

AN ABSTRACT OF THE THESIS OF

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Lion Rookeries

Abstract Approved:

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Northern sea lions (Eumetopias jubatus) were studied at three sites (Rogue Reef, Oregon, Marmot Island, Alaska, and Ugamak Island, Alaska) during the 1982, 1983, 1985, and 1986 breeding seasons. Data were collected on female activity budgets, attendance patterns, births, copulations, population structure, and patterns of seasonal and daily abundance.

Females spent most of their time on land in rest, maternal care, and comfort behaviors. Little time was devoted to sexual, movement, and agonistic behaviors. Significant differences were observed in behaviors between females of different maternal status, at different sites, and at different times-of-day. Females without young rested more, were less aggressive, and spent more time at sea than those with young. Females with pups and older young spent similar amounts of time in nursing, but only those with pups gave other care to their young. Females with pups spent the most time ashore. These differences are due to the necessity of females to attend to their young.

Rogue Reef females were the least active and least aggressive. Females at Marmot Island were more active, more aggressive, and

showed the least change in behavior by time-of-day of any site. Ugamak Island females were intermediate in behavior to the other sites, but showed the strongest time-of-day effects. These differences appear related to thermal, tidal, and substrate differences among the three sites.

Females with pups were the largest group of animals on the rookeries. This group's reproductive cycle and behavior shaped the demographic patterns of primary rookeries, and as a result primary rookeries had many features in common. These included high pupping rates, low pup mortality, low numbers of juveniles, maximum abundance in late June to early July, and low animal abundance during the remainder of the year. Rookeries with few pups (secondary rookeries) had earlier peaks in seasonal abundance, greater pup mortality, and greater variation in juvenile numbers.

Variability in the behavior of females and differences in rookery population structure require care to be exercised when observations are generalized from one site to the population as a whole.

Behavioral and Demographic Characteristics of Northern Sea Lion  
Rookeries

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This thesis is dedicated to the memory of Geoffrey Dimmick.

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# BEHAVIORAL AND DEMOGRAPHIC CHARACTERISTICS OF NORTHERN SEA LION ROOKERIES

## CHAPTER I

### INTRODUCTION

Northern or Steller sea lions (Eumetopias jubatus) are one of the most widespread of the otariid pinnipeds. It breeds from the Kuril Islands and Sea of Okhotsk in the Soviet Union through the Aleutian Islands and Gulf of Alaska and south to central California. Loughlin et al. (1984) estimated the maximum population worldwide in 1974-80 was 290,000 (including some pups), of which more than 150,000 were in southwestern Alaska (i.e., the Aleutian Islands through the central Gulf of Alaska). Recent studies by the National Marine Mammal Laboratory and the Alaska Department of Fish and Game have determined that sea lion numbers in southwestern Alaska have declined by 52% since 1956-60 (Merrick et al. 1987).

An understanding of northern sea lion behavior is important not only to a general understanding of animal behavior, but may also provide insight into the the population decline. Information on maternal strategies may explain why sea lion fecundity is lower than fur seals and phocids. Information on the duration of female trip-making and their attendance of young may provide a indirect measure of feeding success. Knowledge of the variation between sites in seasonal and daily hauling patterns assists in the determination of the best time to count animals.

Numerous studies of northern sea lion behavior have been performed, with results as summarized in Loughlin et al. (1986). However, there are at least two significant subjects which remain to

be addressed. First, an activity budget has not been calculated. Without this unifying behavioral framework it is difficult to fully assess the significance of individual behaviors. Secondly, there has been little study of the variability in the expression of behaviors, whether it be between animals of different reproductive status, between sites, or over time. Species exposed to such a wide range of environmental conditions as are the northern sea lion should exhibit behavioral variability (Odell 1972; Emlen and Oring 1977; Davies and Krebs 1978; Gisinier 1985; Gentry et al. 1986).

This thesis has evolved to a point where I can consider these subjects; however, my initial research plan was far less ambitious. That plan was simply to catalogue behavior at one site - Rogue Reef, Oregon. Subsequently, I was able to expand my study to include one field season at Marmot Island, Alaska, and two at Ugamak Island, Alaska. Serendipitously, each site represents an area affected differently by the southwestern Alaska sea lion population decline. Rogue Reef is in Oregon, an area unaffected by the declines. Marmot Island is in the Gulf of Alaska and has only recently been affected. Ugamak Island is located in the eastern Aleutian Islands and is at the center of the earliest declines.

I have organized the wealth of data collected during these four field seasons under two topics. The first is the behavior of females on rookeries as measured by activity budgets and other behavioral observations. This includes an analysis of the variability in the expression of behaviors.

The second topic addresses the demographic patterns at rookeries. The need for a separate treatment of these patterns

became apparent when I recognized that differences existed in behaviors at different rookeries. Most were relatively slight at my three study sites; however, published results from other sites (Sandegren 1970; Lisitsyna 1981; Withrow 1982; Gisiner 1985) indicated extreme differences in behaviors could exist. One explanation for the differences was that there were different types of rookeries. Thus population structures and patterns of seasonal abundance at different rookeries were analyzed in order to determine how diverse rookery populations were, and if this diversity could be related to behavioral differences.

This thesis is organized into three chapters beyond this Introduction. Chapter II discusses the behavior of female sea lions on the breeding grounds, and includes information on their activity budget, as well as an analysis of differences between female types, sites, and by time-of-day. Chapter III discusses the demographic features of sea lion rookeries as observed at my three study sites and other sites discussed in the literature. Chapter IV presents a summary of the results of Chapters II and III. Appendices are included which summarize the biology of the northern sea lion (Appendix I), show individual field forms used (Appendix II), and describe individual behaviors in detail (Appendix III).

## CHAPTER II

## BEHAVIOR OF FEMALE NORTHERN SEA LIONS ON ROOKERIES

Introduction

Northern sea lions have been the subject of scientific curiosity since Steller's 1751 account from Bering's second expedition. Scammon (1874) presented the first account from U.S. waters, although he did not distinguish between the northern sea lion and the California sea lion (Zalophus californianus). The best early accounts are probably those of Allen (1880) and Elliott (1881). Evermann (1921) published the first detailed description of the species' breeding behavior. Subsequent studies have dealt with various aspects of the animal's breeding behavior and provide a relatively complete catalogue of the northern sea lion's breeding behavior. Most studies, however, focused on some special problem. An overall view of their behavior has largely been neglected since the work of Gentry (1970) and Sandegren (1970). Elementary characteristics of their behavior, such as variation between sites, over time, or between animals remain largely unquantified.

This element of my study had two objectives. The first was to quantify female behavior on rookeries using activity budgets. The second was to determine the variability in the animal's behavior. Three hypotheses were considered with respect to this second purpose:

1. That behavior differed among females by maternal status
2. That behavior differed between rookeries
3. That behavior differed by time-of-day

These hypotheses were tested using female activity budget data collected at the three rookeries, supported by additional data on birthing, copulation, attendance, and hauling patterns.

### Methods

#### Sites and Seasons

I made observations of northern sea lion rookeries at Rogue Reef, Oregon, Marmot Island, Alaska, and Ugamak Island, Alaska (Figure 1). The term rookery is used here in reference to a specific location within a larger site, where sea lions come primarily to breed and secondarily to rest. Each site includes more than one rookery.

The Rogue Reef (RR) site is located three km offshore of Gold Beach, Oregon (Figure 2). Based on my 1982 counts it is the largest northern sea lion rookery south of Alaska. The maximum daily population in 1982 was 1,261 animals other than pups (Table 1). Rogue Reef is a complex of islands, but only Pyramid Island acts as a rookery. This island includes three separate rookeries (R1-R3), as well as a bachelor bull haul-out (R4). I made observations of the three rookeries on Pyramid Island during daylight hours between 23 April through 13 July, 1982 from a shelter located 10 m above rookery R1.

Marmot Island (MI) is 45 km northeast of Kodiak Island, Alaska (Figures 3-4), and is the largest northern sea lion rookery in the world (Loughlin, et al. 1984). The maximum daily population in 1979 included 6,381 adult and juvenile animals (Calkins and Pitcher, 1982). The island includes six separate rookeries (B2-B7) and two

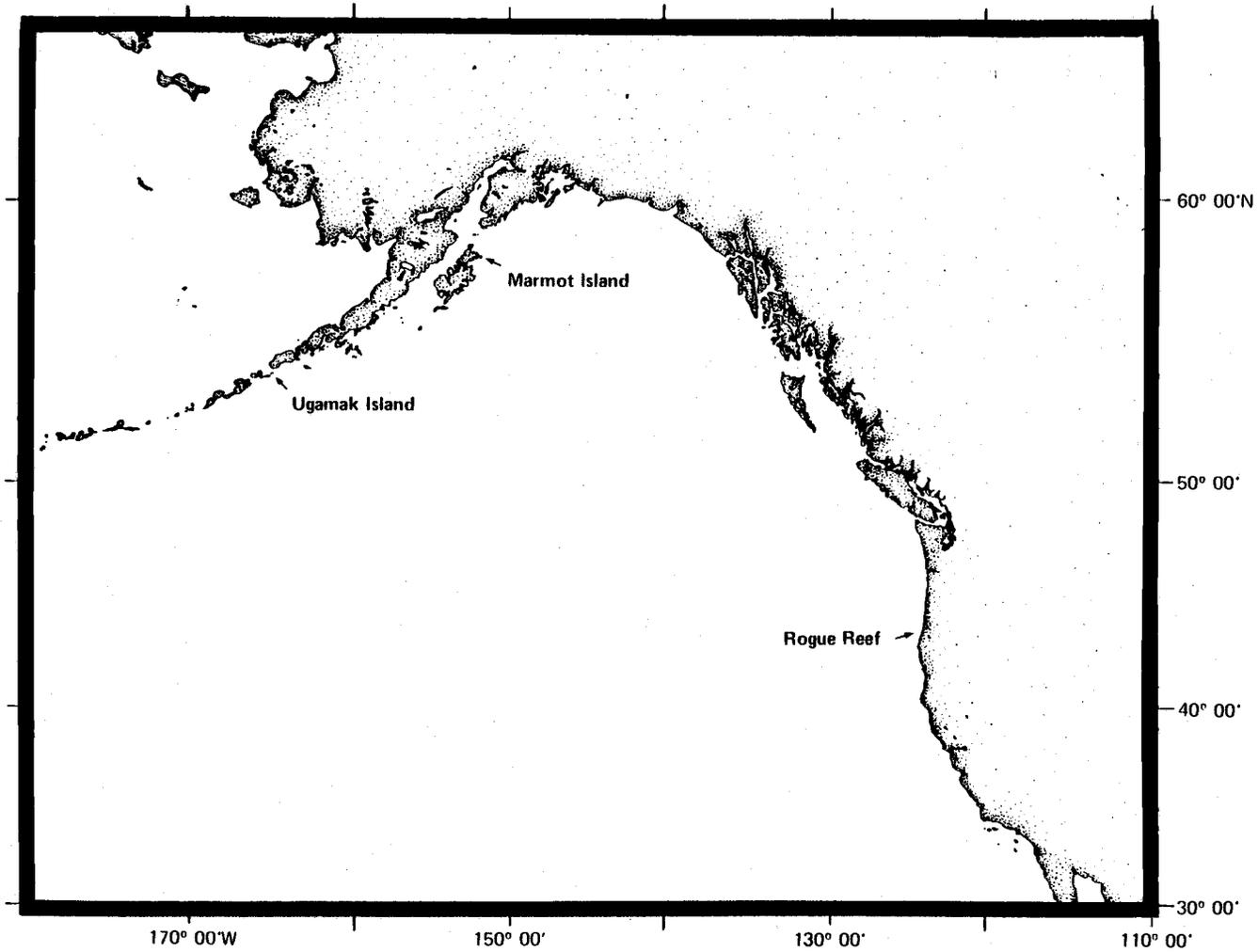


Figure 1. Map of study area.

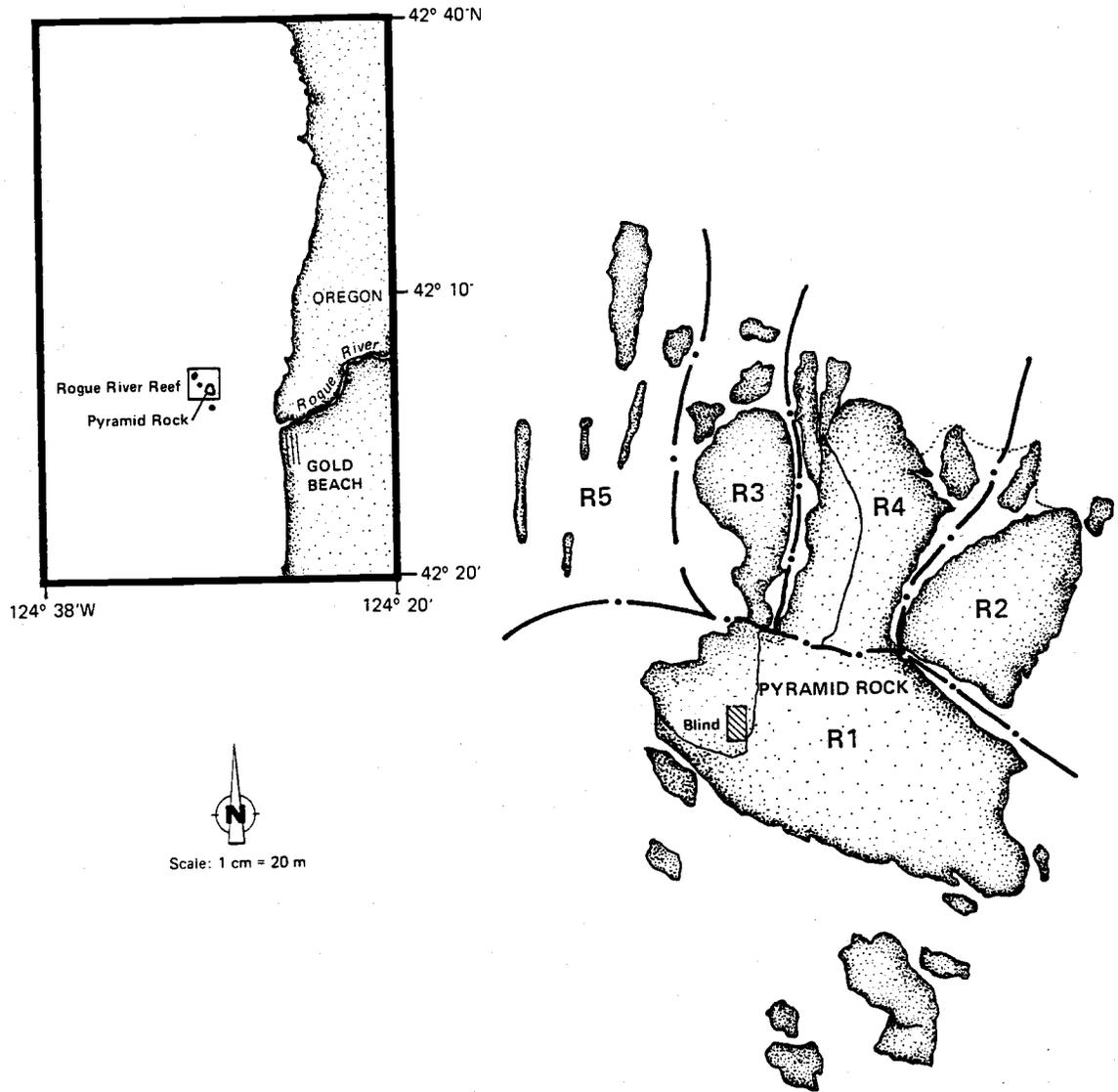


Figure 2. Map of Rogue Reef, Oregon study site.

Table 1. Sampling statistics for Rogue Reef, Beach 2-3 at Marmot Island, and Ugamak Island.

Item	Rogue	Marmot	Ugamak Island	
	Reef	Island	1985	1986
Hours of observation	461	150	143	nc
General log				
Births	311	nc	99	nc
Female Displays	70	1	0	nc
Copulations	322	314	118	nc
Focal event samples				
Births	42	nc	7	nc
Female Displays	39	0	0	nc
Copulations	55	32	55	nc
Focal female samples	220	184	170	nc
Maximum daily population observed at site:				
Adult territorial male	65	109	117	81
Adult other male	67	53	216	268
Adult female	960	1,983	1,765	1,302
Juvenile	169	673	89	100
Pups (alive and dead)	354	1,184	1,694	1,389
Total - non pups	1,261	2,800	2,197	1,751
Total - all	1,615	3,984	3,891	3,140

nc=not collected

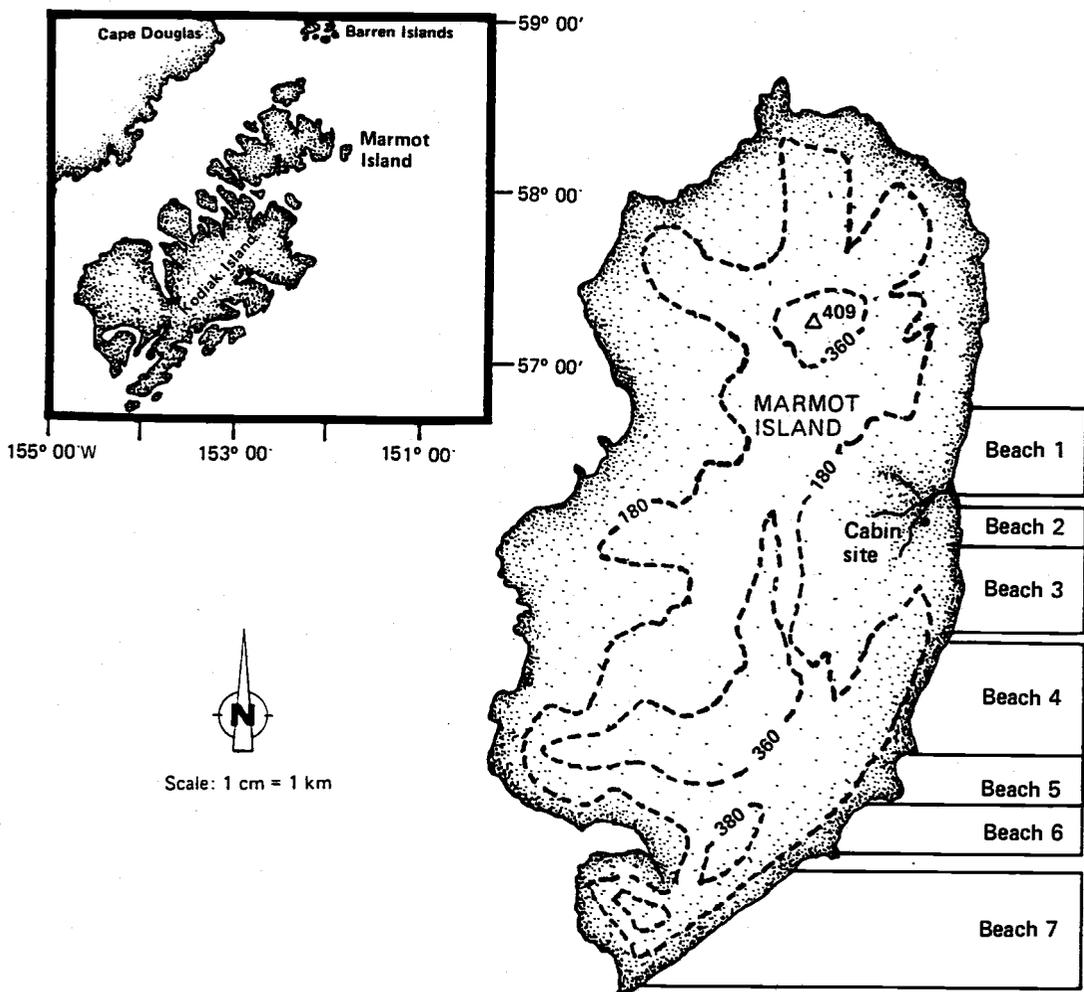


Figure 3. Map of Marmot Island, Alaska study site.

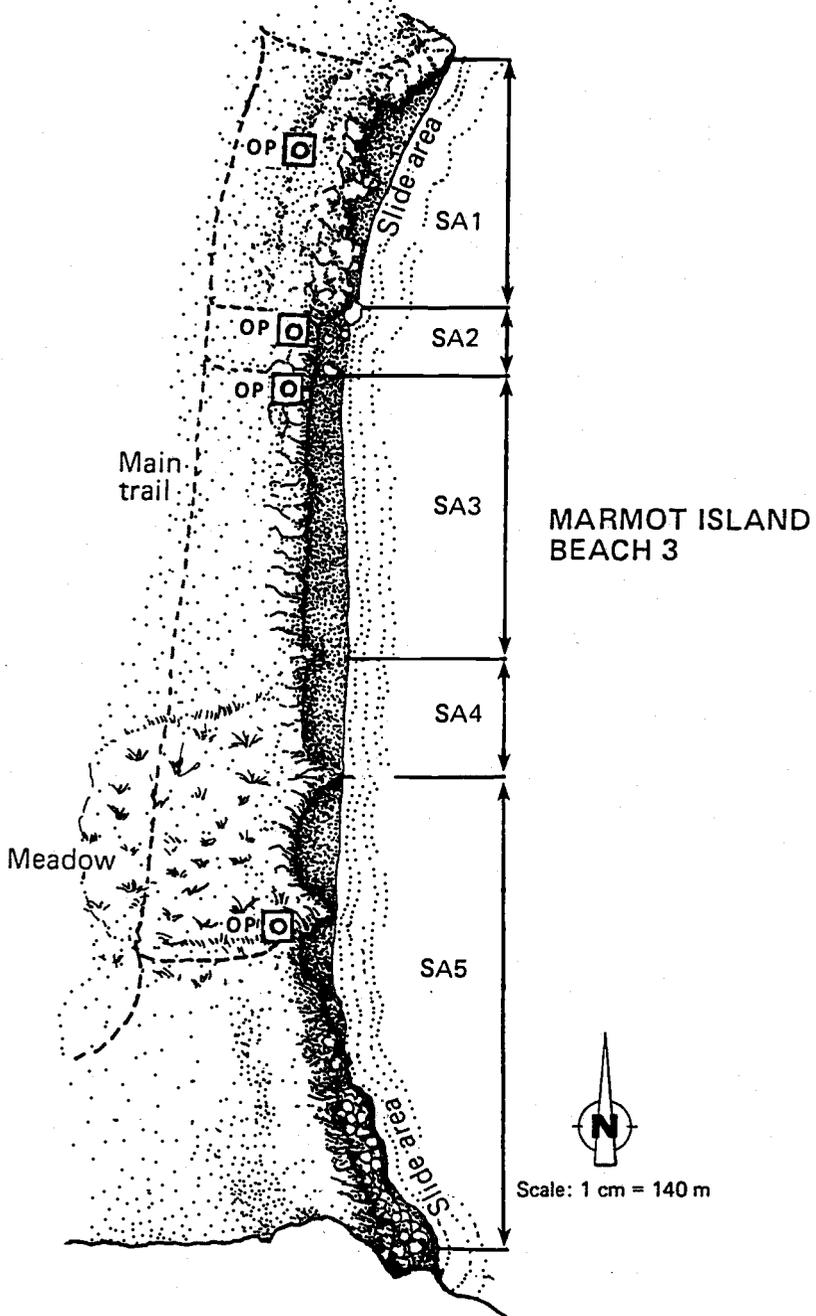


Figure 4. Map of Marmot Island, Alaska's Beach 3 rookery.

bachelor bull haul-outs (B1 and B7). I observed rookery B3 at scheduled intervals between dawn and dusk from 5 June to 7 July, 1983. My observation posts there were located on cliffs approximately 50 m above the beach.

