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Author(s): Vladimir Burkanov, Eliezer Gurarie, Alexey Altukhov, Evgeny Mamaev, Peter Permyakov, Alexey Trukhin, Jason Waite, and Tom Gelatt

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Environmental and biological factors influencing maternal attendance patterns of Steller sea lions (*Eumetopias jubatus*) in Russia

VLADIMIR BURKANOV, ELIEZER GURARIE,* ALEXEY ALTUKHOV, EVGENY MAMAEV, PETER PERMYAKOV, ALEXEY TRUKHIN, JASON WAITE, AND TOM GELATT

National Marine Mammal Laboratory, Alaska Fisheries Science Center/National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115-6349, USA (VB, EG, TG)

Kamchatka Branch of the Pacific Geographical Institute, Far East Branch of Russian Academy of Sciences, 6 Partizanskaya Street, Petropavlovsk-Kamchatsky, 683000, Russia (VB, AA)

Department of Biosciences, P.O. Box 65 (Viikinkaari 1), FI-00014 University of Helsinki, Helsinki, Finland (EG)

Kamchatka Scientific Research Institute of Fisheries and Oceanography (KamchatNIRO), 18, Naberezhnaya Street, Petropavlovsk-Kamchatsky, 683000, Russia (EM)

V.I. Il'ichev' Pacific Oceanological Institute Far East Branch of Russian Academy of Sciences, 43 Baltiyskaya Street, Vladivostok, 690041, Russia (PP, AT)

School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, P.O. Box 755220, Fairbanks, AK 99775-7220, USA (JW)

* Correspondent: eli.gurarie@noaa.gov

Maternal attendance patterns in free-ranging wildlife can provide insight into basic biology, foraging behavior, and population dynamics. We collected detailed visual observations of attendance patterns by adult lactating Steller sea lions (*Eumetopias jubatus*) from 2005 to 2007 on 6 major rookeries in the Russian Far East, including those with an increasing population trend (Sea of Okhotsk), severely depleted populations that were recovering (Kuril Islands), or those that were stable (Commander Islands). Individually identifiable females were observed during the postpartum period, with special attention paid to presence and absence during the day and to departure and arrival times. Within Russia females on several Kuril Islands rookeries exhibited extremely short foraging trip durations (median 6.5–8.0 h) and spent higher proportions of time on the rookery (75–82%), whereas females in the Sea of Okhotsk population had the longest trips (median 19.8 h) and spent the least amount of time on the rookery (60%). Most indices of attendance pattern were more favorable (longer peripartum period, higher proportion of time spent on rookery, shorter trips, and longer visits) than those reported in Alaska and much more so than those in California during El Niño years, where the proportion of time spent on the rookery was nearly half that in Russia. Females >6 years of age had shorter trips and longer visit durations than the youngest females (4–5 years), and older mothers exhibited significantly longer periods of nursing before taking their 1st trip, suggesting greater physical condition for older females. Although trip durations remained constant throughout the season, visit durations shortened significantly as the pups aged, suggesting that increasing nutritional demands of pups are met by more frequent, rather than longer, trips. No apparent relationships between attendance patterns and population status were observed; however, many of the differences in attendance patterns throughout the range of the Steller sea lion could be related to local variation in bathymetry and diet patterns.

Key words: Asian population, Commander Islands, *Eumetopias jubatus*, foraging behavior, Kuril Islands, maternal attendance patterns, postpartum nursing period, Sea of Okhotsk

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Steller sea lions (*Eumetopias jubatus*) range along the North Pacific from northern Japan to California. The United States population has been subdivided into 2 stocks: the western United States stock, which includes all animals west of 144°W and throughout the Aleutian Islands, and the eastern United States stock, including all animals east of 144°W, from southeastern Alaska to California (Bickham et al. 1996). Consistent declines in populations since the 1st trend counts in Alaska in 1956–1960 led to the listing of the western stock as endangered and the eastern stock as threatened under the Endangered Species Act (Gelatt and Lowry 2008). An intense research effort has been underway to identify the causes of the population decline (Loughlin 1998), but definitive causes have proven elusive. A leading hypothesis is that the proximal cause of the decline has been food limitation, whether due to overfishing, environmental changes, or an interaction of the 2 (Atkinson et al. 2008a, 2008b; DeMaster and Atkinson 2002; Loughlin and Merrick 1989; Merrick et al. 1997; Trites and Donnelly 2003).

