

BEHAVIORAL AND PHYSIOLOGICAL
MEASUREMENTS OF MATERNAL
INVESTMENT IN THE STELLER SEA LION,
EUMETOPIAS JUBATUS

LESLEY V. HIGGINS

DANIEL P. COSTA

ANTHONY C. HUNTLEY

BURNEY J. LE BOEUF

Long Marine Laboratory, Institute of Marine Science,
University of California, Santa Cruz, California 95064

ABSTRACT

The onshore and at-sea cycles of females, suckling behavior of pups and their milk intake were studied in Steller sea lions (*Eumetopias jubatus*) during 1983 at Año Nuevo Island, California. Females averaged approximately 21 h ashore and 36 h at sea. The trips to sea lengthened as pups aged, resulting in an overall decline in female time ashore to 30% by the sixth week following parturition. Activity budgets of pups showed no significant differences among suckling time, age and sex. Milk intake, estimated using labeled water studies, revealed that heavier pups consumed more milk than lighter ones (milk ingestion in ml/d = $4.26 + 0.0687 \times \{\text{Pup Mass in kg}\}$). Mean milk intake was 1.78 ± 0.33 liters/d. Mean pup growth rate was 0.38 ± 0.1 kg/d. The results suggest that female attendance patterns are shaped by the increasing nutritional demands of growing pups and their increasing efficiency at suckling.

Key words: *Eumetopias*, Stellar sea lion, female attendance pattern, milk intake, suckling, growth rate, maternal investment.

Prior to making the transition from suckling to self-feeding, pinniped neonates must attain sufficient body weight and energy reserves to maximize the probability of survival during the first year of life. Unlike some phocids, such as northern elephant seals, *Mirounga angustirostris*, (Le Boeuf *et al.* 1972), Hawaiian monk seals, *Monachus schauinslandi*, (Kenyon 1981), and grey seals, *Halichoerus grypus*, (Bonner 1981), otariid females forage at sea intermittently, leaving their pups onshore while they replenish their energy stores. This cycle is repeated many times during the lactation period and is called the female attendance pattern (Gentry 1970).

A typical otariid pattern is exemplified by the northern fur seal, *Callorhinus ursinus*, which increases the duration of foraging trips to sea as the nursing season progresses. In contrast there is no progressive change in the duration of time spent onshore (Gentry and Holt 1986). Milk intake is positively correlated with age and mass of pups, with male pups consuming significantly more than female pups (Costa and Gentry 1986).

The timing of the maternal attendance pattern is an important part of the otariid reproductive strategy and varies among species. Recent attention has focused on the differences in maternal attendance patterns and their relationship to milk composition, geographic location of the rookery, rate of milk consumption, and pup growth rate (Trillmich 1986, Gentry and Holt 1986, Costa and Gentry 1986). It has been suggested that the temporal patterning and duration of foraging at sea and the subsequent time spent onshore nursing are related to distance to the foraging grounds, food availability, latitude and female body mass (Gentry *et al.* 1986). This pattern and the consequent rate of pup provisioning are critical to the pup's survival. Females must balance the time required to replenish their reserves with the amount of time the pup is left alone fasting onshore.

Sexual investment theory suggests that in polygynous, sexually dimorphic species, such as otariids, the male offspring might be expected to receive a higher proportion of maternal resources (Trivers and Willard 1973, Maynard Smith 1980). Male otariid pups are heavier at birth, grow faster (Mattlin 1981, Ono *et al.* 1983, Doidge *et al.* 1984) and ingest more milk than female pups (Ofstedal *et al.* 1983, Costa and Gentry 1986, Trillmich 1986). Costa and Gentry (1986) found that milk intake for male northern fur seal pups is 61% greater than for female pups, and concluded that the mother invests more energy and nutrients in male pups than in females. If male pups receive more milk than female pups, differences in maternal attendance patterns or in pup suckling activity would be expected. However, similar observations led Trillmich (1986) to question the validity of Fisher's (1930) sex ratio theory and differential investment in male and female pups. His observations show that variations in female attendance pattern do not correlate with pup sex. It might also be expected that many of these variables vary as a function of body mass.

