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Maternal attendance and pupping site fidelity of Steller sea lions in Alaska

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MATERNAL ATTENDANCE AND PUPPING SITE FIDELITY OF STELLER SEA LIONS IN ALASKA

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by

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ABSTRACT

MATERNAL ATTENDANCE AND PUPPING SITE FIDELITY OF STELLER SEA LIONS IN ALASKA

by Pamela Parker

From 2001-2005 maternal attendance patterns and pupping site fidelity among individual Steller sea lions (*Eumetopias jubatus*) was studied at Chiswell Island, a small rookery in the Gulf of Alaska. Photo-identification and remotely operated cameras were used to identify and observe individual females without disturbance. Females foraged at sea an average of 3.3 times greater in duration during autumn compared with summer, and average durations of foraging trips during autumn were not significantly different among years or throughout any autumn season.

Pupping site fidelity was defined as giving birth within 5.8 m of a previous pupping location in at least 2 years. Mean frequency of pupping site fidelity was similar for females that gave birth 2-5 times. Distribution of births on the rookery was not random; multiple births occurred at some locations throughout the breeding season, and pups were born more frequently in pupping locations with advantageous physical attributes.

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CHAPTER 1:

PUPPING SITE FIDELITY AMONG INDIVIDUAL STELLER SEA LIONS (*EUMETOPIAS JUBATUS*) IN THE GULF OF ALASKA

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ABSTRACT

Pupping site fidelity (defined as ≤5.8 m between pupping locations in ≥2 years) of Steller sea lions (*Eumetopias jubatus*) was investigated during the breeding seasons from 2001-2005 at Chiswell Island, a small rookery in the Gulf of Alaska. Photo-identification and GPS locations, including elevation of the rookery, were used to determine location of birthing for individual females. Timing of births and storms during summer significantly increased the mean distance among pupping locations, used in different years, for individual females. Sixty-two percent (34/55) of multiparous females (with ≥2 births) exhibited pupping site fidelity at least once from 2001-2005. Mean frequency of pupping site fidelity was similar among females that gave birth 2-5 times. Fifty percent of the births occurred at 22% of the pupping locations during all years, implying multiple births occurred at some locations throughout the breeding season. Competition or aggression among females for specific pupping locations before birth was not observed, indicating the rookery was not overcrowded and many suitable pupping locations existed. Pups were born more frequently in proximity to vertical rock walls and/or cracks, with easy

access to water used for thermoregulation, and greater than 5 m from the surf zone. Multiparous females gave birth at locations with a significantly greater number of advantageous physical attributes than primiparous females. Long-term monitoring of pupping site fidelity in combination with other measures of maternal care will ultimately determine which factors have the greatest effect on pup survival.

INTRODUCTION

Breeding site fidelity, returning to the same rookery in multiple years, has been documented in many pinnipeds including: northern elephant seals (*Mirounga angustirostris*; Le Boeuf and Laws 1994), southern elephant seals (*M. leonine*; Lewis et al. 1996), grey seals (*Halichoerus grypus*; Pomeroy et al. 1994), northern fur seals (*Callorhinus ursinus*; Baker et al. 1995), Hooker's sea lions (*Phocarctos hookeri*; Beentjes 1989), and Steller sea lions (*Eumetopias jubatus*; Edie 1977; Gisiner 1985; Milette and Trites 2003; Raum-Suryan et al. 2002). Few investigators have quantified fidelity in terms of either the locality of pupping at the rookery or the frequency of return to particular locations within a rookery. At smaller spatial scales, some pinnipeds also exhibited some degree of pupping site fidelity within a rookery (Edie 1977; Gentry 1970; Higgins and Gass 1993; Lunn and Boyd 1991; Pomeroy et al. 1994). Pinnipeds that exhibited pupping site fidelity had a tendency to use similar pupping habitat in multiple years, and one hypothesis was that females gave birth in pupping habitats with physical attributes that were advantageous for pup survival (Pomeroy et al. 1994). Studies conducted in the late 1960s and early 1970s indicated that female Steller sea lions gave birth at certain locations within rookeries based on physical attributes of the habitat, such as proximity to water for thermoregulation, territorial bull interactions, and environmental factors (Edie 1977; Gentry 1970; Sandegren 1970).

Observing individual females and their use of specific pupping locations within a rookery can provide information on habitat (rookery) quality and factors that influence where females give birth. Experience with space may increase fitness or reproductive success because animals probably incur lesser costs remaining in a familiar space, territory or home range (Stamps 1995). The impact of pupping site fidelity on reproductive success (i.e. pup survival) is one aspect of female maternal care in Steller sea lions that is not well understood. Female Steller sea lions, like other otariids, give birth to one pup per year on land, and are capable of nursing them until 4 years of age (Gentry 1970; Pitcher and Calkins 1981; Riedman 1990; Sandegren 1970). After foraging elsewhere during winter, females return to rookeries by the end of May, and breeding is usually completed by mid-July (Edie 1977; Gentry 1970; Maniscalco et al. 2006). Females are gregarious but not overly territorial, however, space availability in terms of suitable pupping locations, may determine female distribution on the rookery and degree of female aggregation (Baldi et al. 1996; Emlen and Oring 1977).

The western stock of Steller sea lions is currently listed as endangered under the United States Endangered Species Act (ESA) as a result of continued dramatic decreases beginning in the 1970s (Loughlin et al. 1992; Merrick et al. 1987; Sease and Gudmundson 2002). Ecosystem change is one hypothesis that explains the decline of Steller sea lions (NRC 1996, Paine et al. 2003). Ecosystem fluctuation can alter the local environment at rookeries, such as increasing storms during summer, therefore, it is important to understand where Steller sea lions give birth and how they maneuver on the rookery during high surf conditions or other environmental perturbations.

Availability of suitable pupping areas within rookeries has been an important influence on the evolution of polygynous mating systems in otariids (Stirling 1983). At rookeries with high densities, female dispersion within a rookery has been affected by the density of females and male harassment (Bartholomew 1970; Riedman and Le Boeuf 1982). We studied female dispersion on a rookery with a lesser density of females, and anecdotal observations indicated that male harassment of females did not affect pupping locations. We documented other important factors that influenced female dispersion and selection of pupping locations such as physical attributes of the rookery. We predicted that the selection of a pupping location by females was a learned behavior, and that experienced females (those that gave birth ≥2 years at Chiswell Island) would give birth in pupping locations with a greater number of advantageous physical attributes. If female otariids give birth at their previous pupping locations that contained advantageous physical attributes they may increase their reproductive success (pup survival). They also would maximize their time on shore because they would be experienced with pathways to sea on the rookery, maneuvering within their pupping location, and would possibly be familiar with neighboring males and females.

Because females may give birth at pupping locations with specific physical attributes, we expected a non-random distribution of births at Chiswell Island. We also expected that environmental variables such as weather, physical attributes of the rookery, and access to water while on shore affected the distribution of births. We were concerned with where females gave birth within the pupping area of the rookery and if pups survived 24 h after birth.

METHODS

Study area and data collection. - This study was conducted at a small rookery on Chiswell Island (59°36.13'N, 149°34.05'W), in the northern Gulf of Alaska 65 km south of Seward, Alaska. Steller sea lions at Chiswell Island are part of the endangered stock west of 144°W longitude (Fig. 1). In July of 1956, the earliest published aerial photographic census indicated there were 1459 adult and 564 Steller sea lion pups (Mathisen and Lopp 1963). Since 1956, the number of sea lions using Chiswell Island decreased rapidly through the 1980s, currently with about 90 breeding animals producing approximately 50-80 pups per year (Maniscalco et al. 2002, 2006). Chiswell Island is composed of granite rock and is variable in terms of steepness, structural variability, and protection from environmental factors.

To conduct a long-term monitoring study of the Steller sea lions at Chiswell Island, the Alaska Sealife Center contracted with SeeMore Wildlife Systems, Inc. of Homer, Alaska to install remote-operated cameras in October 1998

(Maniscalco et al. 2006). Six cameras were used during the breeding season (May-August) for complete coverage of the rookery, however, only 2 cameras could be viewed and operated at the same time from the Alaska Sealife Center in Seward, Alaska (Maniscalco et al. 2006). This remote-monitoring system allowed us to observe the sea lions in their natural habitat on a year-round basis without disturbance and without difficulty of sampling in harsh weather conditions.

Data for this study were collected in conjunction with a study of maternal investment of identifiable females from 2001-2005 (Maniscalco et al. 2006). Individual females were identified by their natural markings such as scars, fungal patches, and flipper uniqueness. Females were photographed from as many angles as possible under different lighting conditions, and the photographs and an index of pelage wetness were entered into a Microsoft Access database with additional written details concerning individual identification. Females that were identified in any year from 2001-2005 were considered known females. Parity was determined for females that gave birth more than once (multiparous) at Chiswell Island, and for primiparous females with distinctive natural markings or flipper tags that were never, before their first year of pupping, observed giving birth at Chiswell Island (Maniscalco et al. 2006).

Times of births were recorded to the nearest minute opportunistically from 2001-2005. For births that were not observed we used the time halfway between when females were and were not observed with a pup, only when the period of no observations was <8 h. Detailed information was recorded during births including weather conditions, use of habitat, and any interactions with other animals. Digital photographs and high-quality video tapes (6 h duration) were used to document births. The pupping area of the rookery was approximately 40 x 20-m, and was divided into sections based on the locations pups were born from 2001-2002. Each section of the rookery was given a reference number that was used to determine the pupping location within (±) 0.01 m for each female that gave birth from 2001-2005.

GPS positions (± 0.01 m accuracy) including elevation were determined for each birth observed for all years using Leica Geosystems equipment. The physiography of the rookery also was determined at 0.5 m intervals using a GPS along transects parallel to the tide line, spaced 1 m apart on the rookery. Physical attributes of the pupping area were noted including structural features such as: cracks (<45° angle and <0.5 m tall), rock walls (≥45° angle and ≥0.5 m tall), tide pools, descriptions of slope (relative change in slope), roughness of terrain (smooth = even surface, or rough = uneven surface), and approximate distance from the surf zone.

Habitat characterization and data analysis. - To visually represent the data, GPS points corresponding to each birth were displayed in ArcMap (ESRI, Inc.). A 5 x 5-m grid was overlayed on the pupping area and the observed number of births per quadrat from 2001-2005 was used to test whether births were randomly (Poisson distribution) distributed. A chi-squared test was used to compare the expected (Poisson) number of births with the observed number of births per quadrat.

The most common physical attributes within the pupping area used by females were quantified using a scoring system (App. I). A similar method was used by Edie (1970) to classify and test the significance of factors that influenced the distribution of births of Steller sea lions at Cape St. James, British Columbia. Grids with square quadrats ranging in size from 2 x 2 to 8 x 8-m were overlayed on the pupping area of Chiswell Island. Quadrats with <50% available pupping habitat were not included in the analysis. Quadrats were scored using criteria (hypotheses) that were developed from observations of females that gave birth from 2001-2002 at Chiswell Island and from previous studies that characterized the pupping locations of Steller sea lions (App. I). Each scoring criterion had an associated value used to score quadrats, thus, quadrats with the greatest scores contained more physical attributes considered advantageous. Linear regression analyses were performed to compare the number of births with quadrat scores for each grid size for each year. The greatest coefficient of determination for each year was used to determine the average quadrat size needed to characterize physical attributes within pupping locations.

The definition (size) of a pupping location was determined by calculating the distance between births that occurred within 24 h of each other using GPS locations that corresponded to each birth for all years. This determined the respective distance between females that gave birth. The least frequent distance between births was determined from a frequency distribution that defined the radius of a pupping location within 24 h after birth. Distances between pupping locations were determined by calculating the distance between the center (point) of each pupping location. The time between births that occurred at the same pupping location was calculated for all years. A birth was classified as occurring at the same pupping location if the distance between 2 locations was 0 m. The most common pupping locations were determined by the number of births that occurred per location for all years.

The distances (± 0.01 m) between pupping locations used in different years from 2001-2005 by individual females were calculated. Paired comparisons were conducted for known females to determine if the distance among pupping locations used in different years increased in the year with a summer storm or when there was a social interaction between females. Frequency of pupping site fidelity for individual females was determined for females that gave birth 2-5 times by calculating all distances among pupping locations used from 2001-2005. To determine if pupping site fidelity occurred by random chance, a randomization test was conducted by selecting 5 random grid points on the pupping area of the rookery. One hundred trials were conducted and each trial was considered a good representation of 5 random pupping locations that could be used by a female. Distances among the 5 points were calculated by the same method used to determine the frequency of pupping site fidelity for individual females.

