

## INTERSEASONAL AND INTERANNUAL MEASURES OF MATERNAL CARE AMONG INDIVIDUAL STELLER SEA LIONS (*EUMETOPIAS JUBATUS*)

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We studied maternal care in Steller sea lions (*Eumetopias jubatus*) at a small rookery in the northern Gulf of Alaska over the course of 4 summers, 2001–2004 and 3 autumn seasons, 2002–2004, using remotely operated video cameras. Perinatal periods were long ( $\geq 10.0$  days); although varied between years. Timing of parturition was earlier and perinatal periods longer for multiparous females compared to females considered to be primiparous. Summer foraging trip durations were short ( $\bar{X} = 16.5$  h), increased during August, then did not change significantly over the course of the autumn ( $\bar{X} = 55.7$  h). Individual lactating females spent a greater proportion of their time on shore during the summer and a greater proportion of their time at sea during the autumn. The amount of time that females nursed their pups also increased significantly from the summer to autumn. Long perinatal periods and short foraging trips during summer indicate that sea lions are likely finding sufficient food nearby. Our data also suggest that Steller sea lions reach an upper plateau in duration of foraging cycles as early as mid-August and large increases above that plateau may indicate difficulty finding sufficient food during the winter months.

Key words: birth timing, *Eumetopias jubatus*, foraging cycles, maternal care, perinatal period, remote video, Steller sea lion

Steller sea lions (*Eumetopias jubatus*) have become the focus of much research since they were listed as threatened under the Endangered Species Act in 1990 and the western stock was further up-listed to endangered status in 1997 (United States Federal Register 62:30772–30773). One of the leading hypotheses for the Steller sea lion decline has been nutritional stress (Alverson 1992; Rosen and Trites 2000; Trites and Donnelly 2003) caused by changes in prey abundances (Anderson and Piatt 1999), although it is generally accepted that this is not currently a problem (Pitcher 2002; Trites and Donnelly 2003). A valuable and noninvasive method of making inferences about food quality and availability to otariids can be achieved by examining aspects of maternal care such as maternal attendance and nursing durations. This can be best accomplished by tracking the same individuals over long time periods to avoid the inherent variation of measuring behavioral characteristics of different individuals between seasons and years.

The link 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 both temporal and spatial scales. For example, parturition can be delayed in Antarctic fur seals (*Arctocephalus gazella*) during years of low krill abundance (Boyd 1996; Lunn and Boyd 1993). Short perinatal periods and longer foraging trips have also been attributed to low food abundances in many species including California sea lions (*Zalophus californianus*—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). Significant decreases in suckling time have also been correlated with periods of El Niño in *Z. californianus* (Ono et al. 1987) and *E. jubatus* (Hood and Ono 1997). Therefore, observations of this type may also be useful for identifying major changes in prey availability at any latitude.

Female Steller sea lions typically become reproductively mature at 4 to 5 years of age, give birth from late May into early July, and nurse their offspring for about 1 year (Pitcher and Calkins 1981). Timing of parturition has been shown to vary with latitude and year, possibly due to food availability (Pitcher et al. 2001) and/or photoperiod (Temte and Temte 1993). The perinatal period (time from parturition to the females' next foraging trip to sea) ranges from 3 to 10 days (Hood and Ono 1997; Merrick 1987) and may fluctuate interannually and with breeding location (Milette and Trites 2003). Furthermore, foraging trips by lactating females tend to

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increase as their pups age (Higgins et al. 1988; Trites and Porter 2002) and also can vary between years and locations (Hood and Ono 1997; Milette and Trites 2003).

In this study, we examined several parameters of maternal care 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 behavior in this species. Patterns observed allow us to make inferences about changes in food availability from year to year as well as seasonal changes in the energetic needs of growing offspring. The results of this study were compared and contrasted with similar studies of Steller sea lions and other otariids.

## MATERIALS AND METHODS

**Study area.**—This study was focused at Chiswell Island ( $59^{\circ}36.13'N$ ,  $149^{\circ}34.05'W$ ), located in the northern Gulf of Alaska 65 km south of Seward, within the range of the western (endangered) stock of Steller sea lions (Fig. 1). During July of 1956, the earliest published census, there were 1,459 adult and 564 Steller sea lion pups counted at this site (Mathisen and Lopp 1963). However, the number of sea lions using Chiswell Island declined rapidly from that time through the 1980s and there was little known use of the island as a rookery during those years (National Marine Fisheries Service, in litt.). Recently, it has been used by about 90 breeding animals producing about 60 pups per year (Maniscalco et al. 2002).

