Behaviour of Lactating Steller Sea Lions (*Eumetopias jubatus*) During the Breeding Season:

A Comparison between a Declining and Stable Population in Alaska

by

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ABSTRACT

Female attendance patterns and activity budgets of Alaskan Steller sea lions (*Eumetopias jubatus*) were compared at two sites using scan sampling over two summer breeding seasons in 1994 and 1995 at Sugarloaf Island (a declining population) and Lowrie Island (a stable population). The goal was to document female behaviour and to determine whether there were behavioural differences between the two sites that were consistent with the hypothesis that Steller sea lions in the area of population decline were food-limited. The perinatal period (time from birth of pup to the mother's first feeding trip) averaged 10.1 days in the area of population decline compared to 8.0 days in the stable area, counter to initial predictions. The first shore visit following the perinatal period was significantly longer in the area of population decline compared to the stable population. Females from both populations exhibited a diel haul out pattern where the majority of returns and departures to and from the rookery occurred between 1800 - 0600 hours. Similarly, the mean length of female foraging trips at both populations increased as their pups grew older, whereas shore visits became shorter.

Foraging trips were significantly shorter in the area of population decline, again countering initial predictions. The mean length of maternal foraging trips in the area of population decline was 19.0 hours compared to 25.6 hours for the stable population. In contrast, shore visits and the perinatal period were significantly longer in the area of decline, again countering initial predictions. The mean length of shore visits for the declining population was 26.9 hours compared to 22.6 hours where the population was stable. The average foraging-attendance cycle for both populations was 47.1 hours. Maternal attendance patterns responded in a similar way between years.

Activity budgets for the proportion of time spent at sea during daylight observations were consistent with the maternal attendance results. Lactating females in the area of population decline spent less time foraging at sea (35.9 %) than females from the stable population (46.4 %). More time was spent resting ashore in the area of population decline (49.6 %) compared to the stable population (38.9 %). Females from the area of population decline spent more time suckling their pups and were twice as aggressive compared to the females from the stable population. Overall, lactating females from both populations spent a consistent 85 % of their time foraging at sea and resting onshore. Mothers from both populations spent an average of 36.7 % of their total time with pups. A comparison of female Steller sea lions to other female otariid and phocid species showed that the partitioning of activities is related to differences in lactation strategies, social organization, predation, or thermoregulation.

Behavioural observations of maternal attendance patterns and activity budgets are not consistent with the hypothesis that Steller sea lions at the declining site in the Gulf of Alaska have greater difficulty obtaining prey compared to the stable population in southeast Alaska.

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In Memory of
Michael A. Bigg,
my
inspiration

❀

GENERAL INTRODUCTION

Background

The world population of Steller sea lions (*Eumetopias jubatus*) has been declining since the late 1970s (NMFS 1992; Loughlin *et al.* 1992; Trites and Larkin 1996). Two genetically distinct stocks of Steller sea lions have been identified: eastern and western stocks divided at 144° W near Cape Suckling, Alaska (Figure 1.1; NMFS 1995; Bickham *et al.* 1996). They were listed as a *threatened* species under the U.S. Endangered Species Act in 1990 and were reclassified in 1997 as *endangered* in the western part of their range. (U.S. Federal Register 62:2434355). Food-limitation is one of the leading hypotheses to explain the overall decline (Hoover 1988; NMFS 1992; Merrick 1995) but this hypothesis has been very difficult to test. One means of gaining insight into the nutritional status of Steller sea lions is by observing their behaviour.

My goals were to compare the behaviour of lactating Steller sea lions from the declining and stable populations using two methods: maternal attendance patterns and activity budgets. The maternal attendance pattern refers to the cycle time a mother sea lion spends feeding at sea and caring for her pup on shore. This maternal cycle occurs at regular intervals throughout the breeding season. Activity budgets refer to the proportion of time engaged in various activities.

If the declining population of Steller sea lions was nutritionally stressed, I expected females to spend more time at sea searching for enough prey to meet their metabolic needs compared to females in the stable population (see Chapter 2). This *a priori* expectation was based on the well documented biological effects of the 1983 El Niño-Southern Oscillation which increased the sea level and sea-surface temperatures in the eastern Pacific Ocean (Cane 1983; Fielder 1984; Barber and Chavez 1983). Arntz *et al.* (1991) showed that the 1983 El Niño event had both short and long term effects on the prey populations of pinnipeds. For example, pinniped prey availability changed because of polewind, inshore-offshore, or bathymetric migrations. Body condition, growth rates, survival, and reproductive capacities of prey species were also reduced. The invasion of new species also modified the abundance of normal pinniped prey species. All these changes had some effect on the availability, vulnerability and nutritive value of pinniped prey populations. The result was that females of several otariid species increased their feeding time at sea during the El Niño event (Trillmich and Limberger 1985; Costa *et al.* 1985: Ono *et al.* 1987; DeLong and Antonelis 1991; Heath *et al.* 1991; Majluf 1991). Mortality also increased in several species that were severely deprived of prey (Trillmich and Limberger 1985; Ono *et al.* 1987; Delong and Antonelis 1991; Francis and Heath 1991; Majluf 1991). A more recent study during a moderate 1992 El Niño, showed that lactating Steller sea lions at Año Nuevo Island in California also spent more time out at sea (Hood and Ono 1997). Antarctic fur seals (*Arctocephalus gazella*) also increased their foraging trip durations in response to reduced prey availability (Costa *et al.* 1989).

The attendance pattern includes the regular foraging-attendance cycle as well as the *perinatal period* (the time between the pup's birth and the mother's first feeding trip), during which time the mother suckles her pup and fasts onshore. During the 1983 El Niño event, female California sea lions (*Zalophus californianus*) spent less time onshore during the perinatal period (Ono *et al.* 1987). Thus, another *a priori* expectation was that lactating Steller sea lions in the area of decline should have a shorter perinatal period if they were nutritionally stressed, since they would have less energy reserves at the onset of parturition (see Chapter 2).

Activity budgets were an alternative way to describe the time females spend feeding at sea. Instead of estimating the length of individual foraging trips, activity budgets estimate the total proportion of time females spent at sea during the study period (see Chapter 3). In a sense, it is more useful to know the total time spent at sea than the mean length of individual foraging trips because the duration and frequency of foraging trips can vary between individual females or populations, leading to some confusion about the overall foraging effort over the breeding season.

I also used activity budget analyses to describe how sea lions partitioned their time while on shore. I was particularly interested in estimating the proportion of time females spent suckling their pups between the stable and declining populations since this is a measure of how much energy is transferred from the mother to the pup, and is a possible indicator of the nutritional status of lactating Steller sea lions. During the 1983 El Niño, Ono *et al.* (1987) found that female California sea lions returned from feeding trips with reduced milk yields, and that their pups spent less time suckling, grew more slowly, and suffered increased mortality during the food shortage year. Steller sea lion pups at Año Nuevo Island in California also suckled less during the more moderate 1992 El Niño event (Hood and Ono 1997). Similarly, the northern fur seal population (*Callorhinus ursinus*) at San Miguel Island in California also experienced decreased pup production, high pup mortality, and lower weights of pups during the 1992 El Niño year (Melin and Delong 1994). Thus, my final *a priori* expectation was that lactating Steller sea lions in the area of decline would spend less time suckling their pups.

In summary, otariids observed in California, Peru, and the Galapagos Islands during El Niño responded to reduced prey availability by increasing the length of their feeding trips, decreasing their perinatal period and suckling their pups less. Thus, I assumed that lactating Steller sea lions in Alaska would respond in a similar way if they were food-limited in the area of population decline.

Reproductive biology of Steller sea lions

Steller sea lions belong to the eared seal family Otariidae, and breed on offshore rocks during the summer. They are moderately polygynous. Males arrive on the breeding areas in mid-May and defend territories until mid-July (Gisiner 1985). Females begin to arrive in early June and give birth to a single precocial pup during June and early July, although most pups are born by mid-June. Following parturition, females remain onshore fasting and suckling their pup for about one week before departing on their first feeding trip to sea. This *perinatal period* is a valuable measure of physical condition because it reflects the energy reserves lactating females acquire for the first part of lactation (Bowen 1991). Following the perinatal period, the maternal attendance pattern becomes cyclic by alternating feeding trips to sea with suckling young onshore. Females may care for their pups for as long as three years, although most pups are believed to be weaned before their first birthday (Pitcher and Calkins 1981).

Study sites and materials

With the help of three field assistants, I compared maternal attendance patterns and activity budgets for Alaskan Steller sea lions breeding on Sugarloaf Island (58°53′N, 152°02′W) in the area of population decline, and on Lowrie Island (54°53′N, 133°30′W) where the population has remained abundant (Figure 1.1). Field assistants were initially trained in the laboratory to observe sea lions and conduct behavioural scans using video tapes of Steller sea lions recorded during the breeding season, and by a protocol manual I designed myself. Moreover, at least one field assistant with prior experience observing Steller sea lions was assigned to each island in both study years. Binoculars (8 X 35) and spotting scopes were used to observe the animals. Photographs and sketches were used to identify focal animals.

Sugarloaf Island has an elevation of about 370 m and is approximately 81 ha with steep grass covered slopes on all sides. The rookery used on Sugarloaf Island is a flat rock out crop with boulders scattered throughout. Approximately 100 adults used this rookery during the summer breeding season. An observation blind was constructed approximately 20 m above the rookery and on sunny days it was possible to get within 10 m of the rookery without the sea lions being aware of the observer.

Lowrie Island is approximately the same size as Sugarloaf Island, but it is not as steep or as high. The rookery used for observations was large and on a steep rock outcrop in comparison to the rookery on Sugarloaf Island. It was occupied by about 300 adults during the summer breeding season. The observation blind was about 60 m above the rookery and separated from the rookery by a small surge channel.

Overview of thesis

My thesis is divided into four chapters. In this first chapter, I have provided the reader with background information about the declining population of Steller sea lions in Alaska and the *a priori* expectations of the El Niño effect that I based my hypotheses on. I have also provided a brief description of Steller sea lion reproductive biology so that the reader has a better understanding of their social organization, behaviours, and cycles that occur during the breeding season. Finally, this first chapter introduces the reader to the location of the rookeries used for the study.

The second chapter compares the maternal attendance patterns between the stable and declining population and focuses on the perinatal period, and the mean length of foraging trips and visits ashore. In this chapter, I also explore temporal patterns, and the changes in the duration of foraging trips and visits ashore as the pups grew older. Finally, I describe how the maternal cycle is correlated to the time of day (diel cycle).

The third chapter compares the activity budgets between the two Steller sea lion populations. The activities I chose to compare were time at sea, resting ashore, alert, grooming, nursing, aggression, passive interactions, vocalizing and mother-pup associations. The activity budgets of female Steller sea lions were also compared to females of other otariid and phocid species to gain an understanding how activity budgets differ between genera and species. Chapters 2 and 3 were written to stand alone. There are therefore some redundancies in their introductions and discussions, since both chapters compare the stable and declining Steller sea lion populations and discuss the time females spent foraging at sea.

In the last chapter, I review my major findings and their implications for the nutritional status of Steller sea lions in the area of decline. I also discuss the usefulness of observation and radio-telemetry to compare behaviour and the various biases inherent in each method. Finally, I provide suggestions and insights for future research that could be undertaken.

