

10 Attendance and Diving Behavior of South American Fur Seals during El Niño in 1983

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INTRODUCTION

When we studied the diving and attendance behavior of the South American fur seal in Peru in January and February 1983, the strongest El Niño (EN) in over 100 years was in progress (Cane, 1983). Sea surface temperature (SST) at Punta San Juan, our study site, averaged $22.4 \pm 0.8^{\circ}\text{C}$ (mean \pm SD; range 21.0–24.5°C; Pesca Peru, unpubl. data), while in normal years average January SST is 15.5°C and February SST is 16.0°C (Zuta et al., 1978). These high temperatures resulted from a massive influx of warm water coming from the west.

The warm water influx results from a decrease in the atmospheric pressure gradient between the eastern subtropical Pacific and Indonesia. This gradient change relaxes the trade winds and generates a gigantic Kelvin wave that crosses the Pacific in less than 2 months. When this wave reaches the South American coasts, the sea level rises, the thermocline is depressed, and the mixed surface layer becomes thicker. Coastal upwelling continues, but the water transported to the surface is warm and poor in nutrients (Cane, 1983; Kerr, 1983; Fonseca, 1983).

Phytoplankton, which is homogeneously distributed in the mixed layer, is directly affected by these changes. When the thermocline and the mixed layer are deep, the nutrients and light available for photosynthesis decrease. The resulting reduction in primary productivity causes proportional reductions in growth and the reproductive success of zooplankton, fish, and all organisms in the higher trophic levels of the ecosystem (Barber and Chavez, 1983; Fonseca, 1983), including sea birds (Murphy, 1936; Idyll, 1973; Boersma, 1978; Schreiber and Schreiber, 1983). It also brings economic crisis

to the Peruvian fishing industry; the fish either disappear or cannot be caught by normal methods (Paulik, 1971; Schaeffer, 1970).

Data from echo soundings (IMARPE, unpubl. data) show that fish that normally live near the surface or migrate toward it during the night stay down in cold subsurface waters below the thermocline and away from intolerably high surface temperatures. To indicate the extent of this effect, the 14°C isotherm was 300 m deep at long. 85°W (off Peru; Toole, 1983) in October 1983, whereas it is normally at about 175 m (Meyers, 1979).

Such drastic changes must affect the hunting success of nightly feeding fur seal mothers and may lead to a negative energy balance. Thus collection of data on fur seal feeding behavior in 1983 constituted a unique natural experiment on the effect of varying food availability on maternal behavior. This study provides the first data on the effect of EN on a marine mammal, and shows that many fur seal females under such conditions were unable to obtain enough energy to support themselves and a dependent young.

MATERIALS AND METHODS

This study was made at the guano bird colony at Punta San Juan (lat. 15°22' S. long. 75°11' W) between 10 January and 12 February 1983. Fur seals are protected inside the guano bird reserve, but are nevertheless frequently disturbed by people and are easily stampeded. To avoid massive disturbances during the attendance study, we chose to observe animals in a cove with about 60 m of shoreline that was made inaccessible by steep cliffs all around.

Censuses were made from the cliff top with 8× or 10× binoculars. Adults and 1- or 2-year-olds could easily be distinguished, but the sexes were usually impossible to distinguish among young fur seals and were sometimes uncertain for adults of intermediate size.

For marking, blown eggs filled with a commercial hair bleach (Clairol Born Blonde) were thrown at the seals from the cliff; four pups and four females (not related to each other) were marked in this way. The study area was searched for marked animals at least five times daily. All females suckling pups were always carefully checked. Adults that were not seen were assumed to be absent, and marked pups that were not found were assumed to be without their mothers. On many days observation in the study area was almost continuous. The durations of presence and absence of females were measured to the nearest half day.

All dead animals were noted during the checks for attending females. Within one day, carcasses of pups were either opened by vultures or were visibly bloated. After about 3 days the carcasses had disintegrated completely. Double-counting of carcasses was thus avoided.