**The remote-controlled video system.**—The Alaska Sealife Center contracted with SeeMore Wildlife Systems, Inc. of Homer, Alaska to install remotely operated cameras to study Steller sea lions at Chiswell Island without disturbing them. Cameras were installed in October 1998 and 6 cameras were functional at the peak of the breeding season for complete coverage of the entire rookery, although only 2 could be viewed and operated at the same time from the Alaska SeaLife Center in Seward, Alaska. Each camera was equipped with 12–18 $\times$  optical and digital zoom functions mounted in fully weatherproof housings and had remotely controlled pan, tilt, zoom, and windshield wiper-washer functions. Audio and video signals were sent via Category 5 cable (24 gauge, solid conductor, twisted-pair outdoor cable manufactured by Graybar Electric, St. Louis, Missouri) to a central control tower on Chiswell Island, which transmitted the images and sound to the Alaska SeaLife Center via microwave transmission. The cameras and control tower were powered by a 12-volt battery system charged by solar and wind power. At the Alaska SeaLife Center, audio and video signals were viewed and recorded in real time with television monitors and videocassette recorders, while commands for controlling the cameras were sent from custom-made software running on a desktop computer. All equipment associated with the remote-control video system was owned and serviced by SeeMore Wildlife Systems, Inc. ([www.seemorewildlife.com](http://www.seemorewildlife.com)) and use of the video signal was leased to Alaska SeaLife Center for the purpose of wildlife research. This technology allowed us to observe the sea lions in their natural habitat on a year-round basis without disturbance and without impairment by the extreme weather conditions that often occur in the Gulf of Alaska.

**Data collection and analysis.**—In 2001, we began a maternal investment study of many easily identifiable females and continued this work through 2004. All sea lions with unique scars, fungal patches, or other distinct markings were watched closely from their 1st arrival on shore. These animals are referred to as known females throughout this document. Observations took place from the arrival of the 1st female on the rookery (on or after 23 May) until 10 August in 2001 and 2002,

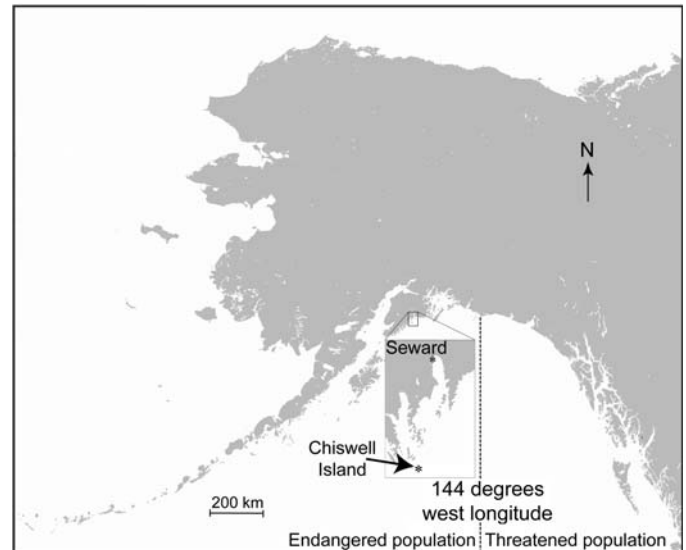


FIG. 1.—Map of Alaska showing location of Chiswell Island within the range of endangered Steller sea lions.

based on the approximate date that similar studies completed summer observations (e.g., Higgins et al. 1988, Milette and Trites 2003). In 2002, we started autumn maternal observations on 15 September, which continued until 5 November. In 2003 and 2004, there was no break in observations after 10 August and we continued until 28 October in 2003 and 18 September in 2004. Summer observations were conducted from at least 0600 to 2200 h daily. Additional morning and nighttime hours were added as light levels allowed with increasing day lengths. After 10 August, observations were made from approximately sunrise to sunset as the diminishing daylight allowed. During 2004 there was also a period of overnight observations by researchers on the rookery at the time of the summer solstice, 17–25 June. We conducted full census counts of all sea lions at the Chiswell rookery daily at 1100 h in all years and at 1900 h from late May through August. We also performed focal-animal sampling and scan sampling (Altmann 1974) at regular intervals daily throughout the study period and ad libitum sampling of events such as births and copulations.

