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The food consumption of South American sea lions (*Otaria flavescens*)

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Summary

This is a study of the food consumption of 4 male and 8 female South American sea lions at Marineland, Antibes, France. The females' average daily food consumption increased for about 5 years after birth, after which it stabilized at around 5 kg/day. The males' average daily food intake reached a peak of about 12 kg/day during their 8th year after which it dropped and stabilized at around 9 kg/day. Adult males ate on average 3% of their body weight each day, and females ate 4%.

Although the animals were allowed to eat as much as they wanted, their food intake fluctuated seasonally. They ate less during the breeding season which was between June and September at Marineland. This is 6 months different from this species' breeding season in the wild in the Southern hemisphere. Energetics of this species are compared in human care and in the wild, and the estimation is made that wild adult males may eat 3700 kg of fish per year, and adult females around 1900 kg per year.

Introduction

South American sea lions (*Otaria flavescens*, Shaw, 1800) live south of Brazil on the east coast, and south of Ecuador on the west coast of South America (Vaz-Ferreira, 1975*a*; 1981). To assess the impact of this otariid on its prey, information is needed about the size and composition of sea lion populations, their seasonal movements, the composition of their diet and their energetic requirements.

The world population of South American sea lions was roughly estimated to be 300 000 in 1981 (Vas-Ferreira, 1981). Not much is known about the sex and age composition of the different geographical populations. Also very little is known about their seasonal movements (Hamilton, 1939; Ximénez, 1976).

The diet of South American sea lions has been studied by stomach content analysis by Hamilton (1934) Vaz-Ferreira (1950), Boswall (1972), Aguayo & Maturana (1973) and Vaz-Ferreira (1981). This species eats mainly fish, crustaceans and molluscs. More detailed information is needed on the prey species taken in different areas, seasons and years.

Very little is known about the energetic requirements of South American sea lions, the amount of food consumed per day, about food intake changes due to the time of year, the age, the reproductive cycle, or about sex-linked food intake differences. This type of information can be derived to some extent from food records of animals kept in zoological parks. The present study analyses the food records of South American sea lions kept at Marineland in Antibes, France, between 1974 and 1992.

Materials and Methods

Study animals

This study concerns the food consumption of 12 South American sea lions (Table 1). The 7 original animals were born in Uruguay, South America. Since 1986 they have produced offspring (Table 2).

Study area

Between 1973 and 1990 most of the animals were kept in a rectangular outdoor pool (35 m × 15 m; approx. 2 m deep). After 1990 the young animals (Ob9, Ob10 and Ob11) were housed in a separate pool (5 m × 20 m; approximately 2 m deep). Ob6 and Ob7 were housed next to the dolphin pool in separate enclosures since 1984 and 1991 respectively. All pools contained natural sea water from the Mediterranean. The water temperature varied from 8°C to 25°C, air temperature from −2°C to 35°C. Adjacent to the pools a land area was available to the animals. Marineland is located 7° 3′ East longitude and 43° 30′ North latitude.

Table 1. The South American sea lions and their relatedness

Code	Sex	Birth date, or est. year	Arrival date	Code sire	Code dam	Origin
Ob0	M	1973	1974	—	—	Uruguay
Ob1	F	1973	1974	—	—	Uruguay
Ob2	F	1981	1-1982	—	—	Uruguay
Ob3	F	1983	28-4-1984	—	—	Uruguay
Ob4	F	1983	28-4-1984	—	—	Uruguay
Ob5	F	1983	28-4-1984	—	—	Uruguay
Ob6	M	1983	28-4-1984	—	—	Uruguay
Ob8	M	1972	29-1-1988	—	—	Spain
Ob7	F	10-7-1989	—	Ob8	Ob2	Antibes
Ob9	F	23-6-1991	—	Ob8	Ob4	Antibes
Ob10	M	4-7-1991	—	Ob8	Ob3	Antibes
Ob11	F	8-7-1991	—	Ob8	Ob1	Antibes

Table 2. The ages of the South American sea lions and the years in which the animals were housed together

	Male Ob0	Male Ob6	Male Ob8	Female Ob1	Female Ob2	Female Ob3	Female Ob4	Female Ob5
1974	1			1				
1975	2			2				
1976	3			3				
1977	4			4				
1978	5			5				
1979	6			6				
1980	7			7				
1981	8			8				
1982	9			9	1			
1983	10			10	2			
1984	11	1#		11	3	2	2	2
1985	12	2#		12	4	3	3	3
1986	13	3#		13	5	4	4*(Ob0)	4*(Ob0)
1987	14D	4#		14	6	5	5	5
1988		5#	16	15	7*(Ob0)	6	6*(Ob0)	6
1989		6#	17	16*(Ob8)	8*(Ob8)	7	7	7
1990		7#	18	17	9	8	8	8
1991		8#	19D	18*(Ob8)	10D	9*(Ob8)	9*(Ob8)	9*(Ob8)
1992		9#		19		10	10	10

*=Year in which a pup was produced.
(Ob..)=sire of the pup.
#=In show pool, not in contact with conspecifics.
D=Year of death.