Activity budgets of females with pups or older young were recorded using instantaneous sampling as described in Chapter 11. Time budget observations were made from a distance of 20–50 m using binoculars whenever necessary. Mothers with pups were observed for 35 hours, mothers with yearlings for 40 hours, and mothers with older young for 8 hours.

The body condition of pups was recorded subjectively. Pups were judged to be in poor condition if the bones of the pelvic and shoulder girdle were protruding. In well-nourished pups these bones were deeply embedded in fat.

A TDR, radio transmitter, and flipper tags were placed on one adult female that lacked a pup. The animal was first stalked, hoop netted, and then restrained following the procedures described in Chapter 2. The TDR was on the animal from 15 to 28 January. Drug-induced immobilization was used for recapture because of the fur seals' wariness to approach and the difficult terrain at the recapture site. A telinject 3 ml syringe was shot at the animal from about 30 m distance. The dart contained 300 mg ketamine, 20 mg xylazine, and 150 IU hyaluronidase. Within 2 minutes the animal was immobilized. The seal was mobile again within 2 hours and remained in the area for the next 24 hours.

Blood samples were collected to determine whether blood conditions were measurably affected by the ongoing EN. Samples were taken from eight pups, one immature, and three adult female fur seals. Blood from pups was collected by cardiac puncture. Blood from adults and the immature were drawn from the rear flipper or from the iliac sinus. Samples were immediately capped and placed on ice until they were analyzed one hour later. Standard procedures were used to determine hematocrits and hemoglobin concentration. Oxygen dissociation curves were obtained for whole blood by the mixing method (Edwards and Martin, 1966; Lenfant et al., 1969; Scheid and Meyer, 1978). The blood gas equilibrations were performed in an Instrumentation Laboratory IL 237 tonometer at 37°C. Partial pressures of carbon dioxide ($p\text{CO}_2$) and oxygen ($p\text{O}_2$) were determined in a Corning pH/blood 161 Gas Analyzer at 37°C and calibrated with two humidified gas mixtures. One gas mixture

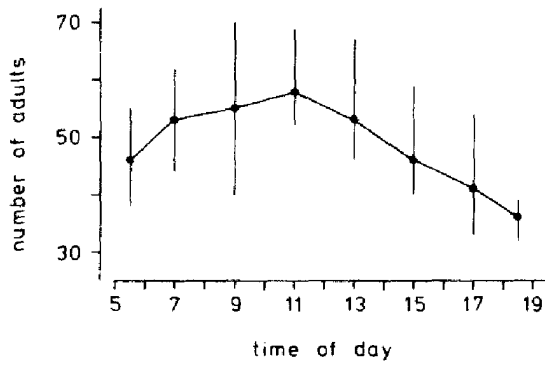


Fig. 10.1. Daily fluctuation in number of adult fur seals in the study area. Averages and ranges from five censuses on 13, 21, 28 January, and 4 and 12 February.

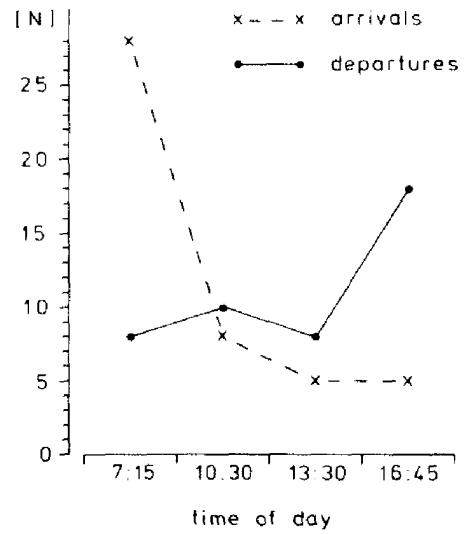


Fig. 10.2 (at right). Distribution of arrivals and departures of females during daylight hours grouped into four time blocks: 0715 = 0530-0900; 1030 = 0901-1200; 1330 = 1201-1500; 1645 = 1501-1830. Arrivals, N = 44; departures, N = 44.