Scan samples were the primary means of determining attendance patterns for known females and were conducted twice during even-numbered hours (0600, 0800, etc.) from at least 0600 to 2200 h during the summer and at least 3 times per day (dawn, midday, and dusk) after 10 August. All scans were recorded in a database with date, time, behavior, area of rookery, and identity of bull if occupying a breeding bull's territory (location and size of bull territories were analyzed separately from this work). During these scans we also noted when known females were absent from the rookery. In some cases, the presence of a female was uncertain because identifying marks were hidden from view. Those situations were entered as "unknown" in the database. If an animal was positively missing from one scan, it was assumed to have departed at the halfway point from the last scan when it was positively identified. The same was assumed for returning animals, except when the pelage was still wet, and then it was assumed that the animal had returned within the last half hour if the previous scan was an hour or more before. Overnight departures or arrivals were assumed to have taken place at 0200 h or the midpoint of nonobservation hours. If observed, actual arrival and departure times were recorded to the nearest minute whether or not they occurred during scan periods. A foraging trip or shore stay was classified as uncertain if there were >3 consecutive

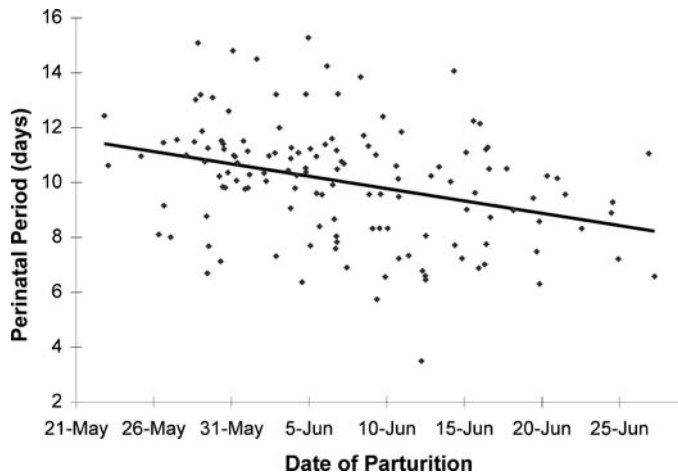


FIG. 2.—Relationship between date of parturition and duration of the perinatal period for Steller sea lions, with data normalized to 2001 levels ( $n = 135$ ).

scan hours of “unknown” status before the female was definitely noted as present or absent. The foraging cycles of lactating females were used in statistical analyses only if there were <50% uncertainties (i.e., unknown status for 3 consecutive scans equals 1 uncertainty) in foraging trip durations. All uncertainties were eliminated from individual female cycles. The required number of foraging trips per female ( $n$ ) needed to conduct paired  $t$ -tests between summer and autumn were determined by using the minimum detectable difference ( $\delta$ ; Zar 1999) calculated from all trips recorded between seasons.

To determine when changes began between summer and autumn foraging trip durations, we calculated mean trip duration and variance in 5-day intervals for all 4 years combined. The date of the midpoint of each 5-day interval was used as the predictor of mean trip duration for each interval in a linear regression. The data were then fit using a 3-stage regression model. This model fit a line that was hinged at 2 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 maternal trip duration and the specific date at which trip durations reached their maximum during autumn. These points corresponded to the minimum and maximum durations of foraging trips that were fit, and the midpoint between them approximated the date of maximum increase in average trip duration. This midpoint was used to delineate between summer and autumn seasons for further comparisons among known females. The 3-stage regression model used in this analysis has 6 parameters: a date = 0 intercept, a slope estimate for the line from date = 0 to the 1st inflection point, date of that inflection point, a slope estimate for the line from the 1st inflection point to the 2nd inflection point, the date of the 2nd inflection point, and finally the slope of the line from the 2nd 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 being fit.

Focal observations were also made on known females for one-half h periods, 6 times daily (at 0700, 0900, 1300, 1500, 1700, and 2100 h) during the summers of 2002 and 2003, and at least 3 times daily during autumn months. Females to be observed were selected from a random table of known females generated in Microsoft Excel. However, if the selected female was not present or not positioned in good view of the cameras, then the next random female on the list was selected and so on until the female chosen was in good view.

Behaviors occurring during each focal period were recorded in real time using Observer Pro 3.0 software (Noldus Information Technology, Leesburg, Virginia). We were primarily concerned with nursing behavior in this study and during focal observations recorded the amount of time spent nursing only when a pup had its mouth on a teat and was actively sucking.