Food

The animals were fed twice a day, once in the morning and once in the afternoon. Until 1990 the diet consisted of on average 50% Mackerel (*Scomber scombrus*) and 50% Herring (*Clupea harengus*), based on weight. Starting in 1990 the diet consisted of on average 40% Mackerel (*Scomber scombrus*), 40% Herring (*Clupea harengus*) and 20% Capelin (*Trisopterus minutus capelanus*). Vitamins were added to the fish after it had been defrosted. During the last feed of the day the animals (except Ob6 and Ob7) 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. Ob6 participated in a show from 1984 and Ob7 from 1991, and as a result they were fed less to allow the trainers to control their behaviour.

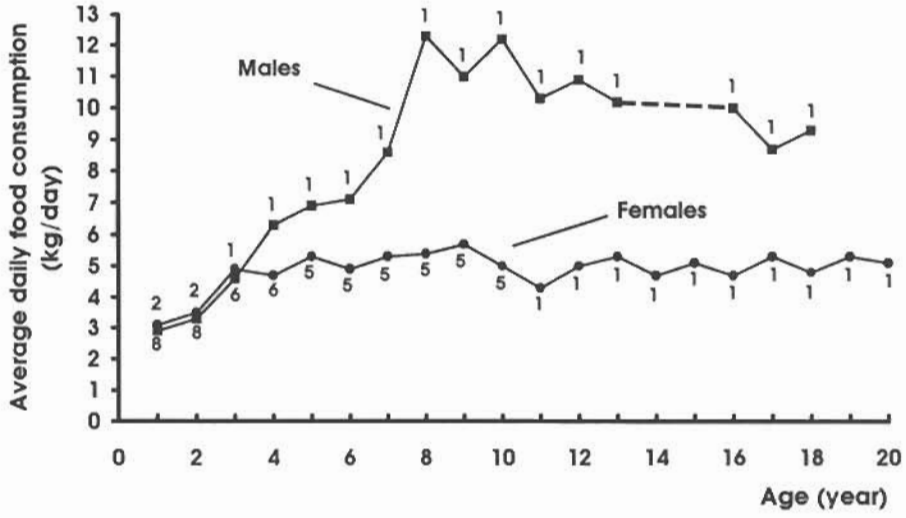

Figure 1. The average annual food intake of 3 male and 8 female South American sea lions at Marineland, Antibes. Age 1 represents the first calendar year after the year of birth. The numbers near the lines indicate the sample size for each age class. The dashed line connects the food intake data of 2 individuals.

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.

Results

Influence of age and gender on food intake

The food intake data of 3 males which were fed *ad lib.* are combined in Fig. 1. Until the age of 2 years their average daily food consumption increased slowly, thereafter it increased strongly to reach 12.3 kg/day at the age of 8 years. After the 8th year, the food intake slowly decreased and stabilized at around 9 kg/day. Data from male Ob6 are omitted in this graph, because his food intake was restricted by the training regime and followed the intake of the females closely.

The food intake data of 8 females which were fed *ad lib.* are also combined in Fig. 1. Up until their third year the females ate similar amounts as the males. Thereafter the females increased their food intake until it stabilized at around 5 kg/day after the age of 4 years.

Looking at individual animals and individual years, no influence of gestation or lactation could be found in the females' average daily food intake.

The pups started to eat fish around the age of 5 months, but often continued to suckle for many months (Table 3).

Age of reproduction

Table 2 shows the ages at which and the years in which the males and females were housed together.

Table 3. Age at which South American sea lion pups at Marineland, Antibes began to eat fish (suckling continued for some time)

Animal	Sex	Birth date	Age onset eating fish (months)
Ob7	F	10-7-1989	5
Ob9	F	23-6-1991	5*
Ob10	M	4-7-1991	7
Ob11	F	8-7-1991	4

*This animal was bottle-fed.

Male Ob0 first successfully fertilized a female when he was 12 years old. Male Ob6 was not housed with females during the study period, and male Ob8 arrived at the age of 16 years, and immediately mated successfully.

Females Ob1, Ob2, Ob3, Ob4 and Ob5 gave birth for the first time at the ages of 16, 7, 9, 4, and 4 years respectively, and first delivered and raised calves at the ages of 16, 8, 9, 6 and 9 years respectively.

