

ATTENDANCE PATTERNS OF CALIFORNIA
SEA LION (*ZALOPHUS CALIFORNIANUS*)
FEMALES AND PUPS DURING THE
NON-BREEDING SEASON AT
SAN MIGUEL ISLAND

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ABSTRACT

The attendance patterns of California sea lions were studied during the non-breeding seasons from 1991 to 1994. Lactating females frequented the rookery to nurse their pups until weaning; most non-lactating females left the rookery for the season. Females spent over 70% of their time at sea except in 1993 when they spent 59% of their time at sea. The mean foraging trip length in the winter and spring ranged from 3.3 to 4.6 d; the mean nursing visit ranged from 1.2 to 1.4 d. The duration of foraging trips and nursing visits was variable over the season for individuals but no pattern of change was detected. Interannual and seasonal differences were not significant for time at sea, visits ashore, or foraging-trip duration before, during, or after the 1992–1993 El Niño event. Pups spent an average of 66.6% of their time ashore and up to three days away from the rookery during their mother's absence. Most females and pups stayed associated until April or May. The results suggest that seasonal movement of prey is more important in determining attendance patterns late in the lactation period than increasing energy demands of the pup.

Key words: California sea lion, *Zalophus californianus*, attendance pattern, El Niño, weaning, maternal behavior, non-breeding season.

The attendance pattern is the alternation of foraging trips to sea and nursing visits on land that a female otariid undertakes to support herself and her pup during the lactation period. The attendance patterns of otariid females have been the focus of many studies because they reflect maternal investment in the pup and may provide an indirect measure of foraging conditions experienced by females during the lactation period (Gentry and Holt 1986, Trillmich 1986, Bengtson 1988, Croxall *et al.* 1988, Higgins *et al.* 1988, Antonelis *et al.* 1990, Boyd *et al.* 1991, Heath *et al.* 1991, Higgins and Cass 1993, Melin 1995, Francis *et al.* 1998, Goebel and Gentry 1998). Most studies have investigated attendance patterns only during the breeding season or in species with relatively short lactation periods. For species with longer lactation periods, such as the California sea lion, most of the maternal investment occurs after the breeding season. For these species, the attendance pattern during the non-breeding season is an important component in evaluating the time a female invests in her pup.

The lactation period of the California sea lion lasts 6–11 mo. Pupping occurs from mid-May through June, followed by breeding from July through mid-August (Peterson and Bartholomew 1967, Odell 1981, Heath 1989). The maternal behavior of California sea lions during the breeding season has been well documented (Peterson and Bartholomew 1967, Odell 1981, Heath 1989, Antonelis *et al.* 1990); after a 5–8-d perinatal period ashore females begin an attendance pattern consisting of 2–3-d foraging trips followed by nursing visits of 1.5–2 d (Heath 1989, Antonelis *et al.* 1990).

The non-breeding season extends from mid-August through mid-May of the following year. The maternal behavior during the non-breeding season has not been studied intensively, yet this period represents up to two thirds of the total time a female invests in her pup. Seasonal changes in prey distribution certainly occur during the 9-mo non-breeding season (Antonelis *et al.* 1984, Lowry *et al.* 1990) and the energy demands of the pup probably increase as the pup grows and becomes more active. In response to these changes, females may have to adjust their attendance patterns. The changes in attendance patterns may be: (1) gradual over time as females increase their time at sea or time ashore (Gentry and Holt 1986) to accommodate increasing energy demands of the pup or to facilitate weaning, (2) cyclical as prey move inshore, offshore, northward, or southward for spawning and migration, (3) seasonally discrete if prey distribution shifts significantly only one or two times during the lactation period (Higgins and Cass 1993), or (4) if pups accompany females on foraging trips changes may be required to accommodate the more limited traveling capabilities of the pup.

In addition to annual and seasonal changes in prey distribution, the foraging environment also changes in response to periodic El Niño events that can cause large-scale, prolonged changes in sea-lion prey distribution and abundance. Such changes in the foraging environment have resulted in significant changes in attendance patterns of many species of otariids (Croxall *et al.* 1988, DeLong and Antonelis 1991, Heath *et al.* 1991, Majluf 1991, Trillmich and Dellinger 1991). During the 1982–1983 El Niño event, the duration of for-

Table 1. Number of California sea lion adult females and pups instrumented with VHF radio transmitters at San Miguel Island, California, 1990–1994. Number of animals with complete record in parentheses.

Period instrumented	Number of lactating females	Number of non-lactating females	Number of pups
Dec 1990–May 1991	27 (21)	2 (0)	10 (1)
Dec 1991–May 1992	21 (21)	4 (1)	—
Mar 1992–May 1992	—	—	7 (6)
Mar 1993–May 1993	6 (3)	—	—
Mar 1994–May 1994	9 (9)	—	9 (8)
Total	63 (54)	6 (1)	26 (15)

aging trips of California sea lions increased and nursing visits decreased during the breeding season (Heath 1989, Heath *et al.* 1991). The effects of the 1982–1983 El Niño event on the attendance patterns during the non-breeding season were not investigated. However, it is likely that they were also altered because the displacement of prey exceeded one year (Arntz *et al.* 1991). Significant changes in the attendance pattern during the non-breeding season could impact weaning behavior and the postweaning survival of the pup. In the second and third year of this study, El Niño conditions prevailed along the California coast, which provided an opportunity to describe the effects of the 1992–1993 El Niño event on attendance patterns during the non-breeding season.