Steller sea lions are found on the Pribilof Islands, Alaska, south to San Miguel Island, California, and in Asian waters on the Kurile Islands, Kamchatka, and the islands of the Okhotsk Sea (Kenyon and Rice 1961). The period of maternal care lasts a year or more; some individuals suckle for up to two years (Gentry 1970, Sandegren 1970, Calkins and Pitcher 1982). Previous studies of Steller sea lions in California and Alaska (Orr and Poulter 1967, Gentry 1970, Sandegren 1970, Gisner 1985), provided data on the reproductive behavior of males and females, but lacked a comprehensive account of individual female and pup behavior.

In order to provide information on the pattern of maternal investment in the Steller sea lion we quantified female onshore and offshore movements, pup growth, milk consumption, and suckling behavior. These data were then used to make comparisons between maternal attendance pattern, milk intake and

pup suckling behavior. Maternal attendance and pup behavior were observed on marked females and known aged pups. Maternal investment was measured by estimating milk intake calculated from radioisotopic determinations of water influx (Nagy and Costa 1980) of freely suckling pups on the rookery.

MATERIALS AND METHODS

This study was conducted from 5 June to 7 August 1983, on Año Nuevo Island, a 3.2 ha island situated about 0.3 km offshore and 30 km north of Santa Cruz, California (Le Boeuf and Kaza 1981). The study area consisted of sloping rocky shelves on the seaward side of the island. Behavioral observations were made from an elevated blind 10 m high within 15 m of the animals.

Behavioral measurements—The activities of 28 females and their pups were followed from birth to departure from the study site, about two months later. Of these females, 18 were marked with colored paint pellets (Nelson Paint Co.) projected from a wrist mounted sling shot. Natural marks and scars were used to identify the remaining females.

Observations of each female were begun after parturition and were carried on daily from about 0500 to 2100. At dawn, all females present were identified and wet animals were recorded as having arrived within 30 min, the approximate time it took them to dry off. Arrivals and departures of known females were recorded throughout the day.

Since observations were not possible at night, females present at dusk and the following dawn were assumed to have spent the night on the rookery. Similarly, females absent at dusk and the following dawn were assumed to have been absent all night. During daylight, no trip was observed to last less than eight hours, the period of darkness. Arrivals and departures occurring at night, as determined by the presence or absence of females in the morning, were assumed to have occurred during the middle of the night, four hours after dark and four hours before dawn.

Pup suckling behavior was recorded from the time of birth to departure of the mother and pup from the study site. Since only six of the 28 pups were marked (*see* below), behavior of unmarked pups was recorded only when they could be identified by association with their mothers. The behavior was recorded in two ways. 1.) The percent of time spent in various activities was determined using a point sampling technique (Altmann 1974), consisting of 12 one-minute scans, five minutes apart, per hour for approximately six hours a day. Pups were classified as being awake, asleep or suckling. Since observations over a 24-h period were not possible, total suckling time was estimated by multiplying the percent of time that a pup suckled by the percent of time that the mother was present on the rookery. 2.) Focal animal observations of suckling bout durations were recorded using the following criterion: A bout was defined as any period in which a pup suckled continuously for more than 30 sec and any pause greater than 30 sec signaled an end to the bout.

Non-parametric statistical tests were used when the data were found to be not normally distributed, otherwise standard parametric tests were used. All

statistics were performed using the procedures described by Sokal and Rohlf (1969).

Measurements of milk ingestion—Nine pups were used in the milk intake and metabolic rate studies. Pups had to be captured opportunistically, when the risk of disturbance to the rookery was low to avoid stampeding the animals. Consequently, not all of the pups were treated in exactly the same manner and milk consumption was estimated in only six pups. Milk intake was calculated from the difference between total water influx and metabolic water production, divided by the water content of mother's milk (Ortiz *et al.* 1984):

$$\text{milk intake} = \frac{\text{total water influx} - \text{metabolic water production}}{\text{milk water content}}$$

Total water influx was determined using the tritiated water method (Nagy and Costa 1980). Nine pups were strapped on a V-shaped restraining board and given a 2-cc intramuscular injection of 0.25 mCi/ml tritiated water (HTO) in sterile saline. Body mass and standard measurements were recorded. Pups were allowed free movement for a three hour equilibration period, after which a 10-cc blood sample was taken from a vein in the pelvic plexus. The pups were then individually marked with hydrogen peroxide and a commercial emulsifier—a bleaching agent (Le Boeuf and Peterson 1969) and released near the site of capture. Six of the nine pups were recaptured within 5 to 24 d. Upon recapture, each animal was weighed and a final blood sample taken. If pup mass increased more than 10%, a second injection of HTO was given, followed by blood collection three hours later to measure the new total body water. All blood samples were frozen and analyzed later for specific activity of tritiated water. The specific activity of tritiated water was determined in 200- μ l aliquots of pure water freeze-trapped from whole plasma and counted in 10 ml of Betaphase cocktail (Westchem, San Diego, CA) in a liquid scintillation counter (Ortiz *et al.* 1978). The specific activity of the injection standard was determined by diluting 50 μ l of injectate in 200 ml of water in triplicate; 200- μ l aliquots were then counted in 10 ml of scintillation cocktail at the same time as the distilled plasma samples.