Seasonal changes

Male Ob0's food intake increased each month until he was 4 years old. From the age of 5 his food intake fluctuated so that he ate less than the annual average in the summer (between June and September) and more than the average in the winter period (Fig. 2A). He also ate much less than the

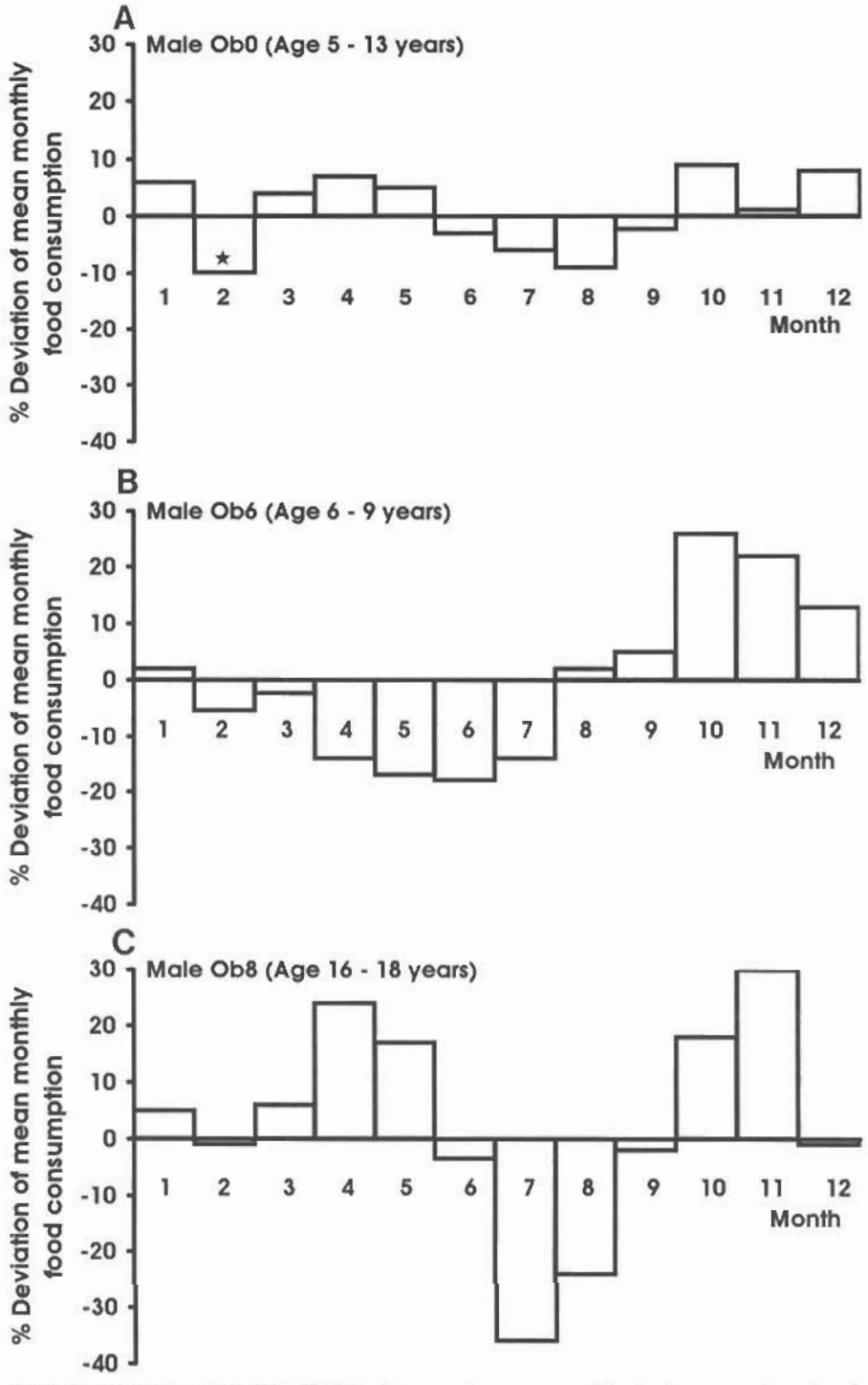

Figure 2. The average deviation (%) from the annual average monthly food consumption of male South American sea lion Ob0 between age 5 and 13 years (A), of male Ob6 between age 6 and 9 years (B), and male Ob8 between age 16 and 18 years (C). *low intake due to illnesses during 3 of the 9 years over which the average was taken.

annual average in February, which was due to gastro-intestinal illnesses in February during 3 of the 9 years over which the average monthly food intake was calculated. Male Ob6's food intake started to fluctuate in a similar way at the age of 6 years (Fig. 2B). He ate less than the annual monthly average between February and July. Male Ob8 arrived at the age of 16 years, and immediately showed an annual food intake cycle (Fig. 2C). He ate less than the annual monthly average between June and September. Both male Ob8 and male Ob0 mated between April and September.