This paper describes the attendance behavior of California sea lion females and pups during the non-breeding season and addresses the following questions: (1) are there significant temporal and annual changes in attendance patterns late in the lactation period? (2) do pups accompany females on foraging trips or travel with females to other hauling sites away from their natal rookery? (3) did the 1992–1993 El Niño event alter the attendance patterns of sea lion females? The answers to these questions provide a better understanding of the role late lactation attendance patterns play in successful rearing of California sea lion pups.

METHODS

We instrumented adult females with VHF radio transmitters (164–165 MHz) at Pt. Bennett, San Miguel Island, California (34°01'N, 120°26'W), during four sampling periods: December 1990 and 1991 and March 1993 and 1994 (Table 1). We also instrumented the pups of these females with VHF radio transmitters in December 1990 and March 1992 and 1994. Transmitters were glued to the pelage on the back using 5-min epoxy resin. In 1994, pups were instrumented with transmitters mounted on flipper tags instead of back-mounted because back-mounted transmitters were lost during the winter molt of pups in 1990. Flipper transmitter tags were attached to the left foreflipper.

The back-mounted transmitters functioned 8–10 mo and had pulse rates of

48–60 per min. The pup flipper transmitters lasted 2–4 mo and had pulse rates of 60 per min. For females, data were collected from December through May 1990–91 and 1991–92 and March through May 1993 and 1994. For pups, data were collected from December through May 1990–1991 and March through May in 1991–1992 and 1994. Females and pups that had incomplete records because of noise or disappearance were not included in the analyses.

A remote radio receiver system with an automatic data logger was stationed on a 100-m bluff overlooking the Point Bennett rookery. This system monitored the presence of instrumented animals. The station consisted of a photovoltaic panel, two marine deep-cycle batteries, a 4-element Yagi antenna, and a programmable scanning receiver and automated data logger housed in a weatherproof container. The radio receiver and data logging system (Advanced Telemetry Systems, Isanti, MN) scanned each radio transmitter frequency for 10 sec every 20 min and recorded the number of signals received for each frequency. Females and pups were considered present if 3–10 signals were received during each 10-sec scan for 3 h or longer. Animals were considered absent when signals were not received for a period greater than 3 h. A reference transmitter was placed in close proximity to the instrumented animals to ensure that the system was working properly when unattended. When researchers visited San Miguel Island, manual radio scans and visual observations of instrumented animals were conducted to verify the accuracy of the automated data logging system.

The 1990–1991 and 1991–1992 study periods were divided into winter (15 December–15 March) and spring (16 March–20 May) for seasonal comparisons of attendance behavior during the non-breeding season. These divisions were based upon seasonal changes in the diet of females (Antonelis *et al.* 1984, Lowry *et al.* 1990).

To assess relationships between physical characteristics of adult females and attendance behavior, the total length ($n = 42$), girth ($n = 14$), weight ($n = 7$) and age ($n = 8$) of a sample of the instrumented females were collected. The smaller sample sizes for weight and age are due to the difficulty of obtaining these measurements with limited personnel. Females were considered lactating if they were sighted nursing a pup or if the teats were clean and milk was ejected when the teats were palpated. Otherwise, females were considered non-lactating. For all pups, weight and sex were recorded.

The distribution of data for nursing visits and foraging trips for individual females was non-normal, and a natural-log transformation did not normalize the data. Therefore, the medians of foraging trip length and nursing visits for each female were used as a measure of central tendency, and the means and standard errors of these medians were computed for summary statistics (*i.e.*, n in the statistical tests represents the number of females rather than the number of trips or visits for the sample). Non-parametric statistical tests were used in comparisons among years and seasons because the medians were used as the basic statistic for comparisons. Statistical tests were conducted using Systat[®] or Minitab[®] software packages with significance at $\alpha = 0.05$.

Table 2. Means and standard errors (SE) of percent time at sea, median foraging trip lengths and median visits ashore (d) in winter (15 December–15 March) and spring (16 March–20 May, 1990–1991 and 1991–1992 for California sea lion females at San Miguel Island, California.

	<i>n</i>	Winter			Spring		
		Range	Mean	SE	Range	Mean	SE
Percent time at sea							
1990–1991	21	68.1–95.4	76.1	0.02	62.4–88.6	72.6	0.01
1991–1992	21	65.5–88.4	75.0	0.01	60.2–84.2	72.4	0.02
1993	3	—	—	—	40.0–82.1	59.4	0.12
1994	9	—	—	—	52.9–82.0	71.6	0.04
Foraging trips							
1990–1991	21	0.6–10.0	4.6	0.57	1.1–6.8	3.8	0.39
1991–1992	21	0.9–6.1	3.3	0.30	0.7–8.9	3.9	0.55
1993	3	—	—	—	0.5–13.0	6.2	0.90
1994	9	—	—	—	0.4–8.9	4.4	0.30
Nursing visits							
1990–1991	21	0.4–3.7	1.4	0.16	0.4–2.3	1.3	0.11
1991–1992	21	0.4–1.8	1.2	0.09	0.3–2.2	1.3	0.11
1993	3	—	—	—	0.8–2.3	1.7	0.19
1994	9	—	—	—	0.4–2.6	1.3	0.06