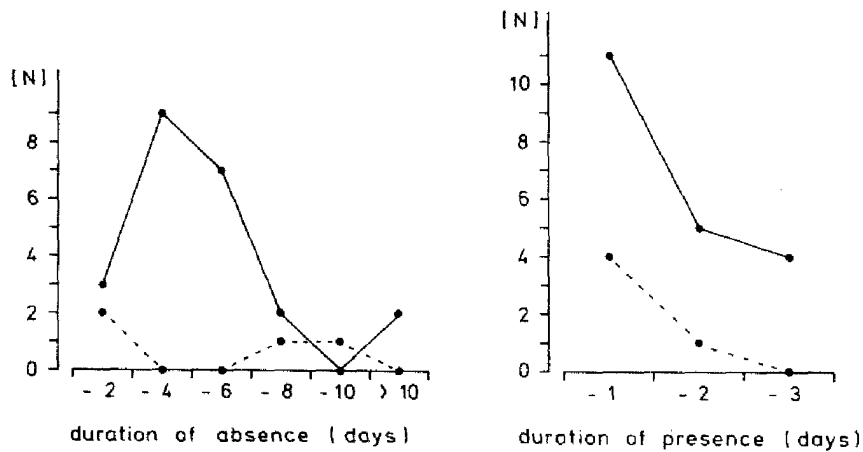


Fig. 10.3. Distribution for duration of (left) absence and (right) presence of females. Solid lines: mothers of pups. Broken lines: females without young.

contained 10% CO₂ and nitrogen, and the other contained 5% CO₂ and 12% CO₂ in nitrogen. Blood pH was measured in a Radiometer PHM 4 pH meter and glass E5021 Ultramicroelectrode.

RESULTS

The Period of Dependence of Young

Most likely, pups were weaned when they were between 1 and 2 years old. At Punta San Juan, fur seal pups are born between October and December. Many females without pups were observed suckling yearlings in December 1979 (Trillmich and Majluf, 1981), and again females were suckling yearlings in January and February 1983. Occasionally mothers were observed with a pup and a yearling simultaneously; such pups were always in poor condition. In our main study area, a pup and yearling pair was observed in a single case out of the sixty mother-and-pup pairs counted on 1 February. The pup later died of starvation. One female simultaneously suckled a male young estimated to be 2 years old, and another male of about 3 to 4 years. Young of about 2 years and older that were still suckling appeared to represent a minority of their age groups.

Daily Fluctuations in Numbers Ashore

Most adult fur seals arrived in the study area in the early morning. The numbers of adults peaked either in the 0900 or the 1100 hour census and then declined toward the evening (Fig. 10.1). This pattern of daily fluctuation in numbers agreed well with direct observations of female arrivals and departures. Arrivals showed a pronounced peak in the morning while departures had a more even distribution and peaked in the evening (Fig. 10.2).

The Female Feeding Pattern

Females with pups spent 23.5% of their time ashore and 76.5% at sea (140 female-days). One female without young and one female that had lost her pup spent 17% of their time ashore and 83% at sea (24 female-days). The distributions of the durations of presence and absence are shown in Figure 10.3. Females with pups stayed ashore for a median duration of 1 day (mean = 1.3 days; N = 26), while females without young stayed slightly shorter periods (median = 0.5 days; mean = 0.8 days; N = 5; Fig. 10.3). This difference approached significance ($p = 0.057$; Mann-Whitney U-test). Females with pups stayed at sea about as long per trip (median = 4.0 days; mean = 4.6 days; N = 23) as females without young (me-