When not conducting censuses, scans, or focal observations, we scanned the rookery for births, copulations, and other interesting or unusual behaviors. Many of these events were recorded using high-quality videotape and also in the database or spreadsheets. Parturitions of known females were recorded to the nearest minute. If they were not observed, we used the point of time halfway between when the females were and were not observed with a pup, provided the period of no observations was <8 h. We also continued to log information on known animals in the database opportunistically at times outside the summer and autumn maternal investment study periods. Females were considered multiparous if they were known to have pupped at least once in a previous year; whereas females were considered primiparous if known from distinctive natural markings or flipper tags and were never, before their 1st year of pupping, observed giving birth on Chiswell Island.

Values are reported as mean  $\pm$  SE. Analyses were performed using SigmaStat Version 2.03 and Systat Version 10. (SPSS, Inc., Richmond, California). Comparisons were made between seasons and years using parametric methods after determining that the data met assumptions of normality and independence.  $P$  values of <0.05 were considered significant. Focal observation data were summarized for activity budgets using Observer Pro 3.0 and transferred to SigmaStat for further analyses.

This study was purely observational and followed the American Society of Mammalogists guidelines (Animal Care and Use Committee 1998). Permits for this research were obtained from the National Oceanic and Atmospheric Administration, National Marine Fisheries Service (782-1532-00 and 881-1668-00) under the authority of the Marine Mammal Protection Act and the Endangered Species Act. Additional Special Use Permits were acquired from the United States Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge to conduct this research on refuge lands.

## RESULTS

*Parturition and the perinatal period.*—The number of pups born on Chiswell Island increased annually from 54 in 2001 to 65, 72, and 80 in the years 2002, 2003, and 2004, respectively. The mean date that births were known to have occurred (within 4 h) was 10 June in the years 2001–2003 and 11 June in 2004 (analysis of variance [ANOVA],  $P = 0.893$ ). However, 13 individual females known to have given birth during all 4 years had later dates of parturition in 2002 (15 June) compared to other years (repeated measures ANOVA,  $P = 0.025$ ). Perinatal periods over all 4 years averaged 10.7 days (range: 1.3–17.1 days). Three females continued to nurse yearlings as well as newborn pups in 2003 and 2 others did the same in 2004. Their perinatal periods were significantly shorter than for other females ( $\bar{X} = 4.8 \pm 1.2$  days,  $P = 0.007$ ) and they were excluded from further comparisons. Perinatal periods were significantly longer in 2002 ( $12.0 \pm 0.4$  days) compared to 2001 ( $10.0 \pm 0.4$  days) and 2004 ( $10.7 \pm 0.3$  days), but not compared to 2003 ( $11.4 \pm 0.4$  days). There was a significant negative correlation ( $r = -0.334$ ,  $P < 0.001$ ) between date of

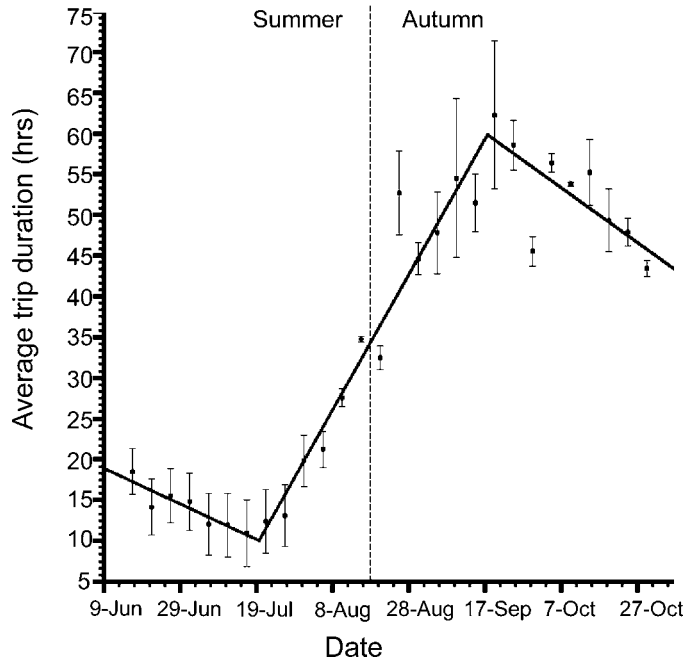


FIG. 3.—Average foraging cycles for all female Steller sea lions and all years combined in 5-day increments. The pattern of change was similar from year to year, although the data were not collected continuously after 10 August in every year.

