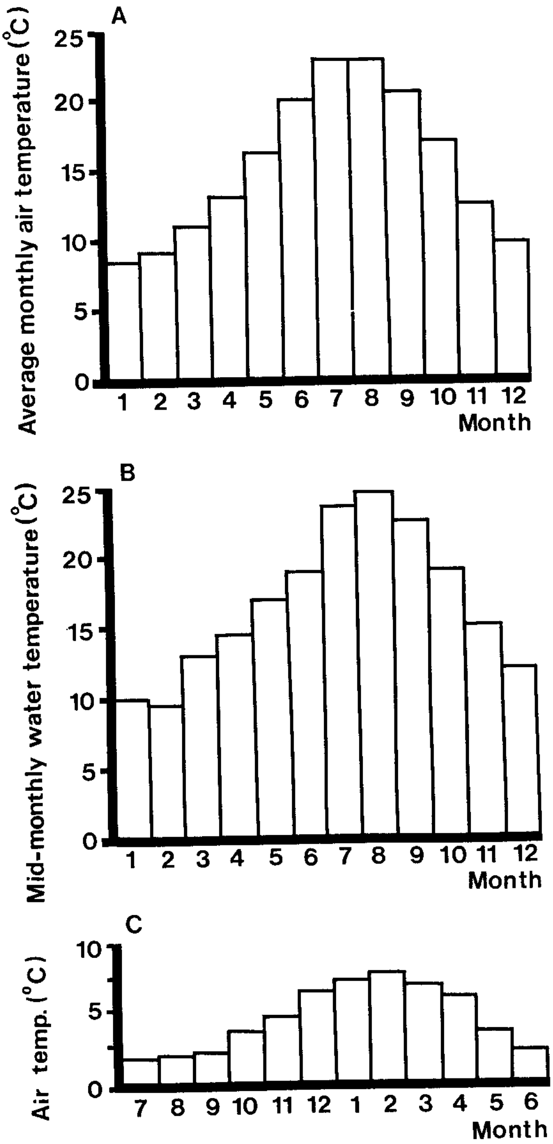

Figure 7. A) The average monthly air temperature at Marineland between 1949 and 1989. B) The water temperature of the Southern elephant seal pool at Marineland recorded on the 15th of each month in 1990. C) The average monthly air temperature at Kerguelen Island between 1952 and 1973 (adapted from Azibane *et al.*, 1977).

weigh 500 kg (between 4 and 6 years old), she was eating around 1.7% of her body weight per day. The difference between Laws' estimate and the data from the present study could be due to the following factors:

1) The difference in activity level between animals in the wild and in a pool. In the wild dives of more than 30 minutes have been observed (Matthews, 1952) during which the seals were probably foraging actively. At Marineland the animals did not have to dive, and thus used less energy, in order to get their food. However, the animals in the present study swam a lot and often stayed submerged on the bottom of the shallow area of the pool with their heads just under water. Except for a reduction in the moult and breeding season, the amount of time spent in the water was similar in the other seasons.

2) The air and water temperatures at Marineland (Fig. 7A & B) are higher than in the Southern elephant seal's distribution area (Azibane *et al.*, 1977; Fig. 7C). Angot (1954) reports water temperatures of 5 to 7°C near the Kerguelen Islands in January and Azibane *et al.* (1977) of temperatures between 2 to 4°C in December. These are summer months on the southern hemisphere, and the reported water temperatures are already less than the winter temperatures at Marineland.

3) Different species of fish have a different energy content per unit of weight (Costa, 1987; Prime & Hammond, 1987). Therefore, food intake quantities cannot simply be compared on the basis of the fresh weight of different food species. The fish species fed to the seals in the present study were not the natural prey of Southern elephant seals. Although the caloric content of the food eaten by the Southern elephant seals at Marineland (50% Herring and 50% Mackerel) was not determined it is clear that its energy content was much higher than that of the natural prey of Southern elephant seals (25% fish and 75% squid; Laws, 1956).

On the other hand the animals in the present study did eat some food during the breeding and moult seasons (probably because they were fed from the hand of the trainer), which would make their food intake higher than that of conspecifics in the wild. Reliable formula to convert the results of the present study to animals of other sizes, or to a different climate or water temperature do not yet exist (Naumov & Chekunova, 1981).

The present study was carried out on only 1 male and 2 females which reduces its representative value. However, most feeding patterns found were present for several years in each animal. Therefore the findings on these 3 animals may have a more general significance. There is thought to be little or no intermixing between the different wild populations of Southern elephant seals and the different growth rates and sizes in different stocks indicate this. Reproductive parameters also differ between stocks (Carrick *et al.*, 1962a; Bryden, 1972; Ling & Bryden, 1981). The animals in the present study come from Kerguelen Island, so the results may only apply to this population. Although the food intake data of the present study are difficult to extrapolate to the food intake of the wild population, the relative difference due to sex and age and changes due to season and breeding stage are probably comparable to those in the field. These changes were controlled by endogenous factors, because the animals at Marineland were offered as much as they wanted to eat.

The importance of fasting in the breeding season and moult is often forgotten in research on pinniped energetics. For instance, Spotte & Adams (1981) studied the energetics of adult female Northern fur seals and attributed all body weight changes to water temperature changes. They failed to take into account the endogenously regulated mechanism that allows females to fast during lactation. Studies on energy requirements (as summarized by Spalding, 1964), should be long term studies involving growing and adult individuals of both sexes, and males and females in different stages of reproduction.

The present study indicates that the food intake patterns in Southern elephant seals are extremely complex. It is risky to use a simple percentage of body weight to calculate the daily food requirement of an entire population of Southern elephant seals. To assess this requirement reliably, information on the geography, water temperature, climate, season, the diet and its caloric content, the digestive efficiency of the different prey species (Keiver *et al.*, 1984; Ronald *et al.*, 1984; Fisher *et al.*, 1991), and the size, sexual composition and age structure of the population is needed. To study the impact of the seals on fish populations, information on the dynamics of the fish stocks is also necessary.

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