Metabolic water production was calculated from metabolic rates determined in five pups by open circuit respirometry (Costa and Kooyman 1982). Of these five, two were also used in milk intake calculations. Pups were placed in a darkened respirometry chamber and two hour measurements were made while ambient air was drawn through the chamber at 20 liters/min. Unidirectional flow was assured by one-way valves on the inlet and outlet ports. The outlet air was passed through a drying tube containing Drierite (CaSO₄, Hammond Co., Xenia, OH) and then through a dry gas meter (American Meter). An aliquot of the metered air was then drawn over a complex of three drying tubes containing Drierite and a CO₂ absorbent (Baralyme, Chemotron Products) and through the sensor of an oxygen analyzer (Ametek, Pittsburgh, PA). Ambient air temperature was monitored with a mercury thermometer, and barometric pressure with an aneroid barometer calibrated against a mercury barometer. \dot{V}_{O_2} was calculated using equation 4b from Withers (1977). Metabolic water

production was determined assuming fat as the sole metabolic fuel yielding 0.523 g H₂O for each liter of O₂ consumed (Ortiz *et al.* 1984).

Milk water, lipid and protein content were assayed in two samples obtained from pups that were actively suckling prior to capture. These samples were collected via stomach tube from the restrained pups and were frozen immediately for later analysis. Milk water content was measured by drying one gram aliquots at 80°C overnight. Fat content of the dried samples was calculated as the weight change after fat extraction with six rinses with di-ethyl ether. Dilution of milk by gastric fluids sometimes occurs (Ofteidal, personal communication) and comparisons of these data to other species must be done with caution.

RESULTS

Parturition—The first birth occurred on 15 June. With few exceptions, females generally spent two or three days at the study site prior to parturition. Females were typically gregarious and remained close together on the rookery even when density was low. After the first pup was born, pregnant females aggregated near the pair, forming a nucleus for subsequent births.

Thirty births occurred at the study site; two were stillbirths. Twenty-six of the births occurred during the day, mostly in the early morning and late afternoon hours. The sex-ratio was 15 males : 14 females, one pup was not sexed.

Female attendance patterns—During the study, 344 foraging trips were recorded. For the first five weeks after parturition, the mean number of trips per female was 13 with a range of 7–25 trips.

Following parturition, females spent a mean of 6.7 ± 2.0 days ($n = 26$, range 3–12) with their pups before going to sea. There was no significant difference in the initial duration of time onshore as a function of the sex of the pup ($\bar{x} = 7.0 \pm 2.2$ days for males and $\bar{x} = 6.5 \pm 1.9$ days for females. Wilcoxon two sample test: $Z = 0.517$, $n_1 = 12$, $n_2 = 13$, $P > 0.05$).

The mean length of the first trip to sea was 20.2 ± 14.3 h ($n = 25$, range 6–62 h). Duration at sea did not vary significantly as a function of latency to go to sea (Pearson product moment correlation = 0.08, DF = 24, $P > 0.05$).

Although only three weeks separated them, females that gave birth later in the season exhibited a significant increase in the duration and variability of the first trip ($\bar{x} = 28.4 \pm 15.1$) when compared to mothers of earlier born pups ($\bar{x} = 10.2 \pm 1.9$) (Mann-Whitney *U*-test, $U = 6$, $n_1, n_2 = 6$, $P < 0.05$). Subsequent trips by the two classes of females were not found to be statistically different.

Females exhibited a cycle in relation to their departures and arrivals (Fig. 1). Fifty-seven percent of the departures occurred between 1600 and 2100. Females returning to the rookery showed less preference for time of day, although 61.6% returned between 2100 and 0900. The lowest number of arrivals and departures occurred during mid-afternoon (1200 to 1400) and reflected an overall reduction in activity on the rookery.

Overall, time spent by females on the rookery decreased with pup age (Fig.