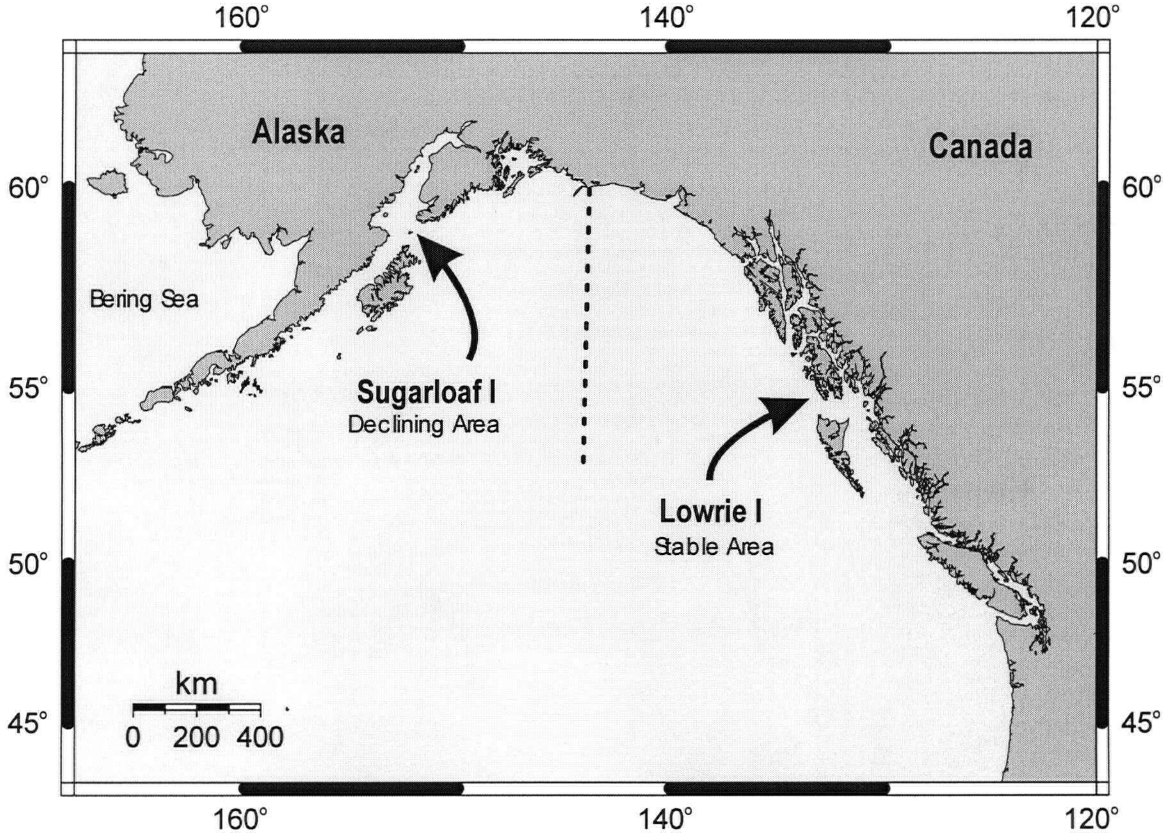

Figure 1.1: Study sites in Alaska. The dashed line (----) shows the division between the western (declining population) and eastern (stable population) Steller sea lion stocks.

2.0 MATERNAL ATTENDANCE PATTERNS

2.1 Introduction

One of the leading hypotheses to explain the overall population decline of Steller sea lions (*Eumetopias jubatus*) is that they are having difficulty finding prey (Hoover 1988; NMFS 1992; Merrick 1995) but this hypothesis has been very difficult to test. One means of gaining insight into the nutritional status of Steller sea lions is by analyzing maternal attendance patterns. Gentry and Holt (1986) suggested that temporal foraging-attendance patterns, feeding trip durations, and time spent on shore suckling young are related to prey availability, feeding locations, and female body mass. The 1983 El Niño event that reduced prey availability for many eastern Pacific pinnipeds demonstrated the plasticity of maternal attendance patterns in response to environmental change. For example, during this El Niño period of reduced prey availability, females of several otariid species increased their feeding time at sea (Trillmich and Limberger 1985; Ono *et al.* 1987; DeLong and Antonelis 1991; Heath *et al.* 1991; Majluf 1991). Furthermore, Ono *et al.* (1987) found that female California sea lions (*Zalophus californianus*) spent less time onshore during the perinatal period. Antarctic fur seals (*Arctocephalus gazella*) also exhibited similar responses to reduced prey availability (Costa *et al.* 1989, 1991). Pup growth and behaviour was also adversely affected during the 1983 El Niño event. Ono *et al.* (1987) found that female California sea lions returned from feeding trips with reduced milk yields, and that their pups were less active and spent less time suckling.

The following study compares maternal attendance patterns for Alaskan Steller sea lions breeding on Sugarloaf Island in the area of population decline, and Lowrie Island where the population has remained abundant (Figure 1.1). My primary goal was to compare the length of perinatal periods and feeding cycles of lactating females between the two sites to gain insight into whether the population decline in the western stock of Steller sea lions is related to nutritional stress. If prey availability is reduced, I expected the Steller sea lions in the declining area to exhibit similar responses to the pinniped species observed during the 1983 El Niño. My secondary goal was to evaluate how feeding cycles changed as pups grew older, and to document any trends in the departure and arrival times of foraging females after parturition.

2.2 Methods

In 1994, my assistants and I observed Steller sea lion behaviour from May 16 to August 11 on Sugarloaf Island and from May 10 to August 1 on Lowrie Island (Figure 1.1). In 1995, observations took place from May 10 to August 14 on Sugarloaf Island and from May 16 to August 4 on Lowrie Island. Observations from both study years covered the entire summer breeding season at each site. Maternal attendance patterns of individually recognizable females with pups was recorded using instantaneous focal scan sampling (Altmann 1974; Martin and Batson 1986). Attendance was recorded hourly from 0600 - 2000 hours on most days but there were several days when observations started as late as 0800 hrs. Two days per week, hourly attendance checks were made between 0600 - 0900, 1300 - 1400, and 1700 - 2000 hours. In 1994, logistic difficulties on Lowrie Island prevented the collection of data on 5 non-consecutive days. There were also several days on Sugarloaf Island in 1994 where female attendance could only be recorded every 6 hours due to poor weather. In 1995, female attendance data were collected hourly and on every day at both sites. Overall, observation efforts for individual focal females ranged from 157 to 554 hours depending on their parturition date. Natural markings such as scars or fungal patches were used to identify lactating females.

Mean length of trips to sea, visits ashore, and the perinatal period

A feeding cycle was defined as a trip to sea followed by a visit ashore. A trip was assumed to have occurred if the female was absent from the rookery and was not observed floating or swimming near shore. I only included trips in my analysis when the females were observed departing and/or hauling out with wet pelage after being absent for a period of time. As a result, the length of feeding trips and visits ashore included in the analysis were accurate to within 12 hours (i.e., the maximum error for a single trip or visit was ± 6 hrs). Overnight departures or arrivals were assumed to have occurred at 1:00 AM (the midpoint of non-observation hours). Trips with an accuracy of greater than

± 6 hours were omitted. Short trips (30 minutes - 4 hours) that met the above criteria were included since they were sometimes the only trip observed for a two day period. I assumed that females found prey close to the rookery on these short trips. Short disappearances (< 30 minutes) from the rookery were not considered to be trips if there was no observation of a female departing, arriving or being wet. Under these circumstances, the female could have moved to another location or may have been missed during a scan.

The perinatal period occurred between parturition and the mother's first trip to sea. It was accurate to within 12 hours (± 6 hrs). The time of the pup's birthday was either known exactly, or within 12 hours if parturition occurred overnight. Overnight births were assumed to have occurred at 1:00 AM (the mid point of non-observation hours). For the first trip to sea following parturition, the female had to be observed leaving and/or arriving to the rookery with wet pelage to be included in the analysis. If the female's first disappearance from the rookery was ambiguous and followed by a regular attendance cycle (~ 24 hrs at sea and 24 hrs ashore), her first trip was omitted and that particular female was not included in the perinatal period analysis. If an ambiguous female disappearance occurred on or shortly after the pup's birth (i.e. up to 4 days later), and was followed by an unusually long visit of 5 to 7 days, the second absence was assumed to be the first feeding trip to sea and that female was included in the analysis if her departure and/or arrival from or to the rookerymet the criteria previously described.

Perinatal periods and the mean length of trips to sea and visits ashore for individual females at both study sites in 1994 and 1995, were compared using a two-factor Analysis of Variance. Mean trip and visit durations for females with less than 5 trips to sea or visits ashore were excluded from the analysis. Probability plots were used to verify that the data were normally distributed.

Length of trips to sea and visits ashore as pups aged

The relationship between pup age and the mean length of trips to sea, and between pup age and visits ashore was determined for mothers with known parturition dates. Some females were omitted from the analysis if the feeding cycle could not be related to the age of the pup. The mean maternal feeding cycle (the length of time at sea and the length of the subsequent shore visit) of all females observed was calculated at 5 day intervals, where day 0 is the pup's birthday. For example, I calculated the mean feeding cycle of females with pups between the ages of 0 - 4 days, 5 - 9 days, 10 - 14 days and so on. Linear regression analysis was used to show trends over time. Using mean values for the trip and visit lengths at each 5 day interval, satisfied the normality assumptions of the regression model.

Departures and arrivals during daylight

The proportion of females arriving and departing to and from the rookery during the day (0600 - 2000 hrs) was analyzed using linear regression to determine if females exhibited a diel foraging trip cycle. To calculate the proportion of departures and arrivals at each hour of the day, I used the following formula:

$$\%\ \textit{departures or arrivals each hour} = \frac{\textit{no. of departures or arrivals each hour}}{\textit{total no. of departures or arrivals}}$$

The proportions were normalized using a slight modification of the Freeman and Tukey (1950) arcsine transformation:

$$p' = \tfrac{1}{2}\left[\arcsin \sqrt{\frac{X}{n+1}} + \arcsin \sqrt{\frac{X+1}{n+1}} \right],$$

where X/n is the actual proportion. This transformation was preferable for the extreme ends of the proportions (Zar 1996).

Departures and arrivals grouped into larger time blocks (i.e., the morning: 0600 - 1200 hrs, and afternoon: 1200 - 1800 hrs) were also compared using a two-factor Analysis of

Variance. Statistical comparisons from 1800 - 0600 hours could not be made due to the lack of hourly observations during this time block.

2.3 Results

Mean length of trips to sea and visits ashore

Depending on the site and the year of observation, the total number of observed trips to sea and visits ashore for 15 - 40 females ranged from 115 - 380 (Table 2.1). Overall, mean trips to sea and visits ashore were about 24 hours long (Table 2.2) but ranged widely from 5 - 53 hours.

Mean trip and visit lengths (for females with 5 or more trips and visits) differed significantly for both sites and years (Figure 2.1). Trips to sea were shorter ($\bar{x} = 19.0$ vs. 25.6 hrs, $F_{1,96} = 12.57$, $p = 0.001$) and visits ashore were longer ($\bar{x} = 26.9$ vs. 22.6 hrs, $F_{1,94} = 6.99$, $p = 0.010$) in the area of population decline than in the stable area. In 1994, females from both populations had shorter trips to sea (20.1 vs. 24.5 hrs, $F_{1,96} = 5.56$, $p = 0.020$) and visits ashore (21.3 vs. 28.1 hrs, $F_{1,94} = 17.16$, $p < 0.001$) than in 1995. Similar trends for mean trip and visit lengths between the study sites and years resulted when females with less than 5 trips to sea and visits ashore were included in the analysis (refer to Methods).

Mean length of perinatal period

Sample sizes for perinatal periods ranged from 13 - 38 observations (Table 2.1). Overall, the mean perinatal period for both sites and years combined was 9.0 days. Significant differences in the perinatal period were found between years ($F_{1,85} = 9.92$, $p = 0.002$) and sites ($F_{1,85} = 20.49$, $p < 0.001$) (Figure 2.1). Females from the declining population had longer perinatal periods ($\bar{x} = 10.1$ days) than the stable population ($\bar{x} = 8.0$ days). Both populations had shorter perinatal periods in 1994 ($\bar{x} = 7.8$ days) than in 1995 ($\bar{x} = 9.5$ days).