Comparisons were made among females using parametric methods after determining that the data met assumptions of normality and independence (Zar 1999). Non-parametric tests were conducted when unequal variances occurred. Distances were reported assuming ± 0.01 m accuracy throughout this document. Data were reported as mean ± standard error (*SE*), and statistical analyses were performed using SYSTAT V. 10 (SSI, Inc.). For all statistical analyses, *P*-values <0.05 were considered significant.

Permits for this research were obtained from the National Oceanic and Atmospheric Administration, National Marine Fisheries Service (Numbers 782-1532-00 & 881-1668-00) under the authority of the Marine Mammal Protection Act and the Endangered Species Act. Additional Special Use Permits to conduct this research on refuge lands were acquired from the United States Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge. This study was purely observational, and followed American

Society of Mammalogists guidelines (Animal Care and Use Committee 1998).

RESULTS

Definition of a Pupping location. - The number of pups born at Chiswell Island increased annually from 54 in 2001 to 80 in 2004, then decreased to 54 in 2005 (Table 1). Of the 325 pups born from 2001-2005, 297 births were observed within ± 4 h of their occurrence (237 births by known females and 60 by unknown females). An average of 91.5% of the births was observed each year (range: 82-100%). The distance between births that occurred within 24 h of each other was calculated for 627 occurrences for all years. Females gave birth more frequently ≥3 m away from a location where another female gave birth in the previous 24 h (Fig. 2). Ninety-five percent of all births occurred >2.9 m away from births within the previous 24 h; only 1% of births occurred <1 m apart. Therefore, a pupping location was defined as a circle with a 5.8 m diameter (radius: 2.9 m) for 24 h after a birth at Chiswell Island. Females used an average of 40 (± 3.8 *SE*) pupping locations per year, with 91 different pupping locations used from 2001-2005 (Table 1).

Distribution of Pupping Locations. - Births were not randomly distributed within the pupping area of the rookery ($X^2 > 1.0 \times 10^8$, $P < 0.001$). Fifty percent of the births occurred at 22% of the pupping locations during all years, births occurred at the center of these locations (Table 2). These locations (22%) were defined as the most common pupping locations, where 6-11 births occurred per location. The greatest number of births at any pupping location was 11, and only a single birth occurred at 33 of the 91 unique locations from 2001-2005 (range: 1-11 births per location; Table 2).

There was a significant relationship between the habitat scores (based on physical attributes) for pupping habitats (quadrats) and the number of births in those habitats for all years of the study. However, the quadrat size with the greatest coefficient of determination varied among years ranging from 5 x 5-m in 2001 ($r^2 = 0.283$, $P = 0.002$) to 8 x 8-m in 2005 ($r^2 = 0.511$, $P = 0.003$). On average, 48.6% of the variability associated with where births occurred within the pupping area of the rookery was explained by the relationship between scores for pupping habitats (quadrats) and number of births in those habitats. The average quadrat size for all years, with the greatest coefficient of determination, was 6.6 x 6.6-m. Therefore, we defined the size of a pupping location based on physical attributes was approximately 6.6 m in diameter. This implied that physical attributes that were advantageous to females during birth were within a 3.3 m radius. Pups were born more frequently in quadrats with the greatest number of the following physical attributes: rock walls, overhanging shelves (rock wall above and adjacent), cracks, and tide pools. Eighteen quadrats were scored, based on physical attributes, for a 7 x 7-m grid (closest quadrat to 6.6 x 6.6-m) with a median score of 6 (range: -1-13). Therefore, we determined that quadrats with scores greater than the median were the most suitable pupping habitats for giving birth based on physical attributes. Seven of 18 quadrats had scores >6, which were located in or adjacent to the central portion of the pupping area and were >5 m from the surf zone (determined using ArcMap; Fig. 3). The 7 quadrats with the greatest scores contained all combinations of surfaces of the rookery such as: steep (constant change in slope) and smooth (even surface), steep and rough (uneven surface), flat (relatively no change in slope) and smooth, and flat and rough.

The most common pupping locations for all years, where 50% of the births occurred, were mainly within the 7 quadrats with greatest habitat scores (7 x 7-m grid; Fig. 3). Multiparous females gave birth at pupping locations with significantly greater habitat scores ($\bar{x}$ = 8.7 ± 3.2 score) compared with primiparous females ($\bar{x}$ = 6.1 ± 1.1 score; $t = -3.05$, *d.f.* = 140, $P < 0.003$) for all years. Parity was known for 77 of 149 births (50% of the births) that occurred at the most common pupping locations from 2001-2005. Multiparous females gave birth at the most common pupping locations 90% (69/77) of the time, whereas primiparous females only gave birth at those locations 10% (8/77) of the time, however, sample size for primiparous females was minimal.

Pup survival. - Five pups were born <3 m from the surf zone from 2001-2005, three of these pups involuntarily entered the water seconds after birth; 2 mothers of these pups were primiparous females (Fig. 3). Two of the females retrieved their pups from the ocean and one primiparous female did not respond, leaving the pup to be washed away with the ocean currents and presumed to have drowned. This was the only pup that died less than 24 h after birth in all years, whose death was associated with distance from the surf zone. From 2001-2005, no other pups died within 24 h after birth directly related to where their mothers gave birth on the rookery.

Storms in June of 2002 occurred when the majority of pups were too young to swim effectively or climb back out of the sea onto the rookery. These storms were responsible for 11 pup losses representing 17% of the pups born at Chiswell Island in 2002. Of the 11 pups, 6 were born to known females and the pups were an average of 6.5 days old (range: 2.3-14.2 days) when the storms occurred. Only four of those 6 females returned to pup in 2003. Two of those returning females were observed giving birth for the first time at the rookery in 2002 (parity uncertain) and used pupping locations in high surf areas that went totally awash during the storms. In 2003, those same 2 females gave birth at the most common pupping locations, which were in the central portion of the pupping area and farther from the surf zone.

Pupping site fidelity. - Twenty-two females gave birth at Chiswell Island in 2 years, 10 in 3 years, 15 in 4 years, and 7 in all 5 years from 2001-2005. The time between births that occurred at the same location (distance between two births was 0 m) for each breeding season was calculated for 97 occurrences from 2001-2005. Females gave birth more frequently at the same location >3 days after another female gave birth at that location (Fig. 4). Five percent of females gave birth at the same location within 1.8 days of each other from 2001-2005. There were only 2 instances of births that occurred at the same location within 1 day, therefore, 1.8 days was used to determine if timing of birth had an effect on the distance among pupping locations for individual females. There were 8 known females that did not give birth at their most recent pupping location when another female gave birth at that same location within 1.8 days of when they gave birth. For these 8 females, the distance between births in consecutive years was significantly greater if another female had given birth at their previous pupping location within 1.8 days ($\bar{x}$ diff = 7.03 ± 1.98 m; paired $t = 3.55$, $P = 0.009$). We referred to this as the timing of birth effect.

Summer storms also had an effect on the distance among pupping locations for individual females. Six females that gave birth during or just following summer storms in June of 2002 had significantly greater distances between pupping locations used during the storm and 1 other year compared with years without summer storms ($\bar{x}$ diff = 10.93 ± 2.91 m; paired $t = 3.76$, $P = 0.013$). Females gave birth at greater elevations, farther from the sea avoiding high surf conditions associated with those storms. We referred to this as the storm effect.

Pupping site fidelity was defined as an individual giving birth ≤5.8 m from a location she used in a previous year from 2001-2005. Fifty-five known females gave birth at least 2 times from 2001-2005, 34 (62%) of these females exhibited pupping site fidelity at least once. Timing of birth and storm effects had significant influences on the distances among pupping locations used by individual females, thus, we removed all locations with these effects because they would decrease individual pupping site fidelity. We determined that females without pupping site fidelity ($n = 21$) had a significantly greater mean distance between pupping locations compared with females that exhibited pupping site fidelity ($n = 34$; $\bar{x} = 14.4$ m versus $\bar{x} = 7.2$ m; Mann-Whitney rank sum, $P < 0.001$).

Mean frequency of pupping site fidelity was similar for females that gave birth 2-5 times at Chiswell Island, when all distances among locations were considered for each female (Fig. 5). Multiparous females exhibited pupping site fidelity an average of 37% of the time at Chiswell Island. However, when only pupping locations used in 2 consecutive births were considered, mean frequency of pupping site fidelity was greater for females that gave birth 4 or 5 times compared with females that gave birth 2 or 3 times from 2001-2005 (Fig. 6). A randomization test determined that there was less than a 1% chance of exhibiting 37% pupping site fidelity by random chance alone.

Four of 6 females that skipped 1 pupping season exhibited pupping site fidelity at least once. Two females gave birth in 2001 then skipped 3 consecutive years and returned to pup in 2005. One of these females exhibited pupping site fidelity and 1 gave birth 6.96 m away from her location used in 2001. Twelve of 55 females, that gave birth at least 2 times from 2001-2005, gave birth at the same location, where the distance between 2 births was 0 m. Only 1 female exhibited pupping site fidelity every time she gave birth at Chiswell Island from 2001-2005.

DISCUSSION

Female Steller sea lions exhibited breeding site fidelity at Chiswell Island, returning to give birth at the rookery multiple years. Within rookeries, individual Steller sea lions also exhibited pupping site fidelity (Edie 1977, Sandegren 1970), and selection of their pupping locations depended on several environmental factors. For example, Sandegren (1970) indicated pupping locations of Steller sea lions at Montague Island, Alaska had the following common attributes: (1) above the high tide line, (2) shelter from storms, (3) easy access to protected shallow water, (3) gentle slopes, and (4) protection against strong solar radiation. Gentry (1970) determined that births on Año Nuevo Island, California occurred at locations of the rookery near tide pools or spray zones during greater temperatures and speculated that females needed to regulate their body temperature. Edie (1977) also indicated the influences of environmental factors on the distribution and movements of pre-estrus Steller sea lions at Cape St. James, British Columbia. In that study, females gave birth on relatively flat, level locations away from major crevices. Females also displayed different aggressive behaviors as a result of overcrowding at the most common locations. Furthermore, a storm during the summer of 1973 at Cape St. James, caused 30% pup mortality for identifiable females, indicating that using protected locations increased pup survival. Edie (1977) concluded that females were influenced by trade-offs of access, protection, and crowding in addition to favoring less rugged terrain.

The distribution of births on Chiswell Island was not random, which was consistent with previous results. More births occurred at pupping locations that contained a greater number of advantageous physical attributes such as cracks, rock walls, and tide pools. Anecdotal observations indicated that females used rock walls and cracks during births to decrease the chance of displacing their pup once born. Pups born at locations without these attributes tended to slide away from the mother just after birth requiring her to retrieve her pup (Sandegren 1970; this study). This compares with Australian sea lions (*Neophoca cinerea*) and New Zealand fur seals (*Arctocephalus forsteri*) that gave birth at pupping locations characterized by the presence of ledges or crevices for pups to hide within when their mothers were foraging at sea (Bradshaw et al. 1999; Higgins and Gass 1993). At greater densities, south

American fur seals (*Arctocephalus australis*) competed for pupping locations near wet intertidal areas used for thermoregulation, a lack of access to water caused early pup mortality (Cardenas et al. 2005). Our results also indicated that tide pools in pupping locations with the greatest habitat scores were advantageous to females and pups by providing a source of water for thermoregulation. The most common pupping locations on the rookery were all greater than 5 m from the surf zone, which protected pups from surf conditions during high tide when pups were too young to swim effectively.

We also observed that some females gave birth at pupping locations that were <3 m from the surf zone and not the most suitable locations for controlling their pup just after birth. One hypothesis was that females that gave birth at pupping locations with less advantageous physical attributes were inexperienced (<2 years of giving birth) or it was their first time giving birth at Chiswell Island. We observed 2 known primiparous females that gave birth <3 m from the surf zone on relatively steep inclines and their pups involuntarily entered the water within a minute of birth. One of these females exhibited good maternal care by retrieving her pup from the surf, whereas the other female did not respond and the pup presumably did not survive. This was the only pup that died within 24 h after birth because the mother gave birth at a less suitable location. Most of the time we observed a maternal bond between mothers and pups just after birth that was characterized by females picking up pups, nuzzling, and vocalizing.

Our observations that births generally did not occur at the same location within 24 h and that the most common pupping locations had specific physical attributes was similar to other studies, however, those researchers observed females aggressively defending space just before birth. Sandegren (1970) documented maximum aggressiveness just before birth when the density of females was greatest, with female Steller sea lions defending a 3 x 3-m area. Gentry (1970) also observed that females defended a space during birth with a maximum radius of 2.5 m, similar to the 2.9 m we observed. He concluded that aggressive behavior among females during birth protected their pups from other aggressive females. We did not observe aggressive interactions among females before birth that resulted in displacement of a female to another pupping location on the rookery. This implies that the size of space that a female occupies during birth can be influenced by a combination of social and environmental factors. One factor may be more important than another depending on the density of females or the prevailing weather conditions. For example, harsh weather conditions could influence females to extend maternal care by giving birth within a certain distance from advantageous physical attributes thus protecting a pup.