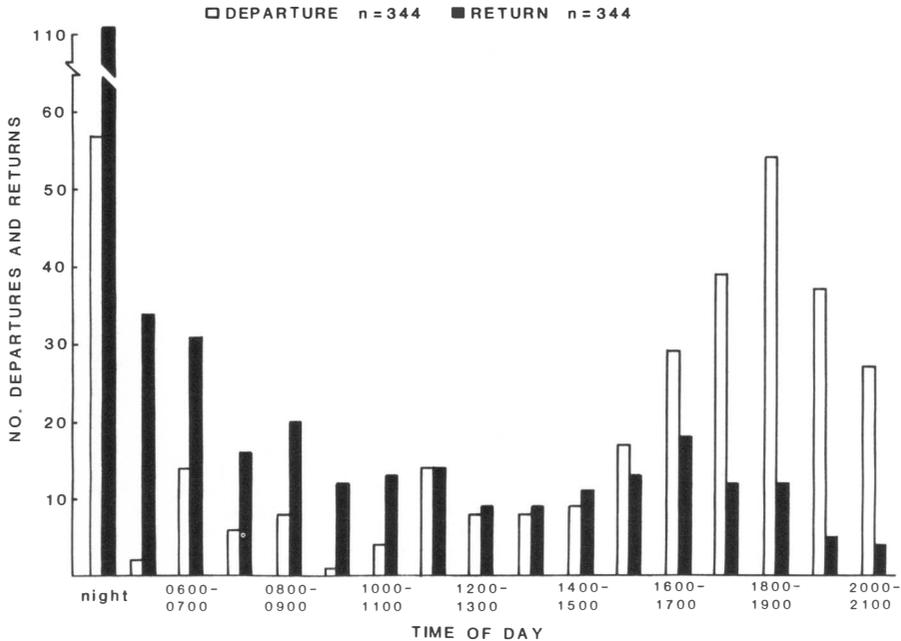


Figure 1. Departures and returns of females with pups as a function of time of day. Nighttime movements, as determined by presence or absence of females in the morning, are grouped together at far left.

2). There was a sharp drop in attendance from the first to the third week, then a more gradual decline until the sixth week when only about 30% of their time was spent on the rookery. Although mothers of male pups appeared to spend less time on the rookery than those with female pups, this difference was significant for only the fifth week (Mann-Whitney *U*-test; $U = 24.5$, $n_1, n_2 = 10$, $P < 0.05$).

Excluding the first trip, females spent 37.0 ± 19.1 h at sea, and 22.6 ± 9.5 h on shore. However, the time spent at sea increased significantly as both female and male pups became older (Fig. 3) (male pups: Kruskal-Wallis test, $H = 17.34$, $DF = 5$; female pups: $H = 14.55$, $DF = 5$, $P < 0.05$). In contrast, no trend was found with pup age and the time spent onshore by their mothers (male pups: Kruskal-Wallis test, $H = 2.88$, $DF = 4$; female pups: $H = 1.40$, $DF = 4$, $P > 0.05$). There was a non-significant trend for females with male pups to spend more time on trips away from the rookery than females with female pups (Mann-Whitney *U*-test, $U = 1.49$, $n_1 = 44$, $n_2 = 47$, $P > 0.05$).

Pup behavior—Pups suckled within two hours of birth but these initial bouts were shorter than later ones. The mean suckling bout duration during the first week was $11.2 \text{ min} \pm 6.28$ ($n = 41$) and increased to $20.9 \text{ min} \pm 6.69$ ($n = 16$) by the fifth week. The longest bout recorded during the first week was 26 min compared to 61 min in the fifth week. Although there was an apparent trend for male pups to suckle longer than female pups it was not significant (Fig. 4) (third week: Two sample *t*-test, $t = -1.286$, $v = 41$, $P > 0.05$).