Table 2.1: The number of females used in the ANOVA for the comparison of perinatal periods, mean feeding trips and mean visits ashore between the two study sites. Mean feeding trips and the length of shore visits were calculated for each female. Total number of trips and visits observed from all the females is shown in brackets.

Study Site	No. of Perinatal Periods		No. of Mean Feeding Trips		No. of Mean Visits Ashore	
	1994	*1995*	*1994*	*1995*	*1994*	*1995*
Declining Area	14	38	26 (210)	40 (380)	26 (215)	38 (350)
Stable Area	13	22	15 (115)	19 (166)	16 (135)	18 (151)

Table 2.2: Maternal attendance patterns of Steller sea lions at both study sites for both years combined (1994-95).

Study Site	Perinatal Period (days)			Trip Lengths (hrs)			Visit Lengths (hrs)			Total Cycle Time (hrs)
	$\bar{x}$	$s_{\bar{x}}$	n	$\bar{x}$	$s_{\bar{x}}$	n	$\bar{x}$	$s_{\bar{x}}$	n	$\bar{x}$ *Trip + Visit*
Declining Area	10.1	0.19	52	19.0	1.10	66	26.9	0.98	64	45.9
Stable Area	8.0	0.23	35	25.6	1.51	34	22.6	1.32	34	48.2

Length of trips to sea and visit ashore as pups aged

Two 'trip' outliers out of 135 individual trips were removed from the 1994 Lowrie Island data (stable population), and one 'visit' outlier out of 242 individual visits was removed from the 1994 Sugarloaf Island data (declining population) because they were not consistent with individual trends. At each age interval, sample sizes used to calculate mean trips to sea and visits ashore varied, ranging from 3 - 39 ($\bar{x}$ = 17) for Lowrie Island (the stable population) and from 4 - 77 ($\bar{x}$ = 30) for Sugarloaf Island (the declining population).

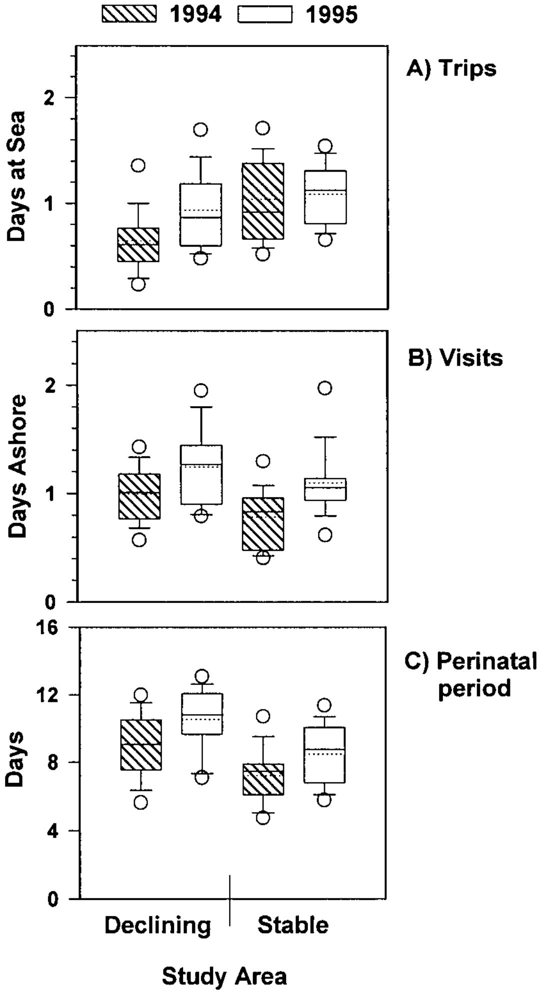

Figure 2.1: Box plots showing the distribution of a) mean trips to sea (n = 100 females), b) mean visits ashore (n = 98), and c) perinatal periods (n = 81) for lactating females from the declining and stable populations. Mean trips and visits were only conducted for females with 5 or more trips or visits. Results show that females in the area of decline had longer visits and perinatal periods, and shorter foraging trips than females from the stable population. For both populations, foraging trips, visits ashore, and perinatal periods were shorter in 1994 than in 1995. The ' ° ' symbol shows the 5th and 95th percentiles, the dashed line (---) shows the mean, and the solid line (—) refers to the median.

Comparing regression slopes and elevations showed significant differences between years in the length of trips to sea and visits ashore as the pups grew older at each site (Figure 2.2). Trips to sea increased as the pups aged in 1995 for females in the stable area, but showed no significant change in 1994 ($t_{13} = 2.97$, $p = 0.01$). In the area of decline, trips to sea increased in both years as pups grew older but were longer in 1995 than in 1994 ($t_{15} = 2.77$, $p = 0.014$). As trip lengths increased through the breeding season, time on shore (visits) decreased at both sites. Visits ashore were longer in 1995 than in 1994 for females from the stable population ($t_{13}= 4.12$, $p = 0.002$) but no differences were detected between years for females in the area of population decline. Overall, females from both populations behaved similarly between years.

When years were pooled, results (Figure 2.2) showed that the length of time the mother spent ashore decreased for both sites as the pup grew older ($F_{1,14} = 7.408$, $p = 0.017$ for the declining area; $F_{1,14} = 14.522$, $p = 0.002$ for the stable area), while the length of trips to sea increased ($F_{1,16} = 7.572$, $p = 0.014$ for the declining area; $F_{1,15} = 4.738$, $p = 0.046$ for the stable area). Although trends were similar between the two sites, the elevation of the population regression lines for trips and visits differed significantly between the two sites. The regression elevation for trips to sea in the area of decline was lower ($t_{32} = 4.54$, $p < 0.001$) than in the stable area, whereas the regression elevation for visits ashore in the area of decline was higher ($t_{29} = 3.72$, $p < 0.001$) than in the stable area, suggesting that females at the two sites partitioned their time at sea and ashore differently.

Decreases in the amount of time females spent ashore were also apparent using both trip number and week as independent variables. This suggests a strong relationship between the length of visits ashore and the age of pups. Although my trip and visit sample sizes for estimating this relationship varied by pup age interval, there was no indication that the regression analysis was biased by individual female trends over time. The majority of females were represented at each age interval and they exhibited similar trends over time.

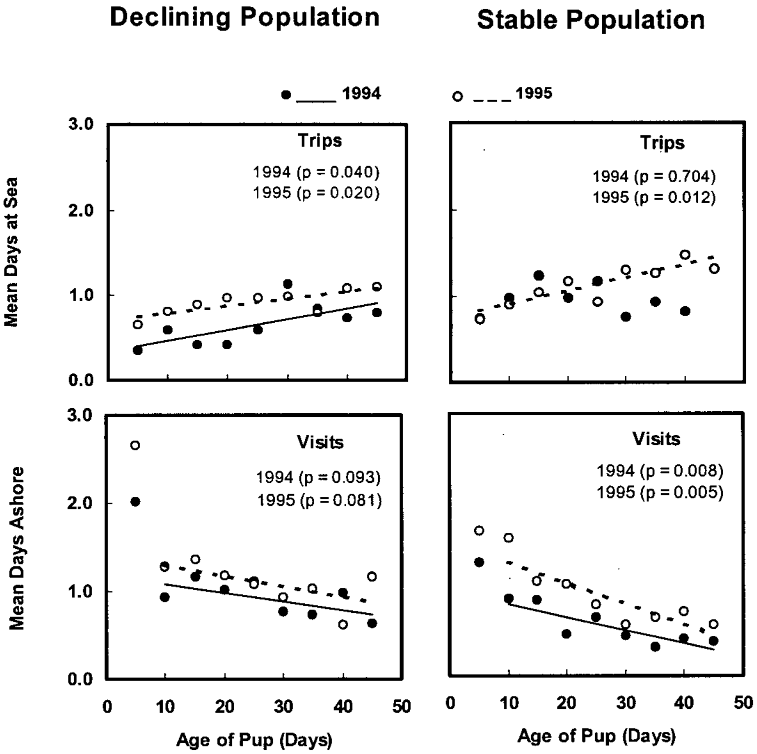

Figure 2.2: The relationship between pup age and the mean length of trips to sea and visits ashore for 1994 and 1995. Mean values were calculated per 5 day pup age period and plotted on the youngest age associated with each pup age interval. Sample sizes for each data point ranged from 3 to 77 observations for 3 to 54 females. The first set of data points (pup age 5 to 9) was omitted from the visits ashore regression analysis because these visits were significantly longer than subsequent visits in the area of decline and longer than in the stable area. Visit lengths ashore decreased whereas trip lengths at sea increased as the pups became older when years were pooled. Moreover, the regression elevations for females in the declining area were significantly lower for trips, and higher for visits than for females in the stable area.

Arrivals and departures

The proportion of females departing the rookery increased during the day (0600 - 2000 hrs) for both populations and on both years (1994-95). The rate of departure for females in the declining area differed between 1994 and 1995 ($t_{24} = 3.361$, $p = 0.006$), but no differences were found between years in the stable area. When years were pooled, regressions were similar between the two populations ($t_{53} = 1.67$, $p = 0.10$) (Figure 2.3).

Arrival patterns were more variable than departures. The rates of return to the rookery in the declining area differed between 1994 and 1995 ($t_{24} = 3.710$, $p = 0.001$) but suggest no significant overall pattern. Arrivals to the rookery where the population is stable were relatively constant over the daylight hours for both years. Pooling both years of data suggests a random return of females to shore by time of day for both populations (Figure 2.3). Whether or not females exhibited a similar pattern of arrival and departure during the night (2000 - 0600 hrs) can not be determined from these data.

Figures 2.4 and 2.5 show the proportion of departures and arrivals that occurred during the morning, afternoon, and night for both sites and years. No significant differences were found between sites for the morning or afternoon. Statistical analysis could not be done for the overnight time block due to a lack of hourly data. In 1994 however, an average of 15.0 % more departures ($F_{1,20} = 22.644$, $p < 0.001$) and 11.5 % more arrivals ($F_{1,20} = 9.532$, $p = 0.006$) occurred during the afternoon. As a result, fewer departures occurred after 6 p.m. in 1994 ($\bar{x} = 51.8$ %) than in 1995 ($\bar{x} = 69.3$ %) (Figure 2.4).

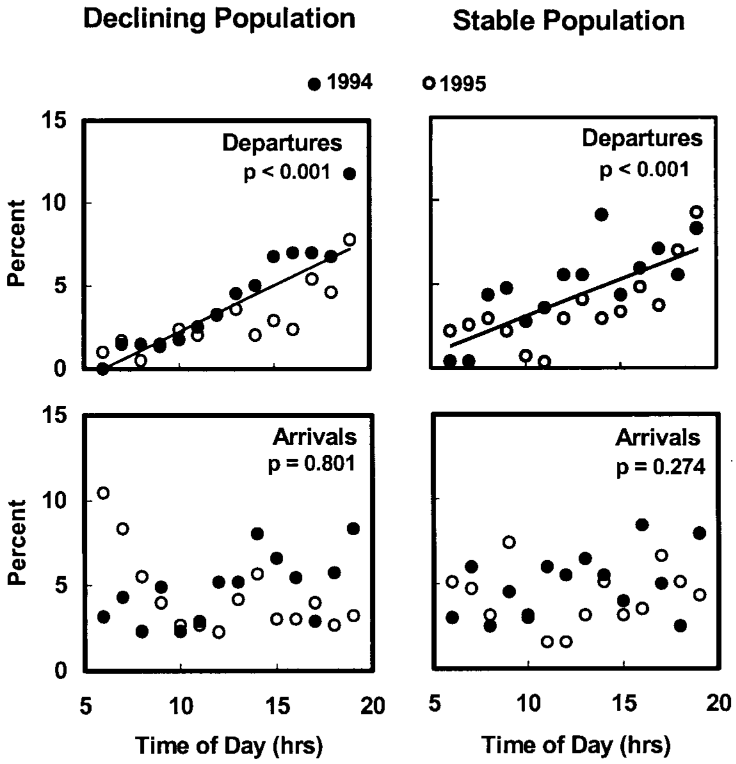

Figure 2.3: The relationship between female departures and returns to the rookery, and the time of day for 1994 and 1995 combined. The percentage of departures and arrivals was calculated for each hour during the observation period. The significant regressions show that the number of females departing the rookery increases as the day progresses whereas there were no significant trends in female arrivals to the rookery during the observation period. The proportion of females departing the rookery during the night (2000 - 0600 hrs) is not shown. For the declining area, the proportion of overnight departure were 39.3 % in 1994, and 59.2 % in 1995. The proportion of females returning overnight for the declining area were 32.6 % in 1994, and 38.2 % in 1995. For the stable population, the proportion of overnight departure were 31.8 % in 1994, and 50.7 % in 1995. The proportion of females returning overnight were 29.9 % in 1994, and 42.6 % in 1995.