Female Ob2 started to show an annual cycle in her food intake at the age of 4 years while Ob1, Ob3, Ob4 and Ob5 showed a cycle at 5 years. They generally ate less than average between March and August, and more than average in the winter months (Fig. 3A–E). The low food intake of female Ob4 in September (Fig. 3D) was due to illness in 1 of the 5 years over which the average was taken.

No obvious moult was detected in the study animals.

Discussion and conclusions

Influence of age and gender on food intake

In the wild, male and female pups have slightly different birth weights. Males weigh on average around 14 kg and females around 12 kg (Vaz-Ferreira, 1981; Capozzo *et al.*, 1991). The pups in the present study started to eat fish around the age of 5 months, but often continued to suckle for many more months. In the wild, juveniles are weaned after the new pups are born. This is usually when the juveniles are 1 year old, but sometimes when they are 2 years old (Vaz-Ferreira, 1981).

Adult male South American sea lions weight about twice as much as adult females (Vaz-Ferreira, 1981; Fig. 4), and the present study shows that the daily intake of adult males is about twice that of adult females. Large sexual differences in food intake after maturation have been observed in other sexually dimorphic pinnipeds such as Grey seals (*Halichoerus grypus*), Steller sea lions (*Eumetopias jubatus*), South African fur seals (*Arctocephalus pusillus*) and Southern elephant seals (*Mirounga leonina*) (Kastelein *et al.*, 1990*a, b & c*; 1991).

In the wild, females are sexually mature at the age of 3–4 years, and males at the age of 5 or more years (Vaz-Ferreira, 1981). The present study shows that females' food intake stabilizes at the age of 3 years, which suggests that they become reproductive when they are full-grown. The male in the present study showed a strong food intake increase between his 6th and 10th year. Because his mane started to appear in that period, suggests that it was the time of sexual maturation.

The animals in the present study were never weighed, but Vaz-Ferreira (1981) reports that in the wild adult males weigh around 350 kg in November–December at the beginning of the breeding season and around 250 kg in January, towards the end of the breeding season (which is summer in the southern hemisphere). Assuming that the average weight of an adult male is around 300 kg, and assuming that the adult males in the present study had similar weights as their wild conspecifics, the adult males in the present study ate around 3% of their body weight every day, averaged over the entire year.

Vaz-Ferreira (1981) reports that adult females normally weigh around 120 kg, and reach a maximum of 144 kg between December and January. Assuming that the average annual weight of an adult female is around 125 kg, and assuming that the adult females in the present study had similar weights as their wild conspecifics, the adult females in the present study ate around 4% of their body weight each day, averaged over the whole year.

Vaz-Ferreira (1981) describes a 3-year-old female of 68 kg. Assuming that the females in the present study were around this weight at the age of 3 years, they ate on average 6.7% of their body weight each day.

Vaz-Ferreira (1981) reports that captive South American sea lions consume about 8% of their body weight daily in fish, he does not mention water temperature, the age or the sex of the animals. His data may have been based on animals that were housed in a colder environment, or fed a diet of a lower caloric content than the animals in the present study. Alternatively, the animals he used may have been growing.

Age of reproduction

It is not clear why male Ob0 did not reproduce until he was 12 years old. Up until the age of 8 years, he was housed only with female Ob1. Possibly these animals were not compatible, or males of this species need to be surrounded by a certain number of females in order to show mating behaviour. The former is probably true, because when females Ob2, Ob3, Ob4 and Ob5 reached sexual maturity he mated with 3 of them, but still not with Ob1. Ob1 did become pregnant immediately after male Ob8 was introduced. Reproductive incompatability may serve to prevent inbreeding (=improve heterosis).