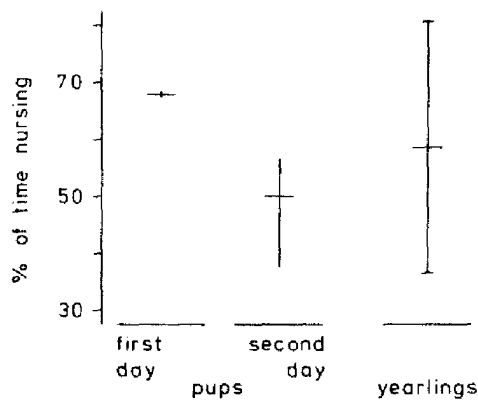


Fig. 10.4. Percentage of time ashore spent suckling by mothers of pups and of yearlings. For pups mean and range of observed values are given. First day (of female attendance): observations on two pups for 20 hours total; second day: observations on three pups for 15 hours total. Yearlings: mean \pm SD of 40 hours observation on seven mother and yearling pairs are given.

dian = 4.5 days; mean = 4.9 days; $N = 4$). No difference was detectable in our small sample ($p = 0.5$; Mann-Whitney U-test).

Of all seals one year old or older that were ashore at the time of the census, on average 13% were together with their mothers; in pups this was 15%. For a median stay ashore of 1 day for a given mother, this percentage attendance leads to a calculated average stay at sea of 6.1 days, slightly higher than the measured mean duration at sea. Perhaps this indicates that mothers with older young tended to stay at sea for slightly longer periods than mothers of young pups.

Female Time Budget Ashore

Similar to the Galapagos fur seal (Chapter 11), South American fur seal mothers spent most of their time ashore lying and sitting ($91.0 \pm 8.5\%$). For thermoregulation they moved to wetted shoreline (walking = 0.7%) or into the water (in water = 0.2%). Thermoregulatory movements led to most interactions, and these accounted for 0.6% of the females' time on land. Aggressive interactions with their own young comprised an additional 0.3% of the females' time.

The proportion of time on shore spent suckling varied with the age of the young and the duration of the shore visit. Mothers of pups estimated to be 2 to 3 months of age and mothers of yearlings

suckled for nearly 60% of their time ashore (Fig. 10.4). In contrast, the mother of a 2-year-old spent only 28% of its time ashore suckling (8 hours of data). The marked pups suckled 68% of the time on the first day of their mothers' attendance and only 50% of the time on her second day ashore (Fig. 10.4). Similar effects could not be evaluated for yearlings since we observed no marked mother and yearling pairs and could therefore not determine the mothers' previous attendance time.

Body Condition and Mortality of Young

During our study period most fur seal pups were in poor body condition. In early February only 8% of the pups were judged to be in good condition, 25% were in intermediate condition, and 68% in poor condition (N = 170). Pups in poor condition weighed on average 5.5 ± 1.2 kg (N = 4).

Many of the pups in poor condition died during our study period, and one of the marked pups died after a 10-day continuous absence of the mother. Of about seventy pups in the study area, at least 29 (41%) were found dead on land during 22 days. This number did not include dead young washed out to sea. The mortality rate appeared to increase during the observation time; during the first 11 days twelve pups died, while during the subsequent 11 days seventeen died. During the same 22-day period four yearlings out of forty yearlings and 2-year-olds (average of fourteen morning counts) were found dead from starvation.

Diving Behavior

Table 10.1 summarizes the three trips to sea by the single female from which dive data were obtained. Each successive trip was longer than the previous one, and most information came from the third and final trip, on which 698 of the 968 total dives were recorded. The first trip was not only unusually brief, but also the average dive

TABLE 10.1. Summary of three trips to sea for one South American fur seal female.

Trip no.	Total dive	Trip length (h)	Depth		Duration	
			Aver. (m)	Max. (m)	Aver. (min)	Max. (min)
1	85	24	63	170	3.3	5.0
2	185	47	39	81	2.8	3.7
3	698	116	27	90	2.3	7.1
Total	968					

TABLE 10.2. Activity budget for three trips to sea of one South American fur seal female.

Trip no.	Rest (%)	Dives/h	Transit times	
			Outbound ^a (h)	Return ^b (h)
1	4	3.5	11.0	6.0
2	0	3.9	8.0	1.5
3	2	6.0	7.5	1.5

^a Time from departure to first dive bout.