birth and duration of the perinatal period in all years combined with birth dates and perinatal periods normalized to 2001 (Fig. 2). Twenty-six multiparous females that had given birth before or during 2002 had a mean date of parturition of 9 June and mean perinatal period of 11.2 days in 2004. Those contrast with 13 primiparous females in 2004 which had a later mean date of parturition (15 June;  $t = 2.22$ ,  $P = 0.032$ ) and a shorter mean perinatal period (9.6 days;  $t = 2.08$ ,  $P = 0.026$ ).

**Foraging cycles.**—We chose 5-day intervals for assessing changes in trip duration because individuals tended to alternate long and short foraging trips and we were interested in seasonal patterns, rather than day-to-day differences. Examination of the initial regression residuals of mean foraging durations indicates that error variance increased with date (Fig. 3). Therefore, we weighted the regression residual calculation at each date by the standard deviation associated with the average trip duration for that date to correct for unequal variance. The model found an initial inflection point at 19 July. Trip duration increased steadily from then until 17 September (Fig. 3). The midpoint between those 2 inflection points was 18 August, which marked the transition from summer to autumn.

Summer foraging trip durations averaged  $16.5 (\pm 0.6)$  h over all years but varied from year to year with known females in 2002 having significantly shorter trips ( $11.5 \pm 0.6$  h) compared to 2003 ( $19.3 \pm 1.8$  h) and 2004 ( $18.1 \pm 0.8$  h) but not 2001 ( $15.1 \pm 1.0$  h; Table 1). Multiparous females ( $n = 24$ ) foraged the same amount of time (17.4 h) as primiparous females ( $n = 9$ ; 17.4 versus 17.6 h;  $t = 0.11$ ,  $P = 0.910$ ) during the summer of 2004. Autumn foraging trips averaged  $55.7 (\pm 3.1)$  h over the years 2002–2004 and were not significantly different in any

TABLE 1.—Mean foraging cycles of all known females combined for summer (1 June to 18 August) and autumn (after 18 August) from 2001 through 2004. Sample sizes ( $n$ ) are number of females tracked. Data with same superscripts in rows were significantly different (Tukey test).  $P$  value is for ANOVA.

	2001	2002	2003	2004	$P$
<b>Summer</b>					
$n$	12	18	16	37	
Foraging trip (h)	15.1	11.5 <sup>ab</sup>	19.3 <sup>a</sup>	18.1 <sup>b</sup>	<0.001
Shore stay (h)	22.3	19.9 <sup>a</sup>	27.5 <sup>ab</sup>	22.4 <sup>b</sup>	0.001
Foraging cycle (days)	1.56 <sup>a</sup>	1.31 <sup>bc</sup>	1.95 <sup>ab</sup>	1.69 <sup>c</sup>	<0.001
Time at sea (%)	40.9	36.7 <sup>a</sup>	40.3	44.7 <sup>a</sup>	0.002
<b>Autumn</b>					
$n$	0	11	12	20	
Foraging trip (h)		52.9	64.2	52.1	0.234
Shore stay (h)		33.2	31.8	26.7	0.089
Foraging cycle (days)		3.58	4.00	3.28	0.130
Time at sea (%)		60.6	65.6	65.0	0.420

year (Table 1). However, observations ended on 18 September in 2004 because females departed the rookery early that year. Trip durations did not change significantly through any autumn season (linear regression  $P$ -values: 2002 = 0.699, 2003 = 0.920, 2004 = 0.509).

Seasonal comparisons among individual females indicate that they foraged at sea an average of 3.3 times longer in autumn than in summer each year. Visits ashore also increased significantly from summer to autumn during 2002 and 2004 but not in 2003 (Table 2). Summer to autumn increases in duration of foraging trips during 3 years and shore visits during 2 years resulted in increases in attendance cycles (1 cycle = 1 shore visit plus 1 foraging trip) of about 2 days overall (Table 2). Individual females spent about 40% of their time foraging at sea during the summer compared to >60% during the autumn (Table 2).