RESULTS

Behavior of Lactating and Non-lactating Females

Attendance records from 54 of 63 lactating females were obtained (Table 1). Lactating females visited San Miguel Island frequently throughout the study periods. Five of the six non-lactating females dispersed from San Miguel Island shortly after instrumentation and did not return to San Miguel Island for the remainder of the study period. The non-lactating females were sighted at San Nicolas Island (85 km SE of San Miguel Island), Año Nuevo Island (286 km NW of San Miguel Island), the Farallon Islands (440 km NW of San Miguel Island), and at various hauling sites along the California coast. One non-lactating female, from 1991–1992, remained at San Miguel Island throughout the study period and exhibited an attendance pattern similar to that of lactating females.

Attendance Patterns of Lactating Females

Interannual seasonal patterns in attendance, 1990–1991 and 1991–1992—In the winter, lactating females spent 76.1% and 75% of their time away from the rookery in 1990–1991 and 1991–1992, respectively (Table 2). The difference was not statistically significant (Mann-Whitney, $P = 0.870$). Foraging trip lengths (4.6 d, 1990–1991; 3.3 d, 1991–1992) and nursing visits (1.4 d, 1990–1991; 1.2 d, 1991–1992) during the winter also were not different

Table 3. Relationship of age and morphometric measurements to median foraging trip length for California sea lion females. Data for all females pooled. R^2 and P -values calculated from simple linear regression.

Parameter	n	R^2 adjusted	ANOVA P -value
Length	46	0.001	0.687
Girth	14	0.001	0.824
Weight	7	0.001	0.983
Length, girth	7	0.261	0.243
Length, weight	7	0.239	0.257
Girth, weight	7	0.526	0.100
Length, girth, weight	7	0.375	0.267
Age	8	0.132	0.196
Length, age	4	0.152	0.530

between years (foraging trips, Mann-Whitney, $P = 0.102$; nursing visits, Mann-Whitney, $P = 0.846$).

In the spring, females spent about 72% of their time away from the rookery in both years (Mann-Whitney, $P = 0.863$) (Table 2). Foraging trip lengths (3.8 d, 1990–1991; 3.9 d, 1991–1992) and nursing visits (1.3 d in both years) during the spring were not different between years (foraging trips, Mann-Whitney, $P = 0.811$; nursing visits, Mann-Whitney, $P = 0.811$).

The durations of foraging trips and nursing visits were positively correlated in both years but more so in 1990–1991 than 1991–1992 (Spearman rank correlation, $r = 0.74$ for 1990–1991; $r = 0.49$ for 1991–1992). The duration of foraging trips and nursing visits were variable among individuals within each year. The variability in foraging trip lengths ($F_{1,581} = 0.016$, $r^2 = 0.000$, $P > 0.899$, 1990–1991; $F_{1,530} = 2.494$, $r^2 = 0.003$, $P > 0.115$, 1991–1992) and nursing visits ($F_{1,588} = 4.372$, $r^2 = 0.006$, $P > 0.037$, 1990–1991; $F_{1,548} = 0.276$, $r^2 = 0.000$, $P > 0.600$, 1991–1992) was not explained by a linear trend through time. Foraging trip length was also not correlated with adult female length, girth, weight, age or combinations of these parameters (Table 3).

Seasonal patterns in attendance, 1990–1991 and 1991–1992—The percent time away from the rookery, the foraging-trip lengths, and nursing visits did not change between the winter and spring in either year (Mann-Whitney. Time away: $P = 0.122$, 1990–1991; $P = 0.372$, 1991–1992. Foraging trips: $P = 0.291$, 1990–1991; $P = 0.443$, 1991–1992. Nursing visits: $P = 0.980$, 1990–1991, $P = 0.734$, 1991–1992). Although most females did not change their behavior significantly between seasons, 19% and 28.6% of the females in 1990–1991 and 1991–1992, respectively, changed their foraging trip length between the winter and spring (Fig. 1a, 2a). The duration of nursing visits changed significantly between seasons for 23.8% and 33.3% of the females in 1990–1991 and 1991–1992, respectively (Fig. 1b, 2b). For the females that changed their pattern significantly, no consistent pattern of change among the females was detected in the percent time away from the rookery

