Variation in maternal attendance patterns and pup behaviour in a declining population of Steller sea lions (*Eumetopias jubatus*)

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Abstract: Maternal attendance patterns of lactating female Steller sea lions (*Eumetopias jubatus*) and the activity budgets of pups on Año Nuevo Island, California, were compared between the 1973 and 1992 breeding seasons to investigate temporal changes in behaviour that may be associated with population decline. Females were absent from the breeding area longer in 1992, which may reflect increased foraging effort. Pups also spent significantly less time sucking and more time swimming in 1992. Suckling time is correlated with milk intake in some otariid species, thus the decreased amount of time 1992 pups spent sucking could reflect a reduction in the total volume of milk produced by females. Pups in 1992 are likely to have spent more time swimming than pups in 1973 because high tide covered a greater proportion of the study site in 1992 than in 1973. An increase in time females spent at sea and a decrease in time pups spent sucking are consistent with behavioural changes associated with reduced prey availability.

Résumé : Les soins maternels assurés par les femelles de l'Otarie de Steller (*Eumetopias jubatus*) et l'emploi du temps des petits ont été comparés au cours des saisons de reproduction de 1973 et de 1992, dans l'île Año Nuevo, Californie, dans le but de permettre l'évaluation des changements de comportement qui pourraient être associés au déclin de la population. Les femelles sont restées absentes des territoires de reproduction plus longtemps en 1992, ce qui reflète peut-être un effort de recherche de nourriture plus intense de leur part. Les petits ont également passé moins de temps à téter et plus de temps à nager en 1992; la durée de l'allaitement est généralement reliée à la quantité de lait consommée chez certaines espèces d'otaries et il est possible que cette diminution du temps passé à téter soit attribuable à une réduction du volume total de lait produit par les femelles. Il se peut que les petits de 1992 aient passé plus de temps à nager que ceux de 1973 parce que les marées hautes recouvraient une plus grande partie du site étudié en 1992. L'augmentation du temps passé en mer chez les femelles et la diminution du temps consacré à l'allaitement chez les petits sont en confirmité avec l'hypothèse de changements comportementaux associés à une réduction de la disponibilité des proies.
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Introduction

The foraging patterns and suckling schedules of lactating female mammals are largely determined by the location and abundance of prey. In otariids, females alternate between feeding at sea and suckling their young on shore. These cyclic behaviours are referred to as female attendance patterns (Gentry and Kooyman 1986). Gentry et al. (1986) suggested that variation in female attendance patterns in fur seals is largely determined by the productivity of the ocean surrounding the breeding area.

In otariids, as in most mammals, species-specific attendance patterns are not fixed, exhibiting plasticity in response to variation in the environment. During the 1983 El Niño, prey availability was reduced for many eastern Pacific pinnipeds. Under these conditions, females of several species spent more time away from the breeding areas while foraging (Trillmich and Limberger 1985; Ono et al. 1987; DeLong and Antonelis 1991; Heath et al. 1991; Majluf 1991). The Antarctic fur seal (*Arctocephalus gazella*) has shown a similar change due to decline in prey availability (Costa et al. 1991). In addition, during the 1983 El Niño, California sea lions (*Zalophus californianus*) spent less time ashore between parturition and the first trip to sea (Ono et al. 1987).

Since otariid females leave their young ashore while foraging, increases in time at sea must be compensated for with increases in milk production to prevent an adverse affect on pup growth, behaviour, and survival. During the 1983 El Niño, when California sea lion females spent more time at sea, milk yields on returning were reduced and pups were less active and spent less time sucking (Ono et al. 1987). Increased mortality was common among several species suffering from severe prey deprivation (Trillmich and Limberger 1985; Ono et al. 1987; DeLong and Antonelis 1991; Francis and Heath 1991; Majluf 1991).