Seasonal changes in food intake

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

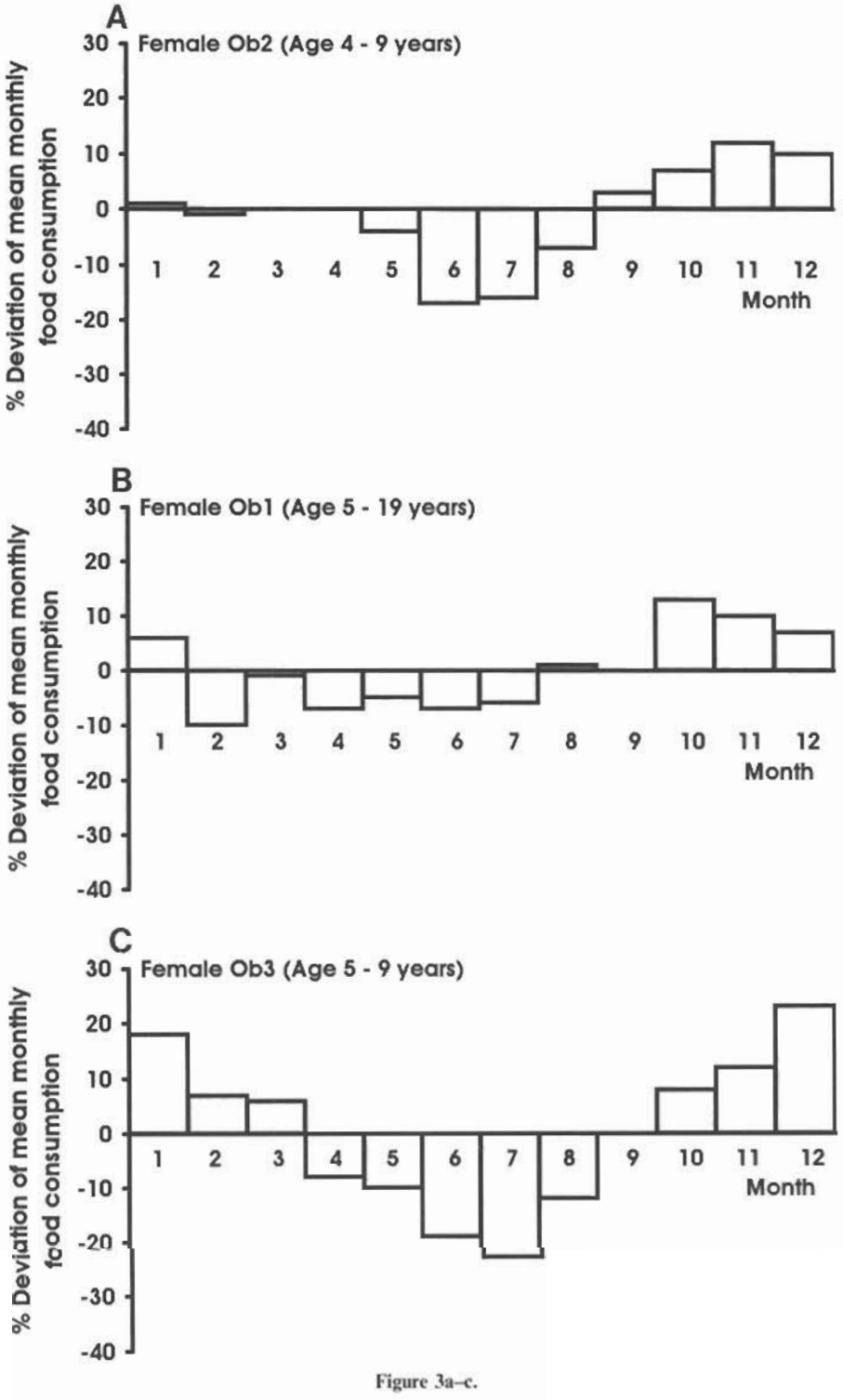
A
Female Ob2 (Age 4 - 9 years)
% Deviation of mean monthly food consumption
30
20
10
0
-10
-20
-30
-40
1 2 3 4 5 6 7 8 9 10 11 12
Month
B
Female Ob1 (Age 5 - 19 years)
% Deviation of mean monthly food consumption
30
20
10
0
-10
-20
-30
-40
1 2 3 4 5 6 7 8 9 10 11 12
Month
C
Female Ob3 (Age 5 - 9 years)
% Deviation of mean monthly food consumption
30
20
10
0
-10
-20
-30
-40
1 2 3 4 5 6 7 8 9 10 11 12
Month

Figure 3a–c.