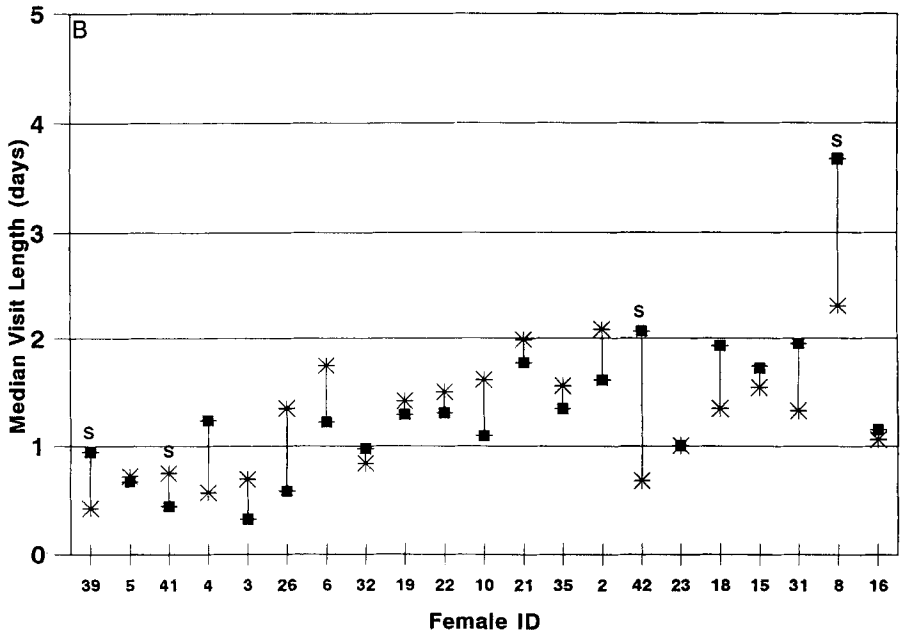
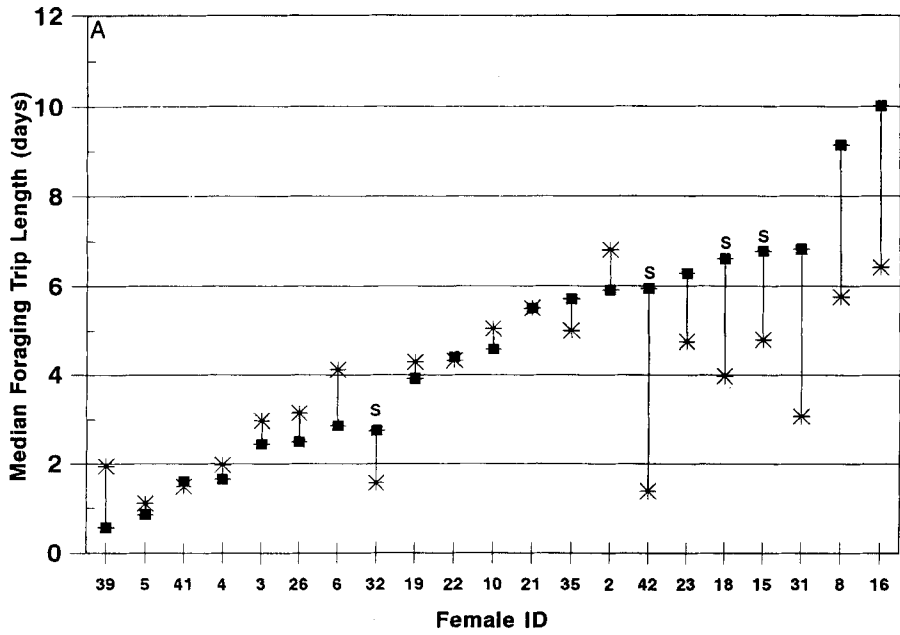


Figure 1a. Seasonal changes in median foraging trip durations for lactating California sea lions at San Miguel Island, California, 1990–1991. “S” indicates significant change between winter (■) and spring (*).

Figure 1b. Seasonal changes in median visit ashore durations for lactating California sea lions at San Miguel Island, California, 1990–1991. “S” indicates significant change between winter (■) and spring (*).