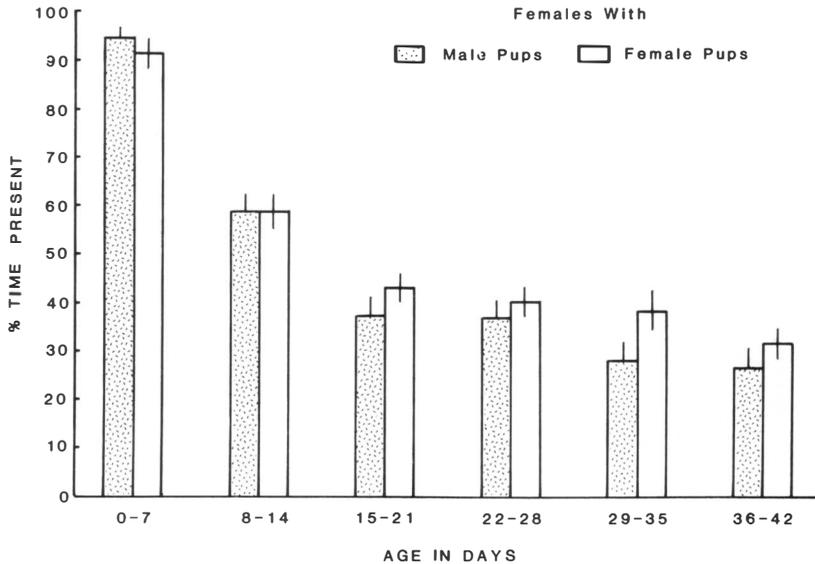


Figure 2. Percent of time females were present on the rookery as a function of pup age and sex. Vertical lines indicate one standard error.

Two-hundred and forty hours of scan sampling were performed, with approximately 15 pups observed at any one time. Each pup was scanned for a mean of 98 ± 38.6 h during the study period. Because the data for each pup were combined into one-week sets and then the mean of each week taken for all the pups, any erroneous results from any single scanned hour were assumed to be averaged out in the final analysis. The data show that as females spent greater amounts of time away from the rookery after the first week, pups suckled more during the time females were ashore between trips (upper part of Fig. 5). The apparent increase in suckling by male pups compared to female pups in this situation can be explained by the longer absences of females with male pups (Fig. 2). However, the total time pups spent suckling, shown in the lower part of Figure 5, remained virtually the same for male and female pups for the six-week period. The results indicate that there are no differences between male and female pups in terms of suckling, and that pups do not increase the overall amount of time they suckle as they age.

Pups spent about 50% of their time sleeping, and this was consistent over all age classes. These data were collected when pups were with their mothers, and do not include the time the mothers were absent.

Milk intake measurements—Of three milk samples obtained, only two were fresh enough for analysis. One from a five-day-old pup contained 68% water and 23% fat; the other from a three-week-old pup contained 65% water and 25% fat. The mean value of 66.5% was used in all calculations of milk intake.

Mean oxygen consumption of five pups was 0.682 ± 0.193 liters O_2 /kg/h. Metabolic water production was calculated as 8.56 ml H_2O /kg/day. Mean total water influx was 54.6 ± 3.5 ml/kg/day ($n = 7$), yielding milk

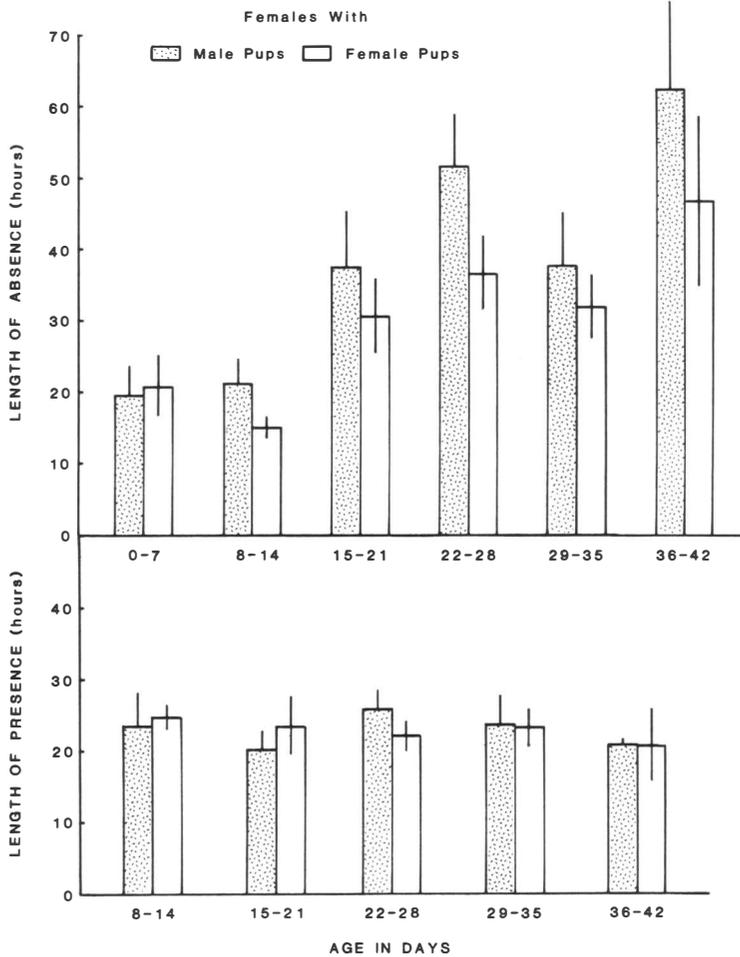


Figure 3. Length of at-sea and on-land intervals as a function of pup age and sex. Vertical lines indicate one standard error.