We examined maternal attendance patterns and pup behaviour in the Steller sea lion, *Eumetopias jubatus*, breeding on Año Nuevo Island. Within the last 30 years, this species has experienced a marked decline throughout most of its range (Merrick et al. 1987; Loughlin et al. 1992), which previously extended from the California Channel Islands (34°N, 120°W) to the Pribilof Islands (58°N, 170°W) in the eastern Pacific, and from the Aleutian Islands to the Kurile Islands (42–45°N,

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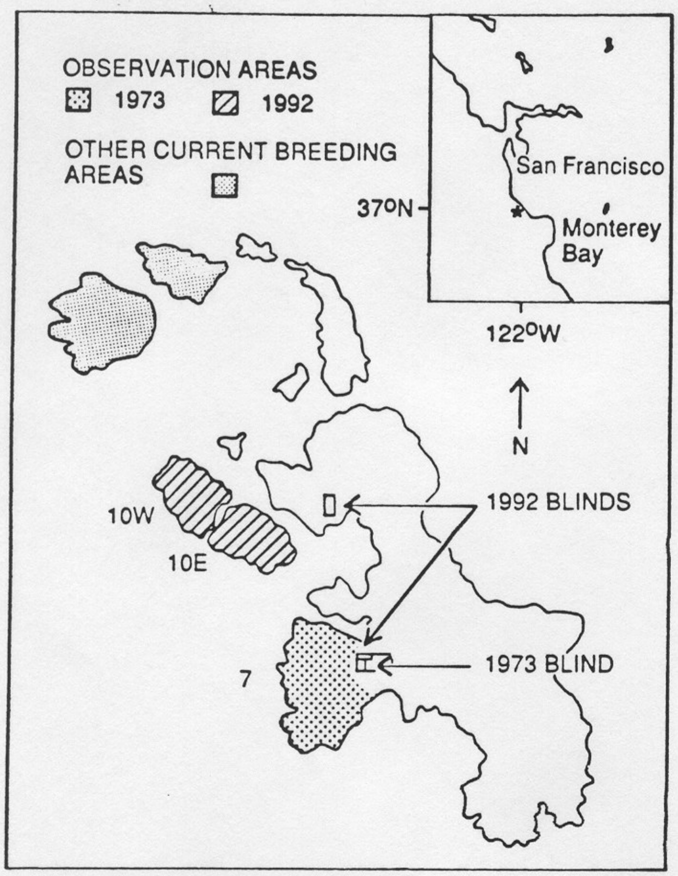
Fig. 1. The 1973 and 1992 observation areas on Año Nuevo Island (adapted from Gentry 1970).



145–155°E) in the western Pacific (Kenyon and Rice 1961; Reidman 1990). Since 1978, *E. jubatus* has failed to breed on the Channel Islands, and the southernmost breeding area now lies approximately 300 km north on Año Nuevo Island (37°N, 122°W; Bonnell et al. 1978; Antonelis and Fiscus 1980). The number of females that return to give birth and breed on Año Nuevo Island each summer declined by at least 85% between 1961 and 1991 (Le Boeuf et al. 1991).

For the first 2–3 months of life, *E. jubatus* pups are left ashore while their mothers forage (Gentry 1970). In our study, the proportions of time that pups allocated to various activities were compared between years to determine if pup behaviour varied. This study was conducted during two El Niño events of moderate intensity (Quinn and Neal 1987; Kousky et al. 1995), thus any effects that these events may have had on the population are assumed to be similar.

Methods

The behaviour of Steller sea lions on Año Nuevo Island, California, was examined between early June and mid-August in 1973 (K.A. Ono) and 1992 (W.R. Hood). In 1973, the behaviours of mother–pup pairs were observed from a blind located approximately 10 m above breeding area 7 (Fig. 1). Similar data were collected in 1992 for those pairs utilizing areas 10E and 10W, since sea lions no longer used area 7 for breeding. Observations were made from a blind located approximately 25 m north of area 10E and from the foghorn house, approximately 100 m east of area 10E (Fig. 1). These blinds were nearly level with area 10E so that a small portion of the study site was not visible. Observations were made with the aid of binoculars (8 × 40 and 7 × 50) and spotting scopes (60× and 15–60×). Observations made between 07:00 and 20:00 were compared between studies.