Ugamak Island (UI) lies 110 km southeast of Dutch Harbor, Alaska (Figures 5-6). The maximum daily population included 2,199 adult and juveniles in 1985, and 1,751 in 1986. The island includes eight separate rookeries and one bachelor bull haul-out. I observed rookery A2 at scheduled intervals between dawn and dusk during two breeding seasons - 31 May to 10 July 1985 and 16 June to 26 July 1986. My observation posts were located on cliffs approximately 50 m above A2.

#### Data Collection

I collected behavioral data by four procedures: logging all occurrences of births, copulations and female displays; focal event surveys of births, copulations, and female displays (Altmann 1974); focal animal surveys of female behavior (Altmann 1974); and monitoring of female movements on and off shore. Each procedure involved direct encoding of the observed behaviors onto field forms (Appendix II) or onto magnetic media using a lap-top computer. Timing of behavioral states was done with a stopwatch or with the built-in clock in the computer. My observations were made with the unaided eye, binoculars, or a spotting scope.

I kept a record of all occurrences of births, copulations and displays. This provided the relative frequency these events occurred within the population. I recorded each event in a log which included

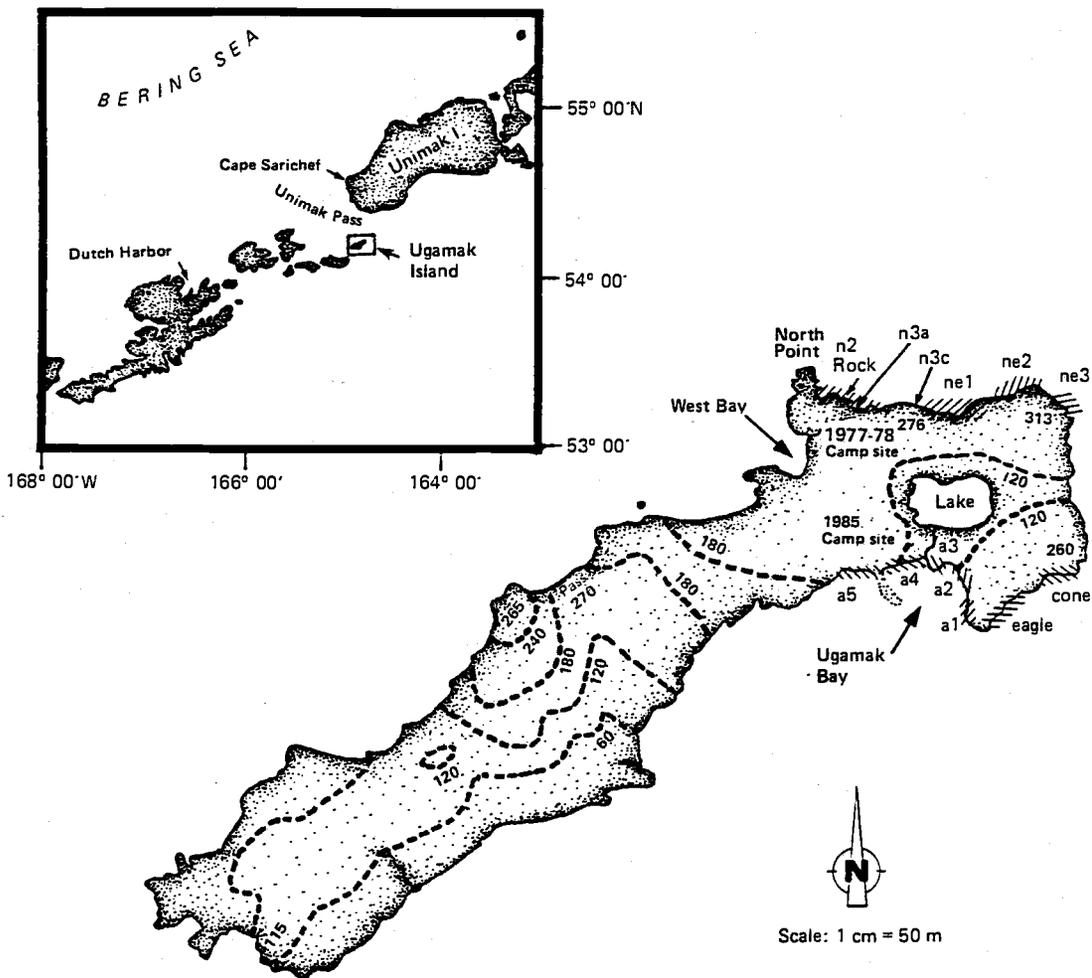


Figure 5. Map of Ugamak Island, Alaska study site.

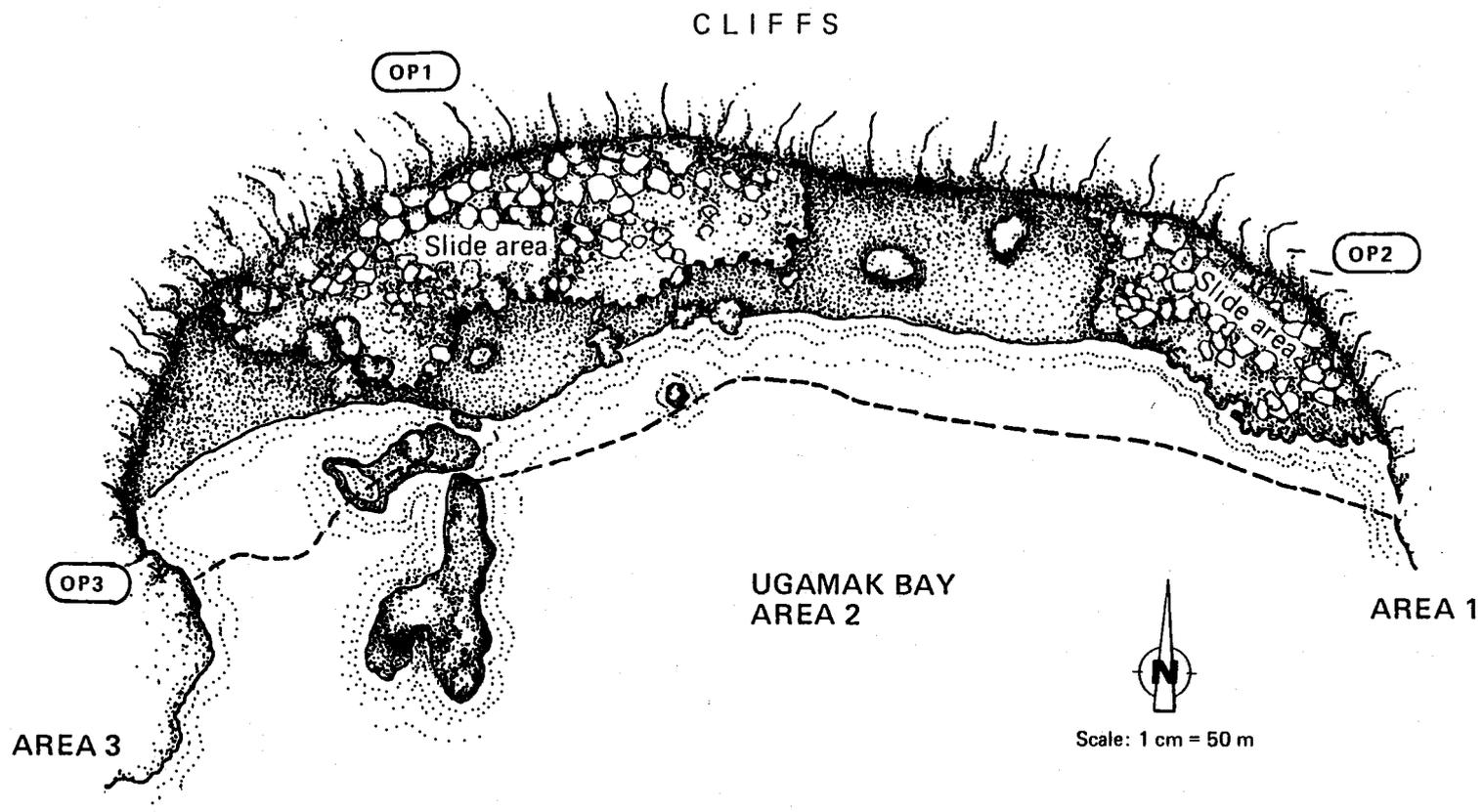


Figure 6. Map of Ugamak Island, Alaska's Beach A2 rookery.

the time, the male territory where the event occurred, the participants, and the outcome.

My focal event surveys provided detailed information on births, copulations, and female displays. These required me to watch an event from its onset to its termination and record the sequence and duration of the series of behaviors involved in the event. I also recorded the time the event began, its locations(s), its participant(s), and its outcome. Predefined sampling periods were initially used in the collection of these data at RR. It was soon apparent these event's aperiodic nature would make it difficult to obtain a reasonable sample size with such a sampling regime. Thereafter, these data were collected whenever the event was observed and a focal animal survey was not being conducted.

I used focal animal surveys to record the chronology and duration of behaviors exhibited by individual females during 15 min intervals. My list of female behaviors was prepared from descriptions in the literature and updated from my field observations. Nine behaviors were considered: 1) rest, 2) comfort, 3) birth, 4) nursing of offspring, 5) other maternal care, 6) female "courtship displays" (Sandegren 1970), 7) copulations, 8) movement, and 9) agonistic interactions (e.g., threat displays and fights). The salient characteristics of each female behavior is described in Appendix III. I also recorded where movements began and ended, the age and sex class of participants in any interaction, and the apparent cause of movements and agonistic interactions.

Once I had begun to analyze the data I created a tenth behavior category which I have labelled as "general activity". This was

calculated as the percentage of females who exhibited a behavior other than rest during the period of observation.

Samples were defined as a 15 min observation of an individual female. Stratified random sampling (Cochran 1977) was used to select females, with male territories defining the strata. Each sampling day was divided into four sampling periods - 0600 to 0959, 1000 to 1359, 1400 to 1759, and 1800 to 2159. Four focal female samples were scheduled for each period during a sampling day. The beginning of work was shifted by an hour each succeeding sampling day to ensure complete coverage of each sampling period.

Attendance (i.e. the time spent on and off shore) of 53 females from A2 beach at UI was monitored between 4 June and 3 July, 1985 (20 females) and between 17 June and 26 July, 1986 (33 females). Forty-two of these animals had pups, three had juveniles, two had both, and six had neither. These animals' locations were recorded two to four times a day between 0700 and 2400 AST for each day of the study period. A history card (Appendix II) was maintained for each female which described her marks, whether or not she had a pup, pertinent life history milestones, and her location during the daily censuses.

If I saw a female once in a day I assumed she was on the rookery for the whole day. I also assumed that a female was absent from the rookery if I did not see her a whole day. Females, particularly those with suckling young, usually return to the same location after feeding. Consequently, if I did not see a female she was probably either at sea or could not be seen on the rookery.

Hourly counts were made of adult females (at RR) or all animals (at MI and UI) for two or three days at each site.

## Analysis

Female behavior was analyzed using two statistics. The first was the proportion of females exhibiting a behavior. The second was their activity budget (i.e., the proportion of the sampling interval devoted to a behavior). The latter was calculated by determining the mean amount of time (in sec) devoted to the behavior, and then dividing by 900 (the duration in sec of the sampling interval).

I analyzed differences by female maternal type (with pup, with juvenile and alone), by site (RR, MI, and UI), and by time-of-day (the four sampling periods) using  $X^2$  contingency table analysis (Fienberg 1980). Time-of-day patterns were analyzed in two ways. First, the frequency a behavior was exhibited was regressed against time. The resulting slopes were then tested to determine if they were significantly different from zero. Secondly, frequencies were ranked for the four hour sampling periods. The period when the most animals exhibited the behavior received a rank of "1" while the period with the lowest frequency received a rank of "4".

Activity patterns of females of different maternal classes were similar at all sites, so those data were pooled by site for analysis by female class. However, analysis of time-of-day patterns indicated that considerable variation existed between sites. Consequently, the data was not pooled for time-of-day analysis and these patterns were considered separately for each site.

Parametric statistics were used to compare values of several other statistics (e.g., duration of births, births per territory). All statistical tests were made at the 0.05 level of significance.

## Results

A total of 754 hours of observation (Table 1) was spent at the three sites. Four hundred and ten births were observed, with 49 recorded in detail. No record of births was kept at MI. Seventy-one female courtship displays were observed, 39 in detail. Copulations were common, with 743 logged and 139 recorded in detail. A total of 574 focal female samples were obtained.

Birth, female courtship displays and copulations were observed in two, seven, and one focal animal samples, respectively. There were too few samples of females with both a pup and a juvenile for statistical comparisons, consequently, they have been excluded from further consideration.

### Rest and Comfort

Females spent 73.8% to 91.8% of their time in passive, rest-like behavior, with 87.0% to 99.0% of the females displaying the behavior (Table 2). As 53.5% to 29.9% of the females displayed comfort behavior, it was the third most common behavior. Significantly more ( $p < 0.05$ ) lone females displayed rest and comfort behaviors than females with pups or with juveniles. Significant differences were not observed between females with offspring, nor in the amount of time devoted to the behavior by any group.

Significant differences were not found between sites ( $p > 0.05$ ) for either behavior (Table 3 and 4).

More females were at rest in the early morning and late afternoon periods at all sites (Table 5); however, Ugamak Island was

Table 2. Mean frequency (Freq) and duration (Dur) of time spent in behaviors by female northern sea lions by maternal status for all sites and seasons.

Behavior	Female Maternal Status					
	With pup (n=299)		With juvenile (n= 77)		Alone (n=198)	
	Freq (%)	Dur (%)	Freq (%)	Dur (%)	Freq (%)	Dur (%)
Rest	93.3	73.8	87.0	74.3	99.0	91.8
Comfort	38.5	4.3	29.9	1.6	53.5	5.5
Nursing	33.9	15.6	30.6	20.0	0.0	0.0
Other care	24.6	1.4	4.5	0.1	0.0	0.0
Movement	12.4	1.1	13.0	1.1	13.6	0.9
Agonistic	56.2	3.8	63.6	2.9	51.0	1.8
General	79.9	na	85.3	na	70.0	na

Table 3. Mean frequency (Freq) and duration (Dur) of time spent in behaviors by site for female northern sea lions unaccompanied by young.

Behavior	Rogue Reef (n=100)		Marmot Is. (n= 54)		Ugamak Is. (n= 44)		All (n=198)	
	Freq (%)	Dur (%)	Freq (%)	Dur (%)	Freq (%)	Dur (%)	Freq (%)	Dur (%)
Rest	98.0	90.9	100.0	91.1	100.0	94.1	99.0	91.8
Comfort	31.0	7.4	31.5	4.0	54.5	3.2	53.5	5.5
Nursing	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other care	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Movement	17.0	0.9	16.7	1.1	15.9	0.5	13.6	0.9
Agonistic	45.0	0.8	59.3	3.8	50.0	2.2	51.0	1.8
General	64.0	na	71.4	na	81.8	na	70.0	na

Table 4. Mean frequency (Freq) and duration (Dur) of time spent in behaviors by site for female northern sea lions accompanied by a pup or juvenile.

Behavior	Rogue Reef (n=120)		Marmot Is. (n=130)		Ugamak Is. (n=126)		All (n=376)	
	Freq (%)	Dur (%)	Freq (%)	Dur (%)	Freq (%)	Dur (%)	Freq (%)	Dur (%)
Rest	90.8	77.4	90.8	68.3	92.9	76.3	92.0	73.8
Comfort	27.5	3.4	41.5	4.6	40.5	3.1	36.7	3.7
Nursing	31.2	15.2	34.9	20.2	35.4	13.8	35.0	17.6
Other care	9.3	1.2	20.5	1.4	29.9	1.1	20.1	1.1
Movement	5.0	0.7	19.2	1.3	13.5	1.4	12.5	1.1
Agonistic	59.2	2.1	72.3	4.2	44.4	4.3	57.7	3.6
General	72.5	na	90.7	na	77.6	na	81.0	na

Table 5. Ranking of frequency of occurrence of behaviors by site and time period (1=0700 to 0959, 2=1000 to 1359, 3=1400 to 1759, 4=1800 to 2200).

Behavior	Rogue Reef				Marmot Island				Ugamak Island			
	1	2	3	4	1	2	3	4	1	2	3	4
Rest	2	4	1	3	1	2	3.5	3.5	2	3	1	4
Comfort	4	2	3	1	1	4	3	2	3	2	1	4
Nursing	3	1	4	2	1	2	3.5	3.5	3	4	2	1
Other care	3	2	4	1	1	4	2	3	3	4	2	1
Movement	2	1	4	3	3.5	3.5	1	2	4	2	1	3
Agonistic	3	1	2	4	4	1	2	3	4	2	3	1
Mean Copulations per hour	2	3	4	1	3	2	4	1	3	1	4	2
Mean Rank	2.8	1.7	3.5	2.0	2.3	2.8	2.6	2.4	3.3	2.5	2.2	2.0

the only site which exhibited a significant difference by time-of-day ( $p < 0.01$ ).

### Parturition

The period of parturition was quite similar at the sites (Table 6). Viable, live births began in mid-May and continued through early July, a period of seven or more weeks in length. The median pupping date at the three sites was between 12 June and 14 June (Table 6).

Differences in the locations of births existed within sites. At RR, births were significantly more frequent ( $t=3.279$ ,  $n=35$ ,  $p < 0.05$ ) in terrestrial territories ( $x=10.13$ ,  $n=22$ ,  $s=9.55$ ) than in semiaquatic territories ( $x=3.8$ ,  $n=15$ ,  $s=6.01$ ). Some females at all three sites apparently preferred to give birth on specific rocks or open spaces, as they contended with other females for those sites.

Based on observed deliveries, parturition at RR showed a bimodal pattern during the day (Figure 7). Numerical peaks were reached in the morning and evening.

Duration of births (as measured from the bursting of the amnion to delivery) averaged 16.8 min at RR and 20.5 min at UI. These differences were not significant ( $t=0.445$ ,  $df=27$ ,  $P > 0.5$ ). The mean duration of caudal presentations was longer than cephalic presentations at RR (31.3 min vs 6.3 min) and UI (27.5 min vs 6.5 min). Caudal presentations accounted for 44% and 40% of the births observed at RR and UI, respectively.

Table 6. Percent of northern sea lion births by week<sup>1</sup> by site, and related statistics

Week Ending	ANI <sup>2</sup>	RR	Site CSJ <sup>3</sup>	UI	MI	WI <sup>4</sup>
<5/01	-6	5.0	5.6	8.7	-8.0	1.9
5/07	-13	14.6	21.2	18.2	-21.3	15.1
6/14	-21	29.5	33.4	33.0	28.3	28.3
6/21	-31	27.1	26.7	23.9	23.5	22.6
6/28	-21	19.5	10.1	9.2	9.9	22.6
7/05	8	4.4	3.0	7.8	9.1	9.5
# born	117	343	197	1063	1069	53
Range:						
Begin	mid-May	5/14	late-May	<6/01	-5/13	5/30
Median	6/14-16	6/14	6/14	6/12	6/13	6/16
End	early July	7/10	early July	7/06	7/02	7/01
Latitude	37°N	44°N	53°N	54°N	58°N	60°N

<sup>1</sup> ANI and CSJ percentages computed from observations of births, all other from pup counts.

<sup>2</sup> Gentry (1970); ANI=Año Nuevo Island

<sup>3</sup> Edie (1977); CSJ=Cape St. James, British Columbia, Canada

<sup>4</sup> Sandegren (1970) from Wooded Island, Alaska for 1967

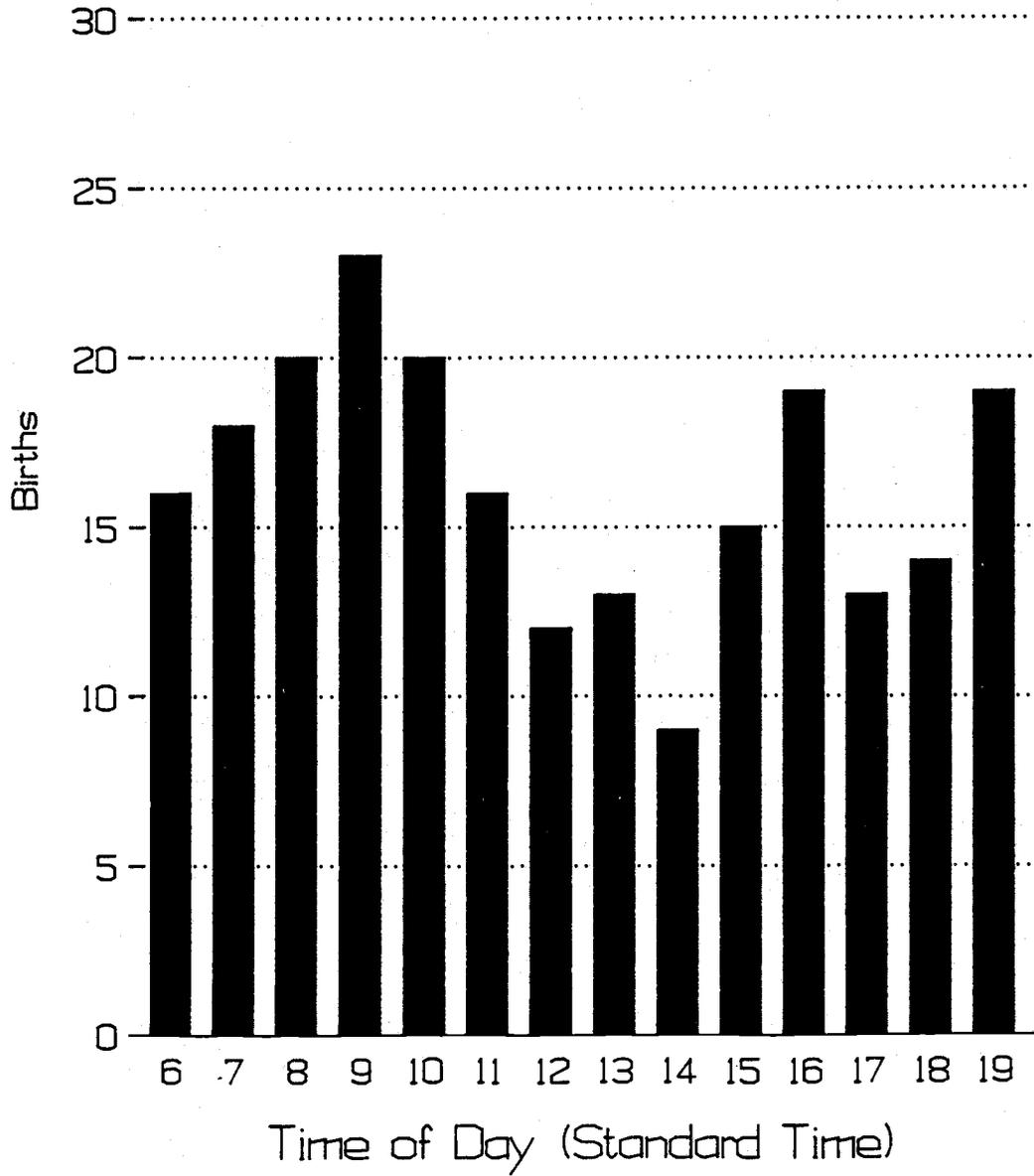


Figure 7. Frequency of northern sea lion births by time-of-day at Rogue Reef, Oregon.