Studies in the 1960s and 1970s documented some degree of pupping site fidelity in Steller sea lions. For example, Edie (1977) observed that 4 of 32 identifiable females gave birth <10 m from where they gave birth the previous year. Gentry (1970) also determined that 24% (30/122) of identifiable female Steller sea lions returned to pupping locations (areas within a rookery) in successive years. He suggested, however, the tendency was greater than he reported, and attributed the lesser percentage to under-sampling individuals. We observed that 62% of the females that gave birth ≥2 times at Chiswell Island from 2001-2005 exhibited pupping site fidelity at least once. We determined that the mean frequency of pupping site fidelity (37%) was similar among females that gave birth 2-5 times at Chiswell Island, when all distances among pupping locations were considered for each female. This indicated that Steller sea lions were capable of identifying a familiar space on Chiswell Island after giving birth ≥2 times. We did not observe a difference in frequency of pupping site fidelity among females probably because we did not know the age of multiparous females. Presumably older females have given birth a greater number of times, thus, they would have more experience with pupping locations on a rookery compared with younger females. Our sample groups of females that gave birth 2-5 times could have consisted of females with varying degrees of experience, which may have inhibited our ability to detect a significant difference in frequency of pupping site fidelity. We also may not have had sufficient sample sizes for detecting significant differences among females of known age. By continuing long-term monitoring of this breeding group of sea lions we will be able to observe a greater number of known age females and determine if the frequency of pupping site fidelity increases with age. In this study, when only pupping locations used in 2 consecutive births were considered for each female, mean frequency of pupping site fidelity was greater for females that gave birth >3 times from 2001-2005. These results indicated that individual pupping site fidelity at Chiswell Island may increase with experience, in terms of number of births, with females returning to their most recent pupping location. Antarctic fur seals (*Arctocephalus gazella)* also exhibited individual pupping site fidelity with a radius of 2-6 m between pupping locations used in successive years (Lunn and Boyd 1991). Higgins and Gass (1993) observed pupping site fidelity in Australian sea lions; 69% of identifiable females gave birth within 5 m of where they gave birth in a previous year. Australian sea lions exhibited pupping site fidelity even when the season for pupping was a 17.6-month breeding cycle. We also observed that female Steller sea lions exhibited pupping site fidelity even when the time between successive pups was >1 year.

Sandegren (1970) reported that the social status and density of female Steller sea lions affected pupping locations on a rookery. Females of lesser dominance gave birth at marginal pupping locations where aggressive females did not give birth, and aggressive females displaced others from the most common pupping locations. However, he observed 90% of all births occurred at three pupping locations in 1967 and at four locations in 1968, leading to overcrowding in the most common locations in the central portion of the rookery (Sandegren 1970). The timing of birth effect indicated that crowding was not a factor at Chiswell Island because multiparous females did not compete for pupping locations they used in the previous year; instead they gave birth at other suitable pupping locations with advantageous physical attributes. In 7 of 8 occurrences of a timing of birth effect, females that gave birth at the location previously used by the returning female also were multiparous. This indicated that the frequency of pupping site fidelity may have increased for multiparous females without the timing of birth effect because density of females was minimal, thus, their previous pupping locations were accessible. In contrast, pupping site fidelity decreased for females with the timing of birth by increasing the distance between pupping locations when density of females was minimal, yet the quality of pupping habitat was the same. Pupping locations with advantageous physical attributes may be the main factor determining where births occur at a rookery when density of females is minimal, because there may be a greater cost for competing for a previous location. In 2004, when the greatest number of births occurred and the timing of birth effect was most frequent, there was a greater amount of suitable pupping habitat available than was needed for the number of females that gave birth. On rookeries where there is limited suitable pupping habitat, we predict that multiparous females would exhibit a greater frequency of pupping site fidelity by competing for their previous pupping locations that contain advantageous physical attributes. Overall, the timing of birth effect seemed to have no other negative influence on maternal care for individual multiparous females (Maniscalco et al. 2006).

Timing of birth within the breeding season and the duration of perinatal period have been used as indicators of maternal care in many pinniped studies (Boyd 1996; Higgins and Gass 1993; Hood and Ono 1997; Le Boeuf et al. 1972; Milette and Trites 2003; Pomeroy et al 1999), and can be related to food quality or abundance before birth (Boyd et al. 1991; Doidge and Croxall 1989). For northern elephant seals and Antarctic fur seals, older females tend to give birth earlier in the season than younger females and are presumably more experienced at prey capture (Doidge et al. 1986; Lunn et al. 1994; Reiter et al. 1981). This may allow them to remain on the rookery and defend a suitable location longer before making a trip to sea, increasing survival of their pup. Older Antarctic fur seals and northern Elephant seals that were in better health and returned to breeding beaches earlier occupied the most suitable pupping locations for protecting pups and giving birth when densities were decreased (Lunn and Boyd 1993; Reiter et al. 1981).

Results of the maternal investment study that was conducted in conjunction with this study documented that the number of primiparous females that gave birth at Chiswell Island increased in 2004 (Maniscalco et al. 2006). In 2004, multiparous females gave birth significantly earlier and had significantly greater perinatal periods compared with primiparous females. We did not observe multiparous females displacing primiparous females from pupping locations before birth, possibly because Chiswell Island was not crowded and many suitable pupping locations existed. Primiparous females gave birth at locations with significantly less advantageous physical attributes that were suitable for pup survival, regardless of the social status or number of females at the rookery. By continuing to monitor this breeding group of sea lions in order to observe primiparous females during birth, we can determine if they return to their first pupping locations or eventually gain status and occupy the most common pupping locations on the rookery. Overall we did not observe a temporal order of pupping locations used within the rookery, whereas, other researchers of Steller sea lions documented that females occupied the most accessible locations first, followed by less accessible locations (Edie 1977; Gentry 1970). At Chiswell Island, individual pupping site fidelity and the number of advantageous physical attributes within pupping locations were the important predictors of when and where pupping locations occurred on the rookery.

Our study has provided important information on how female sea lions respond to environmental pressures. This is especially important if ecosystem fluctuations are occurring in the Gulf of Alaska, causing changes in the local environment at rookeries such as an increase in storms during summer. Although we concentrated our efforts on documenting pup survival within 24 h after birth, we also observed pup mortality during 2 storms at Chiswell Island. Pups of known females that were lost to sea during these storms were an average of 6.5 days old, and all of their mothers were present during the storm. These pups did not survive because they were unable to swim effectively or they could not climb back out of the sea onto the rookery. We could not statistically test if these pups were lost at sea as a direct result of where their mothers gave birth on the rookery. Anecdotal observations during the storms indicated that pups survived because either they moved or their mothers moved them to greater elevations that were more protected during the storms.

Although the storm effect had a negative influence on individual pupping site fidelity by increasing the distance between pupping locations used in different years, it may have had a positive affect on pup survival during subsequent years. Females that gave birth during or just following summer storms of 2002 used pupping locations that were greater in elevation and farther from the sea. Edie (1970) documented a similar response by female Steller sea lions during storms at Cape St. James, British Columbia; he documented that a greater number of births occurred at pupping locations that were more protected and farther from sea during periods of high waves. Pup loss during the storms probably occurred from inexperience in maternal care in terms of maneuvering pups on the rookery. Examining behaviors of experienced and primiparous (inexperienced) females during storms that occur during summer is useful for understanding the relationship between maternal behavior and pup loss at rookeries.

Territorial bull behavior is another factor that has potential to affect individual pupping site fidelity and the distribution of births on a rookery. In 2005, we observed the greatest number of first-year bulls occupied territories within the pupping area of the rookery. Anecdotal observations also indicated that male boundary displays and fighting was greater in 2005. Territorial bull Steller sea lions that are familiar neighbors have less aggressive interactions than new neighboring bulls (Gisiner 1985). Gisiner (1985) documented that extreme bull fighting had a direct and adverse affect on females, which caused them to move away from areas where fighting occurred for several days. In 2005, there were fewer births within territories occupied by the bulls involved in the majority of the aggressive interactions indicating that territorial bulls may have had an effect on individual pupping site fidelity and the distribution of births. In contrast, female south American sea lions (*Otaria flacescens*) aggregated within bull territories to reduce harassment by males and increase reproductive success by decreasing pup mortality.

Availability of suitable pupping areas within rookeries has been an important influence on the evolution of polygynous mating systems in otariids for the following reasons: births occur on land, males are attracted to females in estrus, and copulations occur after birth (Stirling 1983). In otariids, density of females and territorial behavior of males influenced female dispersion within a rookery and female reproductive success (pup survival; Bartholomew 1970; Riedman and Le Boeuf 1982). For example, Cassini (2000) developed a cost-benefit model of pup survival, with female-female competition for space as the cost and reduced male harassment as the benefit. That model predicted that the size of female aggregations at suitable pupping locations was regulated primarily by avoidance of male harassment and secondarily by female competition for space.

At Chiswell Island, however, density of females was minimal, and anecdotal observations indicated that male harassment of females did not affect pupping locations. Distribution of births was influenced by the quality of the pupping area within the rookery, therefore, females were distributed based on suitable pupping locations. Our observations indicated that selection of a pupping location was a learned behavior because experienced females gave birth more frequently at locations with more advantageous physical attributes, compared with primiparous females. Female Steller sea lions at Chiswell Island may have learned site-specific motor skills for rapid, safe, and consistent locomotion within pupping locations (Stamps 1995). Multiparous females that gave birth at their previous pupping locations probably increased their reproductive success (pup survival) and maximized their time on shore because they were experienced with pathways to sea on the rookery, maneuvering within their pupping location, and possibly were familiar with neighboring males and females. Therefore, it seems plausible that females gave birth at the same location in consecutive years when their location was not occupied by another female and their pup survived the previous year.

Selection of a suitable pupping location also was advantageous to female otariids for mother-pup recognition after birth. Lactating Antarctic fur seals, that were translocated with their pups away from their original pupping locations, returned to their original pupping locations (± 1.5 m) within 24 h after release; and their pups were left to navigate back to their original pupping locations on their own (Lunn and Boyd 1991). That study concluded that within-year pupping site fidelity was a function of mother-pup recognition because females used a combination of familiarity of space and vocalization to recognize their pups. Lunn and Boyd (1991) implied that mother-pup recognition was important during times of greater densities of females to avoid separation from their pups, which was the main cause of pup mortality in that study. Pupping locations also have been documented as "home spots" for lactating female otariids that allowed reunion with their pups after foraging trips at sea; this is a low-cost strategy that minimizes search time when used with vocal recognition of the pup (Phillips 2003; Sandegren 1970). Thus, inter- and intra-annual pupping site fidelity was considered a learned behavior that increased female reproductive success. Success increased because females gave birth at suitable pupping locations with advantageous physical attributes in consecutive years and used those locations throughout lactation to help recognize their pups after separating on the rookery or after returning from foraging trips.

Fidelity toward a particular pupping location occurred at Chiswell Island from a combination of the following factors: familiarity of space, pup survival, experience with rookery weather conditions, advantageous physical attributes within pupping locations, and probably other unidentified factors. It is important to consider the results of this study in a site-specific manner. Weather conditions and terrain vary among rookeries throughout the range of Steller sea lions, therefore, the physical attributes within pupping habitats that are advantageous to females during birth also may vary (Calkins et al. 1999; Call and Loughlin 2005; Kucey 2005). Chiswell Island is a small breeding rookery compared with other rookeries in the Gulf of Alaska, however, because there were fewer animals we could collect detailed information on individual females for five years. Our results were comparable with other studies of otariids, including earlier Steller sea lions studies, and we provided new information on factors that affect maternal care among individual female Steller sea lions. We intend to continue long-term monitoring of this breeding group of sea lions, and eventually determine more factors that affect individual reproductive success in Steller sea lions.

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TABLE 1. - Number of Steller sea lion pups born, number of births observed within ± 4 h, and number of pupping locations used by females annually.

Year	# pups	# observed births	# pupping locations
2001	54	50	36
2002	65	53	37
2003	72	61	42
2004	80	29	54
2005	54	54	32
Total	325	297	*91

* Number of unique pupping locations combined from 2001-2005 at Chiswell Island, Alaska.

TABLE 2. - Number of Steller sea lion births per location with the number and percentage of locations used.