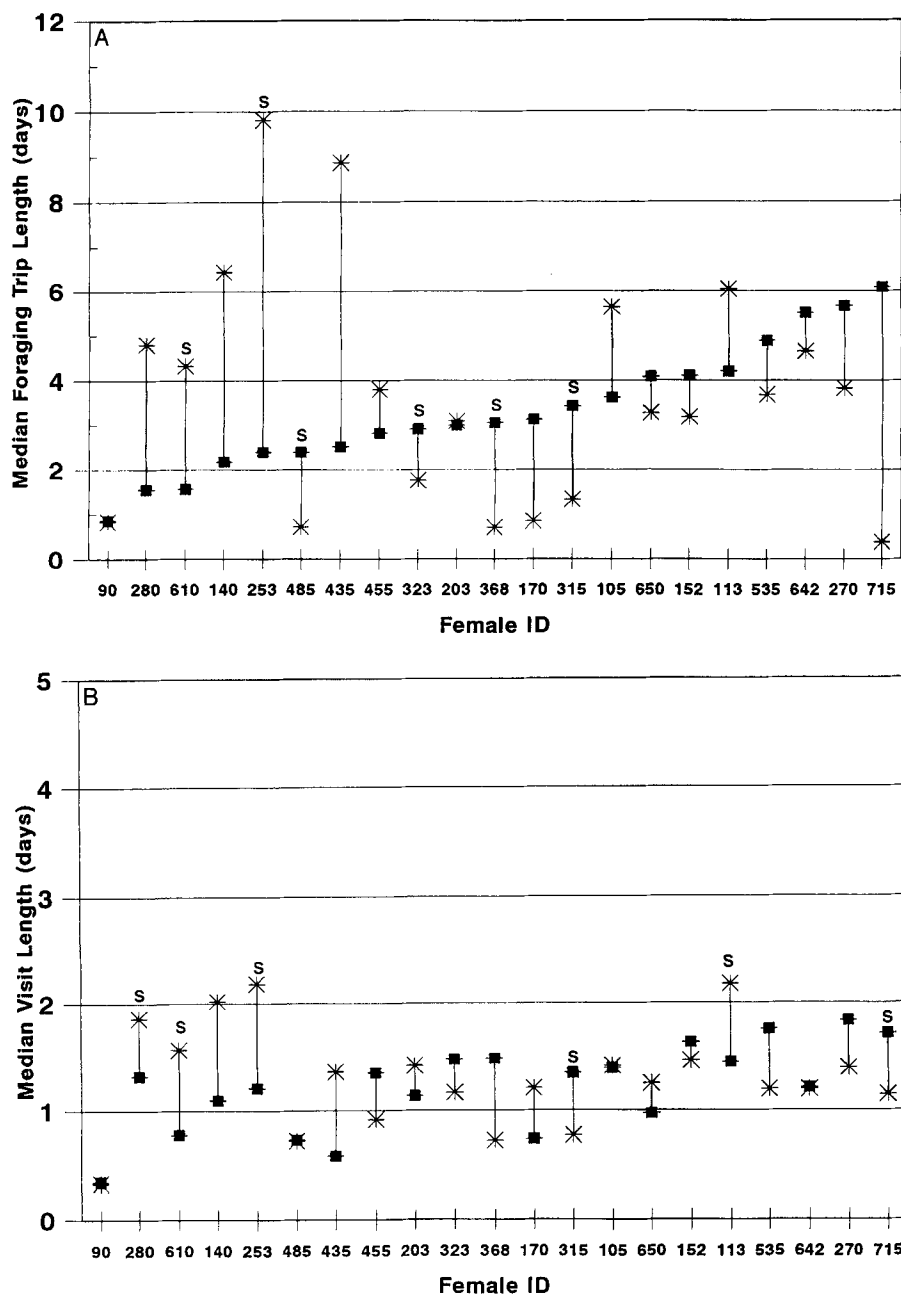


Figure 2a. Seasonal changes in median foraging trip durations for lactating California sea lions at San Miguel Island, California, 1991-1992. "S" indicates significant change between winter (■) and spring (*).

Figure 2b. Seasonal changes in median visit ashore durations for lactating California sea lions at San Miguel Island, California, 1991-1992. "S" indicates significant change between winter (■) and spring (*).

Table 4. Dates of departure from San Miguel Island for California sea lion females and their pups. Negative number for days between departures indicates number of days that pup left before female and positive number indicates that female departed before pup. No pups instrumented in 1993.

Year	Female I.D.	Date of last departure	Pup I.D.	Date of last departure	Days between departures
1990–1991	F91-10	18 May 91	P91-17	5 May 91	-13
1991–1992	F92-113	16 Apr 92	P92-680	1 May 92	+15
	F92-203	2 May 92	P92-060	3 May 92	+1
	F92-270	15 May 92	P92-402	8 May 92	-7
	F92-315	20 May 92	P92-008	9 May 92	-11
	F92-323	15 Apr 92	P92-032	20 Apr 92	+5
	F92-642	20 May 92	P92-772	22 Apr 92	-28
1994	F94-1	22 May 94	P94-13	26 May 94	+4
	F94-2	5 May 94	P94-15	10 Apr 94	-25
	F94-4	3 Apr 94	P94-11	6 Apr 94	+3
	F94-5	5 May 94	P94-20	29 May 94	+24
	F94-7	29 Apr 94	P94-12	30 Apr 94	+1
	F94-8	12 May 94	P94-14	7 Jun 94	+26
	F94-9	21 Apr 94	P94-17	24 May 94	+33
	F94-10	11 May 94	P94-19	24 May 94	+13

(Wilcoxon Signed Rank, $n = 4$, $P = 0.062$, 1990–1991; $n = 6$, $P = 0.253$, 1991–1992), foraging trip lengths (Wilcoxon Signed Rank, $n = 4$, $P > 0.20$, 1990–1991; $n = 6$, $P > 0.50$, 1991–1992) or duration of nursing visits (Wilcoxon Signed Rank, $n = 5$, $P > 0.50$, 1990–1991; $n = 6$, $P > 0.20$, 1991–1992).

For 15 female-pup pairs (1 pair in 1990–1991, 6 pairs in 1991–1992, 8 pairs in 1994), there was no relationship between the foraging trip length of females and the sex ($F_{1,13} = 0.691$, $P > 0.502$) or capture weight ($F_{1,14} = 0.047$, $P > 0.831$) of their pups. The data for pups were pooled because of small sample sizes in each year and because the average pup weights in 1991–1992 and 1994 were not different (t -test, $P = 0.853$).

El Niño and spring attendance patterns, 1991–1994—Comparisons of spring attendance patterns before, during and after the 1992–1993 El Niño event indicate that it did not significantly affect the percent of time away from the rookery (Kruskall-Wallis, $P = 0.750$), foraging trip length (Kruskall-Wallis, $P = 0.969$), or duration of nursing visits (Kruskall-Wallis, $P = 0.666$) of females (Table 2).