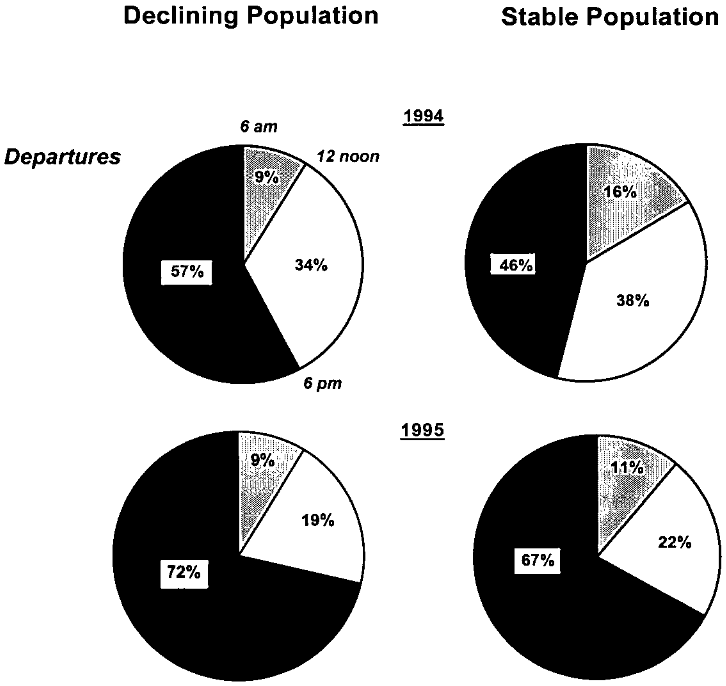

Figure 2.4: The proportion of female departures from the rookery that occurred during the morning (0600 - 1200 hrs), afternoon (1200 - 1800 hrs), and overnight (1800 - 0600 hrs) for both sites and years. Significantly more departures occurred during the afternoon in 1994 compared to 1995.

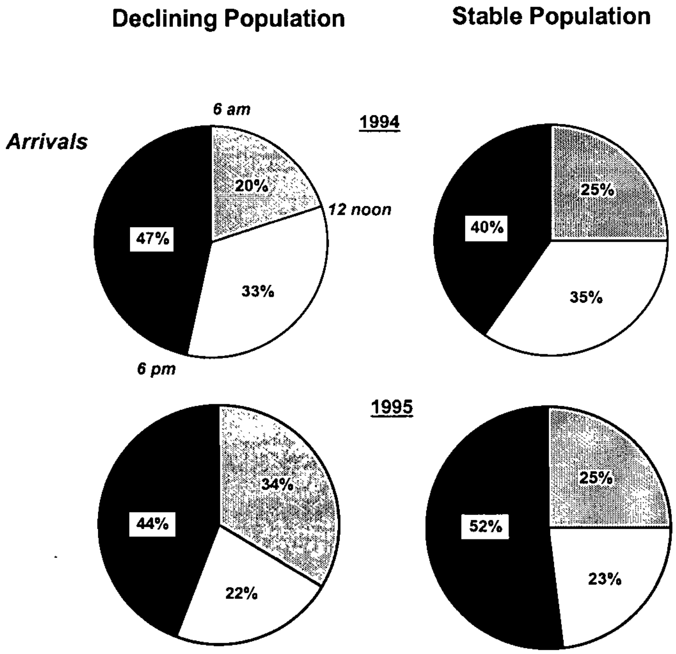

Figure 2.5: The proportion of female arrivals to the rookery that occurred during the morning (0600 - 1200 hrs), afternoon (1200 - 1800 hrs), and overnight (1800 - 0600 hrs) for both sites and years. Significantly more arrivals occurred during the afternoon in 1994 compared to 1995.

2.4 Discussion

Nutritional stress

Behavioural observations of Steller sea lions showed consistent diurnal patterns in the departure time of females seeking food, and temporal patterns in the length of feeding trips and in the time females spent with their pups. However, there were differences between sites in the magnitude of maternal attendance patterns that were not consistent with the food limitation hypothesis. Based on the responses of pinnipeds during periods of prey reduction, longer perinatal periods, shorter trips to sea, and longer visits ashore at Sugarloaf Island (in the Gulf of Alaska population decline) suggest that these lactating Steller sea lions were not nutritionally stressed during the summer. Instead, the data suggest that the abundant population at Lowrie Island (in the Southeast Alaska area of population growth) is perhaps the one that was nutritionally stressed.

During the 1983 El Niño event when prey availability was reduced, nutritionally stressed pinnipeds along the eastern Pacific coast lengthened their foraging trips to meet their metabolic needs (Trillmich and Limberger 1985; Trillmich and Dellinger 1991; Ono *et al.* 1987; DeLong and Antonelis 1991; Heath *et al.* 1991; Majluf 1991). In my study, females from the declining area, which have been hypothesized to be nutritionally stressed, had shorter foraging trips to sea than females from the stable area. Brandon and Davis (unpubl. data, pers.comm.), and Andrews (pers.comm.) who used radio and satellite tracking tags on lactating Steller sea lions, also report shorter maternal foraging trips in the area of decline compared to the stable area.

On the surface, it would appear that the abundant population in Southeast Alaska was nutritionally stressed, not the declining population in the Gulf of Alaska. However, it could also be argued that prey abundance was sufficient at both sites and that the differences in foraging trip duration between the two sites reflected differences in the distance to foraging grounds. Although new evidence suggests that female Steller sea lions commence looking for prey as soon as they leave the rookery, and that they do not capture all of their prey in a single area (Andrews, pers. comm.), concentrations of prey may still differ spatially between the two study sites, leading to the observed differences in foraging trip duration.

Differences in the relative abundance of major prey items may also explain the observed differences in foraging trip length between the two study sites. Since the 1980s, the declining population of Steller sea lions in the Gulf of Alaska and Aleutian Islands have been feeding primarily on walleye pollock (*Theragra chalcogramma*) or Atka mackerel (*Pleurogrammus monopterygius*) (Merrick *et al.* 1997). In contrast, the eastern Steller sea lion population which is stable, has retained a more diverse diet consisting of a higher proportion of fatty fishes such as Pacific herring (*Clupea pallasi*), Pacific sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*) and smelt (*Clupeiidae* spp.) (Trites and Calkins, unpubl. data). The relative high abundance of pollock in the area of decline compared to other prey species may reflect the shorter maternal feeding trips I recorded since it may not be energetically feasible for females to seek out scarce prey. In contrast, the eastern population of Steller sea lions may not encounter a high abundance of any one type of prey, resulting in longer search periods that results in capturing a wider variety of prey, such as fatty fishes.

Dietary differences between the western and eastern Steller sea lion populations may be a key factor in explaining the decline. Recent evidence suggests that the population declines in the Gulf of Alaska and Aleutian Islands could be related to the quality and diversity of prey that Steller sea lions feed upon (Alverson 1992; Merrick *et al.* 1997). The sharpest population declines have occurred in areas with the lowest diet diversity (Merrick *et al.* 1997). Alverson (1992) has suggested that the Steller sea lions are declining because they have been eating too much pollock during the summer and not enough of the fattier fishes such as herring. This has been referred to as the 'junk food hypothesis'. The caloric value of pollock is lower than fattier fishes and nutritional quality of pollock may adversely affect the health of all pinnipeds if consumed in large quantities (Geraci 1975; Thompson *et al.* 1998; Rosen and Trites, in review). Shorter maternal feeding trips in the area of decline support this hypothesis since females may be lacking energy to go on longer foraging trips.

Another possible explanation for the observed differences in foraging trip duration at the two sites are density dependent effects. The Steller sea lion population at Sugarloaf Island numbered an estimated 20,500 pups and adults at its peak in 1979 compared to about 4,000 in 1994 (Trites and Larkin 1996). The adult population of Steller sea lions in the declining area could now be below its summer carrying capacity, such that the prey base is abundant for the population that remains. Since the present Lowrie Island adult population is approximately three times larger than the Sugarloaf Island population (it has grown from approximately 11,000 in 1979 to 13,500 in 1994 (Trites and Larkin 1996; Calkins *et al.* 1999)), females from the larger Lowrie Island population may need to spend more time finding food because they are depleting prey abundance near the rookery at a higher rate over the breeding season than at Sugarloaf Island (Central Foraging Theory). However, if reduced prey abundance was a significant factor, females giving birth late in the season should have longer first feeding trips than females that gave birth earlier on (Gentry and Holt 1986). Unfortunately, I was unable to test whether the length of the first feeding trip to sea differed between early and late pupping females because the majority of my focal females with known feeding trip lengths gave birth in the early part of the breeding season (i.e., before June 15th) in both 1994-95. However, the trend appeared to be that early pupping females had longer foraging trips than the late pupping females. Boyd *et. al* (1991) was able to test this hypothesis and found that female Antarctic fur seals giving birth early in the season spent a significantly greater proportion of their time at sea during lactation than those giving birth later on.

Differences in foraging trip length have also been correlated to different age classes for northern fur seals (*Callorhinus ursinus*). Gentry *et al.* (1986) and Goebel (1988) have shown that older, larger females, which gave birth earlier in the breeding season tended to dive deeper and have shorter foraging trips than the younger, smaller females which tended to give birth later on in the season. Given this evidence, it seems possible that foraging trips were shorter in the area of decline because the age structure is older, compared to the stable population. More studies with known aged females are required to test this hypothesis.

In addition to the shorter feeding trips, I also observed longer perinatal periods in the area of decline. This suggests that female Steller sea lions had more energy reserves for fasting in the declining area at the onset of parturition than females in the stable area. In contrast, Ono *et al.* (1987), found that female California sea lions exhibited shorter perinatal periods during the prey shortage caused by the 1983 El Niño. Physical condition of females during the perinatal period may reflect winter or spring prey availability rather than summer feeding conditions near the rookeries.

Compared to the stable area, females in the area of decline spent more time on shore between trips to sea, and spent more time suckling their pups during daylight (Chapter 3). Longer visit lengths in the area of decline suggest that females returned from foraging trips satiated and with sufficient energy reserves to suckle their young and meet their own metabolic needs.

Temporal patterns

Maternal attendance patterns at both the declining and stable sites were similar between years. The most intriguing finding was that perinatal periods, feeding trips, and visits ashore were shorter in 1994 than in 1995. Interannual similarities in Steller sea lion attendance behaviour between the two study sites may reflect large scale changes in prey availability in the North Pacific Ocean. Longer feeding trips in 1995 suggest that prey were more difficult to obtain in 1995 compared to 1994. The longer perinatal periods in 1995 may reflect better winter feeding conditions such that females would have returned to the summer breeding islands in good physical condition. Such possibilities underline the need for future research on maternal attendance patterns to be conducted in parallel with prey abundance studies during the winter and summer seasons. This will help to determine potential correlations between prey abundance and the duration of perinatal periods and feeding trips.