In Russia Steller sea lions are found in the western Bering Sea, on the Commander Islands, along the east coast of Kamchatka, along the Kuril Islands, on Sakhalin Island, and around the Sea of Okhotsk (Burkanov and Loughlin 2005; Ognev 1935). Recent genetic evidence together with branded animal resighting patterns indicate that the Kamchatka, Kuril, Sakhalin, and Sea of Okhotsk populations constitute a separate Asian stock, and the Commander Islands population aligns with the western stock (Baker et al. 2005). Population trends in the Commander Islands have mirrored western population declines, with an estimated 86% decline since 1977 (Burkanov and Loughlin 2005; Burkanov et al. 1991). The Kuril Islands population appears to have stabilized since 1989 following a prolonged period of decline and is showing a recent increasing trend, with an annual growth of 7.7% per year since 2004 (Burkanov et al. 2008).

Unlike most phocids, lactating otariid females periodically leave their pups unattended on the rookery to forage, balancing a need to replenish energetic reserves at sea and provide milk for their dependent offspring on shore. The durations and frequencies of foraging trips and onshore visits are collectively referred to as maternal attendance patterns. These patterns reflect bioenergetic constraints and local food abundance and have been compared between populations to test food-limitation hypotheses (Altukhov et al. 2008; Andrews et al. 2002; Brandon 2000; Gentry 1998; Milette and Trites 2003; Trites and Porter 2002). Sea lions might be expected to adjust their trip lengths as a response to food availability, such that nutritionally stressed populations can spend more time searching for prey at sea and less on land than stable populations. This relationship has been reported for several other otariid species. Antarctic fur seals (*Arctocephalus gazella*), South American fur seals (*A. australis*), Galapagos fur seals (*A. galapagoensis*), northern fur seals (*Callorhinus ursinus*), and California sea lions (*Zalophus californianus*) all have been shown to make longer trips when prey is scarce (Boyd 1999; Costa et al. 1989; DeLong and Antonelis 1991; Heath et al. 1991; Majluf 1991; McCafferty et

al. 1998; Ono et al. 1987; Trillmich 1986, 1991). A similar response had been reported for Steller sea lions at Año Nuevo Island during a moderate 1992 El Niño event (Hood and Ono 1997).

Although changes in food availability can affect maternal attendance patterns, a straightforward relationship between maternal attendance patterns and long-term changes in sea lion populations has not been demonstrated. Several researchers have noted that the stable or increasing southeastern Alaska population exhibits longer foraging trips than depleted populations from western Alaska, contradicting expectations (Andrews et al. 2002; Brandon 2000; Milette and Trites 2003; Rehberg et al. 2009). The results might indicate either that the relationship between food availability and population trend is not as tightly linked as hypothesized, that variability in foraging behavior between locations is greater than adaptive behavioral variation, or that the different populations are at different levels relative to their carrying capacity.

Most studies of attendance patterns during the breeding season have used radiotelemetry, which has the advantage of providing highly precise data, including nocturnal data (Andrews et al. 2002; Brandon 2000; Merrick and Loughlin 1997). However, these studies are costly and can be difficult to implement on full-grown adults that cannot be captured and instrumented easily. Observational studies on large numbers of marked animals are less accurate but provide much more data. In Russia Steller sea lion pups have been branded since 1989, and a dedicated resighting effort has been underway in the past 10 years, with observers stationed at most of the Russian rookeries making daily behavioral observations. Extensive branding (more than 5,000 marked pups between 1989 and 2004) and the long-term resight effort in Russia have provided an extensive multiyear data set and complete knowledge on the origin, age, and resight history of hundreds of reproductive females.

We examined maternal attendance patterns based on data obtained during 3 reproductive seasons (2005–2007) at 6 rookeries from all regions of the Russian range of the sea lion and compared our findings with published results of similar studies elsewhere. These 6 rookeries account for more than half of all Steller sea lions reproducing in Russian waters and include rookeries from depleted, recovering, and stable populations. We had 2 primary objectives in this study. First, by comparing the attendance behavior of a large number of individually marked females, we expected to obtain insights into the behavioral biology of lactating females. Second, by exploring attendance patterns over a large range and over several years, we investigated the role of several ecologically important processes expected to test hypotheses that might explain attendance patterns, including long-term population status, local bathymetry, and diet.

MATERIALS AND METHODS

Study area.—We collected data at 6 rookeries from 3 distinct regions, 4 rookeries on the Kuril Islands, 1 in the