^b Time from end of last dive bout to return onto shore.

TABLE 10.3. Characteristics of South American fur seal dive bouts.

Trip no.	Dive bouts	Average bout duration (h)	Dives/h within bout
1	2	2.4	14
2	5	1.5	15
3	14	3.1	14

depth was more than twice that of the following two trips. The deepest dive (170 m) was also made on the first trip. Dive durations overall averaged 2.5 minutes and the maximum dive time was 7 minutes. When removing the TDR, we noted that the animal had lost about 5 kg body weight since the instrument was attached.

When the seal went to sea, she swam continuously for 7.5 to 11 hours before diving (Table 10.2). For the remainder of her time at sea, she remained active almost constantly. Even on the longest trip of 4.8 days, she was swimming or diving all but 2% of the time. In all trips the rate of dives per hour for the whole sea period ranged from 3.5 to 5.5. The interval from the last dive to the return ashore ranged from 1.5 to 6 hours.

The dive-bout criterion for this animal was 12 minutes. The average bout duration ranged from 1.5 to 3.1 hours, and the dive rate within a bout averaged fourteen dives per hour for all three trips (Table 10.3).

The most frequently attained dive depths were between 11 and 20 m, and between 21 and 30 m (Fig. 10.5). About 55% of all dives were within these ranges. Dive frequency declined rapidly at greater depths, with fewer than 1% of all dives to depths greater than 90 m. Almost all dives occurred between 2000 and 0700 hours

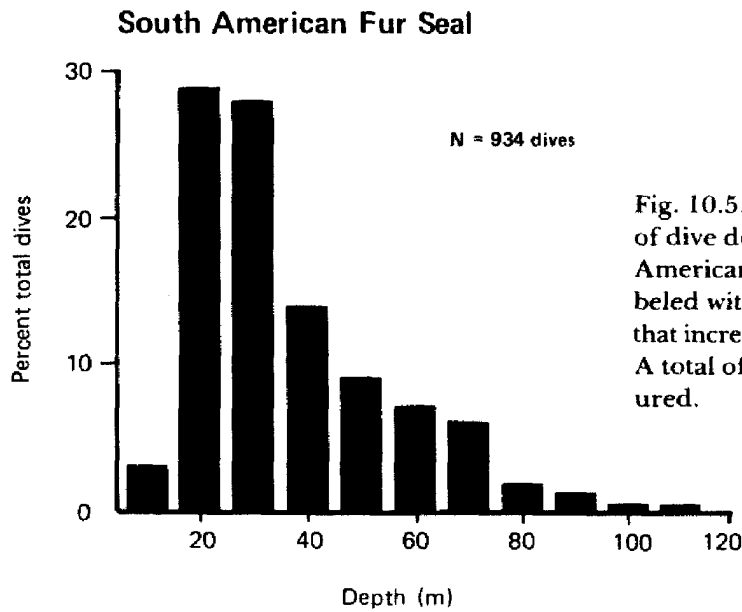


Fig. 10.5. Frequency distribution of dive depths of the South American fur seal. Bars are labeled with the deepest dive of that increment (20 = 11-20 m). A total of 934 dives was measured.