The timing of departures from the rookery and the length of feeding trips appear to be correlated. When feeding trips were longer in 1995, the proportion of departures occurring in the afternoon dropped and overnight departures increased (Figure 2.4).

However, when feeding trips were shorter in 1994, more females left on feeding trips and returned during the afternoon. Arrival times to the rookery also changed in 1995 when feeding trips were longer. In the area of decline, the proportion of afternoon arrivals decreased and more females returned in the morning (Figure 2.5). In contrast, the decreased proportion of afternoon arrivals in the stable area resulted in more females returning overnight. Further research might reveal whether departure and arrival times are an indication of the feeding conditions in any particular year.

Arrivals and departures

Females exhibited a diurnal pattern in their arrivals and departures to and from the rookery. The majority of all departures and arrivals occurred in the evening and overnight (1800 - 0600 hrs). Sandegren (1970), Gentry (1970), Withrow (1982), and Higgins (1988) have all reported a similar diel cycle for Steller sea lions during the summer breeding season. Steller sea lions probably leave on foraging trips during the night because preferred prey make a vertical migration to the surface at night creating a nocturnal peak in prey availability (Beamish 1966; Harden Jones 1968; Hansen 1979).

The proportion of females leaving on feeding trips increased as the day progressed, with about 50 % or more of the departures occurred overnight (1800-600 hrs). Although females returning to the rookery showed less of a preference for time of day, the largest proportion of females returned overnight (40 - 52 %) compared to the morning or afternoon. Similar arrival patterns for Steller sea lion females were reported by Higgins *et al.* (1988). Female northern fur seals appear to prefer departing at night, but they do not appear to have a preferred time of day to return to the rookery (Gentry and Holt 1986) The apparent randomness of arrivals on shore suggest that Steller sea lions may be returning after they have successfully fed and are satiated, rather than returning due to an inherent diel cycle.

Changes in the length of foraging trips

Maternal attendance patterns over the two month breeding season appeared to be similar at both sites. I found that the length of maternal foraging trips increased over the breeding season as pups grew older. Increases in foraging trips as pups age have been reported for the Steller sea lion, northern fur seal, Antarctic fur seal, California sea lion, Galapagos sea lion (*Zalophus californianus wollebaeki*), Cape fur seal (*A. pucillus)*, and South American fur seal (*A. australis*) (Higgins *et al.* 1988; Gentry and Holt 1986; Doidge *et al.* 1986; Boyd *et al.* 1991; Peterson and Bartholomew 1967; Boness *et al.* 1985; Trillmich 1986; David and Rand 1986; P. Majiluf, personal communication ***in*** Oftedal *et al.* 1987b). Only Melin (1995) failed to find a change in the length of foraging trips of California sea lions (*Z. californianus)* over the lactation period. The seasonal increase in foraging trip lengths is probably related to the increasing nutritional demands of the growing pup over time. Milk transfer measurements confirm that both larger and older otariid pups consume more milk than smaller and younger ones (Higgins *et al.* 1988; Costa and Gentry 1986; Gentry and Holt 1986).

Changes in the length of visits ashore

My study showed that the duration of shore visits decreased as the pup grew older. This is consistent with results from some studies, but differs with others. For example, Higgins *et al.* (1988) found that shore visits remained constant as Steller sea lion pups grew older at Año Nuevo Island in California. The constancy of shore visits was also reported for northern fur seals and California sea lions (Gentry and Holt 1986; Melin 1995). In contrast, Antarctic fur seals increased the duration of shore visits over the season (Doidge *et al.* 1986; Boyd *et al.* 1991), whereas Cape fur seals decreased their time ashore from the first to second month following parturition (David and Rand 1986). Higgins *et al.* (1988) speculated that the unvarying duration of shore visits of the Steller sea lions they observed reflected the time needed for females to rest rather than the increasing nutritional demands of their growing pups. However, a mother's resting time may be flexible depending on environmental conditions such as prey availability and location.

If longer foraging trips are insufficient to meet both the mothers metabolic needs and the increased nutritional demands of her pup, mothers may end up resting progressively less during shore visits and forage more frequently to meet nutritional needs. Less time spent on shore should not interfere with the ability of the mother to nurse her pup since pups increase their suckling efficiency as they grow (Higgins *et al.* 1988) and spend approximately two hours suckling for each maternal foraging-attendance cycle (trip to sea and subsequent visit ashore) (Chapter 3). Therefore, under certain environmental conditions, a decreasing trend in shore visits as pups age may reflect increased suckling efficiency. This speculation is consistent with that posed by David and Rand (1986) who suggested that Cape fur seal mothers may decrease their time on shore as pups age to meet the increasing nutritional demands of their pups. However, Doidge *et al.* (1986) hypothesized that Antarctic fur seals spent more time on shore as pups aged because wandering pups caused mothers and pups to reunite less quickly over time. Such differences in findings suggest that maternal shore visits are flexible. Increases or decreases in the time spent on shore as pups grow older probably depend on the prey availability, behaviour of the pups, or the terrain of a rookery that may cause a mother and pup to reunite less quickly.

Early shore visits (after the initial feeding trip) when pups were 5 - 9 days old were significantly longer than subsequent visits in the area of decline, and longer than in the stable area. Longer perinatal periods and shore visits when pups are very young may explain why pups in the area of decline are heavier (Merrick *et al.* 1995) and grow faster (Brandon and Davis, unpubl. data, pers. comm.) than in southeast Alaska. Good female physical condition may also enable mothers to fast longer on shore with their pups after returning from their first feeding trip. An alternative explanation is that the maternal care strategy when pups are very young differs between the two genetically distinct stocks of Steller sea lions.

2.5 Conclusions

Based on the responses of other pinniped populations during periods of prey reduction, my results suggest that lactating Steller sea lions in the area of population decline were not nutritionally stressed during the summer breeding season. Longer perinatal periods, shorter foraging trips, and longer shore visits are inconsistent with the food-limitation hypothesis. However, there are a number of reasons why maternal foraging-attendance patterns between the two populations could differ. First, the distance to foraging locations may vary between the two populations. Next, the relative abundance of major prey species at each site during the summer may cause changes in foraging trip lengths depending on the movement behavior and location of prey. Differences in prey abundance near the rookeries between the declining and abundant population may also be influencing the duration of foraging trips. Another explanation for the variation is foraging trip lengths is that the age structure may differ between the two populations. Older, more experienced females appear to use a different foraging strategy than younger ones. Finally, longer perinatal periods in the area of decline may be linked to feeding conditions during the winter or spring rather than summer feeding conditions. It seems clear that more research is needed to test these specific hypotheses before we can fully understand the meaning of differences in foraging-attendance cycles between the stable and declining populations of Alaskan Steller sea lions.

2.6 Summary

Female attendance patterns of Alaskan Steller sea lions were compared over two summer breeding seasons in 1994 and 1995 at Sugarloaf Island (a declining population) and Lowrie Island (a stable population). Foraging trips were significantly shorter in the area of population decline, counter to initial predictions. The mean length of maternal foraging trips in the area of population decline was 19.0 hours compared to 25.6 for the stable population. In contrast, shore visits and the perinatal period (time between parturition and first maternal feeding trip) were significantly longer in the area of decline, again countering initial predictions. The mean length of shore visits for the declining population was 26.9 hours compared to 22.6 hours where the population was stable. The perinatal period averaged 10.1 days in the area of population decline compared to 8.0 days for the stable population. For both Steller sea lion populations, the mean length of female foraging trips increased as their pups grew older, whereas shore visits became shorter. The first shore visit following the perinatal period was significantly longer in the area of population decline compared to the stable population. Females from both populations exhibited a diel haul out pattern where the majority of returns and departures to and from the rookery occurred between 1800 - 0600 hours. Maternal attendance patterns responded in a similar way between years. Behavioural observations of maternal attendance patterns are not consistent with the hypothesis that Steller sea lions at the declining site have greater difficulty obtaining prey compared to the stable population in southeast Alaska.

3.0 MATERNAL ACTIVITY BUDGETS

3.1 Introduction

One means of gaining insight into the nutritional status of Steller sea lions is to observe their maternal attendance patterns (Chapter 2). Another way is to analyze their activity budgets. Ono *et al.* (1987) found that California sea lion pups suckled less, received less milk, and were less active during the 1983 El Niño event compared to years of normal oceanography. Controlled experiments using terrestrial mammals have also demonstrated that protein-calorie deficiencies can result in hyperaggression, hyperexcitablility, lack of curiosity, anti-sociality, growth stunting and a decrease in physical activity (*see* Chow and Rider 1973; Zimmerman 1975; Simonson 1979; Levitsky 1979 *for behavioural and developmental effects*, and DeMaeyer 1976; Truswell 1976 *for physical effects*).

The following study compares the summer activity patterns of lactating Steller sea lion females in the Gulf of Alaska, where the population continues to decline, and in southeast Alaska, where the population is stable. My primary goal was to determine whether lactating sea lions in the area of decline spent a greater proportion of time foraging and less time caring for their pups compared to the population that is not thought to be nutritionally stressed. My secondary goal was to provide a detailed account of the proportion of time lactating Steller sea lions spent in various activities over the summer breeding season. Although, the reproductive behaviour and social organization of many pinniped species have been examined in considerable detail (e.g. Gentry 1970; Gisiner 1985; Higgins *et al.* 1988; Higgins and Gass 1993; LeBeouf 1974; Stirling 1971; McCann 1980, 1981a, 1982; Miller 1975; Boness and James 1979), the partitioning of activities for different pinnipeds has received less attention (Harwood 1976, Boness 1984, Anderson and Harwood 1985, Tinker *et al.* 1995 for the grey seal *(Halichoerus grypus)*; Crawley *et al.* 1977 for the New Zealand fur seal *(Arctocephalus forsteri)*; McCann 1983 for the southern elephant seal *(Mirounga leonina)*; Miller 1975 for walruses (*Odobenus rosmarus*)), and there is no detailed activity budget for female Steller sea lions .

3.2 Methods

Behavioural observations were collected over the entire summer breeding season at each site (see Chapter 2 for details). The behaviour of individually recognizable females with pups was recorded using instantaneous focal scan sampling at 15 minute intervals (Altmann 1974; Martin and Bateson 1986). Behavioural scans were conducted between 0600 - 2000 hours on five days per week. Observations were spread evenly throughout the day, weather permitting. The mean daily observation effort for both sites and years was 11.9 hours (Table 3.1). Females with total observation efforts (time at sea and ashore) less than 170 hours on Lowrie Island and 219 hours at Sugarloaf Island were omitted from the time budget analysis because these omitted individuals had observation efforts that were less than 110 hours, a substantial drop from my chosen minimum efforts. The number of females used for this analysis ranged from 17 to 47 individuals. Natural markings such as scars or fungal patches were used to identify females.

Table 3.1: Mean daily observation effort (hours) for both study sites and years. The total number of observation days shown in brackets.

	Declining Population		Stable Population	
	1994 (39)	*1995 (50)*	*1994 (26)*	*1995 (34)*
$\bar{x}$	10.4	12.0	13.0	12.4
$S_{\bar{x}}$	0.09	0.06	0.07	0.08

Although many behaviours were recorded in the field (see Appendix 1), I simplified the behaviours into more general categories to document the general activity patterns of female Steller sea lions. The following behaviours were used in the activity budget analysis:

- **absent** - *female not present on the rookery*
- **rest** - *female laying down flat and could have been yawning, changing position without walking, or rubbing nose on the rocks*

- **nurse** - *suckling offspring (pup had to be attached to teat)*
- **alert** - *upright sitting position*
- **groom** - *scratching or rubbing usually in an upright position*
- **passive** - *mostly nuzzling with their pups but also included infrequent interactions with juveniles and other pups*
- **aggression** - *an encounter between individuals using threat displays and calls*
- **other** - *all remaining behaviours including swimming, walking, running, courting, copulations, controlling location of pup*
- **vocalize** - *mother-pup recognition calls*

Of these activities, only vocalizations could have occurred simultaneously with the other eight activities listed above. For example, a female could have been vocalizing to her pup while walking, alert, or swimming. As a result, the reported proportion of time spent vocalizing was scored and analyzed independently (adding vocalizations to the other activities would result in a time budget that exceeds 100 %).