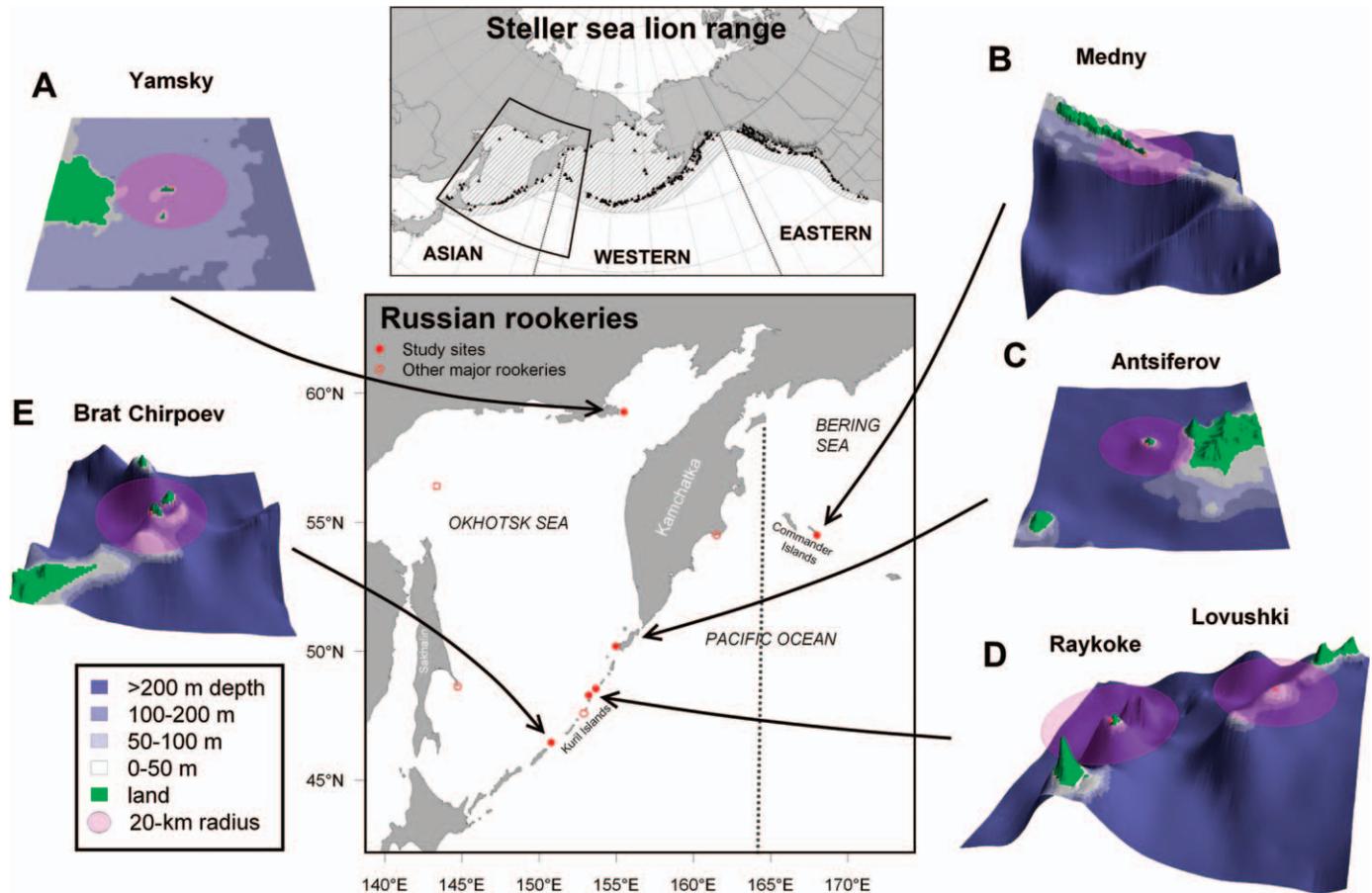


FIG. 1.—Map of Steller sea lion rookeries in Russia. Locations where data were collected are represented by the filled red circles. Empty circles represent other major reproduction sites. The local bathymetry of the study sites is presented in the 3-dimensional plots, with increasingly darker blue representing increasingly deeper waters as per the legend in lower left. The translucent purple circles represent a 20-km foraging radius typical of Steller sea lion females.

Commander Islands in the western Bering Sea, and 1 in the northeastern Sea of Okhotsk (Fig. 1). We characterized the local bathymetry within 20 km of each rookery. This radius was chosen because it accounts for the majority of observed trip distances of satellite-tagged juvenile Steller sea lions in Alaska (Fadely et al. 2005; Loughlin et al. 2003; Raum-Suryan et al. 2004). We also report the proportion of area <100 m in depth within 10 and 20 km, corresponding to the most common diving depths of juvenile sea lions in Alaska (Fadely et al. 2005; Merrick and Loughlin 1997; Rehberg and Burns 2008). All bathymetry data were obtained from the global 30-arc-second General Bathymetric Chart of the Oceans (GEBCO) Digital Atlas (General Bathymetric Chart of the Oceans 2003) and imported into the R statistical programming package (R Development Core Team 2009) using the RNetCDF package (Michna 2006).