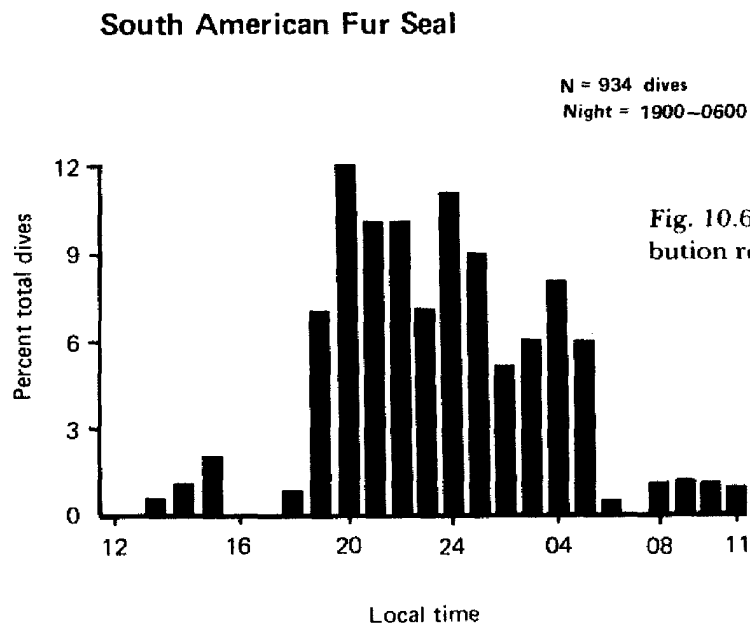


Fig. 10.6. Dive frequency distribution relative to time of day.

(Fig. 10.6). After 2000 hours diving activity rose sharply and remained elevated until 0700 hours, when a sharp decrease occurred. During the night hours the most frequently recorded depth interval was 21 to 30 m, while during the day dive depth was highly variable (Fig. 10.7). The sudden increase in dives and the predominance of deep dives in the early evening compared to other hours are shown in Figure 10.8.

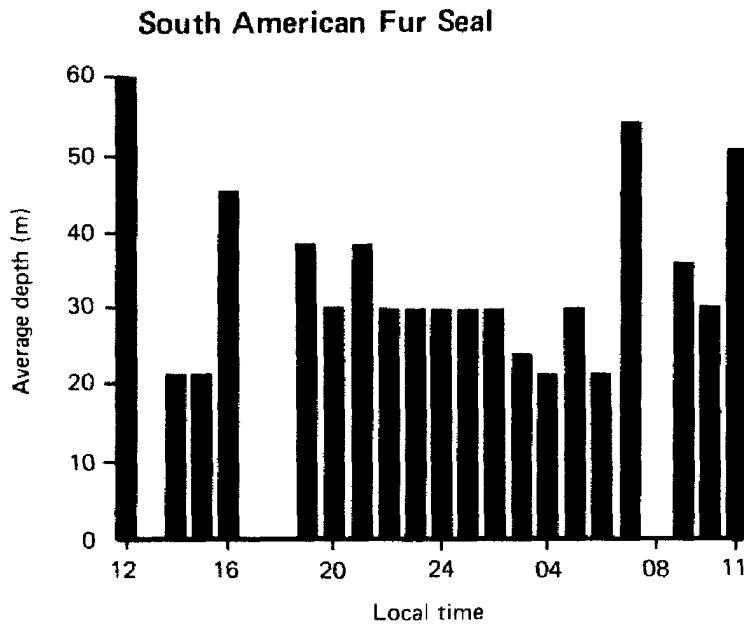


Fig. 10.7. The most frequently attained dive depth relative to the time of day for the South American fur seal.

TABLE 10.4. Hematological parameters for South American fur seals during EN conditions.

	<i>Pups</i>	<i>Older pups^a</i>	<i>Immature^a</i>	<i>Adult females</i>
Sample size	7	1	1	3
Age (months)	2-3	4-5	18	—
Weight (kg) ^b				
Mean	5.4	8.4	17.5	30-40
Range	4.7-6.5	—	—	—
Hemoglobin (g%)				
Mean	14.5	14.0	9.0	16.8
Range	12.4-18.1	—	—	16.5-18
Hematocrit (%)				
Mean	44.1	40.0	24.0	49.3
Range	39-53	—	—	46-51

^a Captured 24 April 1983. All others captured between 15 January and 11 February 1983.

^b Weight estimated by eye.