During the behavioural scans, my assistants and I were occasionally unsure of a female's whereabouts, her behaviour (if she was obscured from our view), or if she was suckling her pup. These behavioural scores were subtracted from the total individual female observation efforts (*adjusted observation effort*) before calculating the proportions for each behaviour. The adjusted observation efforts for each female, which did not deviate greatly from the total effort, ranged from 157 - 340 hours on Lowrie Island, and 194 - 554 hours on Sugarloaf Island.

During each behavioural scan, I also recorded if females were near their pups *(mother-pup association).* A pup was scored as being with his or her mother if it was within one pup length away from the mother. The observation efforts used to calculate the percent association excluded the perinatal period, and observations when the presence of a mother on the rookery was uncertain or obscured from our view. In 1994, observation efforts for mother-pup associations were less than in 1995 because my assistants and I did not start recording associations until June 16th for Sugarloaf Island, and July 9th for Lowrie Island. As a result, observation efforts for mother-pup associations, ranged from 42.0 - 286.8 hours in 1994, and from 115.8 - 491.3 hours in 1995. I did not exclude the smaller observation efforts in 1994 because most of the data for Lowrie Island would have been omitted. The number of females used in 1994 for this analysis is less for Lowrie Island because by July 9th, six of the females we were following had moved their pups away from the breeding area and were no longer seen. The effect of pupping date on time mothers spent with pups was not considered in this analysis.

I used the following formula to calculate behavioural proportions and mother-pup associations:

$$\%\ behaviour = \frac{frequency \times 0.25\ (hrs)}{total\ observation\ effort\ (hrs)}$$

The proportions were normalized using a slight modification of the Freeman and Tukey (1950) arcsine transformation:

$$p' = \tfrac{1}{2}\left[arcsin \sqrt{\frac{X}{n+1}} + arcsin \sqrt{\frac{X+1}{n+1}} \right],$$

where X/n is the actual proportion. This transformation was preferable for the extreme ends of the proportions and yields confident results when statistically comparing the more infrequent behaviours between the study sites and years (Zar 1996).

Once the behavioural proportions were calculated for each female, I averaged the proportions among the females. A two-factor Analysis of Variance was used to statistically compare the data between sites and years.

3.3 Results

Time at sea and resting ashore

Females from the stable population spent considerably more time at sea in 1994 ($\bar{x}$ = 58.5 %) than in 1995 ($\bar{x}$ = 34.2 %) (Figure 3.1 and Table 3.2). They also spent more time at sea compared to females from the declining population in both study years ($\bar{x}$ range: 34.5 - 37.3 %). As a result, the analysis of variance suggests that females from the stable population spent significantly more time at sea ($\bar{x}$ = 46.4 %) than females from the declining population ($\bar{x}$ = 35.9 %) and that females in 1994 spent more time out at sea ($\bar{x}$ = 46.5 %) than females in 1995 ($\bar{x}$ = 35.7 %) (Table 3.3). An interaction between sites and years was also found ($F_{1,112} = 52.15$, $p < 0.001$). In 1995, females from the stable population spent 24.3 % less time at sea whereas females in the declining area spent 2.8 % more time at sea (Table 3.2 and Figure 3.1)

Table 3.2: Individual mean ($\bar{x}$), grand mean ($\bar{\bar{x}}$), and standard error ($s_{\bar{x}}$, $s_{\bar{\bar{x}}}$) percents of total time that lactating females spent in various activities at both study sites. Numbers of females observed are shown in brackets.

	Declining Population				Stable Population				Both Sites Combined	
	1994 (32)		*1995 (47)*		*1994 (17)*		*1995 (20)*		*1994 + 1995*	
	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{\bar{x}}$	$s_{\bar{\bar{x}}}$
absent	**34.5**	1.65	**37.3**	1.28	**58.5**	2.73	**34.2**	1.69	**41.1**	5.83
rest	**51.7**	1.33	**47.4**	1.10	**27.7**	2.05	**50.1**	1.55	**44.2**	5.58
alert	**3.5**	0.21	**5.0**	0.25	**5.3**	0.54	**7.1**	0.61	**5.2**	0.74
nurse	**3.7**	0.31	**5.0**	0.23	**3.5**	0.49	**3.2**	0.29	**3.9**	0.40
groom	**2.2**	0.15	**2.2**	0.11	**2.0**	0.19	**2.7**	0.21	**2.3**	0.15
passive	**1.5**	0.14	**1.2**	0.08	**1.0**	0.10	**0.7**	0.14	**1.1**	0.17
aggressive	**1.1**	0.07	**0.7**	0.04	**0.5**	0.07	**0.4**	0.06	**0.7**	0.15
other	**1.8**	0.17	**1.2**	0.08	**1.5**	0.19	**1.6**	0.29	**1.5**	0.13
-walk	***0.6***	*0.05*	***0.6***	*0.04*	***0.5***	*0.06*	***0.5***	*0.07*	***0.5***	*0.03*
-swim	***1.0***	*0.13*	***0.4***	*0.06*	***0.5***	*0.08*	***0.9***	*0.24*	***0.7***	*0.15*
-misc	***0.2***	*0.04*	***0.2***	*0.03*	***0.5***	*0.08*	***0.2***	*0.04*	***0.3***	*0.08*
vocalize †	**1.1**	0.10	**1.1**	0.08	**0.4**	0.07	**1.6**	0.18	**1.1**	0.25

† Calculated proportion vocalizing is independent of the other combined activities. Vocalizations were not a mutually exclusive category and were scored as a secondary activity during scanning intervals.

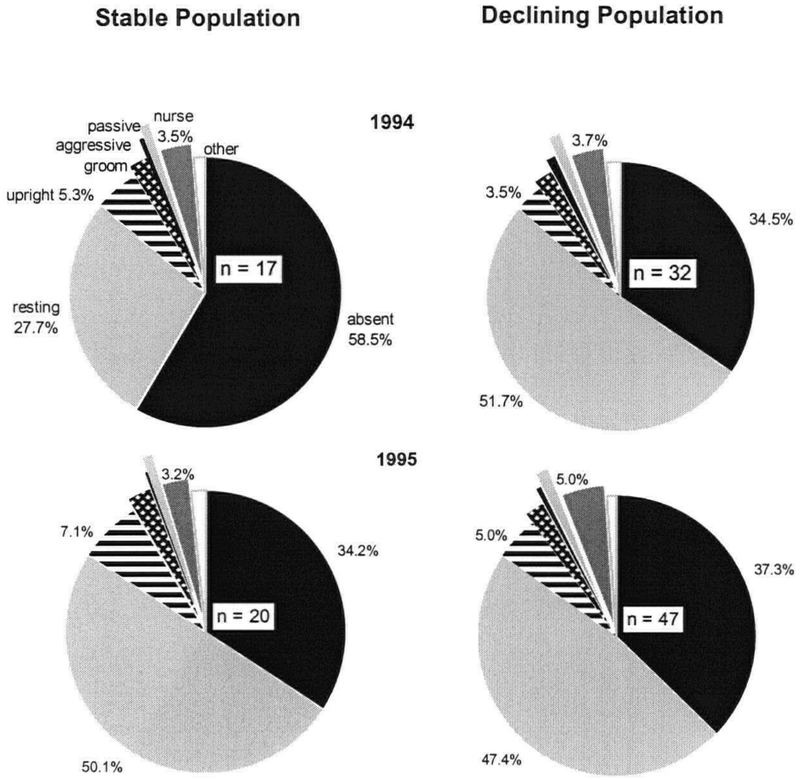

Figure 3.1: Time-activity budgets for lactating female Steller sea lions at Lowrie Island (stable population) and Sugarloaf Island (declining population) in 1994-5. The female sample sizes (*n*) are shown within each chart. ANOVA results suggest that females in the area of decline spent significantly less time out at sea and more time resting ashore. Moreover, females in the area of decline were more aggressive and spent more time suckling their pups. In 1994, females spent more time out at sea and less time resting. Table 3.3 summarizes all the results for between site and year comparisons of female activities.

In 1994, females from the stable population spent only 27.7 % of their time resting whereas in 1995, and for both study years in the area of decline, females spent between 47.4 - 51.7 % of their time resting (Table 3.2 and Figure 3.1). As a result, significant differences were found in time spent resting between sites and years (Table 3.3). Females from the declining population spent more time resting ($\bar{x}$ = 49.6 %) than females in the stable area ($\bar{x}$ = 38.9 %) and more time was spent resting in 1995 ($\bar{x}$ = 48.7 %) than in 1994 ($\bar{x}$ = 39.7 %). There was also an interaction between sites and years ($F_{1,112} = 79.17$, $p < 0.001$). Females spent 22.4 % more time resting in the stable population in 1995, and 4.3 % less time resting in the area of decline (Table 3.2 and Figure 3.1).

Despite the extensive amount of time females from the stable population spent out at sea in 1994, the combined average time spent at sea and resting ashore was relatively stable (≅ 85 %) for both sites and years (Figure 3.1).

Nursing

Pups spent significantly more time nursing in the area of population decline ($\bar{x}$ = 4.3 %) than in the stable area ($\bar{x}$ = 3.3 %) but no differences in time spent nursing were detected between years (Figure 3.1 and Table 3.3). An interaction was again found between the study sites and years ($F_{1,112} = 5.65$, $p = 0.019$). In 1995, females from the declining population spent 1.3 % more time suckling pups than in 1994, whereas females from the stable population spent 0.3 % less time (Table 3.2 and Figure 3.1).

Other activities

The average time females spent alert ranged from 3.5 - 7.1 % (Table 3.2 and Figure 3.1). Significant differences in time spent alert were found between sites and years (Table 3.3). Females from the stable population spent more time alert ($\bar{x}$ = 6.2 %) than females in the area of population decline ($\bar{x}$ = 4.2 %) and in 1995, females spent significantly more time alert ($\bar{x}$ = 6.1 %) than in 1994 ($\bar{x}$ = 4.4 %). Overall, females spent an average of 2.0 - 2.7 % of their time grooming (Table 3.2 and Figure 3.1). No significant differences in grooming were detected between sites or years (Table 3.3).

Females from the declining population were significantly more aggressive ($\bar{x}$= 0.9 %) than females from the stable population ($\bar{x}$= 0.5 %), and in 1994 females were more aggressive ($\bar{x}$= 0.8 %) than in 1995 ($\bar{x}$= 0.5 %) (Table 3.3). Females in the declining area also spent significantly more time interacting passively ($\bar{x}$= 1.4 %) than females in the stable area ($\bar{x}$= 0.8 %). In 1994, females engaged more often in passive activity ($\bar{x}$= 1.3 %) than in 1995 ($\bar{x}$= 1.0 %) (Table 3.3). Although females from both sites spent about 1 % of their time vocalizing, significantly more time was spent vocalizing in 1995 ($\bar{x}$= 1.2 %) than in 1994 ($\bar{x}$= 0.9 %) (Table 3.3).

Table 3.3: Between-site (A) and year (B) comparison of activities for lactating females. The weighted mean of the raw percent ($\bar{x}$) is given along with the mean ($\bar{x}'$) and standard error ($s_{\bar{x}}'$) of the arcsine transformed percents.