During both years, females were identified by means of natural markings and scars that were recorded on identification cards. Black hair dye was remotely applied to some females to enhance identification in 1973 but not in 1992. Females were identified and observed throughout the day so that individual attendance patterns could be examined. Attendance patterns were calculated for females with unequivocal markings and known parturition dates and those that were followed for at least 36 days post partum. The times of observed arrivals and departures were recorded immediately. Night arrivals and departures were assumed to have occurred halfway between the last observation in the evening and the first observation the following morning (adopted from Higgins et al. 1988). During the day, if a female appeared without our having noted her arrival, we calculated her arrival time as halfway between the last thorough search for focal females and her appearance. If we did not observe a female departing, her departure time was calculated as halfway between the last time she was observed and the time we noted her absence. All known females ashore were located every 2–4 h, so the maximal error for missed arrivals and departures was 2 h. In 1992, females were not always observed as they returned to the breeding area, owing to the topography of the area. Wet females were assumed to have arrived within the last 30 min, the approximate time required for the fur to dry (Higgins et al. 1988). Returning females were visible on the 1973 study area. Attendance patterns were not determined for females (*i*) that nursed juveniles, (*ii*) that lost their pup before the end of the study, and (*iii*) that nursed a pup other than their own (if known), and (*iv*) for one female that nursed two pups (1973).

Maternal attendance was examined from parturition through the end of the period onshore or at sea, which includes the 36th day post partum (for example, if a female was at sea during day 36, time absent for that cycle ended on the day she returned to the breeding area). Thirty-six days post partum was chosen as the final day for comparison, since this was the last day for which we have reliable data for all females in the model. The following aspects of maternal attendance were examined: (*i*) duration of the period from parturition to the first trip to sea, (*ii*) duration of the first trip to sea, (*iii*) duration of each period spent on the breeding area, (*iv*) proportion of time spent on the breeding area in each foraging cycle, and (*v*) duration of each period of absence from the breeding area. The study area was disrupted once in 1973 for pup marking. The cycles for females that left the area because of this disturbance were not included in these analyses.

Instantaneous scan samples of all observed pups (Altmann 1974) were obtained hourly to determine activity budgets. In 1973, pups were caught and individually marked. The behaviour of each marked pup was recorded during scans lasting 10–30 min, depending on the time required to identify all individuals. In 1992, pups were not marked. The unidentified pups exhibiting each behaviour were tallied and scans lasted 5–10 min. Behaviours were classified as active, swimming, resting, or sucking. Active behaviour included sitting up, nuzzling, locomotion, play, and swimming. Swimming consisted of any aquatic activities, including nonsocial and social play in the water, diving, and moving in the water from place to place (Ono et al. 1987). This concise definition allowed us to examine swimming as a subcategory of active behaviour. Variation between investigators in methods used for scan sampling may have inflated experimental error, so our interpretation of these results is conservative.

Statistical analyses were completed using the SAS statistical package (SAS Institute Inc, 1989). An arcsine transformation was used to normalize proportional data (Sokal and Rohlf 1969). Between-year comparisons of the interval between parturition and the first

Table 1. Between-year comparison of maternal attendance variables for *Eumetopias jubatus*.