ingestion rates ranging from 1.50–2.35 liters milk/d (Table 1). The mean growth rate of five pups was 0.38 kg/d with an extrapolated birth mass of 17.92 kg. This relationship was highly linear and significant (Pearson product moment correlation, $r = 0.94$, $P < 0.01$). Differences in the quantity of milk consumed were significantly correlated with pup mass and are described by the equation: milk intake (ml/d) = $4.26 + 0.0687 \times$ pup mass (kg) (Fig. 6) (Pearson product moment correlation, $r = 0.88$, $n = 6$, $P < 0.05$). In contrast, there was no correlation between relative suckling time and actual milk intake for the four pups for which there were data (Table 1) (Pearson product moment correlation, $r = -0.40$, $n = 4$). It should be noted however, that the suckling data were collected by scan sampling, and that as such can only approximate actual conditions for individual pups.

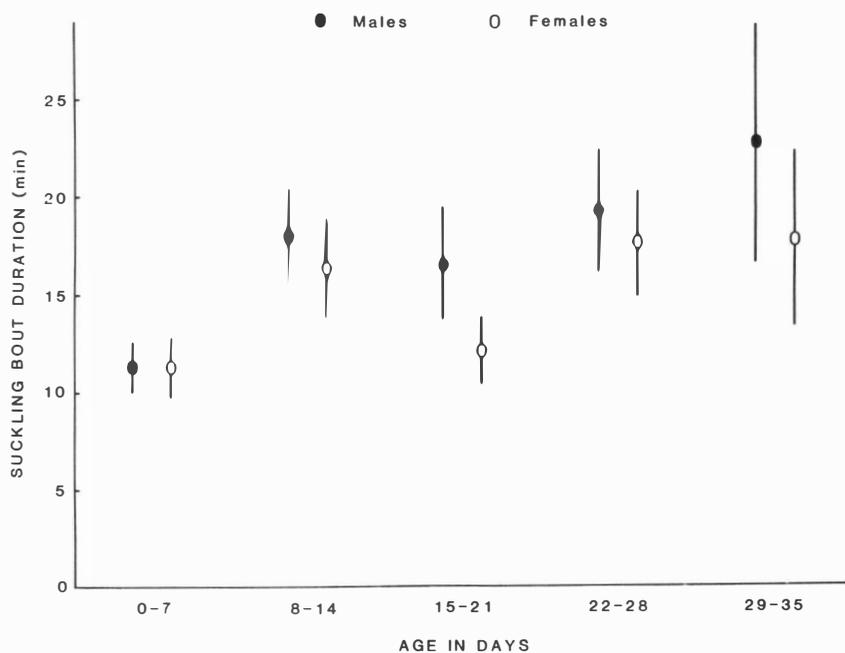


Figure 4. Suckling bout durations of pups according to age and sex. Vertical lines indicate one standard error.