In 1990–1991, 1991–1992, and 1994, females separated from their pups and dispersed from San Miguel Island between April and early June (Table 4). In contrast, of six lactating females instrumented in January and February 1993, three females left in February and early March (prior to 15 March) and were later sighted along the central and northern California coast. It is unknown if their pups were weaned early or died. Of the remaining three females, one female made two trips and one three trips before leaving San Miguel

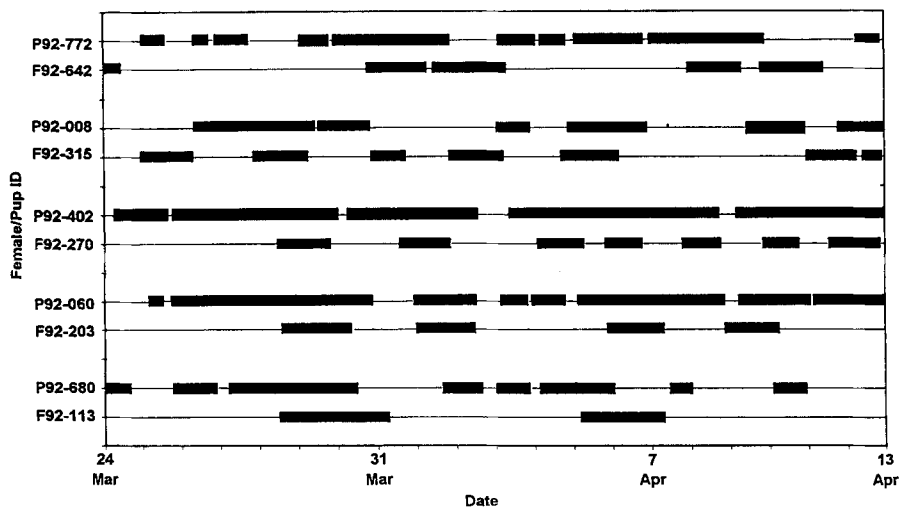


Figure 3. California sea lion female and pup pair attendance patterns, 25 March–14 April 1992 at San Miguel Island California. Thin line indicates time ashore. Bold line indicates time at sea. “F” preceding the sample number indicates female cycle and “P” indicates pup cycle.

Island in mid-April for the remainder of the 1993 study period, and one remained at San Miguel Island, making very short trips to sea throughout the study period. The departure of lactating females prior to mid-March in 1993 was not observed in any of the other study periods.

Pup Behavior

Pups spent more time ashore in 1991–92 ($n = 6$, $\bar{x} = 66.6\%$, $SE = 7.45$) than in 1994 ($n = 8$, $\bar{x} = 6.2\%$, $SE = 2.86$) (Mann-Whitney, $P < 0.001$). The average time pups spent away was 12 h ($n = 6$, $SE = 2.9$ h) in 1991–1992 but ranged from 5.7 h to 26.4 h. In 1994 the average time away was 26.4 h ($n = 8$, $SE = 7.9$ h) with a range of 9–79.2 h (3.3 d). Time away could have been spent at sea or hauled out at an area on San Miguel Island outside the range of the radio receiver station.

Female and Pup Behavior

Females and their pups remained associated throughout the winter and into the spring (Table 4). Figure 3 shows examples of female-pup pair cycles observed in 1991–1992 and exemplifies the patterns observed throughout the spring study periods in 1991–1992 and 1994. The female-pup-pair attendance patterns suggest that pups did not accompany their mothers to sea on foraging trips. However, pups did spend time away from the rookery while their mothers were away. Using the 3-h criterion for status changes, there were some periods when pups and females did not overlap (Fig. 3, P92–772, P92–008,

and P92–680). When data for these pups were examined on an hourly basis, the pups always overlapped with the female but spent several periods less than 3 h with the female while she was ashore.

Pups were considered weaned when there was no overlap between female and pup presence at the rookery based on transmitter signals, but both were known to carry functioning transmitters at the time of separation. Two weaning behaviors were observed: self-weaning by the pup and weaning by the female. Self-weaning was defined as occurring when (1) pups left before the female and the female continued to frequent the rookery after the pup was gone, and (2) the pups were not present at the rookery following the date at which self-weaning was determined to have occurred. Weaning by the female was defined as occurring when (1) the female left the rookery for an extended period of time (a month or more), and (2) the pup continued to frequent the rookery after the female was gone. Based on these criteria, it appears that self-weaning by pups was more common in 1991–1992 than in 1994, although sample sizes were too small to test statistically. In 1991–1992, three of six (50%) pups weaned themselves compared with one of eight (12.5%) pups in 1994 (Table 4). For the only female-pup pair observed in 1990–1991, the pup weaned itself. Ten of 15 females in the female-pup pair sample weaned their pups by leaving San Miguel Island in April and May for at least a month. The pups remained at San Miguel Island from 1 to 33 d after their mothers left. For the remaining five pairs, the pups weaned themselves by departing 7–28 d before their mothers (Table 4).