Of the roughly 16,000 sea lions in Russia, approximately 8,000 reproduce on the Kuril Islands (Burkanov and Loughlin 2005) and are considered to belong to the Asian stock (Baker et al. 2005). The Kuril Islands population experienced a 70% range-wide decline from a peak of >20,000 individuals in the 1960s to a nadir of about 6,000 in the 1990s but has since been recovering steadily (Burkanov and Loughlin 2005; Fig. 2).

Four Kuril Islands rookeries were monitored between 2005 and 2007: Brat Chirpoev, Raykoke, Lovushki, and Antsiferov (Figs. 1c–e). Observers were stationed at rookeries from 25–26 May through 15–21 July all 3 years, conducting dawn to dusk observations (approximately 0530–2300 h) from blinds located on cliff edges or hillsides overlooking the rookeries. These dates captured nearly all pup births on the rookeries and the growth of the pups until most could swim.

Brat Chirpoev (46.5°N, 150.8°E) is a volcanic island located in the southern Kuril Islands group. Brat Chirpoev was the 2nd most productive of the Kuril Islands study sites, with 300–400 pups born each season. Between 1989 and 2004 776 pups were banded on Brat Chirpoev. Bathymetry within a 20-km radius of the rookery ranges from 0 to 2,000 m, with relatively wide accessible shelf areas surrounding neighboring islands (Fig. 1e). A relatively high proportion of the adjacent waters (21% and 17% at 10 and 20 km, respectively) are within 100-m depths.

Raykoke Island (50.2°N, 153.2°E) is a small volcanic island 18 km north of the much larger Matua in the central Kuril Islands. Approximately 250 pups are born annually on Raykoke, making it one of the smaller Kuril Islands rookeries. Between 1989 and 2004 739 pups were banded on Raykoke.

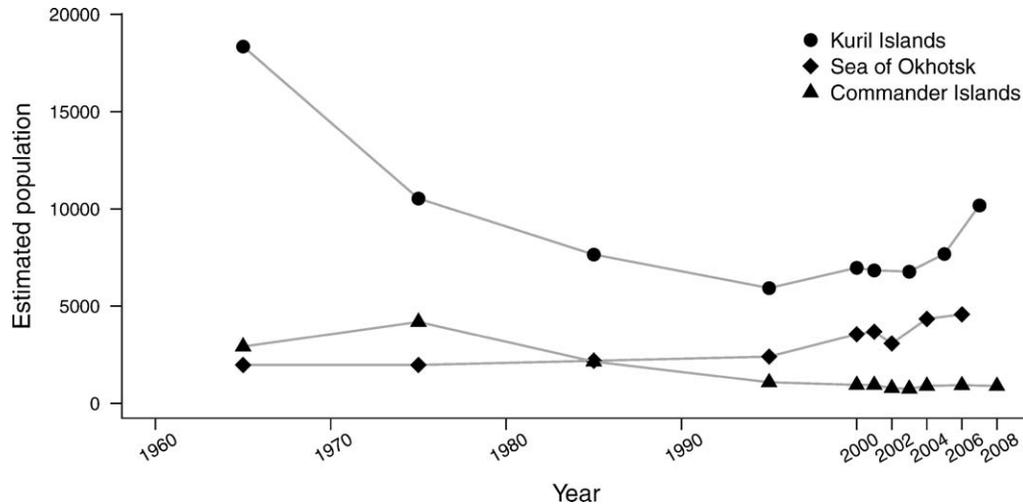


FIG. 2.—Population estimates and trends of Steller sea lions in Russian waters (all ages and sexes) in 3 regions: the Kuril Islands; Commander Islands, including Medny rookery; and the Sea of Okhotsk, including Yamsky rookery. Data prior to 2000 are based on reconstructed decadal abundance estimates (Burkanov and Loughlin 2005). Data since 2000 are based on survey results (Burkanov 2009; Burkanov et al. 2002, 2003, 2008).

Immediately accessible shelf area at typical Steller sea lion is extremely limited (Fig. 1e), with only 5% and 1.4% of the area within 10 km and 20 km, respectively, under 100 m in depth.

Lovushki Islands (48.3°N, 153.8°E) are the exposed edge of a sinking caldera 50 km northeast of Raykoke. Observations were conducted on 400-m-long Dolgaya Rock, one of the larger islands, with a maximum elevation of 30 m. With an annual pup production of approximately 650, it is one of the most productive Kuril Islands rookeries in our study. Between 1989 and 2004 677 sea lion pups were branded on Dolgaya Rock. Bathymetry around Lovushki is very heterogeneous and includes an immediately accessible shelf, with 28% of the area within 10 km and 11% of the area within 20 km of the rookery under 100 m in depth.