				Comparison made with respect to:					
				youngest pups			oldest pups		
	$\bar{x}$	SE	n	df	F	p	df	F	p
Duration of presence (days)									
1973	0.87	0.05	11	1	0.05	0.8271 ns	1	0.20	0.6603 ns
1992	0.85	0.05	14						
Duration of absence (days)									
1973	0.91	0.05	11	1	2.99	0.0974 ns	1	58.81	0.0003***
1992	2.09	0.14	14						
Percent time present									
1973	47.52	1.69	11	1	2.74	0.1111 ns	1	16.55	0.0015***
1992	33.18	1.68	14						

Note: Years were compared using repeated-measures ANOVA with females nested within year. Owing to a significant interaction between age and year, the relationship is described using two repeated-measures ANOVAs (refer to the Methods for more details). Each ANOVA described the same data in an omnibus test: the first describes the disparity between years, with the youngest pups in the model as the reference point (youngest pups), and the second compares years, with the oldest pups as the reference point (oldest pups). The mean, standard error, number of females, and comparison are given (ns, not significant; ***, significant at $\alpha = 0.001$).

trip to sea and the duration of the first feeding trip were made by t tests and were not included in the overall comparison of cycles between years. This period is generally much longer than many of the subsequent cycles and would therefore inflate the means of the overall pattern and act as a confounder. In addition, this period reflects female condition on first arrival at the breeding area rather than prey availability during the season (Doidge and Croxall 1989; Boyd et al. 1991).

Variations in female attendance patterns are compared between years and by pup age using repeated-measures ANOVA, where cycle variables are repeated for each individual and individual females are nested within year (Cody and Smith 1991). In preliminary analysis, a significant interaction was found for duration of absence between age of pup and year ($F_{[30]} = 1.68$, $p = 0.039$). This interaction is due to an increasing disparity in time at sea between years as a function of pup age. Thus, the data violate the assumption of linearity and cannot be compared using a single ANOVA or regression. To describe this relationship, all female cycle variables were compared with two separate repeated-measures ANOVAs. Each ANOVA described the same data in an omnibus test: the first compared years in reference to the second cycle post partum, the youngest pups in the model (the first cycle was not included, as described previously), and the second compared years in reference to the cycle for each female in the model ending 36 days post partum, the oldest pups in the model. With pup age treated as a continuous variable, SAS evaluated the disparity in time at sea between years as a function of pup age, with the lowest age values as the reference point. Pup age varies at the beginning of the second cycle as a function of the duration of cycle 1. Conversely, when age is treated as a categorical variable, SAS evaluated the same disparity with the highest ages as the reference point (T. Heeren, personal communication). The number of cycles occurring within the 36-day period ranged from 12 to 23 in 1973 and from 9 to 14 in 1993. The Bonferroni procedure was used to adjust for multiple comparisons between years for the aspects of female attendance patterns examined (Rice 1990; Haccou and Meelis 1992).

The mean percentages of time that pups spent exhibiting various activities were compared using an ANCOVA. An arcsine transformation was used to normalize all proportional data (Sokal and Rohlf 1969). Scan samples were weighted by the number of individuals observed. Since the ages of individual pups were not known in 1992, the difference between years was examined as a function of date in lieu of age. Since there was no difference between the mean dates of birth of young between years (t test, df = 114, $p = 0.23$), a direct comparison could be made between the specified pup behaviours and date. The interaction between year and date was not significant for any of the behaviours examined, therefore this term was excluded from the final models. Adjustments for multiple comparisons were made using the Bonferroni method (Rice 1990; Haccou and Meelis 1992). Data in tables and text are presented as the mean ± standard error.

Results

Maternal attendance patterns

Maternal attendance behaviour in 1992 was compared with that in 1973. Following parturition, females remained on the breeding area nearly 3 days longer in 1992 (1973: 3.18 ± 0.87 days, $n = 7$; 1992: 5.82 ± 0.60 days, $n = 13$; $t = -2.53$, df = 18, $p = 0.02$). The subsequent first postpartum trip to sea was also longer for 1992 females (1973: 0.62 ± 0.13 days, $n = 6$; 1992: 2.01 ± 0.38, $n = 13$; $t = -2.39$, df = 17, $p = 0.03$).