DISCUSSION

Lactating and Non-lactating Females

Lactating females frequent the rookery regularly to nurse their pups until the pup is weaned. This is similar to the pattern of maternal behavior in the fur seals (Gentry and Holt 1986, Trillmich 1986, Bengtson 1988, Croxall *et al.* 1988, Boyd *et al.* 1991, Francis *et al.* 1998, Goebel and Gentry 1998). Most non-lactating females in this study dispersed away from the rookery during the winter and spring. This contrasts with the behavior of non-lactating northern fur seals which continue to frequent the rookery but have more variability in their attendance pattern (Gentry and Holt 1986). This difference may be because northern fur seal females have no other suitable haul-out sites close to foraging areas other than the rookery, whereas California sea lions have many such hauling sites available to them; *i.e.*, non-lactating sea lion females have many areas for hauling and foraging other than San Miguel Island. Dispersion may allow non-lactating females to exploit different and perhaps more productive foraging areas during the non-breeding season. If there is separation of foraging areas between non-lactating and lactating females, it may indicate that the forage resources near San Miguel Island are limited to supporting juveniles and females with pups during the non-breeding season. Additional study of the annual patterns in non-lactating female behavior is needed to

determine if dispersal from the rookery is characteristic of this component of the population.

Attendance Patterns of Lactating Females

The attendance patterns of lactating females during the non-breeding season were different from patterns in the breeding season for females at San Nicolas and San Miguel Islands in the 1980s (Heath 1989, Antonelis *et al.* 1990). The mean foraging trip was about a day longer and the mean nursing visit was a day shorter during the non-breeding season than in the breeding season. These differences may be authentic but they may also reflect temporal differences or differences in sampling methods. To rigorously address whether there are differences in breeding season and non-breeding season attendance patterns, the same females should be instrumented in both seasons. This requires instrumenting individuals during the breeding season, relocating them after the fall molt, and recapturing and re-instrumenting them for the non-breeding season. We attempted this in 1991–1992 with little success (only four non-lactating females were recaptured).

The most surprising finding of this study was that the duration of foraging trips and nursing visits did not change progressively during the late lactation period. This contrasts with observations of other otariids for which the foraging trip durations increase or decrease during the lactation period (Gentry and Holt 1986, Higgins *et al.* 1988, Boyd *et al.* 1991, Higgins and Cass 1993, Goebel and Gentry 1998). The function of these changes in attendance remains unclear. It has been hypothesized that the changes in the attendance pattern of northern fur seals are related to the increasing energy demands of the pup as it grows (Gentry and Holt 1986, Goebel and Gentry 1998). However, it is also possible that the changes reflect movement of the prey farther from the rookery over the duration of lactation (Higgins and Cass 1993). Under the first hypothesis, we would expect a trend over time as the pup grows. Under the second hypothesis, we would expect more variability in the pattern of change as individual females find or follow prey. Because the changes in attendance patterns observed in our study were not progressive over the lactation period nor consistent among females, we believe the changes observed reflect seasonal movement of prey rather than an increase in the energy needs of the pup. The energy demands of pups increase as the pup grows but most of the energy is required for maintenance (Oftedal *et al.* 1987). Oftedal *et al.* (1987) suggested that the slow growth of pups is a compromise between high maintenance requirements as the pup grows and limited energy investment rate of females due to limited milk storage capacity. Our findings indicate that pups over 6 mo old spend time away from the rookery while their mothers are on foraging trips. If the pups forage during the short trips, they may supplement their diet such that their mother does not have to increase her energy yield to meet the increased energy demands of the pup as it grows. This hypothesis would be consistent with our results and those of Oftedal *et*

al. (1987), because females would not have to increase their foraging trips or nursing visits to maintain their pups.

Variability in the duration of foraging trips among females during the breeding season has been observed for other otariids (Gentry *et al.* 1986, Higgins *et al.* 1988, Costa *et al.* 1989, Boyd *et al.* 1991, Higgins and Cass 1993, Francis *et al.* 1998, Goebel and Gentry 1998). In northern fur seals this variability has been associated with body mass and age of the female (Gentry *et al.* 1986); however, for Antarctic fur seals no such relationships were observed (Boyd *et al.* 1991). No significant relationships between foraging trip durations and the physical parameters of California sea lion females or their pups were detected in this study, although sample sizes were small.

The variability within an individual female's attendance pattern stems from abiotic and biotic environmental forces. The foraging environment of California sea lions is dynamic and females must constantly adjust their foraging behavior and, consequently, their attendance pattern to accommodate changes in prey distribution and abundance. In addition, during the spring, females are preparing their pups for nutritional independence. Some females may change their attendance pattern to facilitate weaning by spending less time ashore or may change the time of day they are ashore (Melin 1995). Therefore, it is not surprising that attendance patterns of individual females during the non-breeding season show considerable variability. The difference between foraging trip and nursing visit medians in the winter and spring for some females exemplifies the flexibility that individual females have in their attendance behavior (*e.g.*, females 253 and 323; Fig. 2a, 2b).

Pup Behavior

The difference in time ashore for sea lion pups in 1991–1992 and 1994 was most likely related to the location of the transmitter on the pup's body. The time ashore in 1994 probably underestimated the time ashore for pups. Flipper transmitters were buried under the body or bodies of other pups more often than the back-mounted transmitters in 1991–1992, resulting in more time "absent" from the rookery for pups in 1994. Therefore, the 66.6% time ashore observed in 1991–1992 more accurately reflects the actual time spent ashore by pups in the spring. However, additional study is needed to accurately determine the time pups spend ashore during the non-breeding season.