## Nursing and Other Maternal Care

Females with young spent 15.6% to 20.0% of their time nursing (Table 2). This time includes breaks of a few sec when young were off teat. Other maternal care was an important activity amongst females with young since 20.1% of the sample females with young were observed giving other maternal care; however, this consumed only 1.1% of their time.

Females with pups nursed about the amount of time as those with juveniles (Table 2). However, females with pups interacted significantly more often ( $p < 0.01$ ) with their young in other maternal care than females with juveniles. Females with pups also devoted more time to other maternal care than those with juveniles, 1.4% and 0.1% of time, respectively.

Insignificant ( $p > 0.5$ ) intersite differences in nursing were observed (Table 4). Significantly more ( $p < 0.05$ ) MI and UI females showed other maternal care to their pups than those RR. The times were not, however, significantly different ( $p > 0.10$ ). Care of juveniles was about the same at RR and MI, while the UI sample was too small for comparison.

Significant time-of-day differences in nursing were observed at RR ( $p < 0.01$ ). There was a trend at both RR and UI towards more nursing in the midmorning and late afternoon (Figure 8). Significantly different time-of-day patterns were observed for other maternal care at each site ( $p < 0.01$ ). This behavior was most common at MI in the early morning, but in later time intervals at RR and UI (Table 5). A midday activity decline was observed (Figure 9).

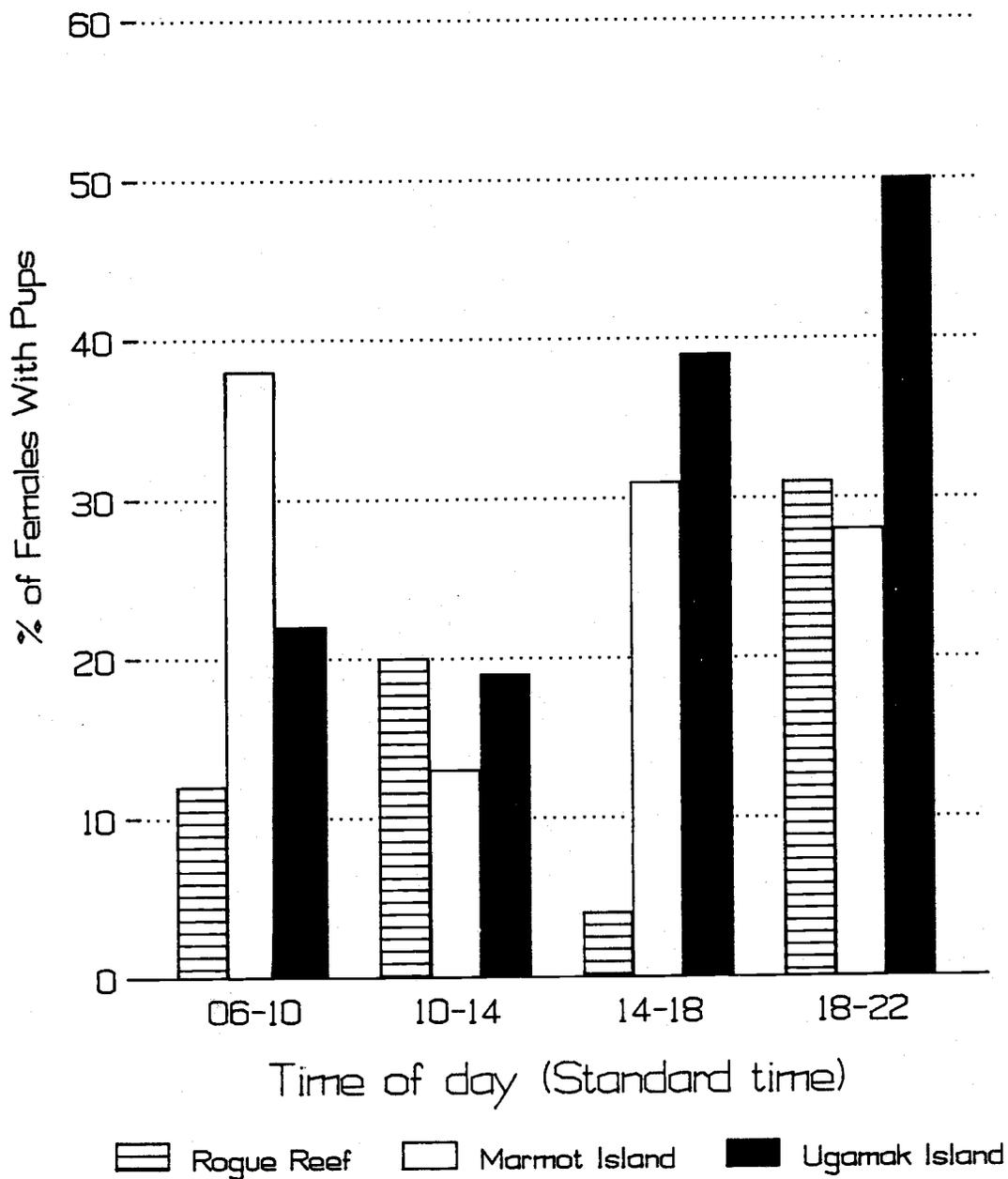


Figure 8. Frequency of nursing by northern sea lion females by time-of-day for all study sites.

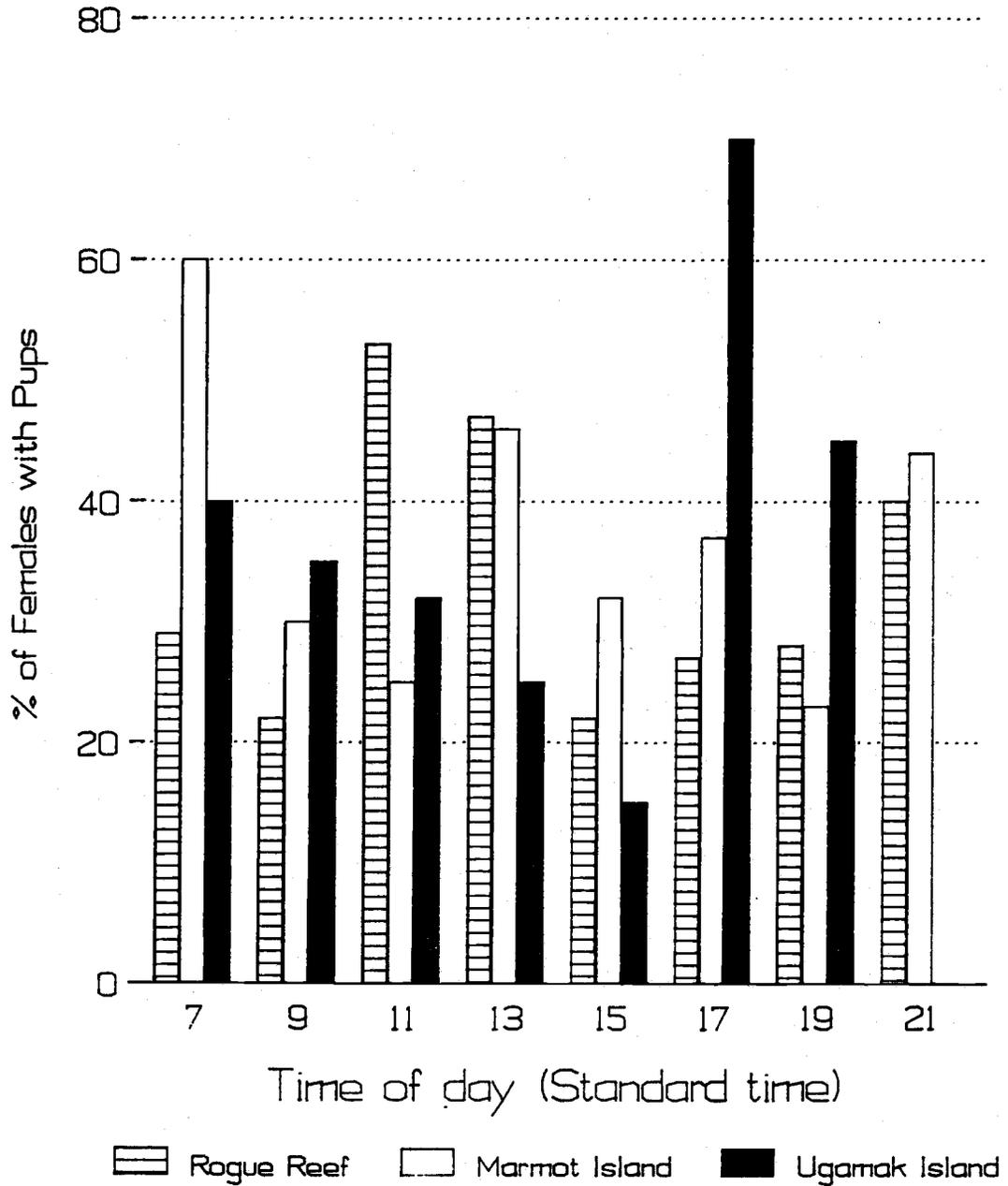


Figure 9. Frequency of other maternal care by northern sea lion females with pups by time-of-day for all study sites.

Only UI showed a significant trend through the day ( $R^2=0.64$ ,  $b=2.05$ ,  $p<0.05$ ).

A seasonal increase in the time females spent nursing was not observed ( $F=1.12$ ,  $p>.05$ ).

### Copulations and Female Courtship Displays

I first observed copulations at the three sites between the end of May and the beginning of June and continued to see them through the first to second week of July (Table 7). Copulations probably began earlier at MI and UI than the dates shown in Table 7, because these were the first observation days there. Thus the period of copulations was about six weeks long at all three sites, somewhat shorter than the period of parturition. The median copulation date was near the third week of June at all three sites.

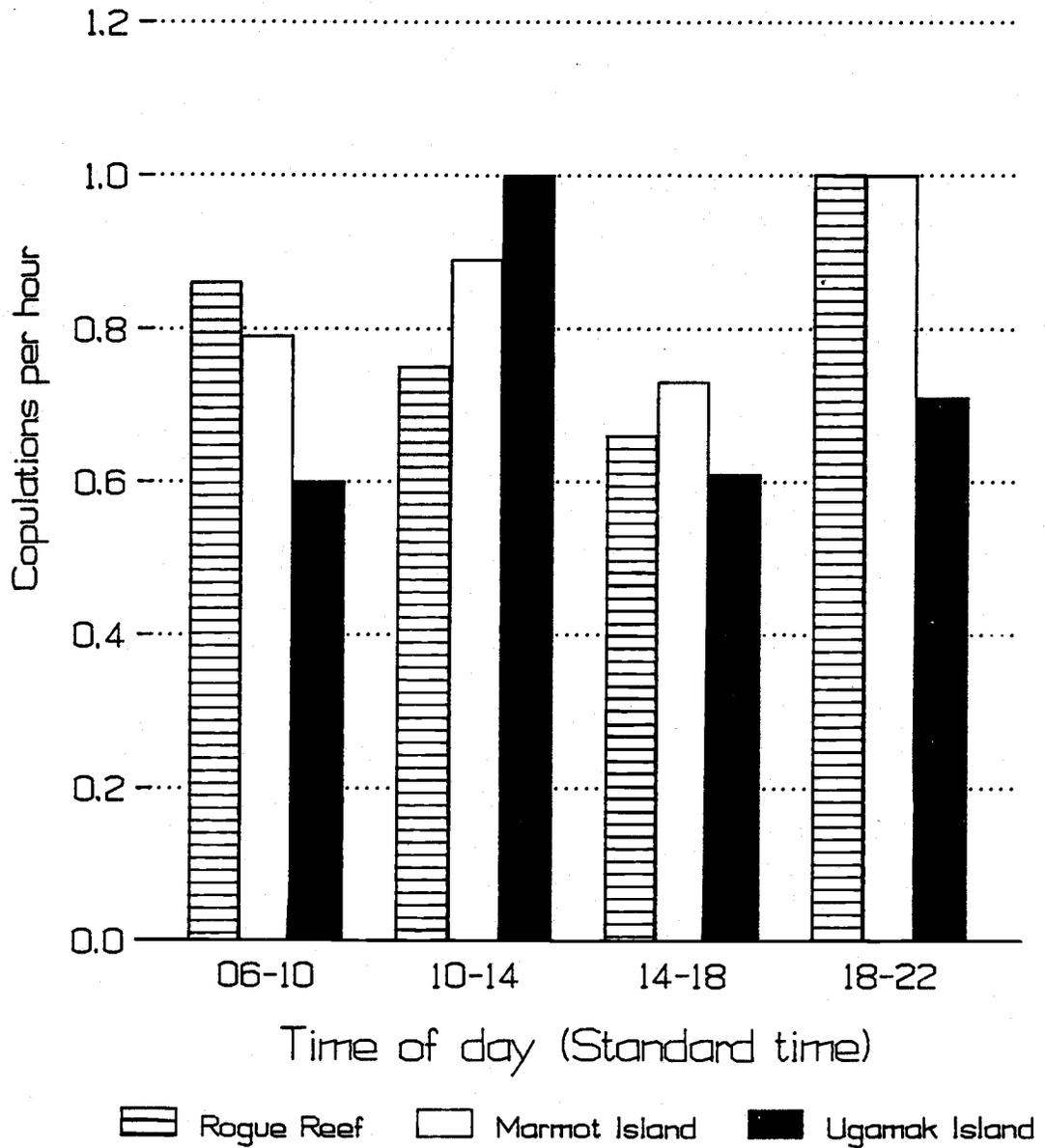
Copulations varied by time-of-day (Figure 10); however, no pattern was apparent.

Fifty-seven female courtship displays were observed at RR and only one preceded a copulation. Twenty-eight (49.1%) resulted from a male's precopulatory investigations, 19 (33.3%) occurred after a copulation, and the remaining 10 (17.6%) occurred in vacuo. Displays occurred in five of the 574 focal female samples, and accounted for less than 0.1% of the activity budget's time. This female behavior was uncommon at all three sites.

At least at RR and MI, most copulations were initiated by the male or begun spontaneously (Table 7). Few were preceded by female actions interpretable as soliciting a copulation. The low numbers of

Table 7. Northern sea lion copulation data by site

Item	Rogue Reef		Marmot Island		Ugamak Island	
	Focal Event	General Log	Focal Event	General Log	Focal Event	General Log
# Obs.	55	322	33	304	51	117
Copulations						
init. by:						
Male	74.5%	52.5%	57.6%	18.4%	13.7%	5.3%
Female	1.9%	.6%	0.0%	0.0%	0.0%	0.0%
Unk.	23.6%	46.9%	42.4%	81.6%	86.2%	94.7%
Female behavior						
after:						
Display	38.0%	27.7%	6.0%	na	80.4%	57.6%
Quiet	45.6%	42.2%	75.8%	na	5.9%	11.5%
Unk.	16.4%	30.1%	18.2%	na	13.7%	30.9%
Duration (min):						
Mean		17.3		29.3		16.4
Range		6.8-31.1		7.6-107.0		9.0-25.0
n		46		32		51
Mounts per copulation:						
Mean		1.4		4.7		1.2
Range		1-5		1-23		1-6
Seasonality						
First		31 May		<4 June		<6 June
Median date		22 June		15 June		20 June
Last		13 July		>7 July		8 July



Copulations per hour normalized to maximum daily rate

Figure 10. Frequency of copulations by northern sea lion males by time-of-day for all study sites.

male initiated copulations recorded in the general logs were due to the difficulty in observing the beginning of the event.

I timed 129 copulations from the initial mount through the final dismount. The average duration of these copulations was 19.8 min, with an average of 2.1 mounts per copulation (Table 7). The duration of copulations at MI (29.3 min) was significantly longer than at RR (mean=17.3 min,  $t=4.04$ ,  $df=76$ ,  $p<0.01$ ) and at UI (mean=16.4 min,  $t=4.79$ ,  $df=85$ ,  $p<0.01$ ). The mean number of mounts was greater at MI than at RR and UI.

#### Movements and Attendance

All females probably move in the rookery during the day, however, only 12.4% - 13.6% of the focal females were observed moving from their rest sites (Table 2). Movement consumed 1.0% of the activity budget. Most (68.6%) of the movements were within the rookery. The number of females moving to or from the water was underreported, however, because many females returned from the sea in the early morning hours before observations were made and because females moving out of the water were not in territories and would not have been sampled.

There was not a significant difference in frequency of movements by female type (Table 2).

The proportion of females with young moving and the amount of time spent in movement was greater at the two Alaska sites than Oregon (Table 4). The proportion of females moving at MI was significantly greater ( $p<0.05$ ) than at RR. The proportions were also greater at MI than at UI and at UI than at RR.

Significant time-of-day differences were only observed at UI ( $p < 0.001$ ). Data collected at UI in 1985 indicated that females began arriving in the early morning and continued to arrive in decreasing numbers until midday (Figure 11). There was then a period with no net movement, followed in the late afternoon by a period of increasing departures. This pattern of daily occupancy was similar to that obtained from the hourly counts of animals made at the three sites (Figure 12). The number of animals increased from early morning lows to a maximum in the midday and was followed by a decline beginning in the late afternoon. Populations were within 10% of the daily maximum between 1000 and 1800 hr at RR and UI, but not at MI.

Attendance data collected at UI provides more information on female movements to and from the sea. The 53 females made 195 trips of a day or more in duration (Table 8). There were also at least 97 trips of less than a day. The latter were identified by the female's observed departure from the rookery in the evening or her arrival in the morning, and her presence the following or previous day, respectively. These short trips were typically some of the first trips the female made after parturition (Figure 13;  $R^2 = 0.86$ ,  $b = -4.36$ ,  $F = 64.0$ ,  $p < 0.01$ ). Four of the 53 females made only short trip during the study period, while 11 females made only long trips.

Female attendance varied with maternal status (Table 8). The perinatal period (the time to the first trip) of 17 females was 9.8 days. Excluding the perinatal period, these females spent 66% of their time onshore. Their average time in attendance was 2.3 days (228 visits) and time absent was 1.2 days (238 trips). Trips made by 10 females, whose dates of parturition were known, followed a pattern

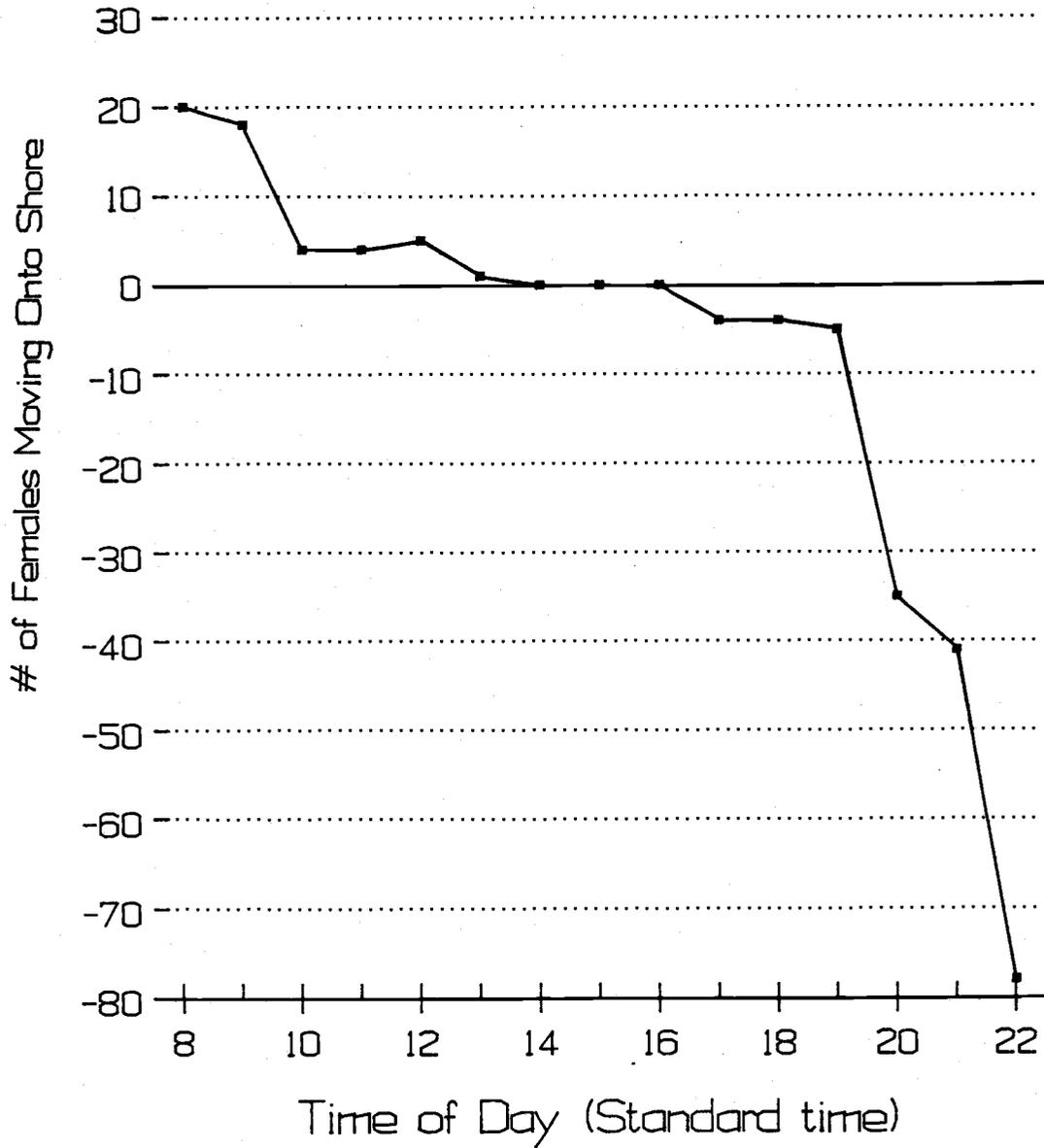


Figure 11. Net movement on and off shore of northern sea lion females by time-of-day at Ugamak Island.

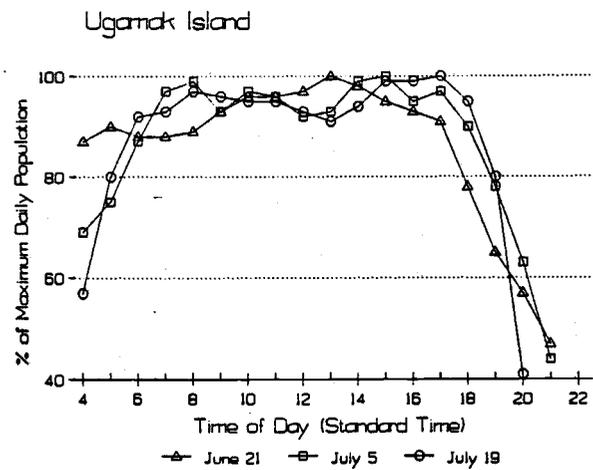
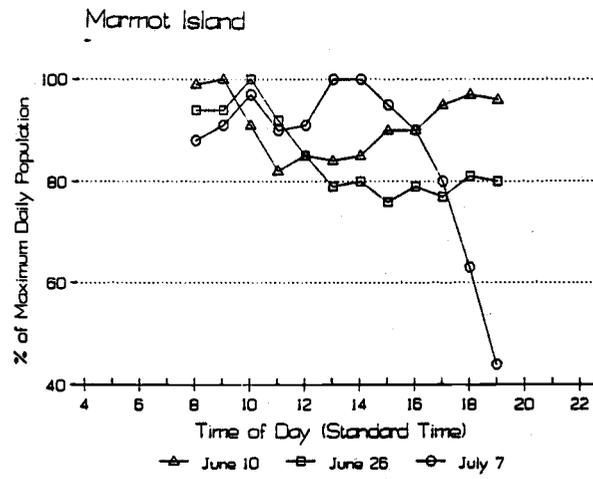
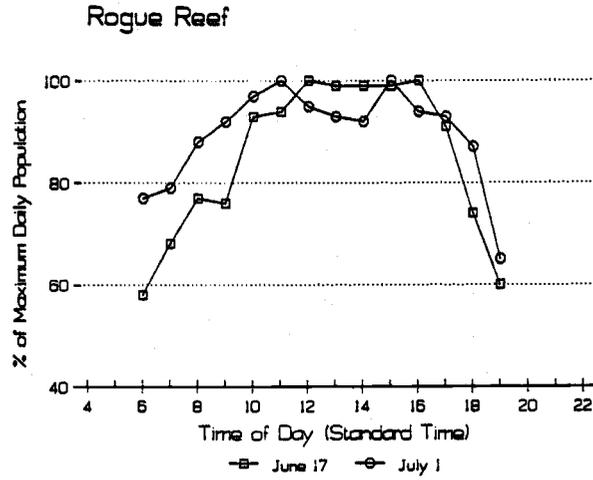


Figure 12: Northern sea lion hourly occupancy patterns by study site.