# births/ location	# locations used (*n* = 91)	% of locations used	% of births (*n* = 297)
1	33	36.26	11.11
2	17	18.68	11.45
3	9	9.89	9.09
4	6	6.59	8.08
5	6	6.59	10.10
6	5	5.49	10.10
7	7	7.69	16.50
8	4	4.40	10.77
9	3	3.30	9.09
11	1	1.10	3.70

(*n*) Sample sizes are total number of different locations used and total number of births that occurred from 2001-2005.

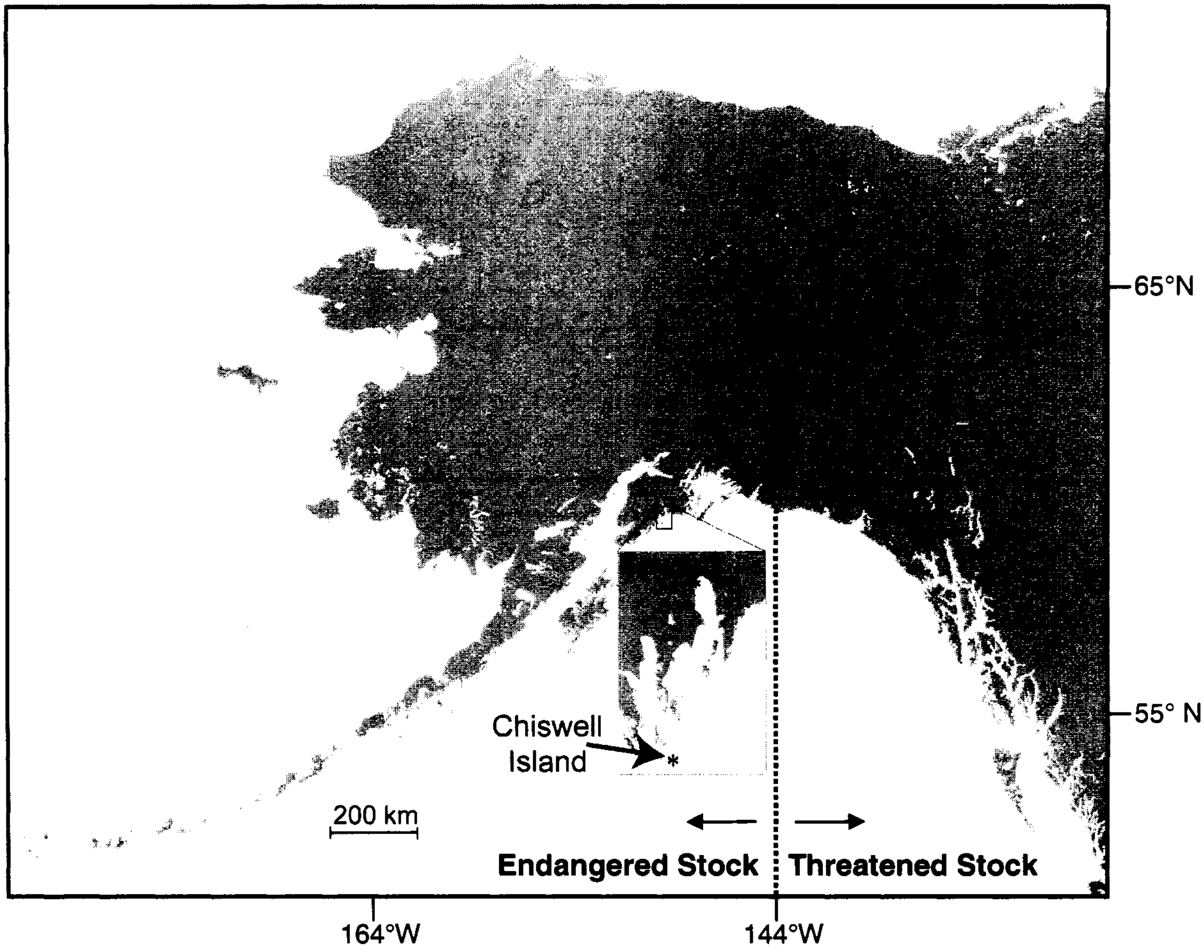

FIGURE 1. - Location of Chiswell Island in Alaska within the range of the endangered stock of Steller sea lions, west of the 144°W longitude.

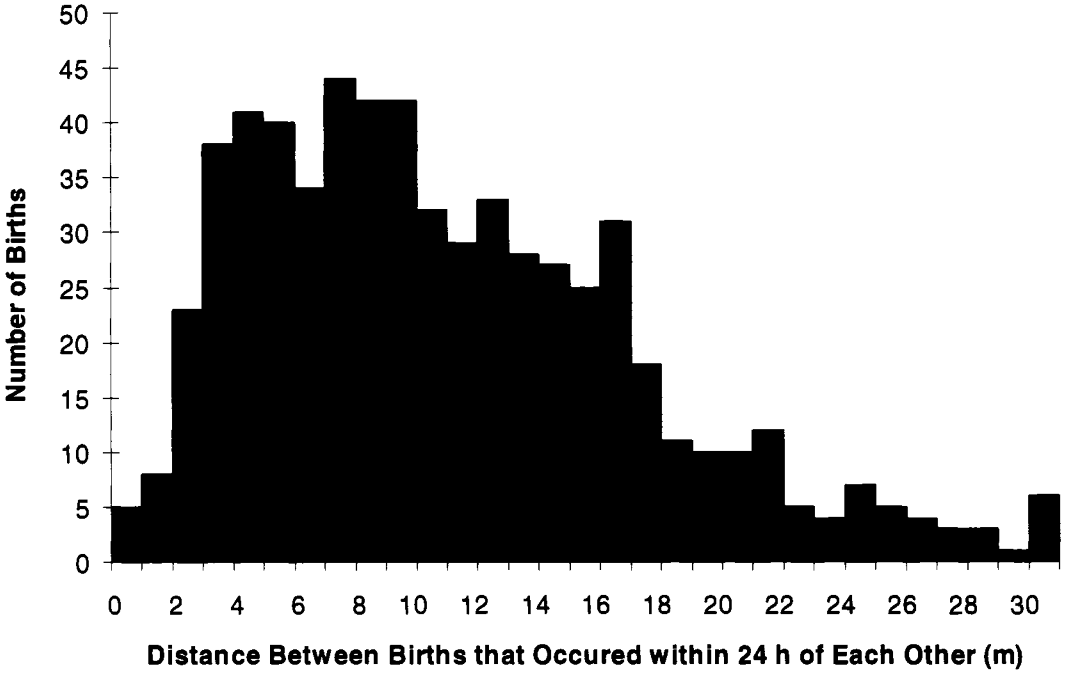

FIGURE 2. - Frequency of the distance between births that occurred within 24 h of each other. Sample size was 627 distances calculated from a total of 297 births from 2001-2005. The pupping area of the rookery was approximately 40 x 20-m.

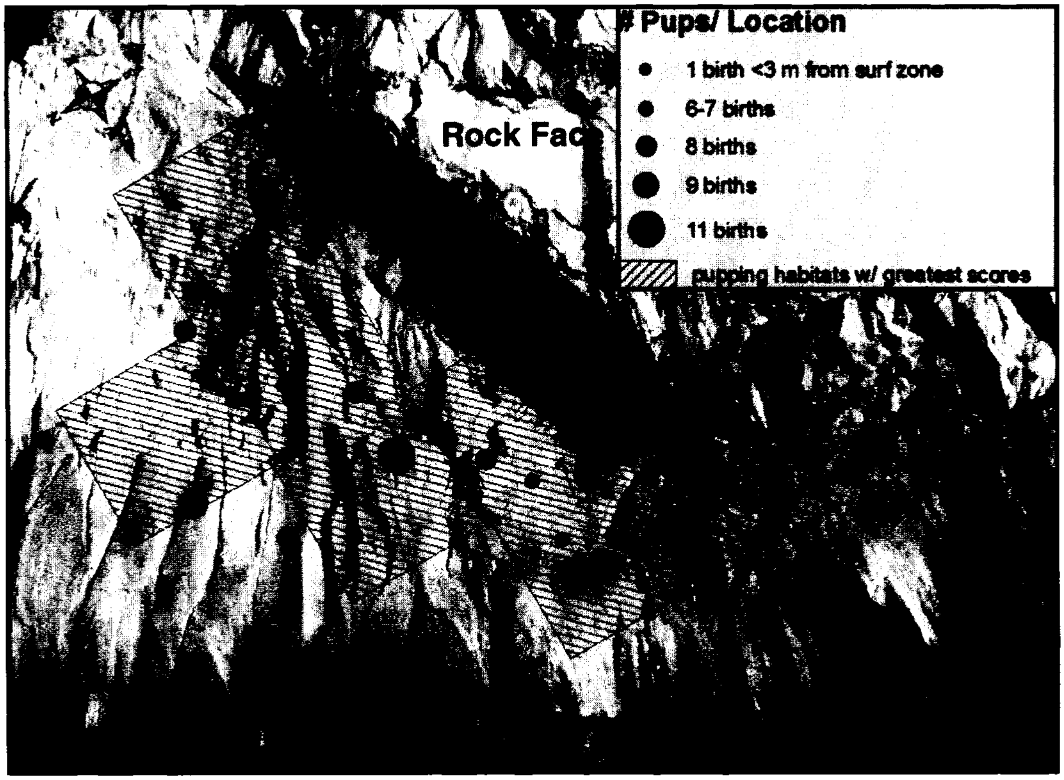

FIGURE 3. - Aerial photograph of the pupping area on Chiswell Island indicating the most common pupping locations for all years were mainly within quadrats with the greatest habitat scores. The smallest circles represent locations where a single birth occurred <3 m from the surf zone. A 7 x 7-m grid (as indicated by the shaded box) was used for this analysis.

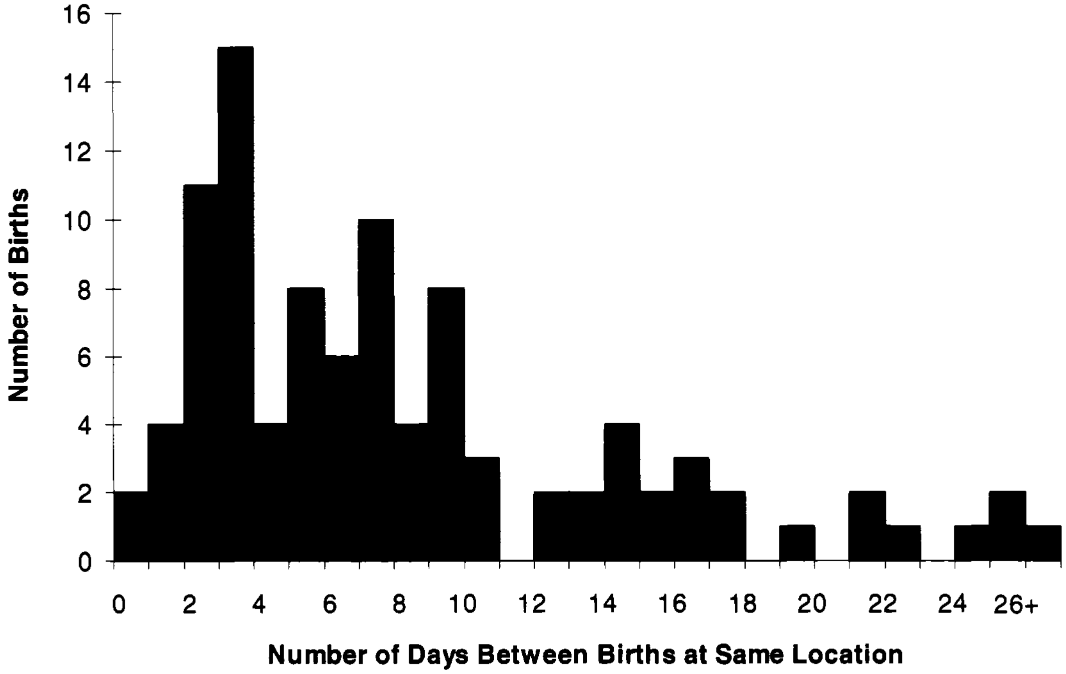

FIGURE 4. - Frequency of the time between births that occurred at the same location. Sample size was 97 occurrences calculated from a total of 297 births from 2001-2005.