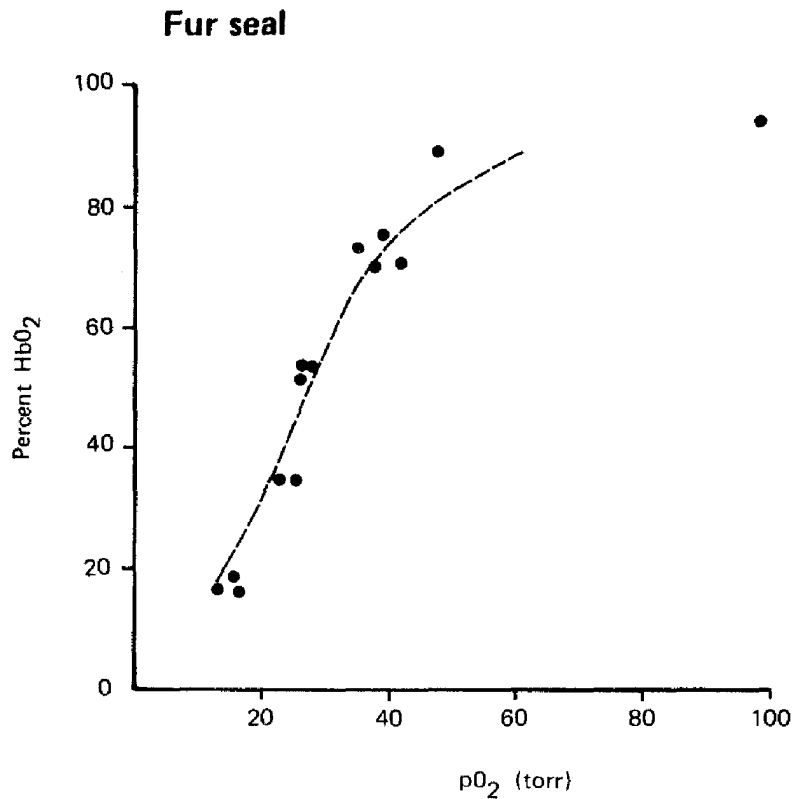


Fig. 10.9. Oxygen dissociation curve for three South American fur seals at pH = 7.4, pCO₂ = 45 torr, temperature = 37°C.

that these long absences were in any way compensated by increased milk transfer from mother to pup during attendance periods (compare with the similar data for the Galapagos fur seal, Chapter 11). The poor body condition and high mortality of pups corroborate this conclusion and suggest that, unlike the northern fur seal, the pup-rearing behavior of this species is not adapted to long periods of maternal foraging. Apparently the quality of milk and the uptake and storing abilities of the young become insufficient if mothers repeatedly remain at sea for more than 5 days.

Strong EN events apparently led to reduced foraging success of females and disrupted normal periodic patterns of female attendance and foraging. At least two factors contribute to this breakdown of the system: (1) absolute density of prey items in the surface layers may be strongly reduced; (2) prey at great depth can only be caught at high energetic cost (long diving time, reduced success rate per dive). These and perhaps other factors may change the benefit to cost ratio of foraging and may induce females to rest in the foraging

area during daytime instead of returning to the colony. Overly long stays at sea and/or reduced milk quality and volume may then quickly lead to loss of the pup.

The dive data obtained from a single, nonsuckling female may not accurately characterize the shore and sea cycle of lactating females. However, the duration of stays ashore or at sea did not differ significantly between females with and without pups (Fig. 10.3a, b). Presumably, the dive behavior would also be similar since the means of finding and catching fish would be the same for suckling and nonsuckling females. This assumption is based on the premise that similar durations at sea mean the animals forage in areas where fish distribution and abundance would be the same.

If we assume that the female swam at 2 m per second (Chapter 15), then the feeding areas may have been as much as 50 to 80 km from the colony. However, the interval from the last dive to arrival ashore (1.5 hours) may better reflect the usual distance from the colony. A 1.5-hour swim time would correspond to about 11 km distance. The 7- to 11-hour interval between departure and the first dive may represent searching within this 11 km range for prey that, due to the EN, was difficult to find. We interpret the female's obvious weight loss over the 11 days from release to recapture as evidence of low success in finding food. Her lean condition was similar to that of many other adult and immature seals in the colony.