Table 8. Duration (days) of trips and shore visits of female northern sea lions at A2 rookery of Ugamak Island during 1985 and 1986 breeding seasons.

Female with	First Visit <sup>1</sup>			Trip Duration			Visit Duration <sup>2</sup>		
	n	x	Range	n	x	Range	n	x	Range
Pup	19	9.8	2-15	238	1.2	.5-5	228	2.3	.5-10
Juven.	3	4.7	3-6	22	1.4	.5-4	21	1.4	.5-3
Both	2	2.5	2-3	17	0.9	.5-3	15	1.4	.5-5
Alone	7	2.6	1-5	15	2.8	.5-13	15	1.3	1-2

<sup>1</sup> First visit is in days postpartum for females with pups, and days after first observation for all others

<sup>2</sup> Excludes perinatal period

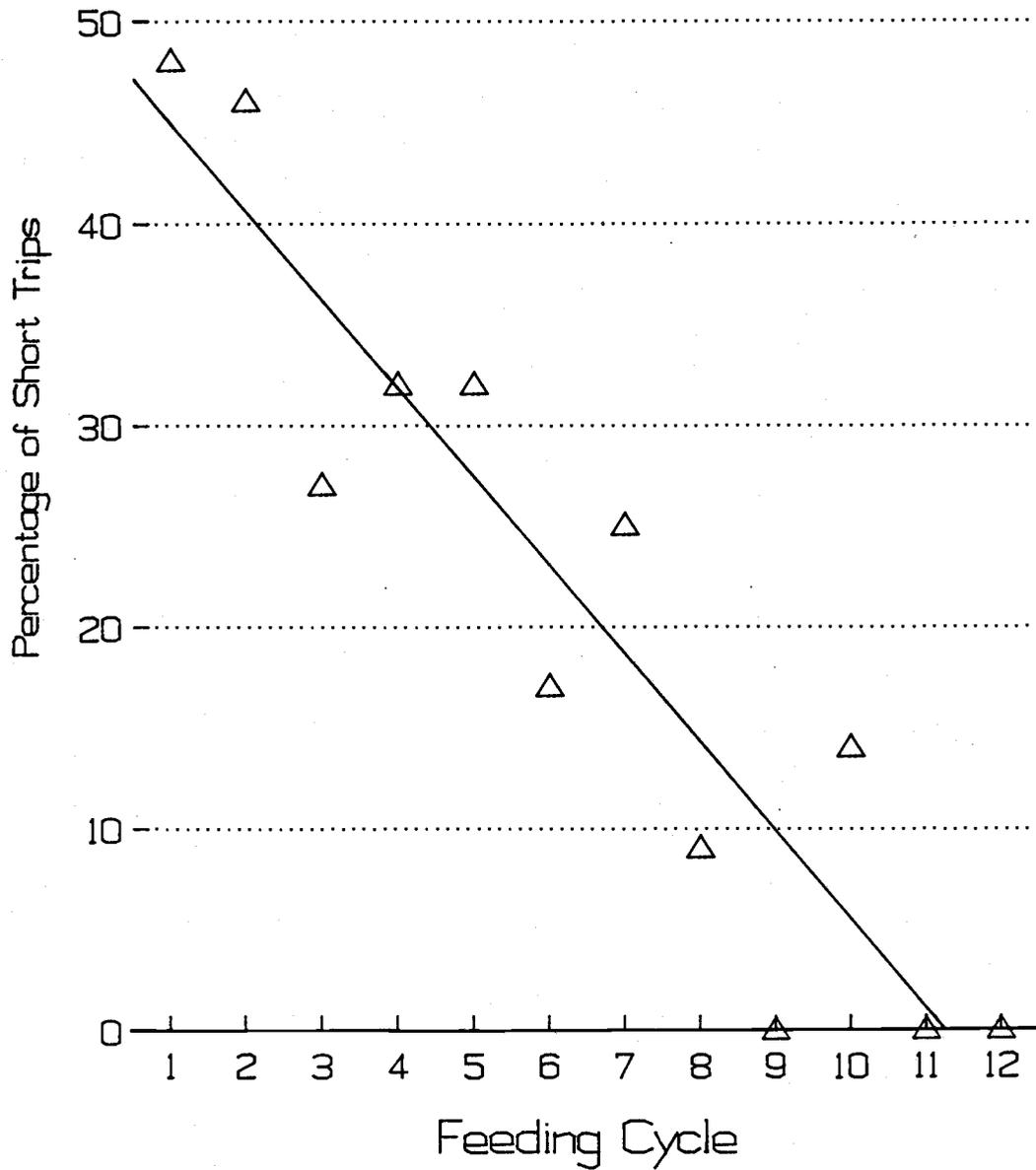


Figure 13. Percentage of short trips (<1 day) by feeding cycle made by female northern sea lion at Ugamak Island.

of decreasing attendance times through the third week postpartum (Figure 14). The proportion of time onshore stabilized between the third and fifth weeks. The trips of these ten females and six others, whose perinatal periods were only partially observed, were analyzed by feeding cycle (the combination of sequential absence and attendance periods). The proportion of time spent at sea by these sixteen females increased until by cycle 9 and 10, trips and visits were in parity at about a day each (Figure 15). The time at sea remained relatively constant through the period, while the time on land decreased.

Females attending a juvenile or both a pup and a juvenile went to sea sooner and spent less time in attendance (Table 8). Seven unaccompanied females were absent longer (2.8 days) and spent the least proportion of time on land.

#### Agonistic interactions

Agonistic interactions consumed little of the female's time (2.9%) but was a common activity with 55.6% of the focal females interacting aggressively with other animals (Table 2). Of the 323 samples including these interactions, 99.1% involved vocalizations, which were typically open mouth threats. Few interactions progressed beyond this; only 7.4% involved physical contact and 6.8% included biting. Behaviors such as locking mouths, head nodding, and belly slapping were rare.

Females with young spent more time in aggressive behavior than lone females (Table 2), however, the differences were not statistically significant ( $p > 0.05$ ).

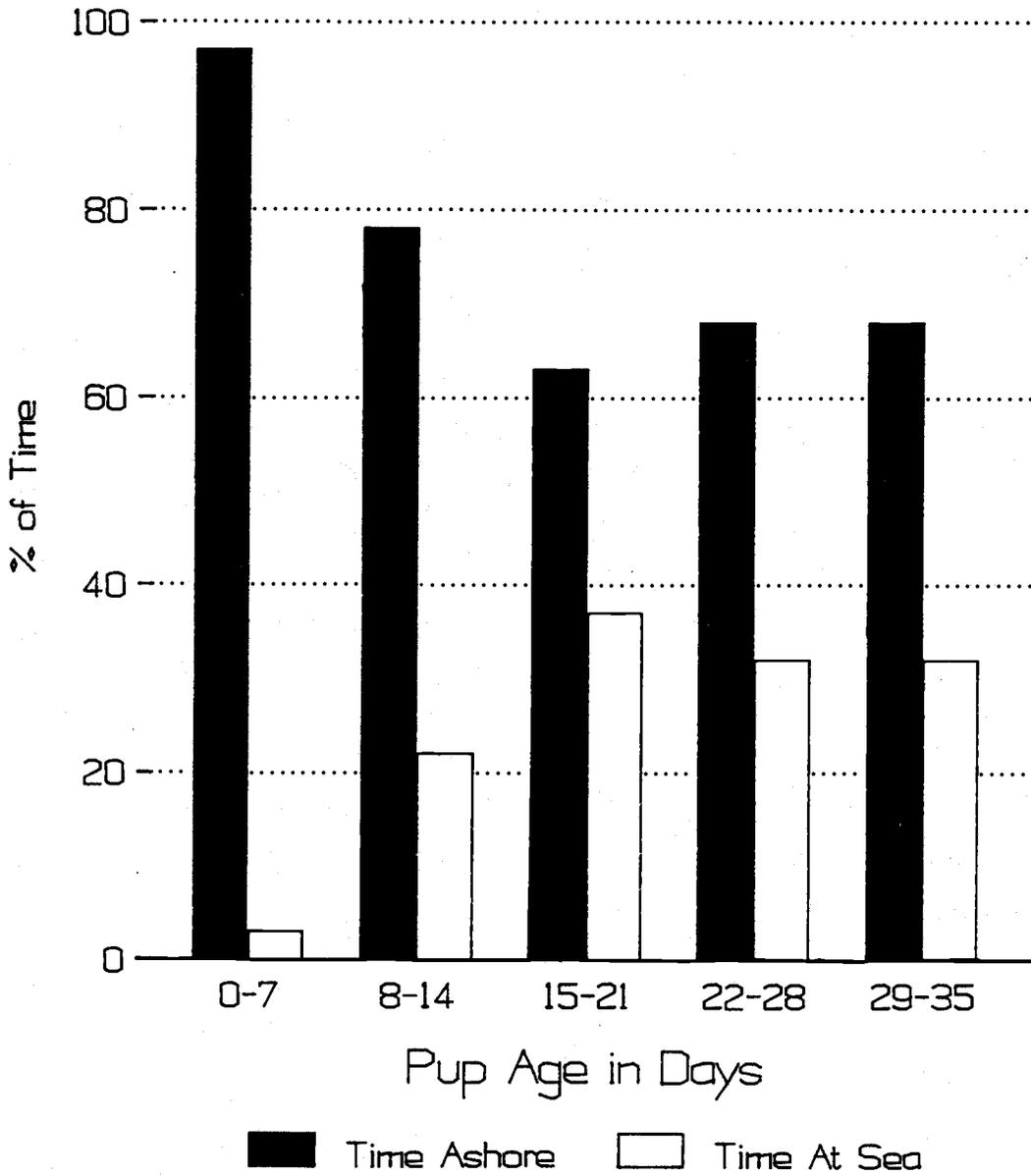


Figure 14. Percentage of time northern sea lion females with pups spent on and off shore at Ugamak Island.

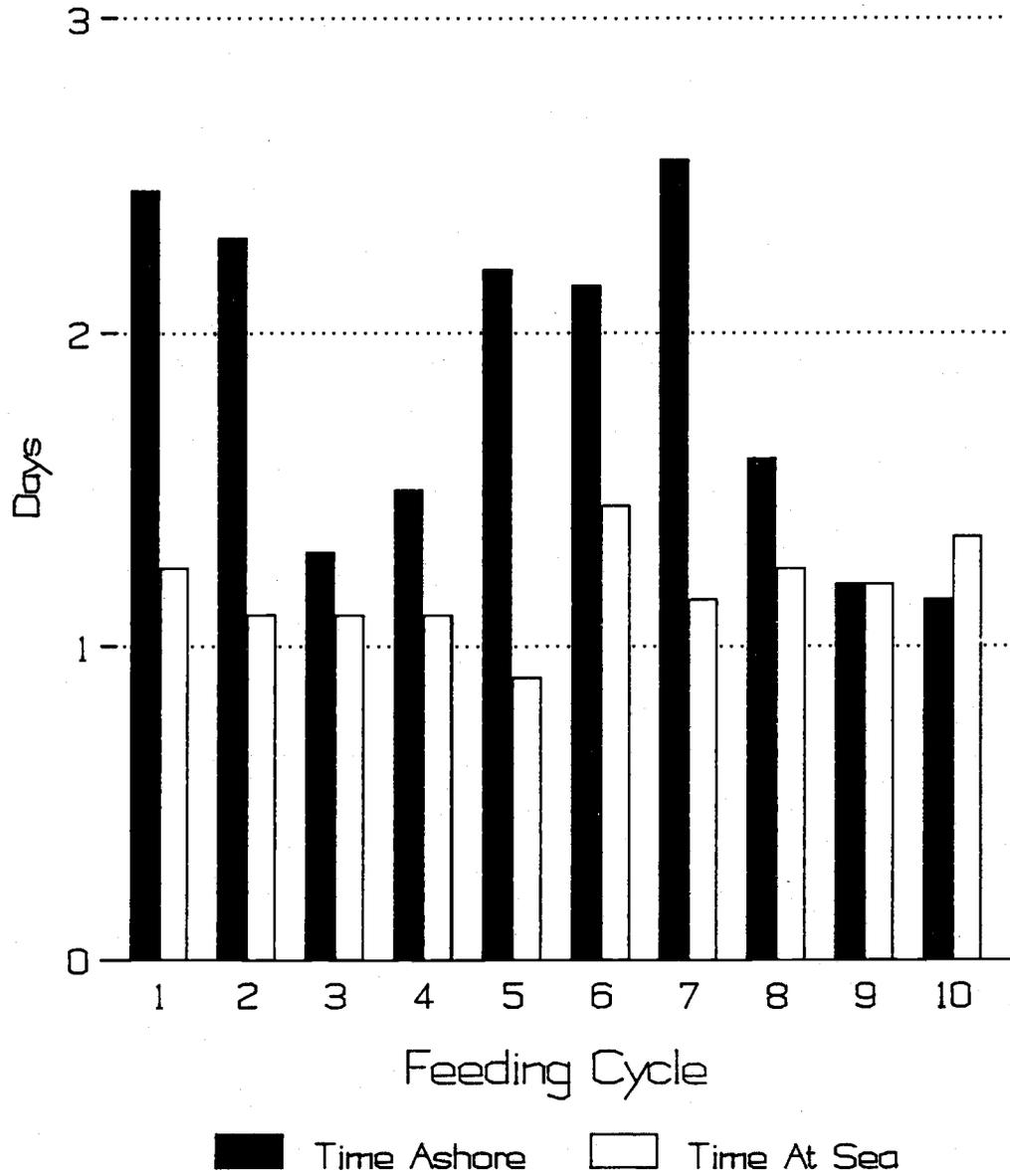


Figure 15. Duration (days) of time northern sea lion females with pups spent on and off shore by feeding cycle at Ugamak Island.

There were differences between sites in the duration and frequency of agonistic interactions (Table 3 and 4). Females at the two Alaska sites spent more time in agonistic behaviors because of more prolonged vocalizations. Significantly more females had interactions at MI than at the other two sites ( $p < 0.01$ ).

Fine scale geographic differences existed. At RR, females on the R2 rookery were more aggressive than those on R1 (64% vs 51%). The frequency of interactions at the five MI subareas was significantly different between them for all females as a group ( $p < 0.01$ ), as well as for females with pups ( $p < 0.01$ ). Females with pups in the open beach area (SA2-4) were less aggressive than those in the enclosed areas at either end of the beach.

The proportion of females showing aggression was significantly different ( $p < 0.01$ ) by time-of-day; however, the duration of aggressive behavior did not change significantly. The frequency of aggression was at an ebb in the early morning and then increased (Table 5; Figure 16).

The frequency of interactions decreased slightly during the the breeding season but not significantly so ( $p > 0.05$ ). At RR, the only site where observations were made prior to the onset of breeding, 69.0% percent of the females were involved in agonistic interactions in May, but only 52.6% in June-July. This was a significant difference ( $p < 0.05$ ). Females also spent more time interacting in May (2.7%) than in June-July (1.5%). This change was most pronounced in single females, some of whom were probably parturient in May. Their time in these interactions fell from 2.6% to 0.9% of their time.

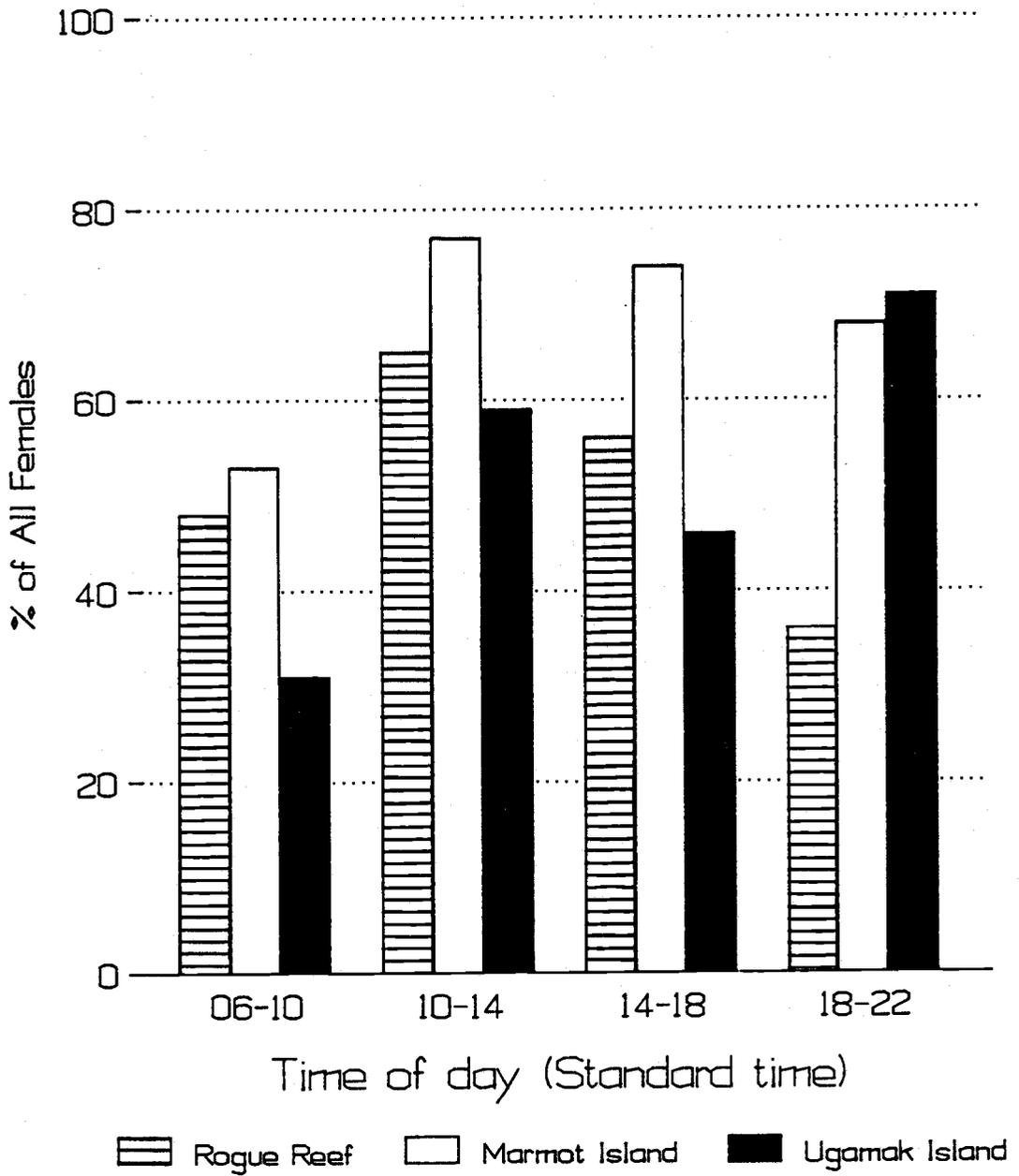


Figure 16. Frequency agonistic behaviors are exhibited by northern sea lion females by time-of-day for all study sites.

Agonistic interactions were stimulated most frequently (Table 9) by another animal moving nearby (33.1% of interactions), another animal touching her (26.3%), or by another animal vocalizing (24.4%). Another 2.2% involved a female protecting her pup. Clearing a pupping or rest area was a relatively uncommon cause (5.4% of interactions) but may occur at least once for all parturient females as they come ashore to pup. Finally, about 8.3% of the interactions involved a female responding to an investigating male.

Interactions were usually with another adult female (65.7%; Table 9); this was predictable because adult females made up 70% to 80% of the population at the three sites. A disproportionate share of the interactions (18.0%) were directed towards territorial males (4% to 5% of the population). The incidence of interactions with juveniles (15.6%) was appropriate to their numbers (4% to 24% of the population).

#### General Activity

This category provided a measure of the proportion of females who were active. Significant differences did not exist between female types overall (Table 2). However, the percentage of females active at MI (86.6%) was significantly greater ( $p < 0.01$ ) than at RR (69.3%). Females were also more active at UI (78.9%) than at RR but the differences were not significant ( $p > .05$ ) nor were significant differences found between MI and UI. Analysis by maternal class indicated MI females with pups (88.5% active) and with juveniles (95.3% active) were significantly more active ( $p < .01$ ) than lone females (71.4% active). Significant differences were not found

Table 9. Percent of focal female agonistic interactions by stimulus and class of interactant by site, excluding pup interactions and unknowns

<u>Stimulus</u>	Rogue Reef (%)	Marmot Island (%)	Ugamak Island (%)	All (%)
Another animal moves	27.4	33.1	38.7	33.1
Another animal moves and touches	40.4	32.1	6.7	26.3
Another animal vocalizes	14.8	17.7	40.8	24.4
Males investigates female	4.9	9.1	10.5	8.3
Clear pupping or rest area	8.9	7.6	0.4	5.4
<u>Another animal touches pup</u>	3.6	0.4	2.9	2.2
<u>Class of interactant</u>				
Adult territorial male	15.3	16.6	22.3	18.0
Other adult male	0.4	0.0	1.7	.7
Adult female	64.1	59.7	75.2	65.7
<u>Juvenile</u>	20.2	23.7	0.8	15.6

between MI females with pups and with juveniles or between female types at other sites.

Activity patterns were different at each site. Activity at RR was low in the early morning, increased in the midday, decreased again in the afternoon, and then increased again in the evening (Table 5). Females at MI remained active throughout the day. Finally, at UI activity was at an ebb in the early morning and then increased throughout the rest of the day. Differences were significant at RR ( $p < 0.05$ ) and UI ( $p < 0.01$ ) but not at MI ( $p > 0.05$ ). At UI activity increased throughout the day and the trend had a positive slope significantly different from zero ( $R^2 = 0.59$ ,  $b = 2.69$ ,  $p < 0.05$ ).

### Discussion

Northern sea lion behavior appears to be constrained by the timing of major life history events. Median parturition and copulation dates and the duration of the breeding season were consistent between most sites. Daily patterns of abundance were similar at the sites. Even the same behaviors were displayed at each site, and, maternal care aside, by all female classes. They retain, however, plasticity in their behavioral repertoire as evidenced by the significant differences observed in the frequency and duration of the expression of behaviors. As such it appears that individual northern sea lion females all utilize the same behavioral suite but modify its expression to suit their maternal status and local environmental conditions.