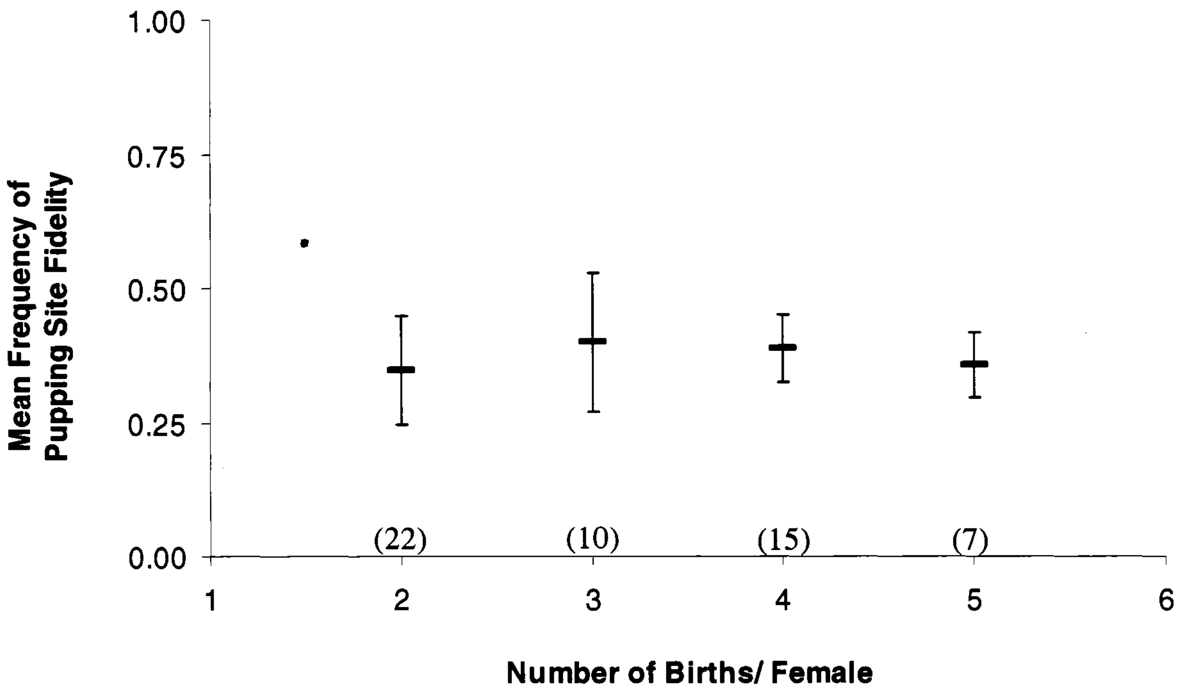

FIGURE 5. - Mean (horizontal line) frequency of pupping site fidelity for known females that gave birth 2, 3, 4, or 5 times at Chiswell Island from 2001-2005 (vertical line is *SE*). Numbers in parentheses indicate sample sizes, the total number of females was 55. Frequencies were determined by dividing the number of distances between pupping locations that were ≤5.8 m by the total number of distances among locations for each female. All pupping locations for each female were included in this analysis.

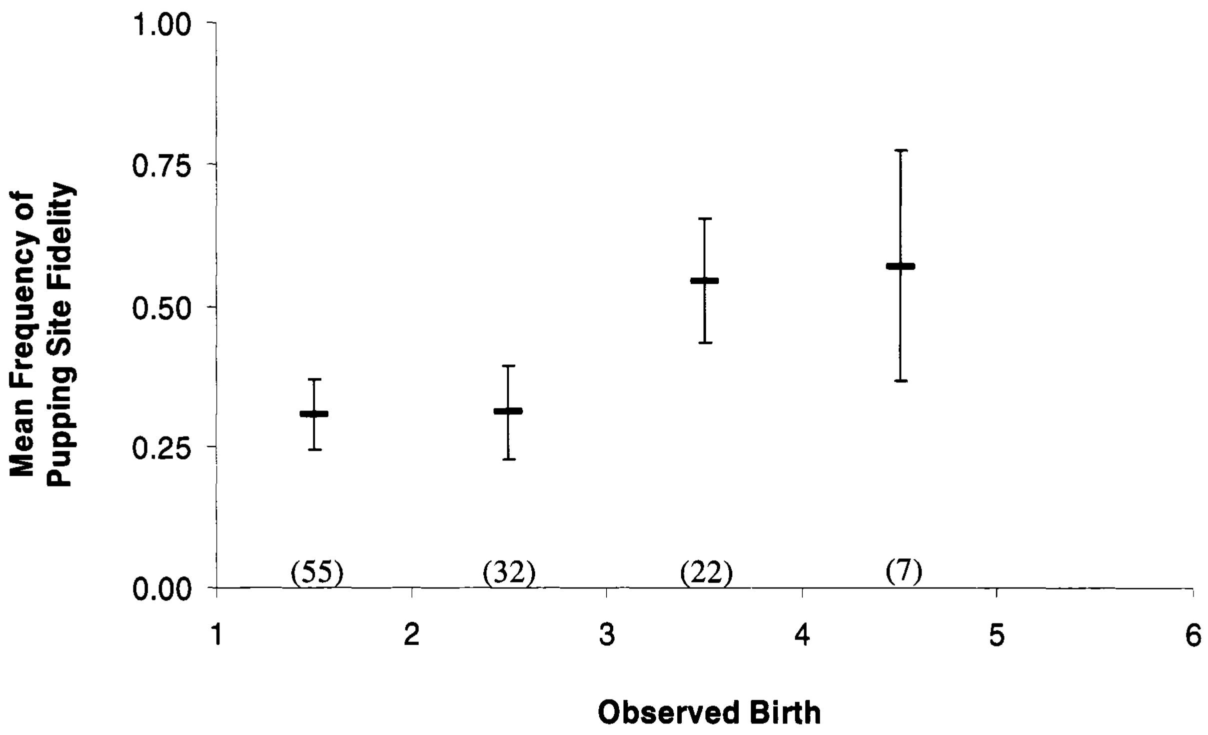

FIGURE 6. - Mean (horizontal line) frequency of pupping site fidelity for known females that gave birth 2, 3, 4, or 5 times at Chiswell Island from 2001-2005 (vertical line is *SE*). Numbers in parentheses indicate sample sizes, the total number of females was 55. Females exhibited pupping site fidelity by giving birth ≤5.8 m from their most recent pupping location at Chiswell Island.

APPENDIX I

Scoring criteria used to determine the number of advantageous physical attributes in pupping locations.

	Scoring Criteria	Scoring value
1	A rock wall (≥45º and ≥0.5 m tall) in a pupping location is advantageous for protecting pups during and following birth.	1
2	An overhanging shelf (rock wall above and adjacent) in a pupping location is advantageous for protecting pups during and following birth.	2
3	A crack (≤45º and <0.5 m tall) in a pupping location is advantageous for protecting pups during and following birth	1
4	A tide pool in a pupping location is advantageous for females and pups for thermoregulation during time on shore following birth.	1
5	A pupping location with an area that is flat and rough covering at least 1 m^2 is advantageous for controlling a pup during birth.	1
6	A pupping location with an area that is flat and smooth covering at least 1 m^2 is advantageous for controlling a pup during birth.	1
7	A pupping location with an area that is steep and smooth covering at least 1 m^2 is disadvantageous for controlling a pup during birth.	-1
8	A pupping location with an area that is steep and rough covering at least 1 m^2 is disadvantageous for controlling a pup during birth.	-1
9	Giving birth ≥5 m from the high tide line is advantageous for protecting pups from the surf.	1
10	Giving birth ≥2-4 m from the high tide line is disadvantageous for protecting pups from the surf.	-1
11	Giving birth ≤1 m from the high tide line is disadvantageous for protecting pups from the surf.	-2

CHAPTER 2:

INTERSEASONAL AND INTERANNUAL MATERNAL ATTENDANCE AMONG INDIVIDUAL STELLER SEA LIONS (*EUMETOPIAS JUBATUS*) IN THE GULF OF ALASKA

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ABSTRACT

We studied maternal attendance patterns in Steller sea lions (*Eumetopias jubatus*) at a small rookery in the northern Gulf of Alaska during 4 summers, 2001-2004 and 3 autumn seasons, 2002-2004 using remotely-operated video cameras. Duration of foraging trips averaged 16.5 (± 0.6 *SE*) h during summer for all years combined but varied annually. Duration of foraging trips averaged 55.7 (± 3.1) h during autumn, and there was no significant difference among years or throughout any autumn season. Mean duration of foraging trips was the same for multiparous and primiparous females during summer of 2004. Individual females foraged at sea an average of 3.3 times greater duration in autumn compared with summer. Mean duration of shore stays (time spent on shore between foraging trips) also increased significantly from summer to autumn during 2002 and 2004 but not in 2003. Females spent an average of 37.0% of their time at sea during summer compared with 63% during autumn. Maternal attendance behavior has evolved with a combination of seasonal unpredictability in the environment and increasing energy demands of offspring. Lesser durations of foraging trips during summer indicated that there was sufficient prey near the rookery and females

could cope with the energy demands of their offspring. Mean duration of foraging cycles plateaued during mid-August, therefore, durations of foraging cycles greater than that plateau may indicate decreases in availability of prey during autumn and winter, or excessive energy demands of the growing offspring.

INTRODUCTION

The maternal care of pinnipeds is unique among mammals because females give birth on land or ice but feed entirely at sea (Bonner 1984). Following birth, pinniped pups are completely dependent upon their mother for nutrition (Boness and Bowen 1996). Lactation is more energy intensive than gestation, therefore, the duration of the lactation period is a crucial component of maternal care (Millar 1977). Among pinnipeds, phocids generally do not forage during lactation and usually wean their pups within 4-50 days, whereas, otariids exhibit a greater range of lactation weaning their pups in 4-36 months (Atkinson 1997, Bonner 1984; Gentry and Kooyman 1986). Lactating otariid females alternate between foraging trips at sea and nursing periods on shore; these cyclic behaviors are referred to as maternal attendance patterns (Gentry and Kooyman 1986).

Most researchers have investigated attendance patterns of lactating females only during the breeding season or in species with lesser lactation periods. In species with greater lactation periods, such as Steller sea lions (*Eumetopias jubatus*), the majority of maternal care occurs following the breeding season. For this species, documenting attendance patterns during non-breeding seasons is important for understanding how females provide nourishment for offspring that need sufficient body weight and energy reserves to survive their first year of life (Riedman 1990).

Female Steller sea lions can live up to 30 years, and usually give birth on land to 1 pup per year. Weaning time is typically 1 year, but immature sea lions have nursed up to four years (Gentry 1970; Pitcher and Calkins 1981; Riedman 1990; Sandegren 1970). The perinatal period (time from parturition to the females' next foraging trip to sea) ranges from 3 to 12 days (Hood and Ono 1997; Maniscalco et al. 2006, Merrick 1987) and may fluctuate inter-annually and among rookeries (Maniscalco et al. 2006; Milette and Trites 2003). After foraging elsewhere during winter, females return to rookeries by the end of May and breeding season is usually completed by mid-July (Edie 1977; Gentry 1970; Maniscalco et al. 2006).

The western stock of Steller sea lions is currently listed as endangered under the United States Endangered Species Act (ESA) as a result of continued dramatic decreases beginning in the 1970s (Loughlin et al. 1992; Merrick et al. 1987; Sease and Gudmundson 2002). One of the leading hypotheses for declines in Steller sea lions has been nutritional stress caused by bottom-up forces (Alverson 1992; Hunt et al. 2002; NRC 1996; Rosen and Trites 2000; Trites and Donnelly 2003) such as reductions in prey abundance, availability, or quality. Recently, however, it has been generally accepted that nutritional stress is not a current problem (Fritz and Hinckley 2005; Pitcher 2002). Attendance patterns of otariid females have been studied because they can be used as indicators of maternal care of pups, and they may be indirect measures of foraging conditions experienced by females during lactation (Campagna and Le Boeuf 1987; Higgins and Gass 1993; Higgins et al. 1988; Melin 1995; Merrick 1987, Trillmich 1990).

The nutrients required for milk production are gained by females during foraging trips, therefore, how females allocate their time spent at sea and nursing on shore directly influences their maternal investment (Doidge and Croxall 1989). Foraging behaviors of pinnipeds are related to the energetic requirements of individuals and to environmental characteristics (McCafferty et al. 1998). For example, optimum foraging theory (McArthur and Pianka 1966) predicts that animals will adopt foraging behaviors that optimize fitness in specific environmental conditions. Gentry et al. (1986) indicated the variation in attendance patterns of female fur seals was mainly determined by the productivity of the ocean. Thus, duration of foraging trips and shore stays of lactating female sea lions may be determined by the availability and abundance of prey near the rookery.