Despite weight loss and possible poor hunting success, the female adhered strictly to nocturnal hunting rather than attempting to feed throughout both day and night (Figs. 10.6, 10.8). The deepest dives occurred early in the evening (Fig. 10.8) and may have represented initial feeding attempts prior to the vertical migration of fish to the surface. Once feeding began, the diving frequency and dive depth (about 30 m) remained relatively constant throughout the night (Figs. 10.6, 10.7, 10.8), suggesting that the distribution and abundance of fish remained uniform. Because of the EN conditions, we suspect that dive frequency and depth were both greater than normal. However, the dive depths were not as great as we expected them to be; the female did not make any exceptionally deep, serial dives such as northern and South African fur seals make. This result is surprising since the fish population had probably moved to greater depths and, based on her observed weight loss, she had been unsuccessful in obtaining adequate food within the depth range she used.

The steady loss of weight by the female may not have had much effect on her dive abilities. The blood samples obtained from pups

and adults showed O₂ capacity, hemoglobin, hematocrit, and dissociation curves to be approximately the same as those measured for other otariids (Ridgway, 1972; Wells, 1978; Lenfant et al., 1970), suggesting that the diving female probably had a normal blood condition despite her weight loss. If so, then as discussed in more detail in Chapter 15, her blood O₂ stores were probably normal and her aerobic dive limit was not affected. Consequently most of her dive capacities, such as dive depth, duration, and frequency, should have been normal.

SUMMARY

Attendance and diving behavior of the South American fur seal were studied at Punta San Juan, Peru, in January and February 1983. This population faces a tropical environment, quite unlike the more temperate environments experienced by other populations of this species. The study was conducted during EN conditions. We found that many females were unable to support themselves and their dependent young. Low foraging success apparently led to extended trips to sea, acute malnutrition, and eventual starvation of pups and yearlings. Pups were born from October to December. Animals attended the breeding sites throughout the year; there was no evidence of an annual migration. The interval from parturition to weaning was 12 to 24 months. Weaning was slow and not always complete; some females suckled a yearling and a newborn simultaneously. The animal that initiated weaning was not determined. No data were obtained on the attendance pattern before parturition, the interval from parturition to copulation, trips to sea before copulation, or number of visits to land prior to weaning. The duration of most visits to shore was 1.3 days. In the study period females spent 24% of their time on shore, and they spent a maximum of 60% of this time suckling, depending on the age of the young. Females departed for sea in the evening and arrived on shore in the early morning. Foraging absences lasted 4.7 days, but because this was an EN year, such durations may have been longer than normal. No data were obtained on increases in feeding-trip duration throughout the season. Nonmothers had slightly shorter stays on shore than did mothers (0.8 days), but trips to sea were about equal in length.

Blood oxygen capacities, hemoglobin, hematocrit, and dissociation curves appeared to be normal for otariids. Nevertheless, due to the presumed scarcity of food caused by EN, 70% of the pups were

in poor condition and pups suffered a 42% mortality over 22 days of observation.

Diving records were obtained for three trips to sea for one individual. Two trips were short and one trip (4.8 days) was about as long as for uninstrumented animals. The transit times were 7.5 to 11 hours outbound, and 1.5 to 6 hours returning. The number of dives per trip to sea varied greatly, depending on trip duration. Diving activity occurred throughout the night (88% of all dives occurred then), with no dawn or dusk peaks. The dive bout criterion was 12 minutes. The female had an average of seven dive bouts per trip, with durations from 1.5 to 3.1 hours, and a dive rate of fourteen dives per hour. The portion of dive bouts spent submerged was not calculated. All dive bouts were shallow. Dives were continuous ascent or descent with no time spent at maximum depth. Dives lasted on average 2.5 minutes with a maximum duration of 7 minutes. The mean depth of all dives was 29 m and the maximum was 170 m. The most frequently attained dive depths were between 11 m and 30 m. No correlations were made between depth and duration, nor between surface interval and depth of dive. Females spent 2% of their time at sea resting, but time spent swimming and diving was not calculated.