**Nursing behavior.**—We recorded behaviors from 292 half-hour focal samples on randomly selected females during the summer of 2002 and 257 samples during the summer of 2003. Lactating females spent 4.9% of their time nursing while on shore in 2002 versus 6.8% in 2003. Those differences were not significant (Mann–Whitney rank sum test,  $P = 0.929$ ). There were no significant increasing or decreasing trends in the amount of time spent nursing over the course of the 2002 or

TABLE 2.—Paired comparisons of individual female foraging cycles between summer (1 June to 18 August) and autumn (after 18 August). The number of females compared is in parentheses. Asterisk indicates that autumn values were significantly greater than summer values for the same year ( $P < 0.05$ , paired  $t$ -test).

	2002 ( $n = 11$ )		2003 ( $n = 8$ )		2004 ( $n = 20$ )	
	Summer	Autumn	Summer	Autumn	Summer	Autumn
Foraging trip (h)	11.2	52.9*	21.6	67.4*	19.1	52.1*
Shore stay (h)	19.4	33.2*	29.1	31.9	21.5	26.7*
Foraging cycle (days)	1.27	3.58*	2.11	4.14*	1.69	3.28*
Time at sea (%)	36.3	60.6*	41.7	66.5*	47.1	65.0*

2003 summer seasons. During 2002, 8 individual females nursed their pups for a greater proportion of their total activity budget during the autumn compared to summer (8.4% versus 2.9%; paired-*t*,  $P = 0.045$ ). Focal observation data during the autumn of 2003 were too few and too variable for suitable estimates of nursing durations.

## DISCUSSION

This study examined several aspects of maternal care in individual Steller sea lions at Chiswell Island over the course of 4 consecutive summer (2001–2004) and 3 consecutive autumn seasons (2002–2004). The ability to track the same females over successive seasons and years eliminated variability associated with sampling different individuals as most other studies have done and allowed us to examine rookery-wide changes as well as real changes in maternal care among individuals.

*Parturition and the perinatal period.*—The number of pups born at the Chiswell rookery increased every year during this study. Mean date of births (10–11 June) observed at Chiswell Island is consistent with other rookeries in the northern Gulf of Alaska (Pitcher et al. 2001). Later birth dates among individual females in 2002 may have resulted from a period of reduced food availability, causing later breeding, later implantation, or extended gestation (as discussed in Pitcher et al. 2001). Steller sea lions begin active gestation in late September or early October (Pitcher and Calkins 1981) but autumn food availability is not thought to play a major role in influencing the timing of implantation in this species (Pitcher et al. 1998). Rather, implantation is thought to be primarily related to photoperiod in most pinnipeds (Boyd 1991; Temte and Temte 1993). In *A. gazella*, however, it has been suggested that females in poorer condition during autumn may delay implantation (Lunn and Boyd 1993) and that winter or spring seasonal reductions in food availability could extend the gestation period (Boyd 1996). In our study, the later birthdates observed in 2002 are suggestive of either later implantation or an extended gestation period, possibly due to lack of sufficient forage during the preceding autumn and/or winter, whereas the longer perinatal periods in 2002, as compared to other years, are suggestive of more abundant resources during the spring months before parturition. Future comparisons of autumn foraging cycles and fisheries surveys with subsequent-year pupping dates at the Chiswell rookery may provide a better understanding of the role of food availability with the timing of implantation and the duration of gestation in *E. jubatus*.

Food availability before parturition may affect duration of the perinatal period in *Mirounga angustirostris* (Stewart and Yochem 1991), *A. gazella* (Boyd et al. 1991; Doidge et al. 1986; Lunn and Boyd 1993), *Z. californianus* (Ono et al. 1987), and *E. jubatus* (Hood and Ono 1997). Perinatal periods observed in *E. jubatus* at Chiswell Island averaged at least 10 days and are among the longest seen anywhere for this species. Therefore, we may assume that breeding females were probably well fed before parturition during all years of this study regardless of interannual variations in their perinatal periods.

Multiparous, presumably older, females gave birth earlier in the season and were able to stay on the rookery longer after parturition than were primiparous females. Similarly, older females tend to give birth earlier in the season in *A. gazella* (Boyd 1996; Lunn and Boyd 1993) and *Callorhinus ursinus* (Boltnev and York 2001), and this may have increased survivability of pups during years of moderate to high mortality in fur seals (Boltnev et al. 1998). Furthermore, duration of the perinatal period is longer for *A. gazella* females that arrive at the rookery earlier but is not related to maternal age or condition (Lunn and Boyd 1993). We also found a significant negative relationship between date of parturition and duration of the perinatal period in *E. jubatus*. That relationship could not be specifically related to age or condition in our study but was related to parity. This suggests that experienced females provide better postnatal care in terms of attending to their pups for a longer period before reinitiating foraging bouts than do inexperienced females.