### Differences in behavior by maternal status

The most pronounced differences existed between the two basic groups of females - those with and without young. Females without young devoted more time to rest and comfort behavior, time which those with young spent in maternal care. Females with young were more aggressive, as also observed at Año Nuevo Island (Gentry 1970) and Wooded Island (Sandegren 1970). Trip making was different; females with young spent more time onshore than those without. Behavior also varied between females with young. While nursing did not vary between females with pups or with juveniles, only females with pups gave other maternal care to their young. Females with a juvenile were more frequently aggressive, but spent less time in aggression than those with a pup. Finally, females with a pup spent more time on land than those with a juvenile; however, their trip lengths were similar. As such, females with juveniles spent a greater relative amount of time at sea. All of this seems to be a function of the maternal strategies of females.

A pinniped mother has a limited number of ways to promote her young's survival - feeding and protection. In feeding, she balances time used to acquire energy (foraging) with time spent transferring energy to her young (nursing). In protecting her pup she concerns herself with the choice of a pupping site, protection of the pup from others and the sea, and assisting the pup in learning to swim and forage. All of this must be balanced, albeit unconsciously, with a potential decrease in her survival.

The compromises necessary in feeding young manifest themselves in specie's nursing and attendance behaviors. Species which spend

long periods on land postpartum (e.g., those with long perinatal periods or with relatively short trips) nurse less often than those which spend shorter periods ashore. Oftedal et al. (in press) present data on five phocid and five otariid species which indicates that the otariids spend longer times in nursing than phocids. All five of the phocid species continually attend their pups up to weaning, while the otariids have intermittent attendance patterns. Otariid pups compensate for their mother's limited presence by suckling longer and more frequently than phocid pups (Oftedal et al. in press).

Substantial differences exist within this otariids as well (Table 10). Gentry et al. (1986) have proposed a model of maternal strategies which may explain the variability between otariid species. They proposed that fur seals have two different maternal strategies. Species breeding in high latitudes (e.g., the northern fur seal, Callorhinus ursinus, and the Antarctic fur seal, Arctocephalus gazella) wean their young much earlier than those breeding at low latitudes (e.g., the South American fur seal, A. australis, and the Galapagos fur seal, A. galapogensis). These differences could be due to the seal's environment. High latitude climates vary greatly seasonally but are quite similar interannually, while low latitudes have limited seasonal variability and great interannual variability. Gentry et al. (1986) contend that "environmental uncertainty is more important than seasonal change" in shaping a suite of characteristics which include weaning periods, attendance, and foraging.

Behaviorally, northern sea lions are similar to the low latitude fur seals. Northern sea lions have a long weaning period (1

year or more; Calkins and Pitcher 1982), a long pupping period (7 weeks or more; this study), short feeding cycles (4 days or less; Gentry 1970; Sandegren 1970; Higgins 1984; this study), and low milk fat content (21%; Poulter et al. 1965). However, their breeding range is identical to the northern fur seal, a characteristic high latitude fur seal which according to Gentry et al. (1986) has a short weaning period (4 months), a short pupping period (3-4 weeks), long feeding cycles (more than a week), and high milk fat (47%).

The three northern hemisphere sea lions (i.e., the northern sea lion, the California sea lion, Zalophus californianus californianus, and the Galapagos sea lion, Z. californianus wollebaeki) are all similar in maternal strategies. The similarity of maternal strategies between sea lions and low latitude fur seals may represent a conservation of ancestral behaviors. Otariids are considered to have arisen in the North Pacific Ocean from ursid arctoid ancestors more than 22 million years ago (Mitchell and Teford 1973). Ursids today have long weaning periods (up to two years in polar bears, Ursus maritimus; Walker et al. 1968). As such, long weaning periods, like terrestrial parturition, may represent a "phylogenetic legacy" (Stirling 1975). If this was the ancestral form then the evolution of the high latitude fur seal maternal behaviors may have occurred after sea lions diverged from fur seals some 3 million years ago (Repenning et al. 1979). This occurred after fur seals had moved into the southern hemisphere (Repenning et al. 1979), so that the similarity between the northern and Antarctic fur seals could be due to convergent evolution.

The ultimate force shaping the high latitude fur seal's maternal strategies has probably been winter environmental conditions. A combination of ice coverage, increased sea state and decreased sea temperatures makes the seas around the Pribilof Islands and Antarctic hauling sites uninhabitable in winter for all but the larger male fur seals. Faced with these conditions and assuming the animals were too small to endure the winter, natural selection would reinforce those behaviors enhancing survival - rapid weaning of pups and migration to more favorable climates. The larger size of sea lions would allow them to cope better with winter conditions (i.e., relatively less heat loss and more swimming power), and not require migration or rapid weaning. That these two different maternal strategies coexist in the Bering Sea represents independent responses to the same environmental problem.

The significance of these different strategies is apparent in the life history parameters (i.e., fecundity and juvenile survival) of northern sea lions compared to northern fur seals. Northern sea lions have relatively low fecundity (0.26; York pers. comm.) compared to high latitude fur seals (0.34 to 0.36; York in press). Sea lions compensate for low fecundity with high juvenile survival, near 0.78 per year through year 2 (Calkins and Pitcher 1982), compared to 0.14-0.45 per year for high latitude fur seals (York in press). Thus sea lions produce fewer pups, but more survive, perhaps due to the prolonged lactation period and lack of a migration.

Maternal status also appears responsible for variation in agonistic behaviors. These interactions are relatively uncommon in pinniped species (Table 10). However, individual aggressiveness

Table 10. Percent of total activity budgets devoted to behaviors by adult females of various pinniped species.

Behavior	Phocids			Otariids		
	Southern eleph. seal <sup>1</sup>	Gray seal <sup>2</sup>	New Zealand fur seal <sup>3</sup>	S. American fur seal <sup>4</sup>	Galapagos fur seal <sup>5</sup>	Northern sea lion <sup>6</sup>
Rest	82	86-90	68	91	70-96	74
Comfort	na <sup>7</sup>	1	na	na	na	4
Nurse	12	2-4	9	(60) <sup>8</sup>	(30+) <sup>8</sup>	18
Other care	na	1	na	na	2	1
Movement	na	1-5	na	1	2	1
Agonistic	1	1	1	1	1 <sup>9</sup>	4
Sexual	1	1	1	na	1 <sup>9</sup>	1
Other	5	2	22	8	na	-

<sup>1</sup> McCann 1983

<sup>2</sup> Anderson and Harwood 1985

<sup>3</sup> Crawley et al. 1977

<sup>4</sup> Trillmich et al. 1986

<sup>5</sup> Trillmich 1986

<sup>6</sup> This study

<sup>7</sup> Percentages not separated out and are included (if recorded) in the Other category

<sup>8</sup> Also included in rest

<sup>9</sup> Value is for sum of aggression and sexual

increases as parturition approaches and continues for a period of time postpartum. This has been observed in California sea lions (Odell 1972), southern elephant seals (Mirounga leonina; McCann 1982), northern elephant seals (M. angustirostris; Christenson and Le Boeuf 1978), gray seals (Halichoerus grypus; Boness et al. 1982), and northern sea lions (Gentry 1970; Sandegren 1970). Such aggressiveness has been regarded as protection of young, and empirical evidence for this has been provided by Christenson and Le Boeuf (1978) and Boness et al. (1982). My studies also support this hypothesis (Table 2).

Previous studies of maternal aggression have considered only females with pups; thus it is noteworthy that northern sea lion females with juveniles are more aggressive than those with pups. If pup mothers are aggressive because they are protecting their young, then presumably those with juveniles may also be protecting their offspring. Alternatively, since much of this conflict is with the juvenile, this agonistic behavior could be due to the mother attempting to wean her young.

It is also striking that females with pups spend far more time in other maternal care than those females with juveniles. During the first days postpartum the mother and pup learn to recognize each other so that they can be reunited after feeding trips (Sandegren 1970). The pup learns the mother is a source of protection as well as of food, and that the mother can be safely followed to sea. Bonds are constantly reinforced via nurturing behaviors (e.g., nuzzling and nosing). Once the bonds are in place there is apparently no need for further reinforcement.

## Differences in behavior between sites and between times-of-day

Similarity was seen between behaviors at the sites, particularly those behaviors which may be physiologically constrained. The season of parturition was around seven weeks at RR, MI, UI, Año Nuevo Island (ANI), and Cape St. James (Table 6). Mean duration of individual births was consistent at RR (16.8 min), UI (20.5 min), and ANI (16-20 min; Gentry 1970). A midday decline in births was also observed at ANI (Gentry 1970) and WI (Sandegren 1970). A seasonal change in the time females spent nursing was not observed at my sites, ANI or WI (Sandegren 1970; Higgins 1984). The duration of copulations was similar at RR (17.3 min), UI (16.4 min), ANI (15.8 min; Gentry 1970), and WI (16.6 min; Sandegren 1970), but longer at MI (29.3 min). Far more copulations were begun by males than females at my sites as well as at ANI (Gentry 1970; Gisiner 1985). Females with young were the most aggressive (Gentry 1970; Sandegren 1970; Calloway 1972). Most females returned from the sea in the morning and went to sea in the evening (Gentry 1970; Withrow 1982). Trips were usually less than two days in length and females spent at least as much time on land as at sea (Gentry 1970; Sandegren 1970).

Significant behavioral differences were, however, observed between rookeries. Females at RR were the least active, devoted the least care to their young, and were the least aggressive. The MI females, on the other hand, were the most active and aggressive. Females at UI were generally intermediate to the other two sites.

Some differences also existed between these sites and other sites, especially Wooded Island, Alaska (WI). At WI, the period of

parturition was only five weeks long compared to seven at other sites, and individual births took longer (30 min; Sandegren 1970). The period of copulations was shorter as well at WI, five weeks as compared to six or more at other sites (Table 7). The median copulation date was 8 June at WI, compared to 15 June to 22 June at other sites. The female "courtship display" was also more common at WI than at my three study sites and at ANI (Gentry 1970; Gisiner 1985). Differences also existed at ANI. Perinatal periods and trips to sea were longer at ANI in 1983 (Higgins 1984) than at UI in 1985-86, and at ANI in 1967-69 (Gentry 1970). The median copulation date at ANI changed from the third week in June in 1968 to the first week of July in 1977-79, later than I observed at my three study sites.

Daily variation in behaviors was observed. All behaviors except nursing varied significantly by time-of-day at UI. Females at UI were less active in the early morning, and then increased their activity through the day. At MI there was little relationship between time-of-day and behaviors; only other care and aggression varied significantly. Activity levels were relatively high and stable throughout the day. Finally, RR was similar to UI but virtually the opposite of MI. It appears that there may be two patterns - one like UI and RR with low activity in the early morning and high activity in the late afternoon with variability in between, and one like MI, with a peak in the early morning but generally little daily variability.

Site and time-of-day differences may be explained by a combination of local air or substrate temperatures, tidal effects, and the rookery's substrate. Average June noon air temperatures at

RR, MI, and UI (1985) were 17°C, 12°C, and 9°C, respectively. Tidal range on 15 June at RR, MI, and UI was 2 m, 4 m, and 1 m, respectively.

One method of thermoregulation is simply to reduce activity (Whittow 1987). Thus reduced activity at RR, as compared to MI and UI, may partly be a response to higher temperatures. In addition, most animals at RR occupy the R1 rookery, which is a relatively flat ledge elevated well above tidal and surf action. Consequently, animals are not forced to move as the tide rises or when a large surf is running, and activity would be less than sites where animals are influenced by the sea. There is also sufficient topographic relief for animals to select a rest site relatively isolated from other animals. Since animals are not forced to move frequently by rising tides, it is possible for neighbors to habituate. This habituation to the nearest neighbor has been used to explain the decline in male aggression during the breeding season (Gentry 1970). As a whole, RR could be characterized as a highly stable habitat.

Marmot Island represents the other side of the coin - temperatures cool, beaches subject to regular tidal flooding, and substrate relatively featureless. Available hauling space changes throughout the day, and, as a result, MI is a highly variable habitat. Changes in hauling area promote activity throughout the day, and no general time-of-day pattern would emerge. Hauling patterns shown in Figure 12 are an indication of this. Neighboring animals can never habituate on the open beach areas because of their constant movements. Rising tides also increase animals density. As most of aggression results from animals moving nearby (Table 8),

increased activity and density promote an increase in agonistic encounters. More frequent and immediate maternal care may be required, because the mother-pup pair is more frequently separated due to their movements. This may explain why MI maternal care peaks in the early morning period (the period when most animals first come ashore). Environmental uncertainty leaves the mother with no choice but to begin important activities such as nursing immediately upon arrival. To do otherwise may result in her separation from her pup before she has had time to nurse it. Frequency of nursing at MI is lower than at the other two sites; however, the time spent nursing is the same. This indicates nursing bouts are longer at MI, and could be interpreted that mothers have fewer opportunities to nurse (perhaps due to tidal effects), and compensate by nursing longer when they have the chance.

Ugamak Island is less affected by temperatures than RR and less affected by tidal range than MI. In addition, its substrate, which includes numerous large rocks, provides refuges for animals both from the tide and each other. Females with pups at UI are typically located at the back of the beach, out of the range of most surf and tidal action. The tide may force them to move occasionally (though less often than MI females), producing more activity and increasing densities. This would probably promote agonistic behaviors but not to the degree as observed at MI. Being the coolest site there would be less of a tendency than at RR to reduce activity because of temperature. Still, UI is a relatively stable habitat, and as a result it is possible for daily patterns to exist which are driven by females returns to and from the sea. Thus a female returning from a

feeding trip has the opportunity to rest after her arrival, and then once she has rested she can begin her normal pattern of terrestrial activities. As a consequence, activity levels build throughout the day.

Factors other than the abiotic (i.e., temperature, tides, substrate, and topography) may also shape the animal's behaviors. The midday declines in activity may be the results of endogenous rhythms (Gentry 1970). Availability of prey may explain the variation in trip making between Año Nuevo Island in 1983 and UI in 1985-86. Longer perinatal period and shorter trip lengths were observed at UI in 1985-86 and ANI in 1967-69 (Gentry 1970) than at ANI in 1983 (Higgins 1984). Similar changes were observed in the attendance behavior of California sea lions at San Nicolas Island in 1983 (Heath and Francis 1984; Oftedal et al. in press). If El Niño conditions reduced prey availability near ANI and San Nicolas Island, females would return to return to sea sooner postpartum (assuming they first came to shore with low energy reserves) and subsequently feed more frequently and/or longer. The extremely short trip length for UI females may result from the reduced sea lion population in the eastern Aleutian Islands (Merrick et al. 1987), which would make feeding less competitive.

The structure of the breeding population may also have an effect. Populations dominated numerically by females attended by juveniles or without young (as at WI), would probably behave different than those composed mostly of females with pups. This may explain the high numbers of female courtship displays observed at WI, a site with few females with pups (Sandegren 1970).

In summary, significant variation in female behaviors existed both within and between sites. Part of this was due to variation between females of different reproductive status, and part was due to environmental differences. Further studies of northern sea lion behavior must explicitly recognize that such variation can exist. Results would be most comparable between sites with similar demographic characteristics, as those of RR, MI, and UI. Sites with different population structures and different environmental regimes can be expected, *a priori*, to have different behaviors.

## CHAPTER III

## NORTHERN SEA LION ROOKERY DEMOGRAPHY

Introduction

Locations at which northern sea lions spend time on shore can be generally classified as two types - rookeries and haul-outs. Rookeries are sites where most males defend territories and where most parturition and mating takes place, while haul-outs are locations where few or no pups are born and little breeding occurs (Loughlin et al. 1984). While rookeries are composed mostly of adult females and pups with a minority of adult males and juveniles, haul-outs are composed of mostly adult males or juveniles of both sexes in the summer and may include a mix of all groups in the winter. Rookeries are a seasonal phenomena, occurring only during the two month summer breeding period. Some sites change seasonally, acting as rookeries during the summer breeding period, and as haul-outs during the remainder of the year. Others are uniquely one or the other. Over time, haul-outs may become rookeries (Perlov 1980) or rookeries may become haul-outs (Bigg 1985) based on the amount of rookery space required and the history of disturbance at the site.

Variation within types has been recognized for haul-outs. Bigg (1985) classified British Columbia haul-outs into year-around and winter-only sites. He also recognized winter rafting sites in areas with limited onshore winter hauling space. Bachelor bull haul-outs are frequently found near a rookery, as they are in other otariid species, such as the northern fur seal (Peterson 1965), South African fur seal (Arctocephalus pusillus; Rand 1967) and California sea lion.

Haul-outs including only juvenile (i.e. age 1 and 2) animals occur in the Kuril Islands (e.g. Iturup Island; Belkin 1966). The population dynamics and behavior of occupants of haul-outs have been studied by Harestad (1973) and De Blois (1986).

Based on my observations of rookeries in Oregon and Alaska and a review of the literature it appears that rookeries are quite similar in their population structure and patterns of abundance. However, some rookeries, basically those with little pupping, vary significantly from this norm. Since behavioral differences exist between females of different maternal status (Chapter II), different behavioral patterns could be expected at these rookeries. Thus it may be necessary to discriminate between rookery types in order to generalize behaviors observed at a site to the population as a whole.

My objective in this element of my study has been to determine the characteristics of rookeries. I present my findings by first describing my observations of rookery demography at three sites in different areas of the species' range. I will also include here observations by other researchers at these and other sites. I will then discuss specific characteristics of rookeries and the mechanisms which produce these characteristics. Finally, I will discuss seasonal patterns of movements and abundance and role these different sites play.

### Methods

#### Sites and Seasons

Counts of northern sea lion populations were made at Rogue Reef, Oregon, Marmot Island, Alaska, and Ugamak Island, Alaska

(Figures 1-6). A full description of these sites is presented in Chapter II.

Two general types of rookeries were recognized - primary and secondary rookeries. Primary rookeries were locations where most pupping occurred and where there were few juvenile animals. These included the R1 rookery at RR, B3 at MI, and most of the rookeries at UI. Secondary sites were those locations where few pups were born relative to the population size and where most of the juveniles could usually be found. This included R2 and R3 at RR, and perhaps B2 at MI and A1 at UI.

#### Data Collection

Sea lion populations were censused daily, usually at midday, during the study periods. Separate counts were made and recorded for each area within a study site (e.g., at RR for the three rookeries, the bachelor bull area, and the other haul-outs). Animals were tallied by five classes: adult territorial males, other adult males, adult females, juveniles of either sex, and pups. Adult males had to have females located within their territory to be considered as adult territorial males. Visual counts of pups were taken on all days. This was done in the early morning or the late evening (times of low adult abundance) to increase the chance of seeing pups.

Hourly counts were taken on at least three days at each site. Counts were made from dawn to dusk on each of these days.

Animals were counted by my field assistants and myself from the observation sites by unaided eye, with binoculars, or with a spotting scope. At beach 3 at MI it was necessary, due to the amount of time

necessary to count such a large population, that on every other day that the beach be photographed for later enumeration. The resulting slides were later projected onto white paper and the total number of animals counted. Visual counts (by animal type) were made on the remaining days, with pups counted visually every day.

These counts represent a minimum estimate of the number of animals using a rookery. Many females were at sea even at times of peak abundance, and as a result any calculation using female numbers was biased. The limited data available (Gentry 1970; Merrick and Osmek 1986) suggests that no more than two-thirds of females with pups and one-half of those without pups are onshore at times of peak abundance. I have assumed that these proportions are constant between sites (though they probably are not), and ratios involving adult females though in error are at least consistent. Calculations involving other adult males and juvenile suffer from a similar problem. Estimates of the number of adult territorial males are accurate since these animals are typically on the site for the full day.

Pups could not all be seen at MI and as result undercounts occurred there (Calkins and Pitcher 1982). At RR and UI, all of the rookeries could be seen. Comparisons of counts made from cliff observation posts and counts made in the rookery after adults had been driven off (spook counts) indicate that the UI cliff counts were as accurate as spook counts (Merrick et al. 1985). Errors in counting dead pups resulted from not seeing carcasses, pups being swept to sea and never having a chance of being seen, and double counting. All of RR and several beaches at UI were surveyed at the

end of the season to find missing dead pups, and these were added to previously counted living and dead pups to calculate the total number of pups born. This was not possible at MI. Finally, maps were kept of the locations of dead pups at UI and RR, so double counting was minimized. A nearshore current at MI moved carcasses back and forth on the beach on a daily basis, so some double counting occurred.

### Analysis

Ratios were calculated as follows:

1. Adult females per adult male - maximum seasonal count of adult females divided by maximum seasonal count of adult males
2. Adult females per adult territorial male - the seasonal average of weekly calculations of adult females divided by adult territorial males
3. Juveniles per adult female - maximum seasonal count of juveniles divided by maximum seasonal count of adult females
4. Pups per adult females - maximum seasonal count of pups (alive and dead) divided by maximum seasonal count of adult females
5. Pup mortality - maximum seasonal count of individual dead pups divided by maximum seasonal count of all pups (alive and dead)

Data were analyzed using  $X^2$  contingency table analysis (Fienberg 1980) or parametric statistics.

## Results

### Abundance

Adult Females - Adult females numerically dominated the three sites, making up 70 to 90% of the total population, excluding pups (Table 11). Similar proportions were observed at MI in 1979 (70% to 76%; Authmiller and Orth 1979) and at Año Nuevo Island in 1963 (68%; Orr and Poulter 1967). Belkin (1966) recorded a range of 66% to 80% at four "harem" rookeries in the Kuril Islands.

At primary rookeries (e.g., R1 at RR, B3 at MI and A1-A5 at UI), at least 60% of the adult females were accompanied by pups by seasons's end (Table 11). Females accompanied by juveniles and those alone made up a significant proportion which varied by rookery. However, it appeared that no more than 30% of the females, and usually less, were accompanied by juveniles at primary rookeries. The high juvenile rates at some of the MI subareas (e.g., SA1-SA3) was due partly to a large number of unaccompanied juveniles using the subareas for hauling out at high tide.

On secondary rookeries (e.g., R2 and R3 at RR, B2 at MI) the proportion of females with juveniles was still usually under 30%. Single females composed 60% or more of the population on the secondary rookeries.

Females segregated within a site or rookery by reproductive status. I observed that single females and those with juveniles favored resting spot close to the water, while females with pups were located farthest from the water's edge (Edie 1977; Lisitsyna 1981). Births in the protected inner terrestrial areas at RR's R1 rookery

Table 11. Northern sea lion population statistics during pupping period for rookeries at Rogue Reef and Ugamak Island, and for Marmot Island, beach 3 subareas. (ATM=Adult Territorial Male, AOM=Other Adult Male, AF=Adult Female, JV=Juvenile)

Site	Rookery or Subarea	Percentage of Adult & Juvenile Population				Rate Per 100 AF		Pup Mort	AF per ATM
		ATM	AOM	AF	JV	JV	Pup		
RR	R1	4.0	0.0	90.3	5.7	.08	.60	.09	18.5
	R2	3.6	0.0	86.8	9.6	.22	.04	.50	21.1
	R3	4.4	0.0	75.7	19.9	.32	.01	.67	17.1
	Sum	4.0	0.0	85.1	10.9	.18	.35	.12	18.6
MI	SA1	2.0	1.1	73.7	23.2	.47	.40	na	23.7
	SA2	3.6	0.9	72.6	22.9	.50	.50	na	19.1
	SA3	3.8	0.8	72.6	22.8	.35	.64	na	21.8
	SA4	5.6	0.0	81.1	13.3	.21	.75	na	17.5
	SA5	4.0	8.1	78.7	9.2	.08	.87	na	16.7
Sum	3.7	1.2	70.1	24.9	.30	.69	.11	19.2	
UI-85	A1	5.7	6.5	71.9	15.9	.29	.68	.06	na
	A2	5.1	1.2	92.1	1.6	.02	.94	.03	21.0
	A4	6.0	6.4	85.0	2.6	.03	.93	.03	na
	A5	5.2	5.0	82.0	7.8	.10	.83	.02	na
	Sum	5.6	4.2	85.1	5.0	.06	.84	.03	15.6
UI-86	A1	5.8	10.1	63.3	20.8	.33	.60	.04	na
	A2	4.7	2.0	92.0	1.3	.03	.96	.05	20.5
	A4	0.0	100.0	0.0	0.0	.00	.00	.00	na
	A5	4.3	10.5	79.0	6.3	.11	.80	.03	na
	Sum	4.8	7.0	82.6	5.5	.07	.90	.03	16.4

(8.3 per territory) were significantly greater ( $t=-3.27$ ,  $df=60$ ,  $p<.01$ ) than at R2-R3, where births averaged 2.2 per territory. Furthermore, at RR the two rookeries subject to the most wave action (R2 and R3) had a significantly greater proportion of females without pups or juveniles ( $p<0.01$ ) than on R1, the most protected site. Marmot Island's beach 3 is basically one large open beach, but the northernmost subarea (SA1) is the most exposed to wave action and had a significantly higher proportion of females without pups ( $p<0.01$ ) than the other subareas. On the south side of UI, most females with juveniles or by themselves hauled out at A1 or A5 and avoided A2. The processes reverses itself towards the end of the breeding season with terrestrial sites abandoned first and females distributing themselves solely along the waters edge.