The female-pup-pair attendance patterns indicate that pups do not travel with females on foraging trips during the spring. They also do not appear to travel with the female away from the rookery to other hauling sites on San Miguel Island or the California coast. Therefore, sightings of pups along the California coast from January through March are evidence that pups can be weaned as early as 6 mo old. However, suckling pups are sighted in April and May at San Miguel Island. These observations indicate that weaning occurs from January through May.

The dynamics of weaning were not directly investigated in this study, but several observations provide insight into weaning behavior. If female and pup

pairs were ashore during the same time period, they were considered associated and weaning had not occurred. Based on this assumption, it appears that most females wean their pups by leaving the rookery in April and May for at least one month. However, some pups weaned themselves by leaving the rookery even though the female continued to frequent the rookery. Both methods of weaning have also been reported in the northern fur seal; however, self-weaning was more common (77% of the pups self-weaned; Macy 1982). In Antarctic fur seals, pups are weaned by the female based on the pup attaining a threshold weaning weight (Doidge and Croxall 1989). If weaning is condition-dependent in California sea lions, then when foraging conditions are poor, self-weaning and early weaning should be less prevalent because attainment of the weaning size should be more difficult. In this study self-weaning was more common and early weaning may have occurred during the 1992–1993 El Niño event, when foraging conditions were poor. Weaning occurred between two and four weeks earlier in 1991–1992 and 1993 than in 1994, a “normal” year. It is unlikely that this difference was due to the bias of tag placement mentioned earlier, because the opposite result would have been expected to have occurred. The reasons for self-weaning or early weaning during the El Niño conditions are unclear. With the onset of El Niño conditions in January 1992, females may have become nutritionally stressed during the non-breeding season lactation period. As a result, pups may have weaned early because they benefitted more by foraging on their own in more productive foraging areas than remaining with the female near the rookery. In contrast, females in 1993 were nutritionally stressed from the onset of pupping through the lactation period, which may have resulted in more females losing pups because of poor nutrition or weaning pups early to ensure their own survival.

The Effects of the 1992–1993 El Niño on Spring Attendance

The 1992–1993 El Niño did not affect the attendance patterns of females during the non-breeding season in the manner expected; foraging trip lengths were not longer in the El Niño years. This is in contrast to results during the breeding seasons during the 1982–1983 El Niño event in which several species of otariids, including California sea lions, made significantly longer foraging trips in years affected by the El Niño conditions (Croxall *et al.* 1988, DeLong and Antonelis 1991, Heath *et al.* 1991, Majluf 1991, Trillmich and Dellinger 1991). That such an effect was not observed in the attendance behavior during the non-breeding season in this study may be an artifact of differences in the attendance behavior during the breeding and non-breeding seasons. However, it may also be due to the difference in the severity of the two El Niño events. Many of the oceanographic characteristics of the 1982–1983 and 1992–1993 El Niño events were similar (Montasterkoy 1992, 1993; Schwing and Hayward 1995). However, during the 1982–1983 event, the thermocline was severely depressed from November 1982 through December 1983 (Norton *et al.* 1985), which apparently displaced preferred sea lion prey both vertically and latitudinally outside the foraging distance or depth ranges of lactating females (Feld-

kamp *et al.* 1991). The decreased food availability forced females to forage for longer periods of time to obtain adequate energy reserves for their survival and the survival of their pup (Feldkamp *et al.* 1991). In contrast, during the 1992–93 El Niño event, the thermocline was not as significantly depressed (Schwing and Hayward 1995) and the El Niño conditions waned from May 1992 to December 1992 before intensifying again in January 1993 (Montasterkoy 1993). Thus, the displacement of prey during the 1992–1993 event may have been more temporary (several months at a time) than the 2-yr-long displacement which occurred during the 1982–1983 event. Thus, preferred prey was probably available within the vertical and latitudinal foraging range of females and they did not have to increase their foraging trip length to meet the minimum energy requirements of their pups (*i.e.*, enough energy for maintenance but not necessarily growth). The high mobility of sea-lion prey, spatially and temporally, and the annual and seasonal unpredictability of prey distribution and availability requires flexibility in sea-lion foraging strategies. Females may accommodate short-term prey displacement by changing their foraging behavior rather than their attendance pattern. The small sample size of lactating females with complete records in 1993 ($n = 3$ of 6) was the result of shorter lactation periods in 1993, either because of pup mortality or early weaning. This result suggests that females may have altered other aspects of their maternal behavior instead of their attendance pattern to ensure their survival.

The individual variability in attendance patterns of female California sea lions demonstrates maternal behavior that has evolved with the seasonal and annual unpredictability in their environment that occurs during the lactation period. This flexibility in maternal behavior has likely contributed to the successful recovery of the California sea lion population from depleted levels in the 1970s despite significant alterations in their foraging environment from short-term El Niño events (DeLong *et al.* 1991) and long-term shifts in oceanographic conditions (Roemich and McGowan 1995, McGowan *et al.* 1998).

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