*Foraging cycles.*—Long foraging trip durations have been linked to low food availability in several pinniped species and are often associated with El Niño events in the western Pacific Ocean (e.g., Lunn et al. 1993; Majluf 1991; Ono et al. 1987). For example, during the strong El Niño of 1983 when squid, mackerel, and anchovy abundances were particularly low, female *Z. californianus* with pups foraged for significantly longer periods than during the previous year (Heath et al. 1991). In South Georgia, *A. gazella* also make significantly longer foraging trips during years of low krill abundance than in years of abundant krill, as estimated from independent surveys (Boyd 1991). In contrast to those studies, we found that lactating females at Chiswell Island made short foraging trips that were consistent with those found at other Steller sea lion rookeries during the 1990s in the western (declining) population and about half the duration of foraging trips seen in the southeastern Alaska (stable) population (Brandon 2000; Milete and Trites 2003). This suggests that sea lions in the northern Gulf of Alaska have not been food-limited during recent years, at least during summer months. Furthermore, the overall quality of available prey was hypothesized to be the main cause of the western population declines during the late 1970s through the 1980s (Alverson 1992; Rosen and Trites 2000), but there is little evidence that food quality is currently a problem for *E. jubatus* (Pitcher 2002; Trites and Donnelly 2003).

In our study, foraging trip durations remained relatively stable from June through mid-July in all 4 years but increased sharply beginning 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). Increasing foraging trip durations by females with pups up to 2 months of age have been observed in *E. jubatus* (Higgins et al. 1988; Milete and Trites 2003) and other otariids (e.g., Doidge et al. 1986; Gentry and Holt 1986) and are presumed necessary to meet the increasing energy demands of growing pups (Gentry and Holt 1986). Marked increases in foraging trip durations from summer to winter months have also been noted in both *E. jubatus* (Merrick and Loughlin 1997; Trites and Porter 2002)

and *Z. californianus* (Melin et al. 2000). However, those studies were unable to determine when those changes occurred. At Chiswell Island, we observed that these changes did not occur gradually over the course of the summer and autumn seasons but happened over a relatively brief period during the month of August. We suggest that the abrupt increase in foraging trip durations of lactating females may have resulted from a seasonal change in food availability, social independence of pups, a sudden increase in energetic demands of pups or mothers, or a combination of these factors.

Studies on maternal attendance of overwintering California and Steller sea lions have found no significant changes in foraging trip durations over the course of winter–spring seasons (Melin et al. 2000; Merrick and Loughlin 1997; Trites and Porter 2002). We also found no significant change over the course of the autumn season, providing evidence that sea lions in the northern hemisphere may reach maximum foraging cycle durations by early autumn and maintain them throughout the winter. The roughly asymptotic pattern in maternal trip duration that occurs from summer to autumn (Fig. 3) may be a result of pups learning to forage on their own, as suggested by others (Melin et al. 2000; Trites and Porter 2002), or may indicate a behavioral pattern of nourishment and lactation that has evolved to best suit this species during times when food is less abundant. Greater variability in trip durations during late summer and autumn compared to early–midsummer likely indicates that the availability of forage becomes less predictable, and detecting overwintering trends in foraging cycles becomes more elusive with increased variation.

Significant differences in foraging cycle durations between summers at Chiswell Island probably signify a range of plasticity in the behavior of *E. jubatus*, which may be an adaptation for dealing with interannual variations in food availability. The consistency of autumn foraging cycles suggests that they reach a maximum amount of time for foraging and resting, beyond which it may become difficult to maintain lactation or gestation. Our observations of 2.3-day foraging trips for mothers with pups during the autumn months are slightly longer than those reported in southeast Alaska during winter for this species (2.0 days; Trites and Porter 2002), but much shorter than those reported farther west during the late 1980s and early 1990s when the sea lion decline was more acute than at present (8.5 days; Merrick and Loughlin 1997). In *Z. californianus*, pup mortality increased significantly during the 1982–1983 El Niño when foraging trips increased 47% from 1.39 to 2.04 days (Ono et al. 1987). *E. jubatus* may have a greater flexibility in time spent foraging than *Z. californianus* because of their larger size. Yet, foraging durations that exceed 3 times what may be the winter norm (e.g., Merrick and Loughlin 1997, compared to Trites and Porter 2002, this study) could indicate limited food availability. However, Merrick and Loughlin (1997) admit that they probably tracked both lactating and nonlactating females, the latter of which may have biased their foraging trip durations to be longer.