The connection between maternal care and food availability has been documented in pinniped studies associated with El Niño in tropical and temperate latitudes and to a lesser extent at higher latitudes where prey resources vary widely on temporal and spatial scales. Greater duration of foraging trips have been attributed to low food abundances in many species including California sea lions (*Zalophus californianus*; Garcia-Aguilar and Aurioles-Gamboa 2003; Ono et al. 1987), Antarctic fur seals (Boyd 1999; Costa et al. 1989; Lunn and Boyd 1993), south American fur seals (*Arctocephalus australis*; Majluf 1991), and Steller sea lions (Hood and Ono 1997). Duration of foraging trips by female Steller sea lions increased as their pups aged (Higgins et al. 1988; Trites and Porter 2002), and also varied among years and locations (Hood and Ono 1997; Milette and Trites 2003). Documenting maternal attendance patterns provides information on the health of the animal before parturition, during lactation and gestation (Lynn and Boyd 1993), and during extreme weather conditions. This can be best accomplished by observing the same individuals over long time periods to avoid the inherent variation of measuring behavioral characteristics of different individuals among seasons and years.

We observed maternal attendance patterns among individual Steller sea lions at a small rookery in the northern Gulf of Alaska to better understand inter- and intra-annual patterns of maternal care in this species. We predicted that changes in duration of attendance patterns of lactating females would be: (1) a gradual increase throughout the year as females increased their time spent at sea or increased their time spent ashore between foraging trips to accommodate increasing energy needs of the pup, (2) variable but would increase with temporal and spatial changes in prey, (3) altered if the pup is traveling with their mother or on its own, and (4) invariant in autumn because temporal changes in prey or energy needs of the pup would be constant. Overall the attendance patterns of lactating females can indicate seasonal changes in food availability and changes in energetic needs of growing offspring.

METHODS

Study area and data collection. - This study was conducted at a small rookery on Chiswell Island (59°36.13'N, 149°34.05'W), in the northern Gulf of Alaska 65 km south of Seward, Alaska (Fig. 1). Steller sea lions at Chiswell Island are part of the endangered stock west of 144°W longitude. In July of 1956, the earliest published aerial photographic census indicated there were 1459 adult and 564 Steller sea lion pups (Mathisen and Lopp 1963). Since 1956, the number of sea lions using Chiswell Island decreased rapidly through the 1980s, currently with about 90 breeding animals producing approximately 50-80 pups per year (Maniscalco et al. 2002, 2006).

In October 1998, the Alaska Sealife Center (ASLC) contracted with SeeMore Wildlife Systems, Inc. of Homer, Alaska, to install remotely-operated cameras to conduct a long-term monitoring study of the Steller sea lions at Chiswell Island (Maniscalco et al. 2006). Six cameras were used during the breeding season (May-August) for complete coverage of the rookery, however, only 2 cameras could be viewed and operated at the same time from the Alaska Sealife Center in Seward, Alaska. At ASLC, audio and video signals were recorded in real-time using television monitors and VCRs. This remote-monitoring system allowed us to observe the sea lions in their natural habitat on a year-round basis without disturbance and without the difficulty of sampling in harsh weather conditions.

Identifiable females were observed in the maternal attendance study from 2001-2004. Individual females were identified by their natural markings such as scars, fungal patches, and flipper uniqueness. Females were photographed from as many angles as possible under different lighting conditions. The photographs and an index of pelage wetness were entered into a Microsoft Access database with additional written details concerning individual identification. Females that were identified from 2001-2004 were referred as known females. Parity was determined for females that gave birth more than once (multiparous) at Chiswell Island, and for primiparous females with distinctive natural markings or flipper tags that were never, before their first year of pupping, observed giving birth on Chiswell Island (Maniscalco et al. 2006).

In 2001, observations were conducted from the arrival of the first female on the rookery ($\geq$23 May) until 10 August, based on approximate dates that researchers completed similar observations of Steller sea lions during summer (Higgins et al. 1988; Milette and Trites 2003). In 2002, we extended the maternal attendance study and conducted autumn observations from 15 September to 5 November. We conducted observations from 10 August to 28 October in 2003 and to 18 September in 2004. Study periods varied because of limited personnel and overlap with other research projects conducted at Chiswell Island. Observations were conducted during the peak breeding season (May-July) from at least 0600 to 2200 h daily. Additional early morning and nighttime observations were conducted when daylight was available. After 10 August, observations were conducted from approximately sunrise to sunset as the diminishing daylight allowed. In June of 2004, overnight observations were conducted by researchers on the rookery for 9 days. We counted all sea lions at Chiswell Island daily at 1100 h in all years and at 1900 h from late May-August.

Attendance patterns for known individual females were determined from scan samples (Altmann 1974). For all years, scan samples were conducted twice during even-numbered hours (0600, 0800, etc.) from at least 0600 to 2200 h during summer and at least 3 times per day (dawn, midday, and dusk) after 10 August. All scans of known females were recorded in a MS Access database with date, time, behavior, area of the rookery, and whether females were with their pup or not (App. 1). During scans we recorded when known females were absent from the rookery. If the presence of a female was uncertain because her identifying marks were out of view, she was recorded as "unknown" in the database. If a female was not present during a scan, we assumed she departed at the halfway point from the previous scan she was present. The same was assumed for females that returned when scans were not being conducted, except when pelage was still wet (dry weather conditions), and then it was assumed that she returned within the last half hour of the non-observation period. Overnight departures or arrivals were assumed to have occurred at 0200 h or the midpoint of the non-observation period. Actual arrival and departure times were recorded to the nearest minute when observed. Duration of foraging trip or shore stay was recorded as uncertain if there were >3 consecutive scan hours of "unknown" status before the female was positively observed as present or absent. Time spent at sea and attendance cycles (1 foraging trip followed by 1 shore stay) were determined from recorded durations of foraging trips and shore stays of known females.

Data analysis - Attendance patterns of lactating known females were used in statistical analyses only when there was <50% uncertainties of the duration of foraging trips and shore stays (i.e. where uncertainty is >3 consecutive scans of "unknown" status). The minimum number of foraging trips and shore stays per female needed to accurately conduct parametric tests for comparisons between seasons were determined using bootstrapped data (Resampling Stats (Resampling Stats, Inc.; App. 2). Data collected from females during autumn were used because the number of foraging trips and shore stays recorded during autumn was less than summer. Data from the female with the greatest number of foraging trips or shore stays during autumn each year were used in bootstrapping.

To determine when changes in duration of foraging trips occurred between summer and autumn, we calculated the mean duration of foraging trips and variance in 5-day intervals for all years combined. The date of the midpoint of each 5-day interval was used as the predictor of mean duration of foraging trips for each interval in a linear regression. The data were then fit using a 3-stage regression model. This model fit a line hinged at two inflection points, which resulted in 3 different slope estimates. We included the inflection points in the model because we were interested in the specific dates associated with the start of the seasonal increase in mean duration of foraging trips, and when the mean duration of foraging trips reached a maximum during autumn. These points corresponded to the minimum and maximum durations of foraging trips, thus, the midpoint of these points approximated the date of the greatest increase in mean duration of foraging trips. We used this midpoint to delineate between summer and autumn seasons for comparisons among known females. The 3-stage regression model used in this analysis had 6 parameters: a date = 0 intercept, a slope estimate for the line from date = 0 to the first inflection point, date of that inflection point, a slope estimate for the line from the second inflection point, the date of the second inflection point, and finally slope of the line from the second inflection point to the maximum date of the study period. The model was fit numerically using Marquardt's algorithm (Press et al. 1997), a least-squares-minimization algorithm that generates variance estimates for each of the parameters.

We tested the data for normality with a Kolmogorov-Smirnoff test and used a Cochran's test to test for homogeneity of variances. Analysis of variance [ANOVA] was used to make comparisons among years within season for all maternal attendance parameters. A paired *t*-test was used to test for differences between seasons for all maternal attendance parameters for individual females. A two-sample *t*-test was used to compare mean duration of foraging trips among females (multiparous versus primiparous females). Linear regression analyses were conducted to compare duration of foraging trip with date throughout autumn for each year. Data were reported as mean ± standard error (*SE*), unless note otherwise. Analyses were performed with SYSTAT Version 10 software (SPSS Inc., 2000). *P*-values of <0.05 were considered significant.

Permits for this research were obtained from the National Oceanic and Atmospheric Administration, National Marine Fisheries Service (Numbers 782-1532-00 & 881-1668-00) under the authority of the Marine Mammal Protection Act and the Endangered Species Act. Additional Special Use Permits to conduct this research on refuge lands were acquired from the United States Fish and

Wildlife Service, Alaska Maritime National Wildlife Refuge. This study was purely observational, and followed American Society of Mammalogists guidelines (Animal Care and Use Committee 1998).

RESULTS

Depending on the year and season, the number of lactating females sampled was 11-37. The number of observed foraging trips per female was 11-42 during summer (82 ± 5.0 days; standard deviation (*SD*)) and 3-14 during autumn (52 ± 20.0 days; *SD*). The number of observed shore stays per female was 9-39 during summer and 4-15 during autumn. Scatter plots of mean (± *SE*) duration of foraging trip or shore stay versus sample size with increasing precision determined that a minimum of 4 foraging trips and 5 shore stays were needed for each female during fall to accurately test for changes between seasons for all years (randomization test; Fig. 2 and 3). We included 1 female with 3 foraging trips and 1 female with 4 shore stays during autumn in our paired comparisons analysis of individual females.

We were interested in determining changes in the duration of foraging trips from summer to autumn rather than day-to-day differences, therefore, we chose 5-day intervals to remove variability from individuals with varying duration of foraging trips (range: 5.5-168.5 h) during autumn. Examination of the initial regression residuals of duration of foraging trips indicated that error variance increased with date (Fig. 4). To correct for unequal variance, we weighted the regression residual calculation at each date by the standard deviation associated with the mean duration of trips for that date. The 3-stage regression model determined an initial inflection point of 19 July and a second inflection point of 17 September. Mean duration of foraging trips increased from 19 July to 17 September with a midpoint between the two inflection points of 18 August. We determined that 18 August, where the greatest change in mean duration of foraging trips occurred, was the transition of the duration of foraging trips from summer to autumn for lactating females on Chiswell Island from 2001-2004.

Duration of foraging trips averaged 16.5 (± 0.6 *SE*) h during summer for all years but varied annually with known females in 2002 having significantly lesser mean duration of foraging trips compared with 2003 and 2004 but not 2001 (Table 1). Mean duration of foraging trips was not different for multiparous (*n* = 24; $\bar{x}$ = 17.4 h) and primiparous females (*n* = 9; $\bar{x}$ = 17.6 h; *t* = 0.11, *d.f.* = 31; *P* = 0.910) during summer of 2004 (only year with sufficient sample size for analysis). Duration of foraging trips averaged 55.7 (± 3.1) h during autumn from 2002-2004, and there was no significant difference among years (Table 1). Duration of foraging trips did not change significantly throughout any autumn season from 2002-2004 (linear regression *P*-values: 2002 = 0.699, 2003 = 0.920, 2004 = 0.509).

Seasonal comparisons from 2002-2004 among individual females indicated that they foraged at sea an average duration that was 3.3 times greater during autumn ($\bar{x}$ = 57.5 ± 5.0 h) than summer ($\bar{x}$ = 17.3 ± 3.1 h; Table 2). Mean duration of shore stays also increased significantly from summer to autumn during 2002 and 2004 but not in 2003. These seasonal increases in mean durations of foraging trips and shore stays caused an increased mean duration of attendance cycles of about 2 days from summer to autumn (Table 2). Individual females spent an average of 41.7% of their time at sea during summer compared with an average of 64.0% during autumn (Table 2).

Discussion

Although Chiswell Island is a small rookery, it offered a unique opportunity for us to document patterns of maternal attendance for individual females for successive seasons and years. Observing the same individuals between seasons eliminated variability associated with sampling different individuals as most other researchers have done. We documented seasonal changes in maternal attendance among individuals and for all lactating females at Chiswell Island.

Greater durations of foraging trips occurred during periods of lesser food quality or availability in several pinniped species, often associated with El Niño events in the western Pacific Ocean (Lunn et al. 1993; Majluf 1991; Ono et al. 1987). Lactating female California sea lions had significantly greater durations of foraging trips during the strong El Niño of 1983 (Heath et al. 1991) and 1998 (Garcia-Aguilar and Aurioles-Gamboa 2003) when prey abundances were particularly minimal compared with a year without rapid changes in the ecosystem. Similarly, Antarctic fur seals at Bird Island, South Georgia had significantly greater durations of foraging trips during years of lesser krill abundance (Boyd et al. 1994). In contrast, our study indicated that Steller sea lions at Chiswell Island in the northern Gulf of Alaska were not food limited during summers of 2001-2004. The durations of foraging trips of lactating females at Chiswell Island were consistent with other studies of Steller sea lion at rookeries in the western population during the 1990s but about half the duration observed in the southeastern Alaska population (Brandon 2000; Milette and Trites 2003). Quality of available prey was hypothesized as a primary cause of declines of Steller sea lions in the western stock that occurred from the late 1970s through the 1980s (Alverson 1992; Rosen and Trites 2000). However, recent studies and our results indicate that there is little evidence that food quality is currently a problem for Steller sea lions (Calkins et al. 2005, Pitcher 2002; Fritz and Hinckley 2005).