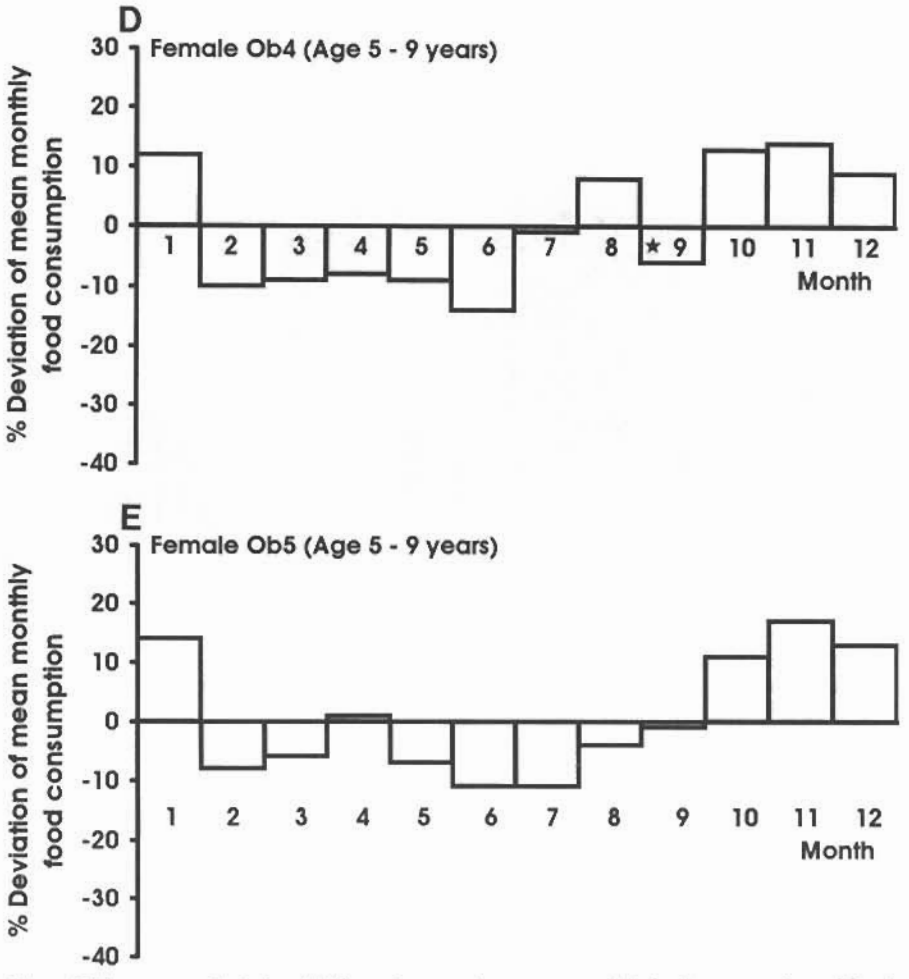

Figure 3. The average deviation (%) from the annual average monthly food consumption of South American sea lion female Ob2 after her 4th year (A), and females Ob1, Ob3, Ob4 and Ob5 after their 5th year (B–E). *Low intake due to illness during one of the 5 years over which the average was taken.

for several months. Probably, any seasonal or regional differences in caloric value of the fish cancelled each other out over the years, and did not lead to annual fluctuation in food consumption.

During the breeding season in the wild, reproductive males haul out on rookeries, and non-breeding male groups form on hauling grounds (Hamilton, 1939). Reproductive males set up territories and fight with neighbouring males to defend them (Vaz-Ferreira, 1981). Male–male interaction occupies only 2.4% of their time, while most of the time (85%) they spend motionless, avoiding waste of energy (Gateño, 1991). Fighting is more common at the beginning of the breeding season. In the wild, the breeding season is between December and February, and births peak in mid-January (Vaz-Ferreira, 1981). The South American sea lions in the present study were kept in the northern hemisphere, which means that they experienced the opposite annual cycle of photo-periods than they would in their natural habitat. As a result, the breeding cycle is shifted by approximately 6 months. Breeding occurs between June and August in the northern hemisphere, and in this period the males of the present study ate less than average and showed sexual behaviour. After the breeding season, wild bulls leave their territories in a generally emaciated condition.

Because annual summer periods with low food intake only occurred after the males had reached the age of 5 years, and because these periods only partially overlapped with the months of the highest

Figure 4. A mature male South American sea lion (left), a mature female, and 2 pups on Isla Marta, Strait of Magellan. Note the sexual dimorphism, which is pronounced in the heads. The male has a characteristic upturned muzzle (Photo: Steve Leatherwood).