Adult males - Adult males comprised about 10% of the rookery populations (Table 11). Total adult male to adult female ratios ranged from a low of 1:3.7 at UI to a high of 1:7.3 at RR. The number of adult nonterritorial males was up to twice as great as the number of adult territorial males. These nonterritorial males were located in the splash zone or at the back of the beach, areas without females. Breeding season ratios of adult territorial males to adult females on rookeries ranged from 1:10 to 1:24 (Table 11). Similar ratios have been observed in the Soviet Union (Belkin 1966; Lisitsyna 1981), Alaska (Authmiller and Orth 1979), British Columbia (Pike and Maxwell 1958), and California (Orr and Poulter 1967). The ratio varied during the breeding season, from a low in the first weeks of June to a high in early July, due largely to the continued influx of

females while the number of territorial males remained largely unchanged.

The ratio of adult territorial males to adult females varied within sites. At RR, the rate was lower on R1 than on R2 or R3, and at MI the rate generally decreased to the south along the beach (Table 11). Orr and Poulter (1967) found ratios ranged from 1:3 to 1:31 at sites on Año Nuevo Island in 1963. Higher ratios (1:12 and 1:31) were found in those rookeries most preferred by females.

Juveniles - Less than 25% of primary rookery populations was composed of juveniles (Table 11). Similar rates have been found at other primary rookery sites by Pike and Maxwell (1958), Belkin (1966), Orr and Poulter (1967), Gentry (1970), Mate (1973), Calkins and Pitcher (1982), and Withrow (1982). The low number of juvenile animals at UI may be a result of behavioral differences in that region or may be due to higher than normal juvenile mortality in the eastern Aleutian Islands.

Many of the juveniles on rookeries appeared to be associated with adult females. All of the juveniles at UI's A2 rookery were still suckling. Authmiller and Orth (1979) observed that upwards to 36% of the juveniles at MI were suckling. This is probably a conservative estimate since it represented only juveniles observed suckling during the daily census.

At UI, where known age and sex animals were available for observation, juveniles were primarily one year of age of either sex. Older juveniles were rarely seen. Data on known aged animals hauling out at MI in 1979 (Authmiller and Orth 1979) indicated that at least 92% of the juveniles there were one or two years of age. This may be

because older males have begun to show male secondary characteristics (e.g., broad necks and head) and are excluded from the rookery by the territorial males (Gisiner 1985). At UI and unlike Gisiner's observations for Año Nuevo Island adult territorial males tolerated juvenile males of at least one year of age. Older juvenile females (3-4 yr) may be on the rookery but may be difficult to distinguish from adults. Authmiller and Orth (1979) observed some three year old females accompanied by pups.

Juveniles appeared to concentrate in areas with few pups. This manifested itself dramatically in the Kuril Islands where juveniles haul-out at sites far removed from the breeding rookeries (Belkin 1966). All sites showed a strong inverse relationship between the pup per female and juvenile per female ratios. The coefficient of determination was 0.90 at RR and 0.92 at MI. Figure 17 presents a scattergram of the census data rates for the two sites, and includes the fitted linear regression lines. The two curves are different ( $F=32.7$ ,  $df=2,4$ ,  $p<0.01$ ), and a combined model provides a poor fit ( $R^2=0.17$ ). Even at UI where there were too few juveniles for valid tests, those sites with the fewest pups (i.e., A1 and A5) had the most juveniles and the greatest number of females without pups.

Pups - Pupping rates at the primary rookeries at RR, MI, and UI were 0.60 per female or greater (Table 11). Rates at other primary rookeries were similar - 0.50 to 0.97 at four rookeries in the Kuril Islands (Belkin 1966), 0.68 at Año Nuevo Island (Gentry 1970), 0.60 to 0.78 at Simpson Reef, Oregon and 0.44 to 0.75 at Orford Reef, Oregon (Mate 1973), 0.78 at Cape St. James (Edie 1977), and 0.95 at Marmot Island's B3 in 1979 (Authmiller and Orth 1979). Note that the

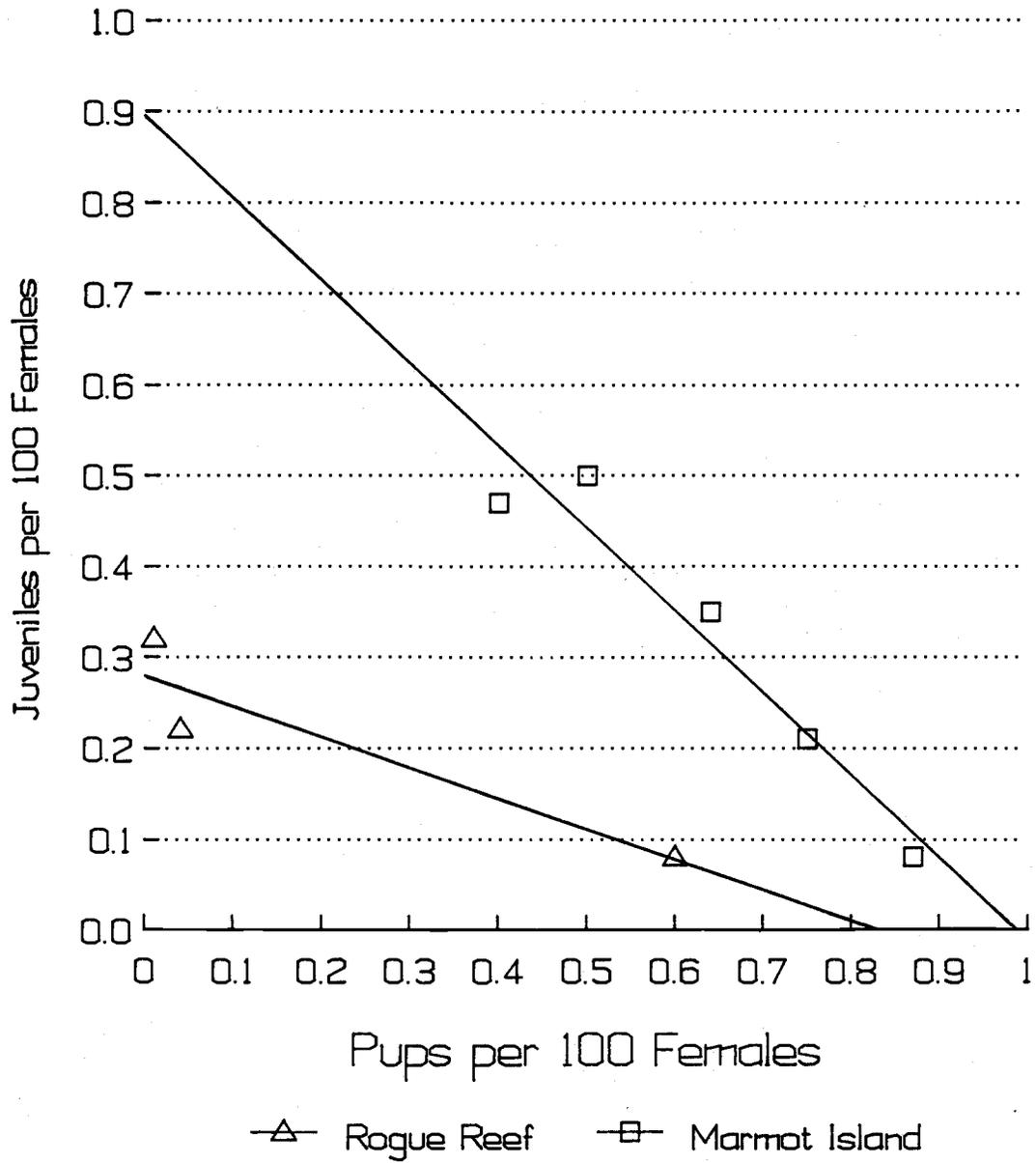


Figure 17. Relationship between pup per 100 females and juveniles per 100 females at Rogue Reef, Oregon and Marmot Island, Alaska.

difference between the counts at MI in 1979 (Authmiller and Orth) and my count in 1983 are due in part to a more complete count of pups in 1979 (a spook count was used). However, these differences may also be due to a recently confirmed decline in pupping there (Merrick et al. 1987).

Pupping varied greatly within a site. As noted earlier births were concentrated in areas away from the waters edge. In addition, the pupping rate on secondary rookeries is lower. For example at RR, the pupping rate at R2 and R3 was less than 10% of R1's (Table 11). These were also areas where most of the premature pups were born. Pupping rates at MI increased from north to south, with the northernmost subarea (SA1) having a rate less than half that of the southernmost (SA5). The rate at beach 2 at MI was 0.16 in 1983 and 0.31 in 1979 (Authmiller and Orth 1979). Intrasite variation has been noted at Año Nuevo Island by Gentry (1970) and in the Kuril Islands by Belkin (1966).

Neonatal pup mortality through the first one to two months postpartum were 12% or less at RR, MI and in both years at UI (Table 11). Similar rates have been observed at MI in 1979 (6%; Authmiller and Orth 1979), Año Nuevo Island (10%; Gentry 1970), and Wooded Island (12%-14%; Sandegren 1970). However, higher rates (up to 82%) have been observed at other sites (Evermann 1921; Pike and Maxwell 1958; Orr and Poulter 1967; Mate 1973; Edie 1977). These observations were usually attributed to pups being swept into the sea by storm swells and their subsequent drowning. It is doubtful that a viable population could be maintained at a site that sustained such mortality year after year. Thus at most sites lower mortality rates,

such as those observed at RR, MI, and UI are probably the norm. At least at these sites, most deaths were probably attributable to starvation due to abandonment or entrapment in crevices, diseases (e.g., Leptospirosis), and congenital defects. Hookworm, a major source of mortality in fur seal neonates (Kenyon and Scheffer 1953), does not appear to be a problem with sea lion pups. Trampling by adult animals may cause some deaths (Orr and Poulter 1967; Gisiner 1985), but from my observations would appear to be rare. The flattened dead pups which have been attributed to crushing are often simply carcasses in advanced stages of decomposition.

Mortality, like pupping itself, varied within a site. At RR, the pup mortality rate was over five times greater on R2 and R3. Most of the R2 and R3 mortalities (7 of 10) occurred early in the pupping season (prior to June 1). Of the 13 dead pups observed in this early period at RR, seven occurred at R2 and R3, three at R1 and three at haul-outs. Half of the pupping on R2 and R3 occurred in this period.

#### Occupancy Patterns

Seasonal patterns - The primary rookeries were largely unoccupied prior to the onset of the breeding season. This is a common characteristic of primary rookery sites throughout the species' range as it has been observed in the Kuril Islands (Belkin 1966; Lisitsyna 1981), in British Columbia (Bigg 1985), and in California (Bonnell et al. 1983). Sites which acted as year-around haul-outs (e.g., R2 and R3 at RR, A1 at UI) were occupied by some females and juveniles at this time.

Populations continued to increase at these and other sites through the second to third week of June and then stabilized (Figure 18; Pike and Maxwell 1958; Edie 1977; Withrow 1982; Bigg 1985).

Ninety percent of the seasonal maximum population could be found at the sites during mid-June to early July. Population peaks followed the median pupping date by one to two weeks (Table 12).

The dates of peak abundance and median pupping were similar between years at UI (Table 12). Data for MI's beach 3 from Authmiller and Orth (1979) were used to calculate the peak population and median pupping dates - 22 June and 18 June, respectively. These were similar to the dates observed at MI in 1983 (Table 12).

Population declines began in early July (Figure 18) at these and other sites (Pike and Maxwell 1958; Orr and Poulter 1965; Belkin 1966; Gentry 1970). By late July the territory structure of the rookery was completely gone. Surveys of the sites in October and November indicated that the primary rookeries were largely empty by this time, although animals remained at other locations at the three sites. Bigg (1985) observed that the December population on rookery sites was only 25% of that observed in July.

It appears that some adjoining primary rookeries are interrelated, such that one is preferred and utilized more heavily than the other. The less preferred rookeries (A4 at UI and perhaps B2 at MI) follow an occupancy pattern similar to other primary rookeries, offset by about a week. At MI, the primary rookery (B3) peaked in population during the week of 25 June, while an associated rookery (B2) did not peak until the week of 2 July (Table 12). A similar pattern was also observed there by Authmiller and Orth

Table 12. Population peaks and median pupping dates at Rogue Reef, Marmot Island, and Ugamak Island rookeries.

<u>Site</u>	<u>Rookery</u>	<u>Population Peak</u>	<u>Median Date Pupping</u>
RR	R1	7/04	6/24
	R2	6/24	6/16
	R3	6/30	na
MI	B2	7/02	6/20
	B3	6/25	6/14
UI-85	A2	6/21	6/11
	A4	6/24	6/14
	South	6/19	6/13
	North	6/25	na
UI-86	A2	6/22	6/17
	A4	-	-
	South	6/20	6/17
	North	6/28	6/20

<sup>1</sup> South includes A1, A2, A4, A5, and Eagle

<sup>2</sup> North includes NE1, and NE2

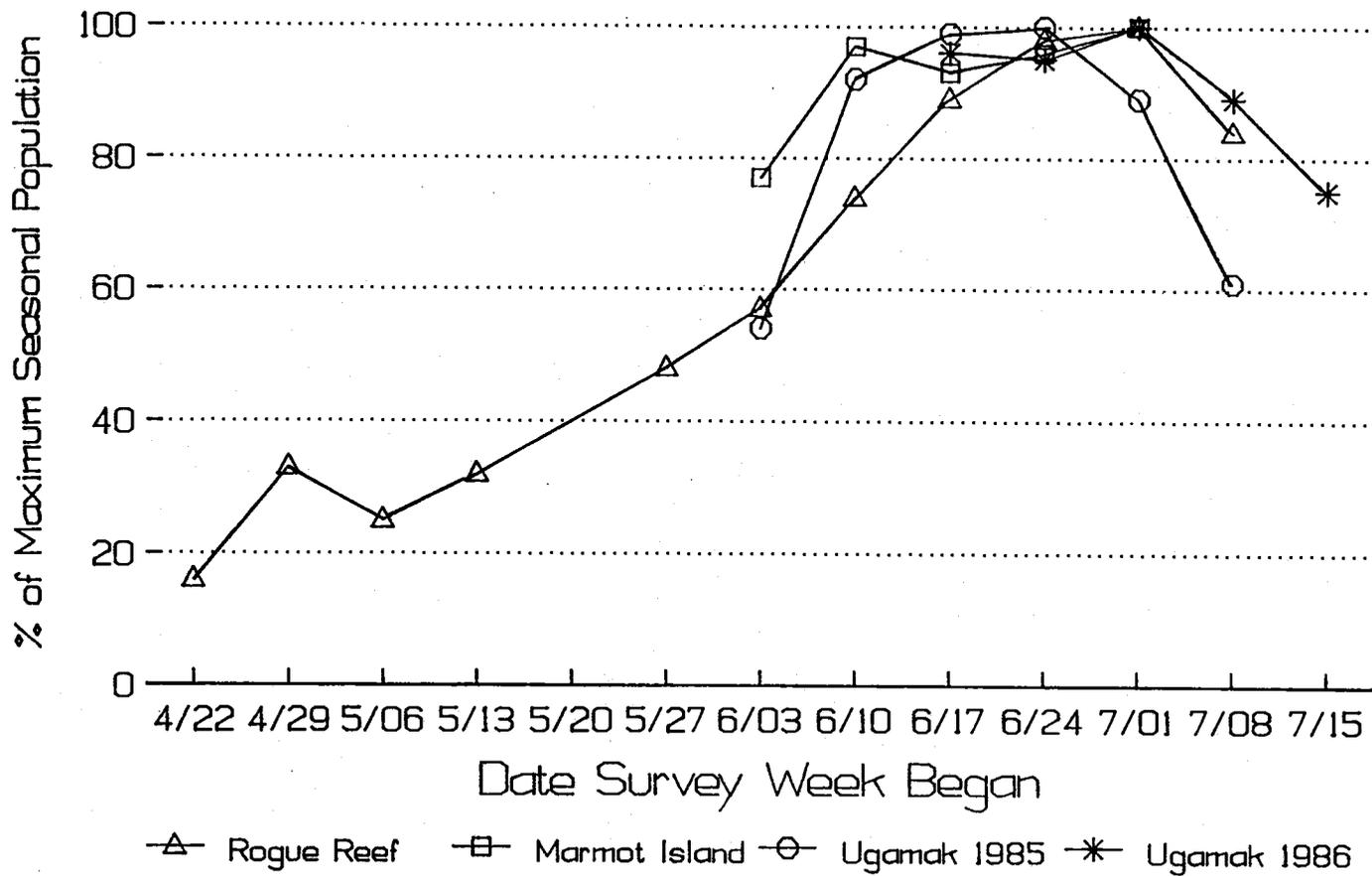


Figure 18. Northern sea lion daily rookery occupancy patterns during June-July by study site.

(1979). Similarly at UI in 1985, A2's population peaked on 21 June while A4 peaked on 24 June. These two less preferred rookeries (i.e. B2 and A4) were largely unoccupied (except for adult territorial males) at the beginning of June when the preferred primary rookery was close to its seasonal maximum. Median pupping dates (the date by which one-half of all pups had been born) were later on B2 and A4 than their associated primary rookeries (Table 12). Finally, population declines observed at MI and UI (Merrick et al. 1987) have affected the less preferred rookeries more than their associated primary rookery. At MI, B2 was occupied by over a thousand animals in 1979 but was empty in 1985 (National Marine Mammal Laboratory, unpublished data); the B3 population remained stable during this period. Similarly at UI, A4 was abandoned by 1986, while A2 remained unchanged.

Secondary rookeries peaked in population a little earlier than the site's primary rookeries. At RR, R2 and R3 were occupied earlier (animals were there year around) than R1, with their populations peaking in late May. Their populations then showed only a slight decline through the remainder of the survey period. Male territorial tenure was also somewhat longer on R2 and R3 (62 days and 61 days) than on R1 (56 days). Withrow (1982) observed that secondary sites at UI peaked earlier than primary rookeries.

### Discussion

#### Rookery Characteristics

Observations at RR, MI and UI, as well as those of other researchers, indicate that the primary rookery type occurs throughout

the range of the northern sea lion and that it has well defined characteristics:

1. Numerical dominance of adult females in the range of 70-90% of the total adult and juvenile population. Most adult females are accompanied by pups.
2. Adult males comprise around 10% of the population, with half or more of these adult territorial males. The ratio of adult territorial males to adult females is 1:10 to 1:24.
3. Less than 30% of the population composed of juveniles.
4. Pupping rates are typically 60 per 100 adult females or greater.
5. Median pupping dates are in mid-June.
6. Pup mortality is usually less than 10%.
7. Few animals use the sites during winter.
8. Peaks in male abundance occur in late May to early June followed by a decline, a period of stability and then a temporary increase in early July.
9. An overall peak in abundance (due to the arrival of adult females) occurs in late June or early July followed by a gradual decline.
10. Daily peaks in abundance occur at midday after an early morning low and followed by a late evening decline as females and juveniles disperse to sea for feeding.

Belkin (1966) and Withrow (1982) also observed sites similar to my primary rookery and classified them as "harem" and "traditional" rookeries, respectively.

Secondary rookeries may have similar numbers of adult males and females, but differ in most other respects. They have little pupping, higher neonate mortality, a wider range in juvenile numbers, different seasonal patterns of abundance and pupping, and may be used year around. Belkin (1966) and Withrow (1982) have also similar rookeries and have labeled them "unproductive" and "peripheral" rookeries, respectively. The site at Wooded Island, Alaska where Sandegren (1970) performed his research is a secondary rookery. It had high juveniles abundance (81% of females were accompanied by juveniles; Sandegren pers. comm. cited in Mate 1973), a low pupping rate (0.10), and a population peak in late May (Sandegren 1970). The Southeast Farallon Island rookery is also a secondary rookery (perhaps with Año Nuevo Island as the primary), as it has low birth rates (0.17), high mortality (a mean of 49% from 1973 to 1982), and numerous juveniles (Huber et al. 1983).

The existence of two different types of rookeries is simply due to chance. I believe this is due to active choice of birthing sites by pregnant females and the resulting exclusion of other females from these areas.

#### Rookery Site Selection

In travelling through the sea lion's domain one is struck by the number of empty beaches which at first glance would appear to be good rookery sites, and yet are not used. Moreover, once a site is chosen as a rookery it remains in use until animals are harassed away from it (Bigg 1985) or until abundance falls so low that the site is not needed (e.g., A4 at UI). Edie (1977) has determined that

parturient females prefer certain characteristics for a pupping site - access to the sea, protection from the sea, gentleness of the terrain, and availability of cooling water. Pregnant females select birthing sites which provide their pups safety from tidal and surf action, but which make them less preferred hauling sites perhaps due to their limited access.

The interior of R1 at RR is an excellent example of this as it is a flat platform well above mean high water and surf action. While well designed for pup safety, there are only three access points at low water. These are guarded by territorial males, who harass transient females. The secondary rookeries (R2 and R3) are more accessible, but they are usually partially awash at high tide or in storms. Females can easily enter and exit without contact with the territorial males. Females with pups seem willing to undergo the potential harassment of the territorial males at R1, in return for the relative safety the rookery gives to the pup. Females without pups prefer the secondary sites.

Differences at the Marmot Island subareas are less striking, as they are on an open beach with unlimited access. However, the two subareas with the greatest pup to female ratios (SA4 and 5) are also the most protected from the sea. The northern two subareas (SA1 and SA2) are subject to flooding by high tides and storms, forcing animals into the rocks at the base of the cliff.

Ugamak Island's rookeries provide an example of fine-scale discrimination between sites, as all the rookeries on the Ugamak Bay side of UI have the requisite characteristics of a primary rookery and yet some are more heavily used. The additional feature there

seems to be the presence of a kelp bed nearshore and the appropriate bathymetry to reduce wave height so as to provide an area for pups to learn to swim. Another feature seems to be the presence of protected tidal pools, again for pups to swim in. These two features are shared at UI only by the two most heavily used rookeries - A2 and NE2.