From 2001-2004, duration of foraging trips during summer at Chiswell Island varied among years, deceasing slightly from early June through mid-July. Mean duration of foraging trips began increasing in late-July, the time when pups were about 30 days old and expending more energy with frequent bouts of play and learning to swim (Gentry 1974). Others have reported that greater durations of foraging trips for female Steller sea lions with pups up to 2 months of age during summer occurred to supplement the increasing energy demands of growing pups (Gentry 1970; Higgins et al. 1988; Milette and Trites 2003). Even greater changes in durations of foraging trips of lactating females from summer to winter have been documented for Steller sea lions (Merrick and Loughlin 1997; Trites and Porter 2002) and California sea lions (Melin et al. 2000). Those researchers observed maternal attendance during the non-breeding season, however, they did not determine when changes between seasons occurred. We observed that changes in duration of foraging trips did not occur gradually from summer to autumn but began to change 19 July. We suspect that this abrupt increase in duration of foraging trips of lactating females may have occurred because of seasonal change in food availability, social independence of pups, a sudden increase in energetic demand of pups or females, or a combination of these factors.

Attendance patterns during non-breeding seasons (mid-August - mid-May), which represent 2/3 of the lactation period, are a crucial component in evaluating the time a female invests in her pup. Therefore, identifying potential factors that influence duration of foraging trips is important. Boyd et al. (1991) indicated that the duration of foraging trips of lactating fur seals could be regulated in two contrasting ways; (1) females may forage until they achieve a net energy gain of some set amount, or (2) females may forage for a set duration before they return ashore with a maximum net energy gain. He concluded that it was probably a combination of the 2 hypotheses because lactating female fur seals may have a minimum net energy gain that must be reached before they return to nurse their pup. They also may have a maximum duration of foraging trip determined from the fasting ability of their pup and their energy storage capacity (Boyd et al. 1991). Maternal attendance patterns, including foraging trips and shore stays, of California and Steller sea lions during non-breeding seasons did not change significantly throughout winter (Steller sea lions: 22 January - 1 April; California sea lions: 15 December - 15 March) or spring (California sea lions: 16 March - May; Melin et al. 2000; Merrick and Loughlin 1997; Trites and Porter 2002). We also did not observe a change in duration of foraging trips throughout autumn (18 August - 5 November), which indicated that sea lions in the northern hemisphere may reach a maximum duration for foraging trips in autumn and possibly maintain that duration throughout winter.

At Chiswell Island, there was a significant increase in mean duration of foraging trips that occurred from summer to autumn and did not change significantly throughout autumn (Fig.3). Greater durations during autumn may have occurred because: (1) pups were learning to forage on their own to supplement their growth as suggested by others (Melin et al. 2000; Merrick and Loughlin 1997; Trites and Porter 2002), (2) females did not need to return to the rookery as often because pups were more efficient at suckling during nursing, or (3) females may have shifted to a maternal attendance pattern that optimized nourishment, lactation, and development of a growing fetus during autumn when food was less abundant. We observed greater variability in duration of foraging trips during autumn compared with the weeks following parturition (Fig. 3). This indicated that availability of prey was less predictable in autumn and detecting trends in attendance cycles during non-breeding seasons was more difficult with increased variation.

Significant differences in durations of attendance cycles (one foraging trip followed by 1 shore stay) among summers at Chiswell Island may indicate that lactating females are capable of alternating attendance patterns when inter-annual variations in food availability might occur. Durations of attendance cycles during autumn were similar among all years, therefore, females may have maximum durations of foraging at sea and resting on shore during autumn regardless of inter-annual variations in food availability during autumn. An average duration of foraging trips of 2.3 days during autumn was greater than reported in southeast Alaska during winter for this species (2.0 days; Trites and Porter 2002), but less than the 8.5 days reported farther west from 1988-1993 when declines of sea lions were more severe then at present (Merrick and Loughlin 1997).

Merrick and Loughlin (1997) observed durations of foraging trips of female Steller sea lions during winter that were 3 times greater than other studies (Trites and Porter 2002; this study). However, they also determined that foraging effort (actively diving for food) was not significantly different between summer and winter by using time-depth recorders attached to females. This indicated that lactating females foraged near the rookery during summer because pups were more dependent on their mothers and/or prey were more abundant near the rookery compared with autumn and winter, when females with pups foraged farther offshore because of seasonal changes in prey availability. The greater duration of foraging trips observed by Merrick and Loughlin (1997) could have occurred because of extremely limited food availability in that winter, however, they admitted that observing both lactating and non-lactating females (post weaning) could have introduced biases that caused the greater duration.

Duration of shore stays of lactating females increased from summer to autumn at Chiswell Island in 2002 and 2004 but not in 2003, which is comparable with other inter-seasonal studies that indicated no change in duration of shore stays (Merrick and Loughlin 1997; Trites and Porter 2002). Shore stays in summer and autumn of 2003 and autumn of 2002 and 2004 were an average 29.8 h and were greater than shore stays observed in most other studies of Steller sea lions regardless of season (range: 15.4-23.0 h; Higgins et al. 1988; Merrick and Loughlin 1997; Sandegren 1970; Trites and Porter 2002). This indicated that lactating females had a maximum duration of time on shore that they needed for rest and nursing between foraging trips. Despite an increased duration of shore stays at

Chiswell Island in 2002 and 2004, lactating females spent a greater percentage of time at sea during autumn (64.0%) compared with summer (41.7%). Steller sea lions in southeastern Alaska had similar attendance patterns, spending a greater percentage of time at sea during winter (Milette and Trites 2003; Trites and Porter 2002). These seasonal changes in time at sea resulted from a greater duration of foraging trips without any change in duration of shore stays, therefore, increasing the attendance cycle to about 3 days during winter (Trites and Porter 2002) and 3.5 days during autumn at Chiswell Island. Lactating female California sea lions in southern California had similar attendance patterns with an average 75.5% of their time spent at sea during winter (Melin et al. 2000).

The foraging environment of Steller sea lions is dynamic. Lactating females must adjust their attendance patterns to accommodate changes in prey distribution and availability, increased harsh weather conditions that occur during autumn and winter, growing offspring along with preparing them for independence, or other unidentified factors. Some females may change their attendance patterns to facilitate weaning by spending less time on shore and more time at sea. Therefore, it is not surprising that variability in duration of foraging trips occurred during autumn. Our observations of individual females from summer to autumn indicated that maternal attendance behavior was influenced by a combination of seasonal unpredictability in the environment and increasing energy demands of offspring. Lesser durations of foraging trips during summer indicated that there was sufficient prey near the rookery, and that females did not forage far from the rookery. Therefore, we predict that durations of foraging trips during summer that greatly exceed durations during autumn may signify critically low food availability during summer.

It has been generally accepted that nutritional stress is not a current problem for Steller sea lions (Calkins et al. 2005, Fritz and Hinckley 2005; Pitcher 2002). Our results indicated that lactating females were not food limited during summer, and attendance patterns during autumn were consistent in all years indicating prey availability was not different among years. However, long-term effects of chronic nutritional stress such as delayed maturation, changes in mean date of parturition, greater weaning time of offspring, reduced female and offspring body mass, and decreased fecundity are difficult to determine without studying greater numbers of sea lions during long time periods. Chiswell Island is a small rookery, so sampling greater numbers of sea lions is not possible, however, observing the same breeding female Steller sea lions inter- and intra-annually for long time periods can be done. Comparing maternal attendance patterns of individual females with other maternal care parameters such as timing of birth, perinatal periods, and pup survival may indicate if Steller sea lions are being subjected to long-term effects of chronic nutritional stress.

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TABLE 1. - Average duration of foraging trip (h), shore stay (h), attendance cycle (days), and time at sea (%) for all known females for summer (1 June to 18 August) and autumn (>18 August) from 2001-2004.

	2001		2002		2003		2004		
Summer	*mean*	*SE*	*mean*	*SE*	*mean*	*SE*	*mean*	*SE*	*P*
n	12		18		16		37		
Foraging trip (h)	15.1	1.0	11.5^{ab}	0.6	19.3^{a}	1.8	18.1^{b}	0.8	<0.001
Shore stay (h)	22.3	1.8	19.9^{a}	0.7	27.5^{ab}	1.3	22.4^{b}	1.0	0.001
Attendance cycle (days)	1.6^{a}	0.1	1.3^{bc}	0.1	2.0^{ab}	0.1	1.7^{c}	0.1	<0.001
Time at sea (%)	40.9	2.4	36.7^{a}	1.3	40.3	1.7	44.7^{a}	1.3	0.002
Autumn									
n	0		11		12		20		
Foraging trip (h)			52.9	5.1	64.2	7.3	52.1	4.1	0.234
Shore stay (h)			33.2	2.3	31.8	2.2	26.7	2.1	0.089
Attendance cycle (days)			3.6	0.2	4.0	0.4	3.3	0.2	0.130
Time at sea (%)			60.6	2.8	65.6	2.7	65.0	2.7	0.420

(*n*) Sample sizes are number of females observed in each year. Values with same superscripts in rows were significantly different (Tukey test). *P*-values <0.05 were considered significant (ANOVA).

TABLE 2. - Mean, standard error (*SE*), and range of duration of foraging trip (h), shore stay (h), attendance cycle (days), and time at sea (%) were compared using paired *t*-tests of individual female Steller sea lions (*n*) between summer (1 June to 18 August) and autumn (>18 August) from 2002-2004.

		Summer			Autumn			Mean	
	n	Range	*Mean*	*SE*	Range	*Mean*	*SE*	*Diff.*	*P*
Foraging trip (h)									
2002	11	7.9-15.2	11.2	0.7	30.2-88.0	52.9	5.1	41.7	<0.001
2003	12	13.3-38.2	21.6	2.9	37.2-112.0	67.4	9.1	45.8	0.001
2004	20	11.1-27.6	19.1	1.0	20.9-89.9	52.1	4.3	33.0	<0.001
Shore stay (h)									
2002	11	16.6-21.3	19.4	0.4	23.7-47.4	33.2	2.3	13.8	<0.001
2003	12	18.7-36.8	29.1	2.0	25.6-46.7	31.9	2.4	2.9	0.202
2004	20	13.4-32.5	21.5	1.1	11.0-52.0	26.7	2.1	5.2	0.019
Attendance cycle (days)									
2002	11	1.1-1.5	1.3	0.0	2.4-4.7	3.6	0.2	2.3	<0.001
2003	12	1.4-3.0	2.1	0.2	2.7-6.6	4.1	0.5	2.0	0.002
2004	20	1.3-2.3	1.7	0.1	1.9-4.8	3.3	0.2	1.6	<0.001
Time at sea (%)									
2002	11	29.9-44.1	36.3	1.4	50.0-79.9	60.6	2.8	24.3	<0.001
2003	12	28.8-53.6	41.7	2.6	55.0-75.0	66.5	2.3	24.8	<0.001
2004	20	35.4-59.9	47.1	1.7	45.5-83.3	65.0	2.8	17.9	<0.001