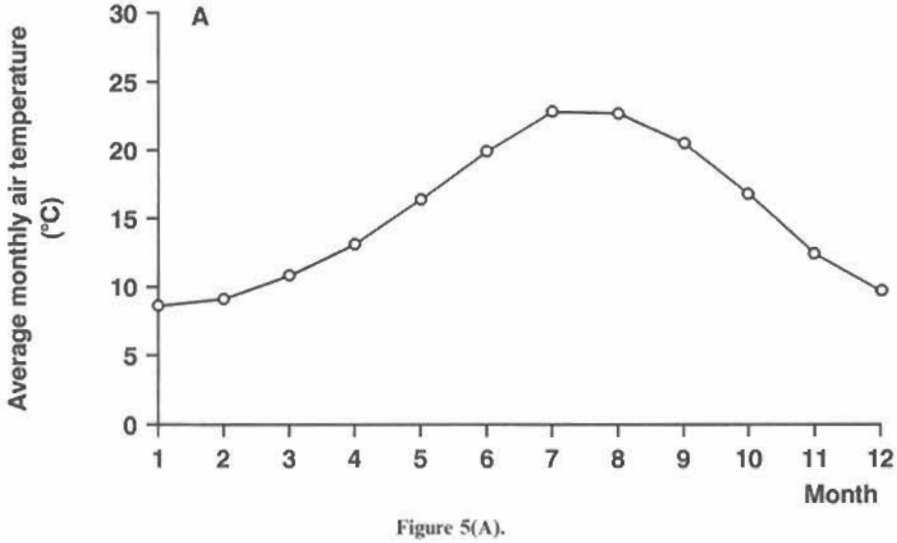

Figure 5(A).

air and water temperatures (Figs. 5A & B), the decrease in food consumption cannot be entirely a thermoregulatory adaptation. Because the males in the present study were given as much food as they wanted, it seems plausible that their reduction in appetite between June and September was caused, at least partly, by endogenous factors. The seasonal fluctuations were the strongest in male Ob8 which was highly sexually active, and less in male Ob0 which showed little sexual behaviour. Male Ob6, which was separated from females, also showed a smaller seasonal fluctuation in food intake than Ob8. This suggests that male hormones influence food intake.

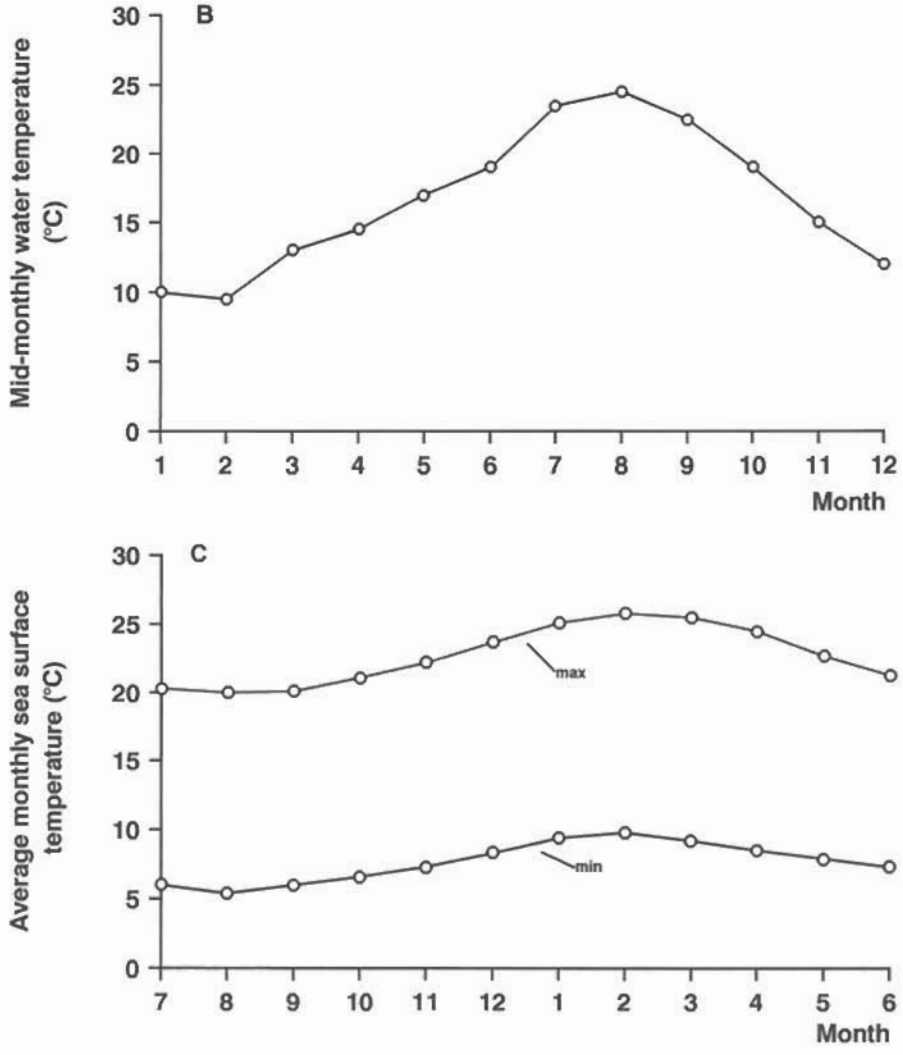

Figure 5. (A) The average monthly air temperature at Marineland between 1949 and 1989, (B) The water temperature of the South American sea lion pool at Marineland recorded on the 15th of each month in 1990 and (C) The average minimum and average maximum monthly sea surface temperatures over a 10 year period in the South American sea lions' distribution area (Source: Royal Dutch Meteorological Institute).