Antsiferov Island (50.2°N, 153.2°E) is a small, circular volcanic island about 18 km west of the southern end of Paramushir Island in the northern Kuril Islands. Between 1996 and 2004 550 pups were branded on Antsiferov, and 280–320 pups were born annually during the years of our study. Waters immediately around the island drop off rather steeply, with only 7.6% of the area within 10 km under 100 m in depth (Fig. 1c). However, the proximity to Paramushir makes an additional shelf area available, such that a slightly higher proportion of accessible area exists within 20 km (8.8%) than within 10 km.

The northern Sea of Okhotsk Steller sea lion population, accounting for about 30% of Russian sea lions, has increased steadily from about 2,000 animals in the 1960s to almost 5,000 in 2005 (Burkanov and Loughlin 2005; Fig. 2). This population reproduces primarily on 2 major rookeries, Iony Island in the northwestern Sea of Okhotsk (pup production >1,000) and Yamsky Islands in the northeast (about 480 pups—Burkanov and Loughlin 2005). Attendance pattern observations were made only on Yamsky Islands in 2007 (59.3°N, 155.5°E). The rookery is on Matykil Island, the

largest island in the group at about 4.6 km long and 1.6 km wide at the widest, where 3 observers performed daily observations from a blind 40 m above the rookery. Yamsky is the northernmost rookery in Russia and among the most northern reproductive sites for Steller sea lions in the world. When the sea lions arrive in May, the island often is surrounded by ice floes, although the active currents in the mouth of Shelikhov Bay help maintain open water. Yamsky rookery is well within the continental shelf and is surrounded by a featureless shallow sea bottom, with 100% of depths within 20 km under 100 m (Fig. 1a).

The Commander Islands, Medny and Bering, are the westernmost links in the Aleutian chain. The sea lions populating these islands belong to the western stock (Baker et al. 2005) but travel regularly to the eastern coast of Kamchatka (Burkanov and Calkins 2008; Burkanov and Loughlin 2005). Sea lions reproduce on Medny Island (52°N, 168°E), the smaller of the 2 islands, on a strip of gravel and rocky beach at the southeastern tip of the island. Approximately 200 pups are born annually on Medny. The sea lion rookery overlaps with a large northern fur seal rookery that can produce more than 30,000 pups annually (I. A. Blokhin, Kamchatka Research Institute on Fisheries and Oceanography [KamchatNIRO], pers. comm.). The Commander Islands are on a wide ridge near the edge of a shelf break dropping to the North Pacific to the south and the shallower Bering Sea to the north. About 88% of the area within 10 km and 48% of the area within 20 km is <100 m in depth (Fig. 1b).

The total number of nonpup sea lions on the Commander Islands decreased sharply from more than 4,500 in 1977 to fewer than 600 in 2002 (Burkanov and Loughlin 2005; Loughlin et al. 1992). The population appeared to have stabilized at a depressed level during the years of our study (Burkanov et al. 2008; Fig. 2).

Between 1996 and 2004 621 pups were branded on Medny Island. Observers were stationed on Medny Island from 22–25

May through 14–17 August in 2005–2007. Observations were performed daily from 2 observation points located 40 m above sea level on the cliffs overlooking the beach.

Data collection.—The standard methodology for observers on all islands was to be present in the blinds from dawn (0430–0600 h) to dusk (2200–2330 h). All branded and naturally marked animals were photographed daily with digital cameras through telescopes to confirm identifications precisely. During the first 3 h of the morning and the last 3 h in the evening the rookery was scanned visually at half-hour intervals, and the presence or absence of every branded or naturally marked reproductive female was noted. The frequency of rookery-wide scans was reduced to once per hour during the middle of the day when activity by the animals on the rookery was minimal.

The rookery-wide scans were supplemented by explicit observations of arrival times and departure times of certain focal females. Focal females were either branded or otherwise naturally marked adult females that gave birth in areas that were well observed from the blinds. Naturally marked animals usually had large, distinctive scars, which made their resighting probability similar or better than that of branded animals. Parturition, nursing, copulation, and occasional deaths were noted whenever observed.

Often, exact arrival and departure times of an animal were unobservable, most commonly because they occurred during nighttime hours. In these cases arrivals or departures were assigned arbitrarily to the midpoint of the nonobservation period, usually 0230 h. In other cases observers were asked to make estimates of arrival and departure times based on other constraints. This was possible, for example, when an animal's pelage was still wet when it was 1st observed in the mornings, allowing for an estimate of arrival within an hour of observation, or if a well-observed animal in the evening was clearly absent from its spot during a mass emptying of the rookery. Any indications of arrival and departure times in these cases were recorded as estimated.

The collected arrival and departure times were used to calculate visit durations and trip durations. In those cases when even an estimate of arrival and departures was impossible, the corresponding visit or trip cycle was excluded from the analysis.