The mean durations of attendance variables were determined for all cycles following the first foraging trip until 36 days had passed (Table 1). No difference was found between years for any of the variables focusing on the second cycle post partum. In the second model, 36 days post partum, no difference was found in the periods of time females spent on the breeding area. Females were absent from the breeding area an average of 1 day longer in 1992 than in 1973.

Pup behaviour

Pups spent significantly less time sucking but more time swimming in 1992 than in 1973 (Table 2). The proportions of time spent resting and exhibiting active behaviours did not vary. There was a significant increase in time spent swimming as function of date, yet there was no change in the proportions of time pups spent resting, active, or sucking with date.

Table 2. Percentages of time *Eumetopias jubatus* pups spent sucking, resting, active, and swimming compared between years.

	$\bar{x}$	SE	n		df	F	p
Proportion of time spent sucking							
1973	10.30	0.01	561	Between years:	1	8.47	0.0074***
1992	2.63	0.01	452	Between years by date:	1	1.94	0.1642 ns
Proportion of time spent resting							
1973	43.92	0.01	561	Between years:	1	0.02	0.8830 ns
1992	49.48	0.01	452	Between years by date:	1	1.48	0.2234 ns
Proportion of time spent active							
1973	45.79	0.01	561	Between years:	1	2.91	0.0881 ns
1992	48.15	0.01	452	Between years by date:	1	0.45	0.5046 ns
Proportion of time spent swimming							
1973	2.21	0.01	561	Between years:	1	57.57	0.0001***
1992	11.38	0.01	452	Between years by date:	1	5.01	0.0255***

Note: Comparisons were made using ANCOVA weighted for sample size within scan samples. The mean, standard error, sample size, and comparison are given (ns, not significant; ***, significant at $\alpha = 0.001$).

Discussion

Maternal attendance patterns

Based on the very small sample size, during the initial postpartum period of attendance, female *E. jubatus* remained on the breeding area in 1992 nearly twice as long as those in 1973. The amount of time females spend on the breeding area prior to their first postpartum trip to sea is likely to be influenced by prey abundance and (or) quality before parturition (Doidge and Croxall 1989; Boyd et al. 1991). A decrease in the postpartum period of attendance was observed in California sea lions during the 1983 El Niño (Ono et al. 1987). In our study, 1992 females remained on the breeding area longer, perhaps reflecting reduced resource availability at foraging grounds used in the prepartum period in 1973. Following this period, females in 1992 spent more time at sea during their first trip than those in 1973.

Increased duration of foraging trips by lactating females has been correlated with food shortage in many mammalian species, including several otariids (Trillmich and Limberger 1985; Ono et al. 1987; Costa et al. 1991; Boyd et al. 1991; DeLong and Antonelis 1991; Heath et al. 1991; Majluf 1991), hyenas (Hoffer and East 1993), and macaques (Hill and Agetsuma 1995). In our study, variation between years was not evident during the early stages of lactation. However, trip duration increased with pup age in 1992 but not 1973, which led to a difference between years for the eldest pups examined. These results suggest that prey availability for lactating females may have been reduced in 1992. However, variation in foraging duration can also be associated with differences in foraging effort or distance to prey (Gentry et al. 1986).

Gentry (1970) and Higgins et al. (1988) collected data on *E. jubatus* attendance patterns on area 7 of Año Nuevo Island in 1968 and 1983. In 1968, 56% of 25 focal females were absent from the breeding area for approximately 1 day, although exact times were not given (Gentry 1970). These findings are somewhat similar to the duration of absence found in 1973. In 1983, females were absent from the breeding area, on average, for 1.54 days (SD = 0.80 days), which is midway between the 1973 and 1992 values. The average time that females were present on the breeding area, 0.94 days (SD = 0.40 days), is similar to that observed in 1973 and 1992. The increased time spent foraging in 1983 compared with 1973 could be associated with either a reduction in prey availability due to the very strong El Niño which occurred that year, a difference in distance to prey, or the small sample sizes associated with the study.