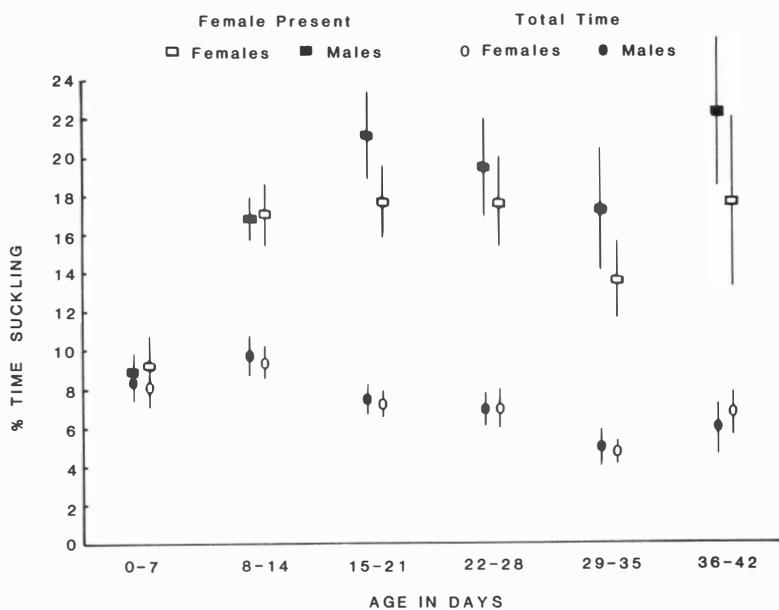


Figure 5. Percent of time male and female pups suckled during the mother's presence on rookery and total percent time male and female pups suckled, including absences of the mother. Vertical lines indicate one standard error.

Table 1. Age, mass, and milk intake rates for experimental pups. Milk intake was estimated from the metabolic water production (MWP) calculated from oxygen consumption measurements and the total water influx (TWF) measured by the dilution of tritiated water.

Pup	Sex	Age (d)	Mass (kg) (range)	MWP (ml/kg/d)	TWF	Milk intake (liters/d)	Suck- ling % time
1	F	20-38	28.4 (26.1-30.8)	8.56	50.723	1.80	1.8
2	M	15-40	29.5 (25.0-34.0)	8.56	52.337	1.94	7.5
4	M	7/8-7/22 ^a	20.0 (17.7-22.3)	8.76 ^b	58.496	1.50	
5	M	5-23	23.0 (18.5-27.5)	8.56	54.101	1.54	9.1
6	M	11-33	30.7 (25.8-35.6)	8.56	59.432	2.35	4.5
9	F	7/24-8/2 ^a	24.5 (22.8-26.2)	11.2 ^b	52.751	1.57	
		\bar{x} =	25.4		54.640	1.78	5.7
		s =	4.2		3.53	0.33	3.2

^a Age unknown, dates given instead.

^b Actual rates measured.

DISCUSSION

The cycle of arrivals and departures observed indicates that female Steller sea lions forage preferentially at night. This is corroborated by the incidental catch of Steller sea lions in the walleye pollock fishery in Shelikof Strait, Alaska. Seventy-three percent of the sea lions caught in trawl nets were caught between 2000 and 0500; the majority were caught between 2300 and 0300 (Loughlin and Nelson 1986).

It is likely that increasing nutritional demands of pups require females to spend more time at sea foraging and that this accounts for the lengthening of foraging trips. Heavier pups consumed more milk than lighter ones and since pups gained approximately 0.38 kg a day it follows that milk intake would increase because pups get larger as they get older. Sex differences can be accounted for by variations in pup mass as well because male pups are larger than female pups. A similar relationship was reported in northern fur seals, where increased milk consumption in older as well as larger pups was found and sex related differences dropped out when milk consumption was plotted against pup mass (Costa and Gentry 1986). As pups grow larger, they also develop greater energy reserves allowing longer fasting intervals between feedings, allowing the females to spend more time foraging (Millar 1977). Increases in the duration of foraging trips were also found in Galapagos sea lions, *Zalophus californianus wolfebaeki*, (Trillmich 1986), California sea lions, *Zalophus californianus*, (Peterson and Bartholomew 1967, Boness *et al.* 1985), Northern fur seals (Gentry and Holt

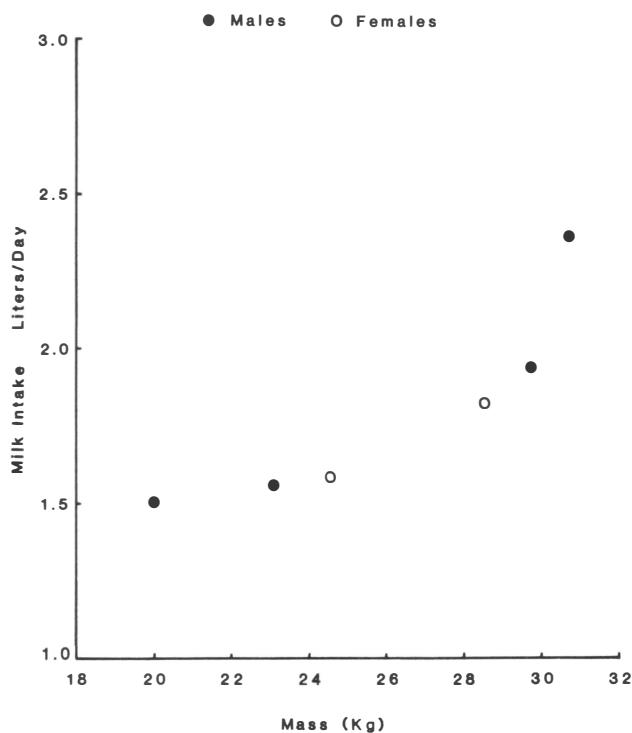


Figure 6. Milk intake in liters per day as a function of pup mass.