To improve the effectiveness of this method the observers worked on alternating 24-h cycles from midday to midday, such that the observer was familiar with the animals that departed in the evenings and could better recognize whether an animal returned on the following morning. The estimation methodology for arrival and departure time is broadly consistent with methodologies in visual studies of maternal attendance patterns on Año Nuevo Island (Higgins et al. 1988) and in various sites in Alaska (Maniscalco et al. 2006; Milette and Trites 2003; Trites and Porter 2002). All field data collection conformed with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Analysis.—For consistency among the attendance observations we restricted the data for analysis as follows. Only

females whose pups survived the reproductive season were used for analysis. Only the periods within 30 days after parturition were included in the analysis. This allowed us to compare the data from females that gave birth later in the season (late June) with those that gave birth earlier in the season (late May and early June) without having the more extended period of observation for the early-birth females bias the comparisons. Those animals that were observed for <10 days were excluded from the analysis. We analyzed only data collected before branding, which occurred on June 28 in 2006 on Medny and between July 1 and 16 on the Kuril Islands in 2005 and 2007. Thus, the observations of the animals ranged from 10 to 30 days, with 90% of the sea lions observed for ≥ 20 days. Although this introduced a slight bias toward shorter periods of observation on branding years and islands, this was an acceptable compromise for increasing the sample sizes. Nearly all adults leave the rookery during branding, and several mothers abandoned the rookeries with their pups shortly thereafter, affecting regular attendance patterns in the short term.

We used the recorded arrival and departure times and parturition dates to obtain several variables of interest: the postpartum period (PPP), defined as the period between parturition and the first departure (Hood and Ono 1997); the trip and visit durations; and the proportion of time spent on shore (P), estimated for each individual using the formula: $\hat{P} = \overline{VD} / (\overline{TD} + \overline{VD})$, where the overbars indicate means and TD and VD represent the trip and visit durations, respectively. We included only those individuals with ≥ 3 visits and trips to mitigate the disproportionate effect of a small sample on the estimate. Because the PPP is almost always much greater than subsequent visits, visit durations and P were calculated after the 1st trip was completed.

Analyses were performed using linear regressions and analysis of variance (ANOVA) using island and year as discrete factors and age of pup in days as a continuous covariate. Because ages of mothers were distributed irregularly (e.g., no marked females were between 12 and 15 years of age), and because the response of many variables to age was not linear, we subdivided age of the mother into 4 discrete groups—4–5 years, 6–8 years, 9–10 years, and >10 years old—and analyzed these as discrete factors. In almost all analyses no differences were found among females >5 years of age. Thus, in the final analyses, females were classified as belonging to younger (4–5 years) or older (≥ 6 years) categories.

Although PPPs were distributed approximately normally, trip and visit durations had right-skewed and heavy-tailed distributions; therefore, these variables were log-transformed prior to analysis. Analysis of P, confined between 0 and 1, was performed using a binomial model with a logit link. We report means and SDs for PPP and medians and interquartile ranges of the data for visit durations, trip durations, and P. Arithmetic means of visit durations and trip durations, which are considerably greater than the median values, also were calculated to facilitate comparisons with other published

TABLE 1.—Summary statistics for postpartum period (PPP) and proportion of time spent on the rookery (P) by female Steller sea lions. The 95% confidence interval (95% CI) for P is analogous to 2 SDs from the mean for the logit-transformed probability data.

Island	Year	No. females	No. trips	No. visits	PPP (SD) in days	P (95% CI)
Brat Chirpoev	2005	19	89	72	13.6 (5.96)	0.84 (0.62–0.93)
	2006	24	152	124	10.6 (3.82)	0.78 (0.53–0.91)
	2007	18	111	110	11.8 (2.77)	0.76 (0.56–0.89)
Raykoke	2005	18	102	92	12.4 (3.40)	0.72 (0.46–0.88)
	2006	21	85	82	14.2 (6.49)	0.55 (0.26–0.81)
	2007	10	39	30	13.2 (3.33)	0.67 (0.48–0.82)
Lovushki	2005	18	123	113	11.9 (3.31)	0.82 (0.57–0.94)
	2006	21	253	247	12.8 (3.75)	0.75 (0.56–0.87)
	2007	21	149	138	10.7 (2.44)	0.74 (0.65–0.87)
Antsiferov	2005	11	57	47	10.1 (3.88)	0.69 (0.40–0.89)
	2006	20	142	128	12.1 (2.84)	0.74 (0.52–0.89)
	2007	15	93	89	14.4 (4.42)	0.69 (0.43–0.87)
Medny	2005	15	97	94	11.7 (6.08)	0.74 (0.46–0.91)
	2006	14	58	54	13.7 (4.46)	0.83 (0.54–0.95)
	2007	14	40	44	17.0 (4.45)	0.59 (0.25–0.86)
Yamsky	2007	21	128	112	10.3 (4.24)	0.59 (0.36–0.80)
Overall totals		280	1,718	1,576	12.4 (4.48)	0.74 (0.55–0.84)

studies, all of which report mean values. We also included accessible depths, defined as proportion of depths <100 m within a 20-km radius, as a covariate in analyses of P (which summarize both the trip and visit durations).