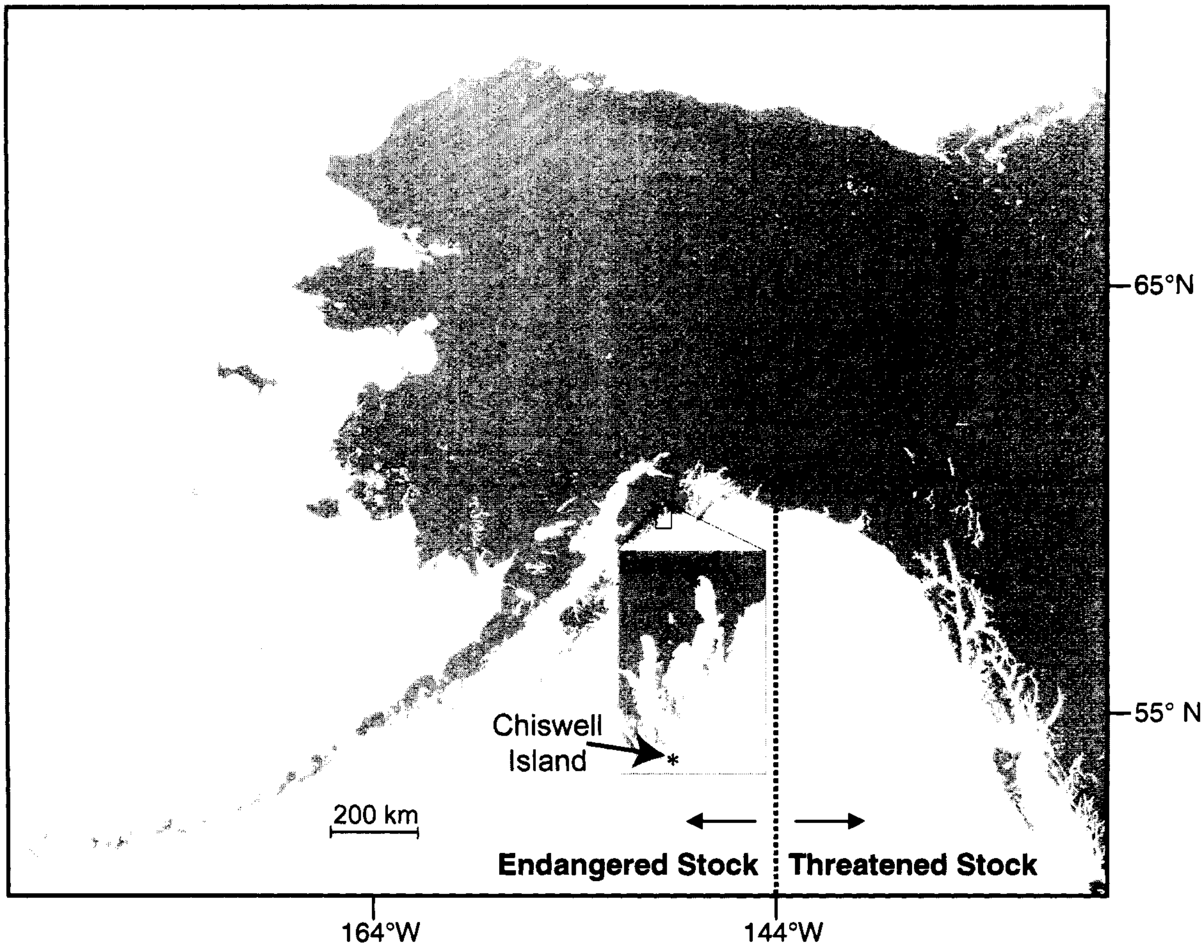

FIGURE 1. - Location of Chiswell Island in Alaska within the range of the endangered stock of Steller sea lions to the west 144°W longitude.

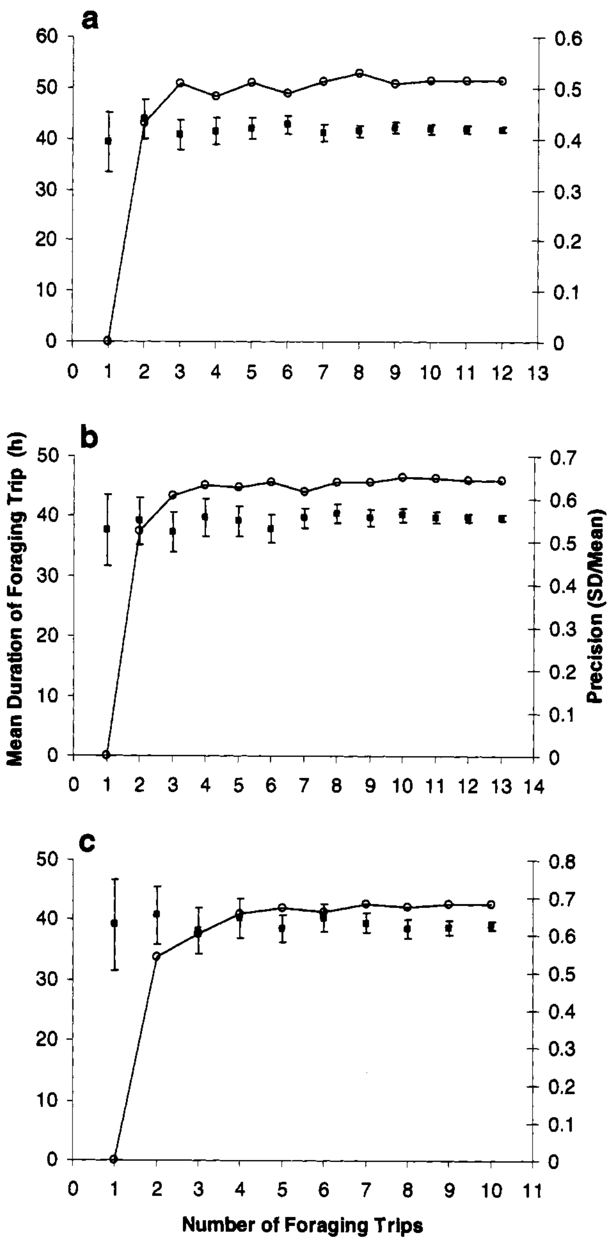

FIGURE 2. - Average duration (± *SE*) of foraging trips during autumn (■) and precision (○) with increasing sample size, plotted from bootstrapped data for a) 2002, b) 2003, and c) 2004.

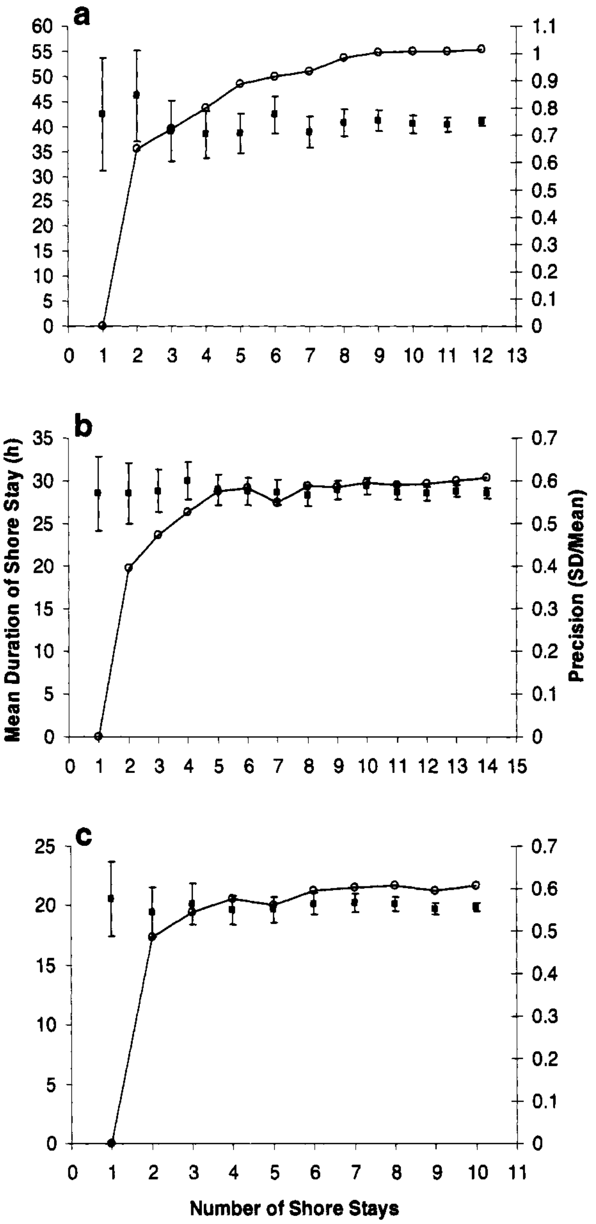

FIGURE 3. - Average duration (± *SE*) of shore stays during autumn (■) and precision (○) with increasing sample size, plotted from bootstrapped data for a) 2002, b) 2003, and c) 2004.

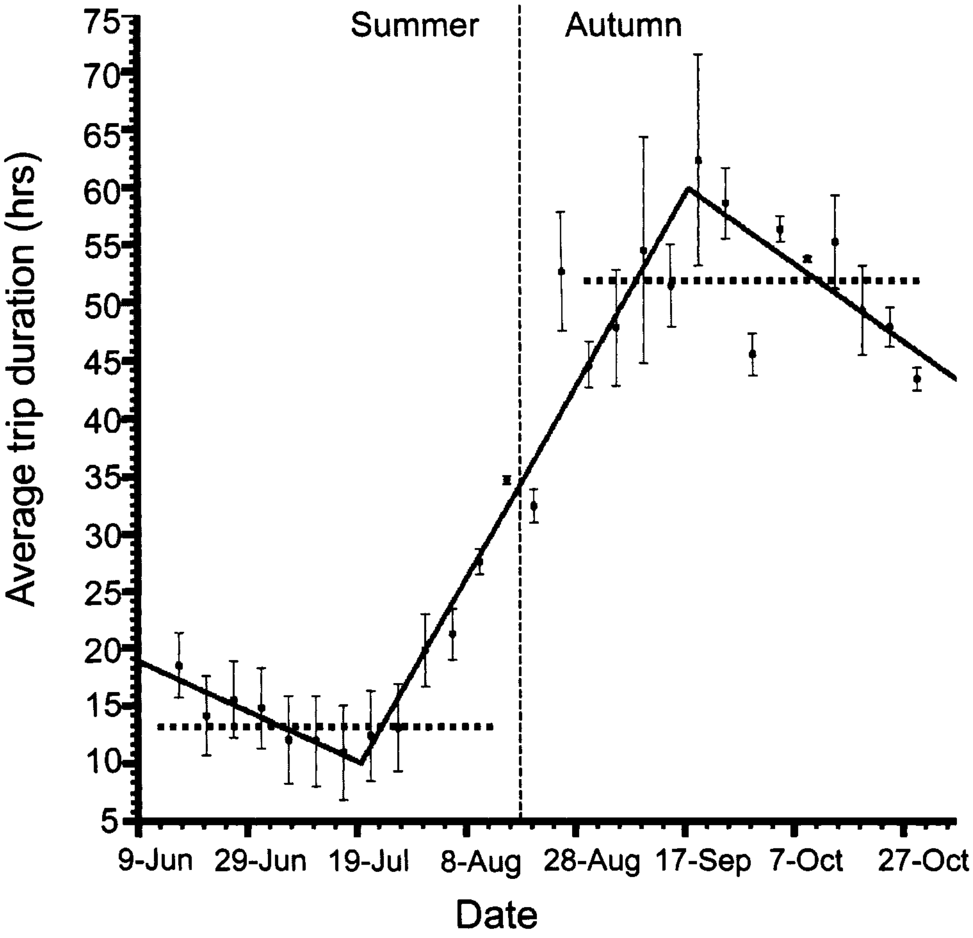

FIGURE 4. - Average duration (h; ± *SE*) of foraging trips for all female Steller sea lions and all years combined in 5-day increments. The pattern of change was similar from year to year, although the data were not collected continuously after 10 August in every year. Summer and autumn were delineated using the midpoint of the inflection points determined using a 3-stage regression model. Dashed horizontal lines represent the general trend in mean duration of foraging trips during each season.

APPENDIX I.

Behaviors used during scan sampling.

Aggressive interaction - threat displays, biting, fighting with another individual
Alert - head up and eyes at least partially open
Giving Birth - when head or tail of the pup emerges to complete delivery
Copulating - male mounting female
Courting - soliciting a male
Entering water - departure from the rocks
Escape behaviors - female leaving territory with the bull attempting to block her
Grooming - scratching with flippers or rubbing on rocks or another sea lion
Hauling out - arriving on shore
Nursing - pup is visibly attached to teat
Other - any behavior not listed here (explained in ‘notes’ section)
Resting - head down and not moving or head up with eyes completely closed
Passive interactions - mostly nuzzling or investigative nosing of another animal
Swimming - in the water no matter what it is doing
Tossing pups - picking up and throwing pups out of the way
Walking - on shore moving from one location to another

Play behaviors for pups:
Object play - pup is tossing or moving an object such as seaweed or feathers
Social play - pup is interacting with others in a playful manner
Solo play - pup is moving body with no purpose such as grooming or walking

APPENDIX II

Resampling stats program (bootstrapping) used to determine the number of foraging trips and shore stays needed to accurately test between seasons.

```
copy (63.5…) data
repeat 100
shuffle data A
take A 1,1 B
mean B C
stdev B D
divide D C E
score C F
score E G
end
mean F H
stdev F I
mean G J
print H*
print I**
print J***
```

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* Grand mean of 100 trials, ** Standard deviation (SD) of the grand mean,
*** Precision determined from SD/grand mean.