1986) and Antarctic fur seals, *Arctocephalus gazella*, (Doidge and McCann 1986).

Pups appeared to adjust their milk intake in response to increasingly longer absences of females. This is shown by the relationship between the time females spent on the rookery and the percentage of time male pups suckled. Male pups suckled more than female pups when their mothers were present; this correlates with longer absences of their mothers. In other words, given that their mothers were present less, male pups suckled proportionately more than female pups and this "catching-up" enabled them to achieve the same percent time suckling overall as female pups. It is unclear whether the increased rate of suckling may have caused the females to spend more time at sea, or if the male pups adapted to their mother's longer absences by suckling more when she was available.

Our data on pup suckling behavior, when compared to the labelled water measurements of milk intake, indicate that suckling behavior is not a good index of the rate of milk ingestion. The combined data for all 28 pups show that overall time spent suckling does not change as a function of pup age or sex. However, measurements of milk intake in five pups show that it is greater in larger pups. If suckling behavior were correlated with milk intake, larger pups should have increased their suckling effort or suckling time. This lack of correlation may be due to a greater suckling efficiency in larger pups that allows

an increased milk intake without an obvious modification of suckling time or effort.

Behavioral observations of suckling time might be better used as an indicator of time required by a pup to suckle, regardless of the amount ingested. The mother's presence on the rookery was found to be longer than the time the pup actually spent suckling, and thus allowed for differences in pup suckling abilities or milk ingestion rate. The constancy of onshore intervals for females may be related to increasing suckling efficiency and the fact that as their pups age, females can transfer more milk in the same amount of time and negate the need to increase their time ashore.

Because of the great size dimorphism exhibited in this species, theory predicts greater maternal investment in male pups (Fisher 1930). However, pup sex seems to have little measureable influence on maternal attendance or pup suckling behavior. Similar findings have been reported in northern fur seals (Macy 1982, Gentry and Goebel, unpublished data). The significant difference in female attendance during the fifth week of this study and the overall trend beginning in the second week suggests that there is an effect that may become more pronounced with time. Moreover, a larger sample may permit a more conclusive test of Fisher's prediction, although female and pup behavior may be sufficiently variable that effects of differential investment are masked and can not be examined with this kind of analysis.

Lastly, the length and variability of foraging trips of Steller sea lions in 1983 might have been affected by conditions caused by the severe El Niño event of 1982–83. Gentry (1970), working at the same study site, found increases in foraging trip duration with an overall mean time at sea of 1.9 d. It would appear that during 1983, trip durations of Steller sea lions were actually shorter than those observed 14 yr previously: Gentry found that 56% of his females took one-day trips, whereas in this study 70% of them did. In addition, Gentry found 19% of foraging trips to be four or more days, whereas in this study only two percent of the trips were of that length. In contrast, Sandegren (1970) reported mean trip duration of only 24 h without any change in trip length over time for female Steller sea lions in Alaska. Such a difference in duration of foraging trips may be due to differences in the distance to the foraging grounds, or that differing methods of data collection make direct comparisons inappropriate.

Attempts were made to follow maternal attendance during 1984. However, subsequent changes in pupping sites on Año Nuevo Island made comparison to later years impossible. This is unfortunate because in other species noticeable effects of El Niño have been reported: Galapagos sea lions experienced drastic pup mortality from the El Niño event (Trillmich and Limberger 1985); and in California during 1983, female California sea lions spent more time at sea than in the previous and following years (Boness *et al.* 1985). Census records of Año Nuevo Island for the years 1982 through 1984 show that the population experienced an all time low during the summer of 1983 (Higgins and Bonnell, unpublished data). Since the numbers of pups were approximately the same for the three years, it would appear that non-breeding animals stayed away from the island during 1983. Whether El Niño was implicated can only be ascertained

when more data become available on how fluctuations in climate and prey distribution modify maternal investment strategies in sea lions.

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