We generated a single estimate of PPP and P per individual per year. Each measurement was considered an individual sample, and standard unbalanced ANOVA techniques were used on appropriately transformed data for inference and factor analysis. However, all individuals perform several trips within a season, leading to potential lack of independence. We therefore considered individual as a random effect in a linear mixed-effects model when analyzing trip and visit durations (Verbeke and Molenberghs 2000).

Because we observed different numbers of animals per island per year and different number of trips per animal, the data were unbalanced. Consequently, we used type III tests for unbalanced ANOVAs and Akaike information criterion (AIC) to compare models (Oehlert 2000). Comparisons of 2 unbalanced samples were performed using the Mann–Whitney *U*-test, and multiple paired comparisons were performed using Tukey's honestly significant difference (Zar 1999). We used a binomial test against equal probabilities for comparisons between PPP of older and younger females in all island and year combinations. All analyses were performed using R (R Development Core Team 2009).

For a meta-analysis we compared our results to summer attendance pattern statistics collected on Steller sea lion mothers on rookeries from the 1960s to the 2000s throughout the geographic range of the species. We report arithmetic means along with the median values of the statistics to conform to the reporting in the other studies, all of which report means despite the skew in the distributions.

Scat data and analysis.—On most rookeries in most years during this study no scats were collected so as to minimize disturbance during attendance studies. The exception was Lovushki Island, on which scats were collected in 2005 and 2007 (Waite 2010; Waite and Burkanov 2006). In addition, we

supplemented the data set with scats collected outside the attendance study period: on Lovushki in 2003 and 2008; Brat Chirpoev, Raykoke, and Antsiferov in 2003; and Yamsky in 2004. All scats were collected opportunistically when the rookery was disturbed for other research purposes, and dried prey remains were identified to the lowest possible taxonomic group by Pacific Identifications, Inc. (Victoria, British Columbia, Canada). Minimum numbers of individual prey items were enumerated by counting a variety of key diagnostic structures. All collection and diagnostic techniques were performed according to methods described in Waite and Burkanov (2006). No scats were collected or analyzed for this study on Medny Island.

RESULTS

Attendance patterns.—In total, 208 females were observed over the period of this study, of which 12 females were observed all 3 seasons, 48 females were observed for 2 seasons, and 148 females for only 1 season. Thus, 280 single-season attendance time series were obtained, an average of 18 per island per year (Table 1). Of the 208 females, 185 were branded and therefore of known age. The ages of the branded females varied from 4 to 18 years, with average ages ranging from 5.6 years on Yamsky Islands to 10.4 years on Lovushki Islands in 2007, reflecting the length of the branding history on these islands. Attendance data analyzed for 2 well-contrasted islands (Yamsky in 2007 and Lovushki in 2006; Fig. 3) illustrate the considerable variation among islands, years, and individuals in all the variables of interest.

The PPP ($\bar{X} \pm SD = 12.4 \pm 4.5$ days) varied significantly among islands ($F_{5,207} = 3.13, P = 0.009$) but not years ($F_{1,278} = 0.29, P = 0.59$), with Yamsky animals displaying the lowest mean ($\bar{X} = 10.3, SD = 4.24$) and Medny animals displaying the highest mean ($\bar{X} = 14.1, SD = 5.43$; Table 1). Other islands were not significantly different from these extremes ($P > 0.10$). The pooled PPP over all the islands was