A) Sites

	Declining Population $n_{females}$ = 79			Stable Population $n_{females}$ = 37					
	$\bar{x}$	$\bar{x}'$	$s_{\bar{x}}'$	$\bar{x}$	$\bar{x}'$	$s_{\bar{x}}'$	df	F	p
absent	**35.9**	36.7	0.63	**46.4**	42.8	0.91	1,112	30.81	< 0.001 ***
rest	**49.6**	44.8	0.51	**38.9**	38.4	0.74	1,112	51.59	< 0.001 ***
nurse	**4.3**	12.0	0.28	**3.3**	10.6	0.40	1,112	8.00	0.006 **
alert	**4.2**	11.9	0.26	**6.2**	14.4	0.38	1,112	29.75	< 0.001 ***
groom	**2.2**	8.7	0.17	**2.4**	9.0	0.25	1,112	1.48	0.227
aggressive	**0.9**	5.7	0.14	**0.5**	4.4	0.20	1,112	26.99	< 0.001 ***
passive	**1.4**	7.0	0.18	**0.8**	5.6	0.25	1,112	18.04	< 0.001 ***
other	**1.5**	7.1	0.22	**1.5**	7.3	0.31	1,112	0.15	0.702
vocalize †	**1.1**	6.2	0.16	**1.0**	5.8	0.24	1,112	2.51	0.116

B) Years

	1994 $n_{females}$ = 49			1995 $n_{females}$ = 67					
	$\bar{x}$	$\bar{x}'$	$s_{\bar{x}}'$	$\bar{x}$	$\bar{x}'$	$s_{\bar{x}}'$	df	F	p
absent	**46.5**	42.8	0.83	**35.7**	36.6	0.74	1,112	31.15	< 0.001 ***
rest	**39.7**	38.8	0.67	**48.7**	44.3	0.60	1,112	38.20	< 0.001 ***
nurse	**3.6**	10.8	0.36	**4.1**	11.7	0.32	1,112	3.43	0.067
alert	**4.4**	12.1	0.35	**6.1**	14.2	0.31	1,112	19.66	< 0.001 ***
groom	**2.1**	8.6	0.23	**2.5**	9.2	0.18	1,112	3.67	0.058
aggressive	**0.8**	5.4	0.18	**0.5**	4.7	0.16	1,112	7.20	0.008 **
passive	**1.3**	6.7	0.23	**1.0**	5.8	0.21	1,112	8.82	0.004 **
other	**1.6**	7.6	0.28	**1.4**	6.8	0.25	1,112	4.22	0.042
vocalize †	**0.9**	5.2	0.21	**1.2**	6.8	0.19	1,112	32.45	< 0.001 ***

† Calculated proportion vocalizing is independent of the other combined activities. Vocalizations were not a mutually exclusive category and were scored as a secondary activity during scanning intervals.

General activity pattern

Resting on shore ($\bar{x}$= 44.2 %) and being away on foraging trips ($\bar{x}$= 41.1 %) were the two major behavioural components of a mother Steller sea lion's time budget (Table 3.2). Sitting upright and alert ($\bar{x}$= 5.2 %), suckling pups ($\bar{x}$= 3.9 %), and grooming ($\bar{x}$=2.3 %) were the next most frequently scored behaviours. The remaining behaviours (passive, aggressive, and other) made up the final 3.3 % of the female Steller sea lion activity budget.

Interannual differences

Comparing the proportion of time spent at sea and resting on shore during daylight hours showed significant differences between the two populations in 1994, but no significant differences in 1995. Moreover, no significant differences in time spent at sea (t_{95} = 0.735, p = 0.464) and resting on shore (t_{95} = 0.400, p = 0.690) were detected between the stable population in 1995 and the decreasing population in both 1994-95.

Table 3.4: Individual mean ($\bar{x}$) and grand mean ($\bar{\bar{x}}$) percents of total time mothers spent near their pup at both study sites. Numbers of females observed are shown in brackets.

	Declining Population				Stable Population				Both Sites Combined	
	1994 (32)		*1995 (47)*		*1994 (11)*		*1995 (20)*		*1994 + 1995*	
	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{x}$	$s_{\bar{x}}$	$\bar{\bar{x}}$	$s_{\bar{\bar{x}}}$
Mother-Pup Association	**34.8**	2.23	**38.6**	1.09	**34.8**	3.47	**38.8**	2.40	**36.7**	1.13

Mother-pup associations

Mothers and pups spent similar amounts of time together at both study sites ($F_{1,106}$ = 0.012, p = 0.914), and on both years ($F_{1,106}$ = 3.181, p = 0.077). The average amount of total time mothers spent with their pup was 36.7 % ($s_{\bar{x}}$= 2.30) (Table 3.4). While mothers were on shore, the average time spent with their pup was 71.6 % ($s_{\bar{x}}$= 4.46). When observation efforts less than 104.5 hours were excluded, results between sites

($F_{1,100} = 0.133$, $p = 0.716$) and years ($F_{1,100} = 3.63$, $p = 0.060$) were similar to the analysis that included the smaller observation efforts.

3.4 Discussion

Time at sea

The activity budgets shown in Figure 3.1 reflect how the lactating Steller sea lions I observed partitioned their time during daylight hours ($\bar{x} = 12$ hours of observation each day). It is not clear whether Steller sea lions partition their time differently at night. However, the tendency in most pinniped studies that have constructed activity budgets is to assume that the behaviour observed during the day is representative of behaviour that occurs overnight (Anderson 1978; McCann 1983; Anderson and Harwood 1985). Thus, applying an average cycle time (time at sea and ashore) of 46.5 hours (Chapter 2) suggests that Steller sea lion females spent an average of 19.5 hours at sea and 27.0 hours on shore, with 1.9 hours of the shore time engaged in suckling their pups.

In the second chapter, I showed that lactating females from the area of population decline took shorter feeding trips than in the stable area. The proportions of daylight hours engaged in foraging, resting ashore, and suckling pups (Tables 3.2 and 3.3) between both populations of Steller sea lions are consistent with this finding and counter my initial expectations. Other studies (Brandon and Davis, unpubl. data; Andrews, pers.comm.) have also found that foraging trips are significantly shorter in the area of population decline.

Lactating females from the stable population (Lowrie Island) spent an extensive amount of daylight hours out at sea ($\bar{x} = 58.4$ %) in 1994 compared to 1995, and compared to females from the declining population. Similar proportions for the 1994 cycle time at sea were reported by Brandon and Davis (unpubl. data, pers. comm.) who followed radio-telemetered Steller sea lion females on Lowrie Island in 1994 and 1995. The increased amount of time spent foraging in 1994 by Lowrie Island females could be related to a difference in prey choice that year. Steller sea lions from the stable population feed on a wider variety of prey than in the area of decline (Alverson 1992; Merrick *et al.* 1997) and the longer cycle time at sea could be related to the movement behaviour of the prey species that were abundant in 1994. Foraging-attendance cycle data collected over several consecutive years may show that cycle times at sea fluctuate frequently from year to year within the stable population, because of the wider variety of prey available for them to forage on.

Resting time

Lactating females in the declining area spent more time resting than in the stable area. However, the most interesting pattern I found in this study was the consistency of the combined time spent out at sea and resting ashore during daylight hours. It was approximately 85 %, regardless of the study year or which Steller sea lion population I observed. Resting time on shore may be the most flexible and expendable activity when time spent out at sea varies temporally. The time devoted to other activities such as grooming, locomotion, swimming, or interactions between individuals appears to stay relatively stable presumably because these activities are infrequent, yet part of their normal behaviour. Lactating females from the stable population spent less time alert in 1994 when more time was spent at sea. It is possible that females may exchange some of the time they spend alert (upright position) to rest more, when time out at sea increases temporally.

Lactating females from the declining population spent significantly less time alert (upright position) than females from the stable population (Table 3.3). Such a difference between the two populations may be related to differences in the geographical features of the two study rookeries. The rookery used where the sea lion population is stable was an exposed, steep, and large sloping rock where vigilance may be more necessary, whereas the rookery used in the area of decline was mostly flat and sheltered on two sides by cliffs. Another explanation could be related to differences in thermoregulatory behaviour between the two populations.

Nursing

Compared to lactating females from the stable population, females in the declining area spent more time suckling their pups despite their shorter foraging trips and total time at sea. In support of these findings, Brandon and Davis (unpubl. data, pers. comm.) reported that Steller sea lion pups from the area of population decline grew faster compared to pups from the stable population. They also showed that pups from the declining population had a trend towards a higher milk energy intake rate in their study, but the differences between the two populations were not significant. Merrick *et al.* (1995) also showed that Steller sea lion pups were heavier in the area of decline. All told, these results suggest that maternal investment in the area of population decline may be greater during early lactation, compared to the stable population. These findings also show no indication that females or pups are food-limited in the area of population decline during the summer.

Aggression

Lactating females in the area of population decline were more aggressive than females from the stable population (Table 3.3). This behavioural difference is the only evidence I found to support the food-limitation hypothesis. Nutritional stress has been shown to cause an increase in aggression in other mammalian species (Dasmann and Taber 1956; Zimmerman *et al.* 1975). However, the increased aggression I observed in the area of decline could have been density dependent. The rookery I used for observations in the declining area was physically small, and occupied by about 100 animals compared to a much larger surface area in the stable area which was used by about 300 animals. Thus, the females on the rookery in the area of population decline were more densely spaced per unit area than in the stable area which may result in more frequent disputes between females.

Comparison to other pinnipeds

Comparing my results to those obtained for other species of pinnipeds shows that the largest proportion of the on-land activity budget for female otariids and phocids during the breeding season is devoted to resting (Table 3.5). Lactating females need to spend large amounts of time ashore during the breeding season to care for their new born pups. The extensive amount of resting ashore is partly due to the energetic costs of lactation either because females fast during the lactation period (phocids) or because they feed regularly at sea during lactation (otariids). It is also important for pinnipeds to stay inactive while on land to minimize the risk of over-heating (Bester and Rossouw 1994). Although it is not clear why southern elephant seals (*M. leonina*) and grey seals (*H. grypus*) spend slightly more time resting on shore than the two otariids I compared (*E. jubatus and A. forsteri*), Pierotti and Pierotti (1980) have speculated that phocids may rest more than otariids because they are generally under greater thermal stress because of winter breeding in temperate to polar regions.

Southern elephant seal females spend considerably less time alert than either grey seals or the two otariids (*E. jubatus and A. forsteri*). On the surface it would appear that morphological differences between the two genera account for this difference, since the alert position for otariids is a sitting or upright position which is easier to maintain for longer periods of time (Bonner 1968; Stirling 1971). However, grey seals spent more time than the other species being alert, suggesting that the threat of predation may be a more probable explanation. Southern elephant seals for example, have no natural predators. Great white sharks (*Carcharodon carcharias*) and killer whales (*Orcinus orca*), are insignificant predators for the southern elephant seal (Carrick and Ingham 1962; Condy *et al.* 1978; Laws 1984) whereas they are significant predators of grey seals, New Zealand fur seals and Steller sea lions (Bonner 1981a; Brody and Beck 1983; Rice 1968; Le Boeuf *et al.* 1982; Ainley *et al.* 1985; Loughlin and Livingston 1986; Mattlin 1987; Bonner 1981b). Both otariid species have no known terrestrial predators (Riedman, 1990). Moreover, grey seal females are more widely spaced during the breeding season than the other species and may need to be more vigilant given that densely spaced groups of females find 'safety in numbers' (*see Hamilton (1971) for the 'Selfish Herd' hypothesis*) .

Table 3.5: Comparison of activity budgets (% time ashore) for female Steller sea lions (*Eumetopias jubatus*), New Zealand fur seals (*Arctocephalus forsteri*), southern elephant seals (*Mirounga leonina*), and grey seals (*Halichoerus grypus*).