Seasonal food intake changes related to the males' 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), Northern elephant seals (*Mirounga angustirostris*) (Ortiz *et al.*, 1984), and Southern elephant seals (Kastelein *et al.*, 1991) also reduce their food intake during the breeding period when they haul out and spend most of their time defending their territories or mating.

In the wild, gravid female South American sea lions haul out some days before their pups are born. Most births occur in mid-January, and cows stay near their pups for some weeks, fasting. The females in the present study reduced their food intake during the summer months. This could have one or several causes; it is the warmest period of the year, food intake is reduced by endogenous factors, or the females are so stressed

by the males that they cannot eat the usual amount. Because the decrease in food intake occurred in both sexes, the warm season and/or endogenous factors seem most likely to be the cause.

To what extent wild South American sea lions store fat reserves before the breeding season is not clear. It may be different between individuals, depending on their physical condition and age (immature or mature) before the breeding season. In South American sea lions, body fat has an important role as an energy store during period of low food intake or fasting, as well as it is important for temperature regulation (Irving, 1969), streamlining, protection of the body from shocks, and bouyancy.

In the wild, not all South American sea lions moult at the same time, and various stages can be seen between April and August (winter). In the present study, no clear moult was detected. This may be because moult in this species is an inconspicuous gradual process.

Ecological significance

How does the present study relate to South American sea lions in the wild?

There is probably a difference in activity level between animals in the wild and in a pool. In the wild, South American sea lions live either near breeding areas or at feeding areas which are often close to the shore. Here they feed near the surface and often rest (Vaz-Ferreira, 1981). Although limited in space, the animals in the present study swam most of the time. However, they did not have to dive for food, so they probably used less energy than wild conspecifics do.

The mean monthly water temperatures at Marineland (Fig. 5B) are within the range that South American sea lions experience in their distribution area (Fig. 5C). This suggests that, if the animals at Marineland spent a similar amount of time in the water as their wild conspecifics (Vaz-Ferreira (1975*b*) observed that in the wild, haul out behaviour is influenced by weather conditions), the energy loss due to thermal conductance would be similar in both situations. However, because it is not known how deep South American sea lions dive, how long they stay there, and what the water temperatures are at those depths, comparisons should be approached with caution.

When the temperature rises, South American sea lions lie belly up on the ground with extremities extended from the body and one or more flippers raised in the air. A very common position in hot weather is sitting with one hind flipper extended above the body. On warm days they throw cool sand on their body, and in very hot weather they often take a dive and return to the rookeries (Vaz-Ferreira, 1981). At Marineland only the latter option for cooling was available to the sea lions.

Different species of fish have different energy contents per unit weight (Costa, 1987; Prime and Hammond, 1987). The fish fed to the animals in the present study were not the natural prey of South American sea lions. Although the caloric content of the food eaten by animals at Marineland (50% Herring and 50% Mackerel) was not determined, this diet is probably of a higher energetic content than the natural diet of South American sea lions, which consists of low-calorie crustaceans and molluscs as well as fish (Hamilton, 1934; Vaz-Ferreira, 1950; Aguayo & Maturana, 1973). Penguins are also part of the diet of adult South American sea lions, but to what extent is not known (Boswall, 1972).

In the wild, adult male South American sea lions eat nothing during the 2 month breeding season because they do not leave the breeding grounds, whereas the animals in the present study ate some food during that period, perhaps because they were fed by hand. This may make the total annual food intake of the animals at Marineland higher than that of conspecifics in the wild, unless the animals in the wild eat much more than the animals of the present study after the breeding season in order to replenish lost fat reserves.

Although the food intake data of the present study are difficult to extrapolate directly to wild South American sea lions, the relative differences due to sex and age, and changes due to season and reproductive state are probably comparable to those in the field. These changes were controlled by endogenous factors, because 10 of the 12 animals at Marineland were offered as much as they wanted to eat, so that changes in food intake were not determined by their keepers. Based on the present study, a conservative food fish consumption estimate for South American sea lions in the wild would be 3700 kg/year for adult males and 1900 kg/year for adult females.

Studies of energy requirements should be long term and involve growing and adult individuals of both sexes, and females in different stages of reproduction. The present study indicates that the food intake pattern in South American sea lions is complex. It is risky to use a simple percentage of body weight to calculate the daily food requirement of an entire population of South American sea lions. 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, and the size, sexual composition and age structure of the population is needed.

Acknowledgements

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