Pregnant females that choose a protected site increase their reproductive success. Theoretically, there would be strong selection pressures acting against females who choose exposed pupping sites, since their pups would have lower survival than those choosing protected sites

That all females do not use the same sites may be due to crowding, competition for choice sites with larger or more experienced females prevailing (Sandegren, 1970), or that some females lack experience in choosing a good site, even though they may be returning to the rookery complex of their birth.

#### Segregation of Females by Type

Exclusion from the primary rookeries of late arriving females and nonpregnant females in general may be a result of the aggressiveness of pregnant and postpartum females, and the preference of nonpregnant females for sites with good access. Females with young are significantly more aggressive than single females (Chapter II; Gentry 1970; Sandegren 1970). Presumably, females would seek to avoid this aggression, and a simple solution would be to avoid aggressive females (i.e., females with pups) by going where they are not. Sandegren (1970) also observed that large females are dominant

over smaller females, so if space is limited (as at A2 rookery on UI), smaller females would locate elsewhere. Finally, as females without pups do not need to be as concerned about storm or tidal effects, they can use sites which are not preferred by females with pups.

Low juvenile abundance on primary rookeries may simply be a function of where the mother decides to haul-out, as it is the juvenile that follows the parent. Alternatively, it may be a result of the weaning process, or active exclusion of juveniles.

#### Patterns of Seasonal Movements and Abundance

During the winter, and much of the fall and spring animals disperse away from rookeries. Males disperse farthest, with males from the continental U.S. dispersing northward and those in the Bering Sea dispersing northward to the ice edge (Mate 1973; Braham et al. 1984). Females, juveniles, and pups use hauling sites less frequently as evidenced by their low abundance at these times of year (Mathisen and Lopp 1963; Braham et al. 1980), but do not appear to disperse far from the rookery sites (Mate 1973). During this time the secondary rookeries may be used as haul-outs.

Males and females begin a coordinated return to the primary rookery sites in the spring. Males arrive at the primary rookeries as early as mid to late April in order to establish territories (Gentry 1970; Mate 1973; Edie 1977). Male abundance peaked in mid-May at RR and then declined, presumably due to the establishment of permanent territories (for the season) and the departure of some of the nonterritorial males. A similar peak was observed in Oregon

by Mate (1973) and in British Columbia by Bigg (1985). This temporary dispersal accounts for the early June peaks seen at sites such as McInnes Island, British Columbia by Harestad (1977).

Female movements lag behind the male's by a month. Temporary stopovers of these animals on their way to rookeries probably account for the late May to early June peaks in female abundance observed at Ship Rock in northern California (De Blois 1986), and at Wooded Island, Alaska (Sandegren 1970). It is during this period that numerous near term abortions are observed at secondary rookeries (e.g., at R2 and R3 at RR). At the Farallon Islands, all 7 premature births observed in 1982 were born between 1 April and 18 May (Huber et al. 1983). Cape St. Elias, Alaska is another secondary rookery with a high number of abortions (20 in 1977 and 21 in 1978) during this period (Calkins and Pitcher 1982).

Most pregnant females continue on to primary rookeries to pup, and begin arriving at about the time territories are established. The first females land on beaches largely devoid of other females, and establish the nucleus of the coming aggregation. Initial low density allows females of all types to enter the beach; however, as the beaches fill, late-comers are met by aggression, forced first to the back of the beach, and then later perhaps precluded from entering the beach at all. This produces an effect whereby some nearby (e.g., A4 at UI) are occupied later. Lone females and those accompanied by juveniles appear to avoid or move away from these primary sites. Thus these females locate themselves elsewhere (e.g., at secondary rookeries such as Wooded Island), producing extraordinarily high juvenile counts at these other sites.

Population increases through June are largely due to the continued arrival of parturient and nonparturient estrus females. The delayed return to sea of postpartum females also contributes to the buildup of animals on the rookeries. The perinatal attendance period ranged from 6 days at Año Nuevo Island in 1983 (Higgins, 1984) to 9 days at Wooded Island (Sandegren 1970) and 10 days at UI in 1985-86 (Chapter II). Females begin feeding trips at the end of the perinatal period, but the proportion of time spent onshore is still high - 50% at Wooded Island to 66% at UI and 63% at Año Nuevo Island (Chapter II; Gentry 1970; Sandegren 1970). Nonparturient females also visit the rookeries to mate, but then quickly return to the sea (Table 8). As a result, the abundance of nonparturient females is considerably greater than it would appear from the rookery surveys.

Beginning in early July the process reverses itself, and primary rookery populations begin to decline. This is due to 1) an increasing proportion of females beginning postnatal feeding excursions, 2) a slight trend towards longer time at sea by these females (Higgins 1984; Chapter II), 3) declining numbers of nonparturient females on the rookeries, and 4) the departure of adult territorial males. Departing territorial males are often replaced by new males, and as a result the territorial structure is maintained beyond the period when most females had undergone estrus. Indeed a second peak in male abundance was observed at RR and UI in late June and early July. Gisiner (1985) noted that many of these new males hold the same territory the next summer. He suggested that late arriving males determine where females are and establish territories the following year in these same locations. This would explain how A4

rookery at UI, which was occupied by over 200 adult females in 1985 but contained only adult territorial males in 1986, could have a well defined territory structure in 1986.

Ultimately, all males leave the rookeries due to the absence of estrus females and the general exodus of female-pup pairs to other locations. Females with pups disperse, once the pups can swim well enough, to secondary rookeries and other haul-out sites. This dispersal would account for the late July peak observed by De Blois (1986) at Ship Rock. By October many rookery sites are again largely deserted.

## CHAPTER IV

## CONCLUSIONS

Summary of Findings

My study of female northern sea lions has revealed that most of their time onshore is spent in rest, maternal, and comfort behaviors. The proportion of time spent in these behaviors represents a compromise between the basic functions of rookeries - hauling out (e.g., rest and comfort) and reproduction (e.g., maternal care). Other behaviors (i.e., agonistic interactions) are of secondary importance.

The semiaquatic nature of pinnipeds requires them to return to land periodically, although the degree this is expressed varies by genera. Lower heat loss on land than in water makes hauling out an energetically efficient location for rest in subpolar and temperate regions (Pierotti and Pierotti 1980), presuming the trip from the feeding grounds to land does not exceed the energy saved on land. Once on land the most energetically efficient behavior is rest. This is a common strategy among pinnipeds (Table 10), as during the breeding season females of several species spent two-thirds or more of their time in rest. Anderson and Harwood (1985) explained this for gray seals as consistent with the limited amount of energy available (gray seals like most phocids do not feed during their 16-21 day lactation period; King 1983). However, data on otariid species (Table 10) indicates that otariids spend similar amount of time in rest as phocids, despite going to sea for feeding much sooner postpartum (4 to 9 days; Gentry et al. 1986). Thus the large amount

of time spent in rest appears to be a general strategy for all land breeding pinnipeds. Presumably, females would spend all their time in rest were it not for the requirements of maternal care, movement, and agonistic interactions (e.g., compare the time in rest for females with and without young shown in Table 2).

Little time was devoted to agonistic behaviors and most of this was confined to vocalizations. Physical contact and biting were rare. Most of the aggression was directed at moving animals, usually other adult females. A disproportionate amount was directed towards adult males. Births and copulations consumed little of the activity budget, but were probably engaged in at one time or another by all females.

I found that significant differences in behavior existed among females, sites, and times-of-day. Females without young rested more while on land, but spent less time there than females with young. They were also less aggressive. Females with pups or with juveniles spent the same amounts of time in nursing and aggression; however, those with pup spent more time on land and devoted more maternal care to their young. The differences between female types reveal the compromise which must be made between rest and care of young. In addition, the greater aggressiveness of females with young is probably due to protection of the young (another aspect of care giving), while nursing requires greater amounts of time on land.

The maternal behavior of northern sea lions is similar to that of other sea lions and low latitude fur seals, and may represent a conservation of ancestral traits. Differences from high latitude fur

seals may be due to the northern sea lion's ability to withstand winter sea conditions and the lack of ice at their hauling sites.

The basic pattern of behavior and timing of life history events was similar at all three sites studied; however, I found significant differences existed in the expression of behaviors. Females at Marmot Island were more active and aggressive than females at the other sites, while those at Rogue Reef were the least active and aggressive. These differences may be due to air temperatures, tides, and site substrates. The Rogue Reef rookery has relatively warm temperatures and is located on a flat ledge elevated above the seas; Marmot Island has cool temperatures, a large tidal range and is an open beach. Females at Rogue Reef can rest without disturbance and can habituate to their neighbors, so activity and aggression are lower. Females there may also rest to remain cool. Marmot Island females, on the other hand, are forced to move as the tide rises and falls, and cannot move to areas isolated from the tide. This movement increases densities at times, and stops animals from habituating to each others presence. As a result, females at Marmot Island are more active and more aggressive.

The significant differences observed between sites in time-of-day effects may be a result of temperature, tides, and endogenous rhythms, all overlaid with the pattern of daily movements. Sea lion females generally return from the sea in the morning and leave in the evening; thus one would expect this to control the daily activity patterns. This appeared to be the case at Ugamak Island where activity increased throughout the day. However, Marmot Island showed no pattern (except for a peak in the morning) and this may be a

result of the constant agitation of the population due to the tidal effects.

Behavioral differences were also found between females at the three sites and those at other sites. Attendance patterns at Ugamak Island were different from those at Año Nuevo Island (Higgins 1984), and may be a result of differences in prey availability. Female courtship displays, which appeared to Sandegren (1970) to be an important behavior in the reproductive cycle at Wooded Island, were rarely observed at my three study sites. This may be a result of differences in the site's population structures. Differences found between sites point out the need to consider the possibility that observed behaviors may be site specific.

The data obtained here are representative of primary (i.e., sites with much pupping) rookeries. A comparison between the three rookeries and other primary rookeries indicates that many similarities exist. Most of the animals on primary rookeries are females accompanied by pups. Pupping rates are high, and neonatal mortality is relatively low. Juveniles may be present but the trend appears to be towards low numbers. Seasonal abundance peaks in late June, a week or so after the median pupping date; however, many primary rookeries are abandoned during the nonbreeding season.

A second type of rookery also exists, one where there are few pups and many juveniles. Pup mortality is higher there, and there may a greater number of premature births at these sites. Peaks of abundance occur earlier, and the sites appear to be used more frequently in the nonbreeding season than do the primary rookeries.

That two types of rookeries exist represents another aspect of the variability in female behavior; in this case it is the differences in site preferences of females of different maternal status. Parturient females choose sites (and locations within them) which improve the chance of their pup's survival; ones which have gentle terrain and protection from the sea. Other females may favor a site with better access to the sea, a site which may not necessarily be safe for pups. Females with pups may also actively exclude other females and juveniles from the pupping rookeries. This explains why sites such as Wooded Island, Alaska have extraordinarily high numbers of adult females accompanied by juveniles.

Both types of sites play a role in the species' annual reproductive cycle. The secondary sites may be used during the nonbreeding season as haul-outs. Then during the return of females to rookeries for pupping and mating, females may use these sites for premature births. Most pregnant females, however, continue on to the primary rookeries to give birth. Some single females and some with juveniles also use the primary rookeries, but others are forced off by the aggressiveness of females with pups. Other nonparturient females may never go to the pupping rookeries, and may mate at the secondary sites. Exclusion of nonreproducing females from the primary sites reduces aggression resulting from crowding, and as a result may also improve pup survival.

The behavior of females on pupping rookeries and the use of different types of rookeries are two elements of a suite of behaviors which enhance the survival of the species. Such behaviors represent the adaptation, over evolutionary time, of the terrestrial behaviors

of the sea lion's ursine ancestor to an aquatic existence. The behavioral variability observed in this study indicates that the animal's behavioral repertoire remains sufficiently plastic for them to respond to environmental differences.

### Significance of Rookery Types

The importance of discriminating between types of rookeries can be demonstrated through the answer to two of the questions which originally motivated this research:

1. Is the reported variation in the juvenile to adult female ratios a latitudinal cline?
2. Why were so many female "courtship displays" observed at Wooded Island (Sandegren 1970)?

Variation in the juvenile to female ratio can be largely explained by differences between the two rookery classes. The proportion of females accompanied by juveniles was 81% Wooded Island in 1967-68 (Sandegren, pers. comm. cited in Mate 1973). Since this was so much higher than rates in southern areas (e.g., 2% at Año Nuevo Island; Gentry 1970) it occasioned speculation that there might be a latitudinal cline in these rates (Mate 1973). However, Wooded Island appears to be a secondary rookery. Thus it should not be compared with primary rookeries. Ratios for primary rookeries were 2% in Año Nuevo Island, 11% at Simpson Reef, Oregon (Mate, 1973), 7% at Rogue Reef, Oregon's rookery R1, 25% in British Columbia (Pike and Maxwell 1958), 10-12% at UI in 1977-78 (Withrow, 1982), less than 17% at UI in 1985, and 22% at Marmot Island's beach 3 (with a 6% at SA5 the prime pupping area). Secondary rookery's rates are generally much

higher, and show considerable variation from 29% at Rogue Reef's R2 to Withrow's (1982) 47-51% at Ugamak Island to Sandegren's 81%.

Sandegren (1970, 1976) considered the female courtship displays observed at Wooded Island, Alaska to be important in maintaining the structure of that rookery. He argued that females use the display to stimulate males to maintain territories. Yet the behavior was rarely seen at my three study sites and at Año Nuevo Island (Gentry 1970) and males still maintain territories. Both cases may exist. At my sites and at Año Nuevo Island the existence of females with pups ensures that many females will always be on the site during the breeding season, and the males can anticipate that these females will come into estrus eventually. However, at Wooded Island, where few pups are born, males have no assurance. Females may come and go with no assurance they will ever be seen in estrus. Thus females using the site need a method by which to retain the males interest and stimulate them to remain on the site. The female courtship display may be that method. This hypothesis could easily be tested by observing behavior at another secondary rookery such as Cape St. Elias, Alaska.

#### Conclusion

Four years of fieldwork with northern sea lions has led me to the conclusion that it is female behavior which dictates the life of rookeries. Females set the seasonal pattern of rookery use as they return to pup and mate. Females select sites based on their needs for pupping and protection of pups. Female movements control the daily activity of rookeries.

Males play a subordinate role as they will only maintain territories on sites occupied by females. Even though males arrive earlier than females it appears males simply return to sites where females were the previous year.

I found no evidence that females actively select mates; however, by selecting only a few sites for mating (i.e., rookeries), females set the stage for intrasexual selection to act on males. This ensures that the most "fit" males have access to females.

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## APPENDICES

## APPENDIX I

## REPRODUCTIVE BIOLOGY OF NORTHERN SEA LIONS

Ontogeny and reproduction

Males exhibit seasonal spermatogenesis, with active sperm found between late April and early August (Pitcher and Calkins 1981). Mating occurs between late May and early July throughout the range (Belkin 1966; Gentry 1970; Pitcher and Calkins 1981). Females mate 11 to 12 days after parturition (Gentry 1970; Sandegren 1970), with 100% of females age six and over ovulating, and 87% of those between ages eight and 20 becoming pregnant. Implantation occurs in late September through early October after a delay of three to four months (Pitcher and Calkins 1981). Gestation period is 354 days. Mating and pupping occurs on land in areas defended by adult territorial males (Belkin 1966); Edie (1977) described parturient females choosing a pupping site. Sandegren (1970) provided a detailed description of parturition. Sex ratios at birth are close to parity (Calkins and Pitcher 1982; Gentry 1970). Birth rates are 60-75% throughout the sea lion's range (Belkin 1966; Gentry 1970; Pike and Maxwell 1958; Withrow 1982). Premature births (usually fully formed stillbirths) occur as early as February, with viable births occurring from late May through early July (Belkin 1966; Gentry 1970; Mathisen et al. 1962; Pitcher and Calkins 1981). Pupping peaks in the 2nd to 3rd week of June (Belkin 1966; Withrow 1982). Crowding and aggression may delay pupping (Sandegren 1970). There is a diurnal cycle in pupping, with the peak in the morning (Gentry 1970;

Sandegren 1970). The pupping rate at night is 50% that of the daytime rate (Gentry 1970; Sandegren 1970).

Average fetal weights in Alaska in February are 4.3 kg with no sexual differences, and rapid growth occurs from then until birth (Calkins and Pitcher 1982). Twinning is rare. Newborn pups are about one m long, weigh 16-23 kg, and have a thick, grayish-brown coat, which is molted to a dark brown coat after six months; male and female pups 6-10 weeks old weighed about 40 kg (Belkin 1966; Calkins and Pitcher 1982; Mathisen et al. 1962; Scheffer 1945). Growth is rapid during the first two years (Fiscus 1961; Loughlin and Nelson 1986), body weight may double in the first seven weeks (Scheffer 1945) and body length may increase up to 80 cm during the first year (Mathisen et al. 1962) and double the birth length by three years of age (Spalding 1964). Yearlings average 179 cm (Mathisen et al. 1962). Pups are capable of swimming at birth (Gentry and Withrow 1978), with most pups swimming well by five weeks old (Sandegren 1970; Mate 1973). Most pups are weaned in their first year, although the presence on rookeries of females with suckling subadults (from 2% of females at Año Nuevo as found by Gentry 1970, to 81% at Wooded (Lewis) Island, Alaska (Sandegren pers. comm. cited in Mate 1973) indicates that some are not weaned until their second year or later.

Females reach sexual maturity between three and eight years of age (Pitcher and Calkins 1981; Perlov 1971), and may breed into their early twenties (Mathisen et al. 1962). Female weight and length increases through age five, and then levels off (Calkins and Pitcher 1982; Loughlin and Nelson 1986). Males reach sexual maturity between ages three and seven and physical maturity by age 10 (Calkins and

Pitcher 1982; Perlov 1971). Testis weight increases through age nine, with the baculum continuing slow growth through 14-17 years of age (Thorsteinson and Lensink 1962). Males begin to develop secondary sexual characteristics (massive muscular neck, thick pelage, and sagittal crest) at four years of age (Calkins and Pitcher 1982). Males holding territories may range between five and 19 years of age (Mathisen et al. 1962) with 90% between nine and 13 years of age (average of 11; Thorsteinson and Lensink 1962). Females are monoestrous (Gentry 1970; Sandegren 1970) and most adult females breed annually (Pitcher and Calkins 1981). Females commonly live to 30 years of age and males to 18 (Calkins and Pitcher 1982).

### Behavior

Little is known about behavior during the nonbreeding season (August through May). During the winter both sexes haul out on land less frequently and are not concentrated at rookery sites. Mate (1973) noted that males competing for rest sites exhibited behaviors similar to boundary displays observed during the breeding season; however these displays were less frequent and less violent than during the breeding season.

Adult breeding animals and some subadults occupy rookeries during the breeding season. Nonbreeding males, subadults and transient females can be found on separate haul-out sites which are less organized than traditional rookeries. The requirements of rookeries and haul-out sites depend on several factors including: (1) minimal human disturbance, (2) access to and from the water, (3) local abundance of food, and (4) exposure and topography (Mate 1973).

Territorial boundaries follow natural features such as cracks, faults or ridges in rocks (Gentry 1970).

Three general types of territories are used - aquatic, semiaquatic, and terrestrial. Males with semiaquatic territories are the most successful in territorial maintenance (Sandegren 1970). Some territories are stable for up to 60 days (Gentry 1970; Sandegren 1970). The mean size at the Año Nuevo rookery was  $205\text{m}^2$ , though there was a large difference in territory size in the population and over time (Gentry 1970).

Rookery populations exhibit a distinct diurnal fluctuation in number, with a low in the early morning and a high in the late afternoon (Gentry 1970; Sandegren 1970; Withrow 1982). This fluctuation results from a movement of females to and from the sea to feed and to a lesser degree are affected by tide and weather (Sandegren 1970; Withrow 1982). A similar pattern has been observed at haul sites in the nonbreeding season (Kenyon and Rice 1961).

Generally, males copulate only when they acquire a breeding territory (Gentry 1970; Gisiner 1985). Once acquired a territory may be held for up to seven years, with copulatory success increasing through the third year (Gisiner 1985). Territories are established in early May, with boundaries delineated through ritualized threat displays towards neighbors and other encroaching males. Displays are much more common than fights, with 47 displays per fight observed at the Año Nuevo rookery (Gentry 1970). Most of the displays, fighting and turnover in territories occurs in the first weeks of the breeding season. Neighbors appear to habituate and the number and duration of displays decreases over time (Gentry 1970). There is an inverse

relationship between the amount of geographic separation and the number of displays (Gentry 1970).

Parturient females arrive at the rookery 2.8 days prepartum (Gentry 1970). Favored pupping sites have a gentle slope, are above high tide level, are protected from storm waves, and are away from territory boundaries. Females frequently return to the same pupping site in successive years (Edie 1977; Gentry 1970).

Births take 16 to 30 minutes after the amnion bursts (Gentry 1970; Sandegren 1970) and are evenly divided between caudal and cephalic presentations (Gentry 1970; Sandegren 1970). After birth, females may attempt to stimulate inactive pups by lifting and dropping, nipping, flipper slapping, flipper stroking, tooth striking, or nuzzling. The female moves the pup into a position for suckling, with suckling beginning 3 minutes postpartum (Gentry 1970). Pups suckle an average of 230 minutes in 12 nursing periods, with the number of nursing periods declining to 3-4 after several weeks (Sandegren 1970). Females vocalize to the pup and smell it after birth to establish mutual recognition; they generally will not separate until recognition is established (Sandegren 1970). Separation usually occurred by the ninth day postpartum when the females first went to sea (Sandegren 1970). Females return to sea every 1-3 days thereafter (Gentry 1970; Sandegren 1970). Most feeding trips are less than 1 day in length (Higgins 1984; Gentry 1970; Sandegren 1970). Females with pups spent 63% of their time on land, while those without spent 47% (Gentry 1970). Reunification of the female and her pup is by vocalization and olfaction (Ono 1972;

Sandegren 1970). Females usually reject foreign pups that attempt to nurse (Belkin 1966).

Female aggressiveness peaked at parturition and continued at high levels 3-10 days postpartum (Sandegren 1970). Aggression after birthing is caused by conflicts over pups and rest sites (Gentry 1970), and by returning females searching for pups (Ono 1972). Females sometimes bite and toss other female's pup, and will threaten subadults and adult males (Calloway 1972).

Females prefer rest sites with ready access to water for thermoregulation, but out of the splash zone. Females with pups select rest sites which are usually farther inland and more protected than those selected by females without pups (Edie 1977). Most (80%) females with pups at the Cape St. James, Canada rookery mated within 10 m of their pupping sites (Edie 1977).

Males initiate most copulations (Gentry 1970; Gisiner 1985). Females exhibit a display which may be significant to initiating precopulatory behavior in the male (Sandegren 1970). However, Gentry (1970) describes this as appeasement behavior. Males mount and dismount until the female becomes passive and pelvic thrusting can begin. Initial pelvic thrusting is irregular and then becomes more regular, more intense and more frequent upon achieving intromission. The female usually signals the end of the mating by vigorous protests and biting the male. Mating typically requires 16 minutes (Gentry 1970; Sandegren 1970). There are more mounts than copulations (1.6:1) at Año Nuevo, with most of the multiple mounts occurring early in the mating period (Gentry 1970).

Females mate an average of 11-14 days postpartum (Gentry 1970; Sandegren 1970). Eighty-five percent of the Año Nuevo females copulated only once, with the remainder copulating twice within a four day period (Gentry 1970).