Activity	Steller sea lion	[1]New Zealand fur seal	[2]Southern elephant seal	[3]Grey seal	[4]Grey seal
Rest*	75.0	62.8	‡ 81.3	85.8	75.4
Alert	8.8	4.9	1.0	7.3	12.6
Groom	3.9	1.7	—	—	0.5
Walk	0.9	1.4	—	—	—
Swim	1.2	15	—	—	—
Aggression	1.2	0.3	0.9	0.4	0.6
Passive (nuzzle)	1.9	† 1.6	0.3	—	0.8
Nurse	6.6	9.3	12.0	1.8	2.7
Vocalize	1.7	0.1	2.7	0.0	—

* resting values taken from McCann, 1983 do not include suckling
† includes carrying pup in teeth
‡ includes grooming
[1] Crawley *et al.* 1977
[2] McCann 1983
[3] Harwood 1976
[4] values averaged from Anderson and Harwood 1985

A striking difference between the two otariids in Table 3.5 is the amount of time spent swimming. New Zealand fur seal females spent 15 % of their time swimming compared to 1 % for Steller sea lion females. This is probably due to the greater thermoregulatory needs of the New Zealand fur seal since they have a thick, insulative, underfur that is not part of the Steller sea lion pelage. The extensive amount of time New Zealand fur seals spend swimming near shore may also explain why they spend less time resting on shore (62.8 %) compared to Steller sea lions (75 %).

The variation in aggressive activity among the four species I compared may be due to differences in the social organization and dominance hierarchy of females. There is evidence to suggest that older northern elephant seal females *(Mirounga angustirostis)* seek central positions in a rookery to ensure that they mate with the highest-ranking males (Reiter *et al.* 1981) and that dominance increases with age in Australian sea lions (*Neophoca cinerea*), such that high-ranking sea lions of both sexes often move subordinate animals during cold and rainy weather, assuming the vacated spot themselves

(Walker and Ling 1981). Although I never quantified female dominance among Steller sea lions, I often observed larger females aggressively moving other females from a spot on the rookery.

In my study, I quantified passive interactions which consisted mainly of mother-pup nuzzling, but also included passive interactions with other pups and juveniles. However, since the passive interactions other pups and juveniles were rare, I chose to compare this behavioural category with the nuzzling category used in other activity budget studies (see Table 3.5). My comparison of passive interactions suggests that otariid mothers nuzzle their pups more than phocids. This can be related to the different lactation strategies that have evolved for phocids and otariids. Phocids seldom leave their pups during the short lactation period whereas, otariids are regularly separated from their pups when they forage at sea and must find them at regular intervals in a crowded rookery when they return to shore. Because otariids are frequently separated from their pups, mothers need to develop strong mother-pup recognition cues to ensure they are reunited after foraging at sea. Nuzzling involves olfactory investigation and helps the mother recognize her pup.

Pup-attraction calls (vocalizations) are also important mother-pup recognition cues. Southern elephant seals spent the most time vocalizing to their pups (2.7 %), followed by the Steller sea lions (1.7 %), and grey seals did not vocalize at all to their pups. McCann (1983) speculates that mother-pup calls are important for southern elephant seals because they breed in crowded assemblies where the consequences of mother-pup separation are probably more serious than in the more loosely organized grey seal breeding assemblies. New Zealand fur seals spent only 0.1 % of their time vocalizing to their pups. New Zealand fur seal females are well spaced compared to the densely spaced Steller sea lion females during the breeding season (*see Riedman (1990) for a review of pinniped social organization*). As a result, olfactory investigation may be a sufficient cue for New Zealand fur seal mothers to reunite with their pups when they return from foraging trips. Female southern elephant seals by far spent the most time nursing their pups (12 %), and grey seals the least (1.8 %) Milk fat content (46.9 % for *M. leonina*; 52.2 % for *H. grypus*) and duration of lactation are similar (23 days for *M. leonina*; 17 days for *H.*

grypus) for both of these species (*see Oftedal et al. (1987b) for a review of pinniped lactation*), but elephant seal females are much larger than grey seal females, and elephant seal pups gain weight at more than twice the absolute rate of grey seal pups (McCann 1983). New Zealand fur seal mothers probably suckle their pups more than Steller sea lion to compensate for their longer foraging trips of five days (Stirling 1970) compared to one day for Steller sea lions.

3.5 Conclusions

The proportion of time spent at sea during daylight was less in the area of decline than in the stable area. In 1994, females from the stable population spent an excessive amount of time at sea compared to 1995, or the females in the area of decline. The temporal variation in time spent at sea for lactating females in the stable area may be related to changes in the variety of prey available between the two years. Females in the area of decline rested more than females in the stable area. However, the maternal foraging-attendance cycle remained very consistent between the two populations and the study years (~ 85 %). It appears that the proportion of time spent resting on shore is curtailed when time spent at sea increases. Lactating females from the declining population also spent more time suckling their pups compared to females in the stable area. Given that females in the declining area spent less time at sea, and that their pups were heavier and grew faster than in the stable population suggests that maternal investment may be greater during early lactation in the area of population decline. Furthermore, mothers from both Steller sea lion populations spent similar amounts of time with their pups despite the similarity in their maternal foraging-attendance cycle. However, lactating females were twice as aggressive in the area of decline. Although aggression has been shown to be more prevalent in nutritionally stressed mammals, it is more probable that the increased aggressive behaviour in the area of decline was related to the different densities of females at each rookery. These findings do not suggest that mothers or pups are food-limited in the area of decline during the summer breeding season.

This study has also shown that resting is the most important component of the on-land activity budget for female pinnipeds during the summer breeding season. Since lactating pinnipeds need to spend more time on land during the breeding season to care for pups, inactivity is probably the most efficient way to conserve energy and to reduce the risk of overheating while on land. The activity budget comparison of female Steller sea lions to females of other otariid and phocid species showed that variation in the partitioning of activities is dependent on the lactation strategy, social organization, thermoregulation, and predation.

3.6 Summary

Time-activity budgets for lactating Steller sea lions were compared over two summer breeding seasons (1994-5) at Sugarloaf Island (a declining population), and at Lowrie Island (a stable population) during daylight hours. Lactating females in the area of population decline spent less time foraging at sea (36.2 %) compared to females from the stable population (45.3 %). The contrast of this was that females spent more time resting ashore in the area of population decline (49.6 %) compared to the stable population (38.9 %). Females from the area of population decline spent more time suckling their pups and were more aggressive compared to the females from the stable population. Overall, lactating females from both populations spent a consistent 85 % of their time foraging at sea and resting onshore. Females from the stable area were more alert (6.2 %) than females in the area of decline (4.2 %) but the amount of time spent grooming was similar for both Steller sea lion populations (2.3 %). Mothers from both populations spent an average of 36.7 % of their total time with pups and 1.1 % of their total time vocalizing to pups. Mothers in the area of decline spent more time nuzzling their pups (1.4 %) than in the stable area (0.8 %). A comparison between the onshore activities of Steller sea lion females and other pinniped females showed that the partitioning of activities is related to differences in lactation strategies, social organization, predation, or thermoregulation. These activity budgets show no indication that lactating Steller sea lions in the area of population decline are nutritionally stressed.

4.0 GENERAL DISCUSSION

The maternal attendance patterns that I recorded in the area of population decline countered what I expected to observe if the adult females were nutritionally stressed during the summer. The most important differences found in Chapters 2 and 3 were that foraging trips and the total time spent at sea were shorter in the area of decline compared to the stable area. It was also surprising to find that the perinatal period was longer, and that mothers spent more time suckling their pups in the area of decline. Studies during the 1983 El Niño event (which reduced prey availability along the eastern Pacific Coast) clearly showed that lactating pinnipeds lengthened their foraging trips, had shorter perinatal periods and suckled their pups less during periods of food limitation (see Chapters 1, 2 and 3). Based on these *a priori* expectations of what should happen to pinnipeds when food is unavailable, the lactating Steller sea lions in the area of decline did not appear to be food-limited during the summer. The recent finding that Steller sea lion pups are heavier and grow faster in the area of decline compared to the stable population is strong evidence to suggest that lactating females are not nutritionally stressed in the declining population (Brandon and Davis, unpubl. data, pers.comm) However, my conclusions must be interpreted with caution since the abundance of prey available to the two Alaskan populations is essentially unknown, unlike the comparison in California, Peru, and the Galapagos Islands between an El Niño and normal oceanographic year. In Chapters 2 and 3, I discussed a number of alternative explanations for the observed differences in foraging trip length which need careful consideration. Clearly, more research is needed to determine such things as foraging locations, the relative abundance of major prey species, carrying capacity, localized prey depletion near the rookery, and the age structure of the adult females between the two populations.

Some scientists believe that observational studies are too subjective, because observers need to interpret behaviours in the same way, re-identify animals based on natural markings from year to year, and make assumptions about overnight behaviour. There has also been some concern that relying on scarred animals for identification may bias observational studies towards older animals. The proportion of time spent suckling is also a crude measure of milk transfer from the mother to the pup. Cameron (1998) reviewed suckling behaviour as a predictor of milk intake and concluded that there are many confounding factors that need to be tested. For example, suckling abilities can vary with a pup's age and sex, hunger can lead to more frequent suckling, the ability to release milk may vary, and non-nutritive suckling is known to occur during suckling bouts in other mammalian species.

Although there are potential biases associated with behavioural studies, I have shown that my results are consistent with other approaches. For example, my results for maternal attendance patterns between the two populations are consistent with similar studies that have tracked Steller sea lions using VHF and satellite transmitters. Information on attendance patterns can be gathered 24 hours per day in radio-tracking studies compared to observational studies yet there are still some problems associated with this technique. For example, short disappearances become questionable since a sea lion could be onshore, but out of radio contact (e.g. behind a rock). Moreover, radio-tracking is not only an intrusive technique but one which also yields a smaller sample size of females from which to do statistical analyses. At some point, one must start to question the value of intrusive studies in an area where the Steller sea lion population is endangered. For example, disturbing a large rookery to capture an individual can have negative impacts ranging from pup mortality to changes in the social organization and behaviour of sea lions.

Although my study will not lead to the recovery of Steller sea lions, it has nonetheless provided useful biological information that can be incorporated into more eloquent studies that may eventually test the hypothesis that sea lions are nutritionally stressed in the area of decline. Moreover, both observational and telemetry studies that have compared maternal attendance patterns have failed to show indications of nutritional stress during the summer in the area of population decline. It appears that summer comparative studies of this type have fulfilled their purpose, and researchers need to re-direct their hypotheses concerning the decline. Future research needs to focus on different age classes of Steller sea lions. For example, there is a valid hypothesis that juvenile Steller sea lions may be nutritionally stressed. Juvenile studies have already commenced (e.g. Porter 1997) but more studies are required to understand the basic life history and ecology of juvenile Steller sea lions.

The drastic decline of Steller sea lions is alarming for those who have admired the splendor of this majestic sea lion in the wild, and for anyone who appreciates the diversity of species around the world. The collaborative effort of the scientific community and industry to solve the puzzle of this population decline is a crucial step towards their survival, and to further understand ecosystem dynamics. Our concern for the Steller sea lion population decline is most admirable but the proximate cause remains unknown.

5.0 LITERATURE CITED

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7.0 APPENDIX 1

Behavioural Categories for Scan Sampling:

- present on rookery
- not sure if present
- prone and eyes open (lying flat, motionless)
- prone and eyes closed
- upright (sitting) and eyes open
- upright (sitting) and eyes closed
- upright in pool
- groom in pool
- groom
- walk
- run
- swim
- courting
- copulate
- vocalize
- other behaviour
- not sure (on rookery but obscured)
- threat display to other females (open/cross mouth)
- foreflipper slaps
- controlling location of pup
- passive interaction with own pup/juvenile
- aggressive interaction with own pup/juvenile
- passive interaction with other pup/juvenile
- aggressive interaction with other pup/juvenile
- passive interaction juvenile (mother unknown)
- aggressive interaction with juvenile
- aggressive interaction with bird (gull)

- interact with male (if no other category fits)
- threaten male
- running in circles/dive into sea
- look at hind flippers
- birth
- pull out placenta
- nurse pup
- not sure if nursing