Some variation in female attendance behaviour may have resulted from poorer visibility in the study area used in 1992 than in 1973; *E. jubatus* breeding areas on Año Nuevo Island had contracted by 1992, making observations more difficult. This would lead to a bias toward an increase in amount of time absent if a female was ashore but not identified, and toward a decrease in time ashore if the female ashore was recorded as absent. However, this is unlikely to be the only factor contributing to variation between years. We identified nearly all of the females with pups on the study area and only analyzed attendance patterns for females with the most distinguishing markings. We are reasonably confident that all focal females were identified each day when present on the study area (see Methods). Therefore, an increase in the total cycle duration should reflect real changes in foraging patterns rather than a bias in visibility. The fact that Higgins et al.'s (1988) values are intermediate to those obtained in our study gives some support to the assumption that the variation in female attendance patterns observed in this study was due to the differences in behaviour of the animals rather than to differences in study area or methods.

Pup behaviour

The decreased amount of time that pups spent sucking in 1992 versus 1973 may indicate that females in 1992 produced less milk than females in 1973. Trillmich (1986) found that the duration of sucking bouts in Galapagos fur seals was significantly correlated with the amount of milk transferred to young. Higgins et al. (1988) found that this correlation did not hold true for *E. jubatus* on Año Nuevo Island during 1983. However, their intake analysis was based on 4 individuals as opposed to 73 individuals studied by Trillmich (1986). Additionally, Higgins et al.'s (1988) results may have been complicated by the very strong El Niño that occurred during their study. The difference between 1973 and 1992 in time spent sucking could also be attributed to the fact that females were absent from the breeding area for greater periods of time later in the season, and sucking pups could easily go undetected because of the terrain in the 1992 breeding area. Additionally, an increase in a mother's absence decreases the opportunities to suckle a pup. In 1992, the location of the blind may have prevented observation of pups sucking from their mother's side opposite the blind. However, Higgins et al. (1988) found that pups spent 5–10% of their time sucking. These values are intermediate to those obtained in our study, giving some support to the assumption that the variation in pup behaviour in this study was due to the differences in behaviour of the animals rather than to differences in study area or methods.

Time spent exhibiting active and resting behaviours did not differ between studies. The proportion of time spent active should have been lower if milk intake was much lower, as Ono et al. (1987) found in California sea lion pups. The lack of a difference in the time *E. jubatus* pups spent resting suggests that there was little or no difference in energy-conservation requirements of pups between the 2 years. Time spent resting in 1983 was also consistent with our findings (Higgins et al. 1988). Ono et al. (1987) found that time spent resting by California sea lion pups was not different during El Niño. Pups spent more time swimming in 1992 than in 1973. The increase in time spent swimming may reflect thermal stress due to variation in ambient temperature or to the gradual increase in Pacific sea surface temperature (Ono 1993). However, this difference is more likely due to the fact that one of the breeding areas was partially submerged at high tide, which forced pups into the water.

Thus, it appears that female *E. jubatus* have experienced a temporal change in maternal attendance patterns. A difference in foraging time between years is likely to reflect differences in the cost of prey acquisition (Costa et al. 1991). A variety of extrinsic factors may affect foraging cost: prey availability, abundance, and (or) quality may have been lower in 1992, stimulating the females to spend more time foraging with each trip to sea. Females may also have been selecting different prey species, or the same species which may have experienced a shift in distribution. Additionally, other factors, such as predation pressure, are equally likely to influence foraging behaviour. When predation pressure is high, females may choose to forage in areas that are less than optimal (Milinski and Heller 1978); these areas could be farther from shore or have lower prey densities, forcing females to stay at sea longer to obtain a similar nutrient intake. Considering that there was little variation in pup behaviour between years and pup mortality was minimal when females spent more time at sea, it seems probable that females were able to match the increased foraging time with adequate milk output.

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