Both males and females preface movements with a vocal display (Gentry 1970). Konstantinov et al. (1980) and Poulter (1968) have catalogued the sounds produced on land. Territorial male sounds are usually low frequency, with amplitude modulation varying with the type of call. Their sounds signal aggression towards other males, courting of females, or are comfort signals. Females vocalize less, at a higher frequency, and use less amplitude modulation. Pups have a bleating cry like sheep, and their voice deepens as they age. Underwater sounds are like their in-air signals. Poulter and Del Carlo (1971) suggested their underwater sounds are used for locating food; however, Schusterman et al. (1970) indicated that these sounds probably have a social function and are not used for foraging.

The motor components in pup social play are similar to adult male agonistic behavior and are separable into male sexual/female appeasement, aggressive/submissive, and fighting/boundary defense bouts (Gentry 1974). Adult-like behavior patterns were evident by 2 weeks of age; age, sex, terrain and play partner were determinants of motor components (Gentry 1974; Sandegren 1970). Farentinos (1971) found that all age and sex groups, except territorial males, played. The development of swimming by pups occurs in 3 phases: a territorial phase (first 2 weeks after birth); a littoral phase (second 2 weeks); and a pelagic phase (third 2 weeks).

Thermoregulatory behavior is important to the survival and reproductive success of E. jubatus. At substrate temperatures between 10-15° C animals stay dry, cover their flippers, and expose a minimum of body surface to the air; between 20-30° C animals expose their flippers and become wet (Gentry 1973). Flippers are important for thermoregulation by evaporative cooling as well as by conduction and convection. Rear flippers are usually wet first, and this may be important to spermatogenesis in males. Other thermoregulatory measures include the use of shade, urohydrosis, and salt water drinking by males (Gentry 1981).

Grooming is performed by bending the head and neck backwards, and scratching with the hind-flipper claws (Steller 1751). Animals also rub themselves on rocks and on other animals.

**APPENDIX II****FIELD FORMS**

The following are the major field forms and codes (as appropriate) used in collection of data at the field sites.



## GENERALIZED ACTION LOG

FIELD	COLS	ITEMS AND CODES
1	1	RECORD # - 4
2	2-4	DATE
3	5-8	TIME OBSERVED
4	9-11	MAP NUMBER
5	12-13	CELL NUMBER
6	14-15	TERRITORY NUMBER - 00-BOUNDARY; 98-WATER; 99-UNKNOWN
7	16	INITIATED BY TYPE - 1-DOM. ADULT MALE; 2-SUBDOM. ADULT MALE; 3-ADULT FEMALE; 4-SUBADULT; 5-YEARLING; 6-PUP; 7-CALIF. SEA LION; 9-UNKNOWN
8	17-18	INITIATED BY NUMBER - ANIMAL NUMBER IF DOM ADULT MALE; IF ADULT FEMALE THEN 91-WITH PUP, 92-WITH YRLNG, 93-BOTH 99-ALONE; ELSE # OF ANIMALS
9	19	RESPONDENT # 1 TYPE - AS ABOVE
10	20-21	RESPONDENT # 1 NUMBER - AS ABOVE
11	22	RESPONDENT # 2 TYPE
12	23-24	RESPONDENT # 2 NUMBER
13	25	RESPONDENT # 3 TYPE
14	26-27	RESPONDENT # 3 NUMBER
15	28	FOR COPULATION - Y-POST COITAL DISPLAY V-VOCAL DISPLAY; U-UNKNOWN FOR BIRTHS - YEARLING PRESENT ? - Y-YES; N-NO
16	29	WIN - FOR MALE DISPLAYS, D=DRAW; I-INIT; R-ALL RESP; 1-RESP 1, 2-RESP; 3-RESP 3 FOR FEMALE DISPLAYS - Y-MALE INTICED FOR COPULATIONS - Y-INTROMISSION FOR BIRTHS - Y-PUP ALIVE, N-STILLBORN
17	30	ACTION CODE FOR MALES - 1-DISPLAY; 2-DISPLAY+ATTACK; 3-ATTACK ONLY; 4-SNIFF+DISPLAY; 5-SNIFF ONLY; 6-HERDING; 7-BREAK UP FEMALE FIGHT; 8-FOLLOW FEMALE TO WATER. FOR FEMALE DISPLAY - 1-PRECOITAL; 2-POST COITAL; 4-POST INVESTIGATION FOR COPULATION - 1-MOVED; 2-WALKED UP TO & SNIFFED; 3-GENERAL SNIFF; 4-DISPLAY FOR BIRTHS - 1-CAUDAL; 2-CEPHALIC; 3-BREECH; 9-UNKNOWN FOR DEATHS - 1-DROWNED; 2-CRUSHED; 3-ABANDONED; 4-STILLBORN; 9-UNKNOWN
18	31-79	NOT USED
19	80	TYPE - 1-MALE DISPLAY; 2-FEMALE DISPLAY; 3-COPULATION; 4-BIRTH; 5-DEATH; 6-BEGIN BREAK; 7-END BREAK







## DETAILED DISPLAY LOG

FIELD	COLS	ITEM AND CODES
1	1	RECORD # - 5
2	2-4	DATE
***** FEMALE COMPONENT *****		
3	5-8	TIME OF INITIAL RESPONSE
4	9-11	MAP #
5	12-13	CELL #
6	14-15	TERR #
7	16-17	FEMALE # (SEE RECORD 4 FOR CODES)
8	18-19	SEQUENCE # - VOCALIZATION
*	** **	FEMALE MOVEMENT DATA
9	20-21	SEQUENCE # - TO BULL
10	22-23	" - AWAY FROM BULL
11	24-25	" - STATIONARY
12	26-27	" - TO BOUNDARY
13	28-29	" - TO OTHER
14	30-31	" - SLOW GAIT
15	32-33	" - NORMAL GAIT
16	34-35	" - FAST GAIT
17	36-37	" - DRAG POSTURE
18	38-39	" - LIFT POSTURE
19	40-41	" - LIMP POSTURE
20	42-43	" - NORMAL POSTURE
**	** **	INTERACTION WITH BULL
21	44-45	SEQUENCE # - AROUND BULL
22	46-47	" - UNDER BULL
23	48-49	" - STROKE BULL
24	50-51	" - BITE BULLS HEAD
25	52-53	" - BITE BULLS TAIL
26	54-55	" - VAGINAL DISCHARGE
27	56-57	" - URINATE
28	58-59	OTHER #1 - CODE (99-LAST RECORD)
29	60-61	OTHER #1 - SEQUENCE #
30-35	62-73	REPETITION OF FIELD 28 AND 29 FOR 3 TIMES
36	74-77	TIME THIS RECORD ENDS
37	78	RELATIONSHIP TO COPULATION - 1-PRE; 2-POST; 3-NONE; 9-UNK
38	79	MORE RECORDS ? - Y-YES
39	80	TYPE - 2

## \*\*\*\*\* MALE COMPONENT \*\*\*\*\*

3	5-8	TIME MALE RESPONDS
4	9-11	MAP #
5	12-13	CELL #
6	14-15	TERR #
7	16-17	ANIMAL #
8	18	FEMALE IN TERRITORY ? - Y-YES
*	** **	PRECOPULATORY DATA
9	19-20	SEQUENCE # - IGNORE FEMALE
10	21-22	" - CHASE FEMALE

11	23-24	"	- HERDS FEMALE
12	25-26	"	- STROKES FEMALES HEAD
13	27-28	"	- STROKES FEMALES BACK
14	29-30	"	- VAGINAL INVESTIGATION
15	31-33		DURATION OF INVESTIGATION (SSS)
16	34-35		SEQUENCE # - MOUNTS FEMALE
17	36		FEMALE RECEPTIVE ? - Y-YES
**	** **		INTERACTION WITH OTHER BULLS
18	37-38		SEQUENCE # - BOUNDARY DISPLAY
19	39-40	"	- LEAVES FEMALE TO DISPLAY
20	41-42		NOT USED
21	43-44		OTHER #1 -CODE
22	45-46		OTHER #1 - SEQUENCE #
23-36	47-74		REPETITION FOR OTHERS 2-8
37	75-78		TIME THIS RECORD ENDS
38	79		MORE RECORDS?
39	80		TYPE - 1



## FOCAL FEMALE LOG

FIELD	COLS	ITEM AND CODES
1	1	RECORD # - 7
2	2-4	DATE
3	5-8	TIME RECORD BEGUN
4	9-10	INITIAL CELL #
5	11-12	INITIAL TERR #
6	13-14	ANIMAL # (SEE RECORD 4)
7	15	AGGRESSIVE ACTIVITY - TYPE - 1-OPEN MOUTHED VOCAL; 2-CLOSED MOUTH; 3-OTHER VOCAL; 4-BELLY SLAPPING; 5-HEAD NODDING; 6-PUSHING; 7-BITING; 8-PUSH+BITE; 9-CLAP+VOCAL
8	16	AGGRESSIVE ACTIVITY - SEQ. WITHIN RECORD
9	17-19	AGGRESSIVE ACTIVITY - DURATION - SSS
10-21	20-39	REPETITION OF 7,8,9 FOUR TIMES
22	40	NOT USED
23	41	RESPONDENT #1 - TYPE (SEE REC 4)
24	42	RESPONDENT #1 - NUMBER - 1-9
25	43	RESPONDENT #2 - TYPE
26	44	RESPONDENT #2 - NUMBER
27	45-46	NOT USED
28	47	MALE INTERVENE - Y-YES
29	48	PURPOSE - 1-ANOTHER VOCALIZES; 2-OTHER MOVES, NO TOUCH; 3-OTHER MOVES+TOUCHES; 4-OTHER TOUCHES PUP; 5-CLEAR PUPPING AREA; 6-CLEAR REST AREA; 7-TO MALE; 8-OUTSIDE DISTURB; 9-UNK; 0-CALL PUP
30	49	OTHER ACTIVITY 1 - TYPE - 0-HEAD UP & ALERT; 1-PASSIVE REST; 2-COMFORT BEHAVIOR; 3-DISPLAY; 4-COP; 5-BIRTH; 6-SUCKLE; 7-OTHER CARE; 8-NONAGGRESSIVE VOCAL; 9-OUT OF SIGHT
31	50	OTHER ACTIVITY 1 - SEQUENCE #
32	51-53	OTHER ACTIVITY 1 - DURATION - SSS
33-34	54-58	OTHER ACTIVITY 2 - TYPE, SEQ, DURATION
35	59	SUCKLING ? - 1-PUP; 2-YEARLING; 3-BOTH
36	60	NONAGGRESSIVE MOVEMENT - SEQUENCE #
37	61-63	NONAGGRESSIVE MOVEMENT - DURATION
38	64	WHERE - 1-TO WATER, ALONE; 2-FROM WATER ALONE; 3-IN ROOKERY ALONE; 4-TO WATER, WITH PUP; 5-FROM WATER, WITH PUP; 6-IN ROOKERY, WITH PUP; 7-9-WITH SA
39	65-66	MOVEMENT FROM TERR
40	67-68	MOVEMENT TO TERR
41	69-70	FINAL CELL
42	71-72	FINAL TERR
43	73-75	TIME IN WATER - SSS
44	76-79	TIME RECORD ENDS
45	80	TYPE - 1-9

Female History Card

<p>DATE MARKED: <u>6/17/86</u> LOCATION: <u>A2W</u></p> <p>WITH? SUBADULT <input checked="" type="checkbox"/> PUP ALONE</p> <p>DATE PUPPED: <u>6/17/86</u></p> <p>DATE FIRST SEEN WITH PUP: <u>6/17/86</u></p> <p>DATE COPULATED: <u>1 1</u></p> <p>DATE LAST SEEN: <u>7/29/86</u></p>	<p>SUMMARY RECORD FOR : <u>1</u></p> <p>LIGHT BROWN</p> <p>MEDIUM SIZE</p>
<p>COMMENTS:</p> <ul style="list-style-type: none"> <li>- CHASED BY ♀ ON 6/24</li> <li>- MISSING PUP 6/24 - 6/26</li> <li>- OK AFTER 6/26</li> <li>- MOVED TO A3 ON 7/26</li> </ul>	

6/14: _____	6/30: <u>9/13/18/21</u>	7/16: <u>10/15/19</u>
6/15: _____	7/01: <u>9/13/18/22</u>	7/17: <u>-/15/-</u>
6/16: _____	7/02: <u>▲</u>	7/18: <u>▲</u>
6/17: <u>12/16/21</u>	7/03: <u>▲</u>	7/19: <u>▲</u>
6/18: <u>8/15/23</u>	7/04: <u>▲</u>	7/20: <u>9/12/21</u>
6/19: <u>9/15/23</u>	7/05: <u>▲</u>	7/21: <u>▲</u>
6/20: <u>8/15/18/23</u>	7/06: <u>10/14/21</u>	7/22: <u>-/11/14/19</u>
6/21: <u>6/12/18/22</u>	7/07: <u>9/13/18/22</u>	7/23: <u>-/12/17/</u>
6/22: <u>10/-/-/23</u>	7/08: <u>-/-/-/21</u> <sup>GONE</sup> 2200	7/24: <u>-</u>
6/23: <u>9/15/23</u>	7/09: <u>▲</u>	7/25: <u>-/12/20/</u>
6/24: <u>9/14/20</u>	7/10: <u>▲</u>	7/26: <u>-/12/19</u>
6/25: <u>9/14/-</u>	7/11: <u>▲</u>	7/27: <u>A3</u>
6/26: <u>9/21/GONE</u> <sup>A2</sup> 2280	7/12: <u>▲/22</u>	7/28: _____
6/27: <u>▲</u>	7/13: <u>9/-/21/</u> <sup>GONE</sup> 2130	7/29: _____
6/28: <u>▲</u>	7/14: <u>▲</u>	7/30: _____
6/29: <u>▲</u>	7/15: <u>▲</u>	7/31: _____

## APPENDIX III

## FEMALE BEHAVIORAL REPERTOIRE

The salient characteristics of each of the female behaviors are described below:

1) Rest - In this behavior the female was either prone or erect, was not interacting with other animals, and could probably be considered to be resting. In the prone position, the female was positioned on her chest with her flippers either tucked under the body or exposed, depending on the ambient temperature. Groups of females huddled together in contact in the prone position when the ambient temperature was low, presumably for warmth, while at higher temperatures they became separated (Gentry 1976). In the erect position, the neck and chest were held upright with body weight supported by the flippers. She generally appeared more alert in this position than when prone. Defecation usually occurred while the female was in a passive behavior (Stirling 19??).

2) Comfort - Female's scratched or groomed their upper body using their hindflippers, and rubbed their posterior with their muzzle. They would also rub their body and face on rocks, and their face and neck on other females. Animals occasionally repeatedly bit an area of their body. Presumably this behavior was necessary to sooth some form of irritation; sea lions have an anopluran louse on the skin, Antarctophthirius microchir (Dailey and Hill 1970). However, the mutual rubbing displayed between adjoining females or a female and her pup may have a social function. While all females displayed comfort behavior, it was particularly noticeable amongst females about to give birth.

3) Birth - Gentry (1970) and Sandegren (1970) have identified three stages in birthing: active, quiescent, and presentation. The active stage begins with the onset of labor and continues through the bursting of the amnion. This stage is marked by intensive agonistic interactions with other females, usually in concert with the search for a birthing site. Once a site has been established, the female alternates between relatively passive prone and upright positions. There is also considerable lateral rotation of the pelvis, including pressing and lifting of the perineum, as well as stretching and spreading of the hindflippers. Vaginal contractions may also be visible.

The quiescent stage begins with the amnion bursting and continues through the beginning of the presentation. Interactions with other females are uncommon at this stage. Motor components include swimming motions with the foreflippers, arching of the back with the hindflippers raised off the ground, continued lateral rotation of the pelvis to the the left and right, bending of the torso into a U-shape, and rotation of the whole body in circles, while she stares at the perineum. This is accompanied by low, undirected moans, vocalizations toward the perineum (this increases in frequency as birth approaches), and biting of the perineum. She may also sniff the amniotic fluid and occasionally may tear open the amnion.

The presentation stage includes the actual delivery of the pup. Generally, she appears totally oblivious to anything other than the pup. She may continue to move though, dragging the partially emerged pup with her. Vocalizations continue and reach a peak once the pup

has completely emerged. Usually the pup is delivered without her assistance, with the umbilicus breaking spontaneously, leaving the placenta inside. On rare occasions the female may reach back, grab the pup, and pull it free. Females also may break the umbilicus when it remains attached to the placenta. The placenta is delivered sometime later, and while the female may sniff it, she does not eat it. Once the pup is delivered, the female and pup spend considerable time sniffing and vocalizing to each other (Sandegren 1970; Ono 1972). An inactive pup may be stimulated by the female into activity.

4) Suckling - After birth, the female may lift the pup into a suckling position (Gentry 1970; Sandegren 1970) or she may leave the pup to find the position itself. When suckling, the female is usually in a prone position on her side, or upright with her hindquarters rotated to make the teats (four to six) accessible to the pup. The teats are either exposed spontaneously or may require stimulation by the pup nosing the area. The teats appear to remain exposed so long as she is in a nursing position. The female appears to initiate suckling in the first few days postpartum, and thereafter the pup begins the sessions. Females may also be suckled by older offspring (usually yearlings), and in rare instances by both a pup and its older sibling. In the latter situation, the older sibling is dominant to the pup and has better access to the teats. The mother may show aggression towards an older, suckling offspring.

5. Other maternal care of offspring - The most obvious example of this behavior is the vocal exchange between mothers and pups during the first weeks postpartum. This is also accompanied by

mutual olfactory or gustatorial inspections. The vocalizations and inspections appear to be important in establishing mutual recognition (Sandegren 1970; Ono 1972). A second major example is the mother's assisting the pup in its learning to swim (Sandegren 1970). Other examples of maternal care include pup-carrying (where the mother grasps the pup's neck with her teeth and carries it to another area), nuzzling, nipping, tooth rubbing (the mother scrapes her teeth along the pup's back and head), and licking. Mother's do not appear to give other care to older offspring. There is also no paternal care of offspring.

Other care included a variety of behaviors such as the mother's playing with and nosing of her pup, carrying of the pup out of harm's way, and the assistance of the pup in its learning to swim. The first was a relatively common event. Pup carrying was rare but was observed at all sites, although it was never observed in a sample female. Finally, assisting the pup in swimming was observed at both RR and UI, but not at MI. The lack of observations at MI may have been due to lack of observations during the time when pups are going to sea. Pups do not begin swimming in the sea until the fourth week postpartum (Sandegren 1970), thus frequent observations of swimming pups would not be obtained until mid-July, after the end of the MI and 1985 UI field seasons. However, the 1986 field season at UI extended past this period and as a consequence females were frequently seen swimming with pups. These observations indicate that females (presumably mothers) provide moral and occasional physical support, but do not actually teach the pup to swim. During these exercises the mother leads the pup into the sea, swims away from the

beach, usually to another beach, closely followed by the pup. If the pup falls behind, the mother will return to the pup and encourage it with vocalizations and may swim beneath the pup to support it, but by and large the pup is on its own. Through this process the pup builds the motor skills and physical strength for progressively longer forays. It is unknown whether all females provide this assistance to their pups; however, based on the resightings of known UI mothers with their pups on beaches (e.g., A1 and A3) other than the natal beach (i.e., A2) in mid to late July, it appears that many young pups (i.e., one to two months old) follow their mothers for at least short trips. These data on activity budgets include only the behaviors observed on land, thus excluding the time females spent at sea with their pup.

6. Movements - There are two general types of movements: intrarookery and to/from the sea. The former frequently result from agonistic interactions between females or between a female and male (as in the female's precopulatory behavior). Animals rarely change rest spots during the day, unless provoked or they go down to the water. The latter includes movements to and from the sea for thermoregulation at midday (Gentry 1976), and for feeding (returning in the morning and departing at night). Females returning from sea may spend considerable time vocalizing and moving through the rookery searching for her pup. This frequently results in threat displays between females. Movements to the sea are generally more direct and more peaceful, subject to the territorial males' herding tendencies.

7. Play - Females may play with their young (as discussed under other maternal care), with other adult females or by themselves.

Only play with pup occurs within the rookery per se; the remaining play occurs almost exclusively in the splash and intertidal zones. Play with other females (or subadults) includes mock fighting in the splash zone (Farentinos 1971), and chasing and leaping out of the water. Play in the water may be important in the coordination of movements of a group of females so that they can feed together at sea or elude the perimeter of aquatic males. Solo play includes tossing and rolling in kelp, and playing with rocks.

8. Female to female threat displays - This form of agonistic interaction usually occurs over a rest or birthing space, or a pup. The two or more females involved begin by facing-off, sometimes touching noses, and vocalizing. Vibrissae are erect and directed forwards, and the mouth is usually open. The females may then interlock mouths laterally and shake heads rapidly back and forth. The display usually ends at this point, either by one female giving a submission display or due to the intervention of the territorial male. Threat displays may also include head nodding (a rapid vertical nodding) and side slapping. In the latter, the female leans to one side, supporting herself with the foreflipper on that side, and slaps her side and venter with the other foreflipper, producing a loud sound. She may also do this while lying on her side or by slapping a rock, and may direct this towards other females in general, rather than towards a specific animal. Slapping is performed only by a few individuals (Gentry 1970).

9. Female to female fights - In rare instances, threat displays accelerate into actual fighting. This usually involves the females pushing each other at the chest and some grasping of necks and

shoulders. Few wounds are incurred. Some fights involve tug-of-wars over pups, where one female mistakenly identifies another female's pup as her own. The two females will then grasp opposite ends of the pup and a struggle ensues.

10. Female to male precopulatory displays - In this behavior the female moves throughout the rookery, displaying several exaggerated movements. These movements include all or part of the following: the vibrissae are erect and directed forwards, and the female is vocalizing; the head and neck are swung laterally; she alternates between running (from a slow to fast gait) and falling; the hindquarter may be drug on the ground, while there is intermittent urination and vaginal dilation. When a male is encountered, she may bite or snap at him, orient her body towards the male, allowing him to inspect her perineum, and may crawl on the male's back. These displays are most common around the time of estrus and may be used as an advertisement (Sandegren 1970, 1976).

11. Female to male submissive displays - This is the most common form of female to male display and is similar in form to the precopulatory displays, except that the movements are not as exaggerated. This is given to the male when she is being herded or inspected, or when the pup is in danger.

12. Copulation - This behavior can be separated into three stages - mounting, passive, and climax (Gentry 1970). In the first stage, the male is attempting to mount the female. In many cases, she will try to keep away from the male by walking in a slow circle keeping her head in contact with his, and her perineum oriented 180° away from him. She may, as in the submissive display, climb over the

male's back and bite his neck. If she is receptive, she will lower herself slightly while being inspected by the male. Once mounted she may struggle and vocalize, as if trying to escape, or she may be submissive and allow him to mount without a struggle. The choice of behaviors may relate to her estrus state. If the male dismounts prior to copulating she will usually remain in place. If she is very active, then repeated mounts and dismounts by the male will produce a more passive state. Normal behavior after mounting seems to be for the female to keep her head up, looking around somewhat, and with some struggling.

Ultimately, the female will stop struggling and enter the passive stage. She will then lay prone, her hind flippers, her genital area opposed to the male's, and with her eyes closed or open and appearing glazed. She may occasionally raise her head and neck and press them against the male's. This stage may be begun by the initial shallow intromission of the male and ends once thrusting intensifies.

The climax stage begins during the deep thrusting of the male, with the female beginning to struggle again, rising on her foreflippers and vigorously biting the male's neck and lower jaw. Struggling intensifies until the male dismounts, and may include the female defecating or urinating. She becomes passive again after the male dismounts, lying still for a short time. She will then rise, perhaps look and nose her perineum, and move off. Females frequently appear agitated at this point and may be involved in several threat displays with females before she settles back into a rest area. Other males will ignore the female at this time.