Lactating females at the Chiswell rookery also increased the duration of their shore visits from summer to autumn during 2002 and 2004. Yet, other interseasonal studies of lactating

*E. jubatus* found no change in the duration of shore visits (Merrick and Loughlin 1997; Trites and Porter 2002). This was also the case during 2003 at Chiswell Island when the mean duration of the summer visits was similar to autumn. Shore visits in summer and autumn of 2003 and autumn 2002 were approximately 1.3 days long and are on the upper end of those observed in most other *E. jubatus* studies regardless of season (Higgins et al. 1988; Merrick and Loughlin 1997; Sandegren 1970; Trites and Porter 2002). This may indicate a maximum amount of time needed to rest and nurse their pups between foraging bouts. Despite increasing shore stays in 2 out of 3 years, females spent a greater proportion of time at sea during the autumn compared to summer at Chiswell Island. *E. jubatus* in southeastern Alaska show a similar attendance pattern, spending a greater percentage of time on shore during summer and a greater percentage of time at sea during winter (Milette and Trites 2003; Trites and Porter 2002). Those changes result from longer foraging trip durations without any change in shore visit duration, effectively increasing the overall attendance cycle to about 3 days (Trites and Porter 2002), which compares to more than 3.5 days in Chiswell Island sea lions. Melin et al. (2000) also found that lactating *Z. californianus* during winter have foraging cycles that are a day longer at sea and a day shorter on shore compared to summer cycles.

*Nursing behavior.*—We recorded nursing behavior under the premise that the amount of time spent suckling is a measure of energy transfer to the pup, although recent pinniped studies (e.g., Galimberti et al. 2002; Higgins et al. 1988) and a recent review (Cameron 1998) suggest that this may not be the case. On the other hand, time spent suckling in *A. galapagoensis* young was found to be significantly correlated with weight gain (Trillmich 1986). Furthermore, our focal sampling methods include actual suckling time on the teat which may be a more reliable measure of energy transfer than quantifying suckling bouts that can include time off-teat of up to 30 s (e.g., Higgins et al. 1988).

Pups are expected to suckle more as they age to meet increasing energy demands and the insignificant changes in suckling duration that we observed during the summer months may be independent of sampling methods and result from an increase in suckling efficiency over the 1st few months of the pups' lives as suggested by Higgins et al. (1988). Once a young sea lion becomes maximally efficient at suckling, changes in nursing duration such as we observed in individual females from summer to autumn in 2002 may more accurately represent changes in energy transfer as foraging durations increase. Similarly, the amount of milk energy delivered to pups was positively correlated with foraging trip duration in *A. gazella* (Arnould and Boyd 1995). In our study, there was also an increase, though insignificant, in the proportion of time spent nursing between the summer of 2002 and the summer of 2003, which may have indicated that pups were trying to make up for the extended foraging trips of their mothers in 2003.

Increasing milk energy intake with increasing pup age may depend on the species being studied. For example, the fat energy content of female *Halichoerus grypus* milk increases while daily intake of milk by pups stays the same during a short

lactation period (Iverson et al. 1993). Among otariids, fat energy may decrease over lactation while milk ingestion increases in *C. ursinus* (Costa and Gentry 1986) or while milk ingestion remains constant as in *Z. californianus* (Oftedal et al. 1987). Changes in the composition of *E. jubatus* milk over time have not been published and would be necessary to better understand milk energy transfer and its relation to suckling durations in this species.

In all years of this study, measures of maternal care at Chiswell Island appeared sufficient and comparable to similar Steller sea lion studies during the 1990s. Long perinatal periods and short summer foraging trip durations indicated that these animals were able to find sufficient food in the vicinity of the rookery. Intra-annual changes in maternal care occur in late summer but do not change significantly through the autumn season. Increases in summer foraging trip durations may not signify critically low food availability unless they greatly exceed the autumn and winter norms. We intend to continue this study because it will allow us to determine which behavioral measures of maternal care are the best long-term predictors of reproductive health in Steller sea lions.

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