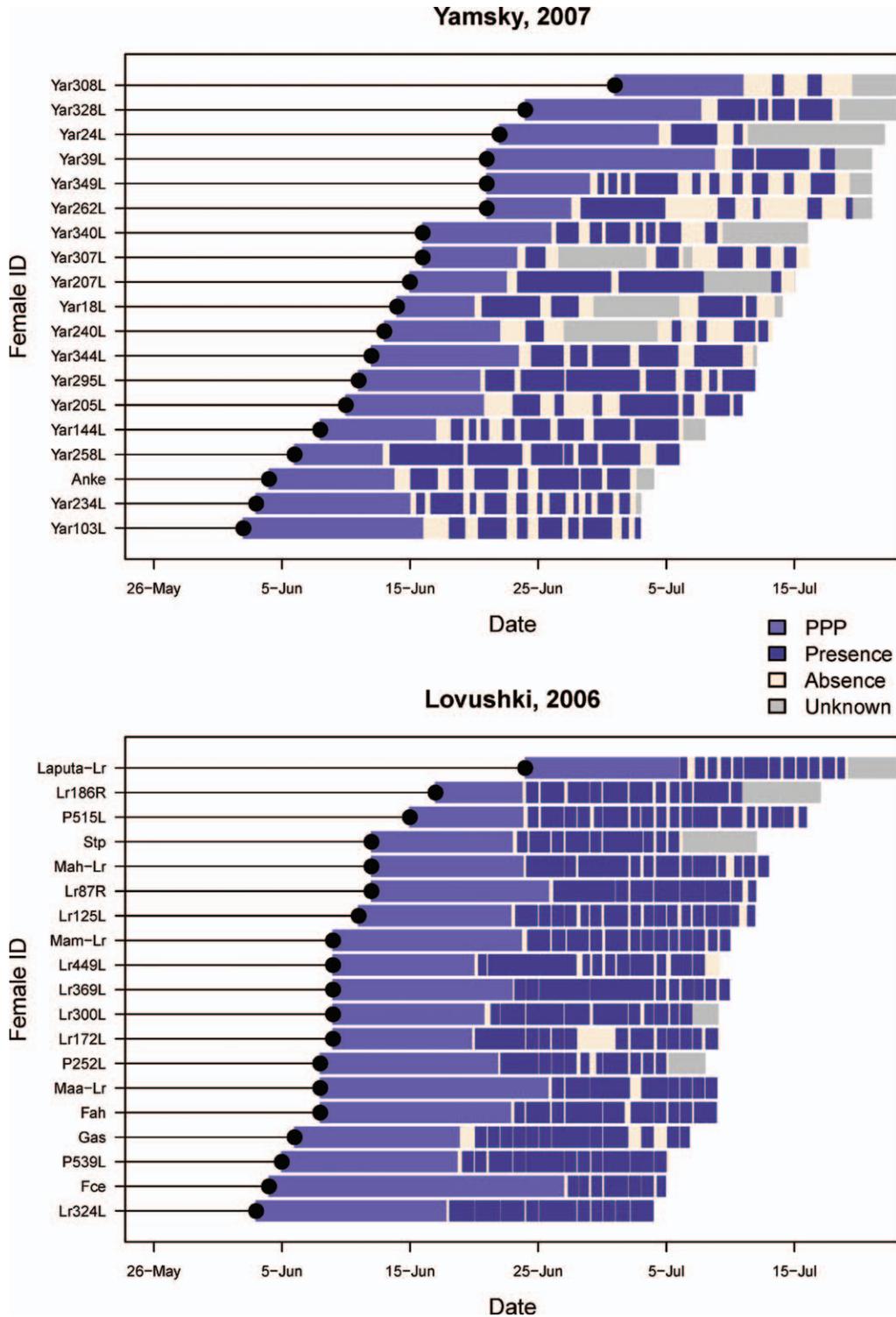


FIG. 3.—Examples of attendance patterns obtained on nursing females on (top) Yamsky Islands in 2007 and (bottom) Lovushki Islands in 2006. Females are identified according to their brands, plastic tag number, or natural markings on the y-axis. Black dots represent parturition dates for the females. Blue bands represent presence, with the lighter blue bands representing the period before the 1st trip (postpartum period [PPP]), and pink bands represent absence. Gray represents omitted observations because either arrival or departure times could not be determined.

higher for older females (6 years and older) than for younger females (4–5 years; \bar{X} = 13.2 and 12.4 days, respectively), but the difference was not significant (U = 4,721, n_1 = 49, n_2 = 203, P = 0.58). However, when the island factor was taken

into account, the interaction term between island and mother’s age was significant ($F_{1,5}$ = 3.12, P = 0.009). More detailed analysis of individual islands revealed that PPP differed by mother’s age on Brat Chirpoev (U = 74.5, n_1 = 6, n_2 = 55, P

TABLE 2.—Medians and interquartile ranges (IQR) for visit and trip durations by female Steller sea lions on all islands and all years.

Island	Year	Visit durations		Trip durations	
		Median (h)	IQR	Median (h)	IQR
Brat Chirpoev	2005	42.1	(25.1–71.0)	8.0	(5.5–13.1)
	2006	38.3	(17.9–62.5)	9.2	(6.0–21.1)
	2007	37.8	(16.8–47.4)	8.6	(7.5–13.3)
	All years	38.7	(19.2–63.2)	9.0	(6.1–16.6)
Raykoke	2005	24.0	(15.9–42.2)	10.6	(6.3–19.2)
	2006	28.8	(14.8–59.9)	21.8	(12.5–41.1)
	2007	39.6	(25.4–47.7)	20.1	(11.6–24.0)
	All years	30.5	(16.1–47.6)	15.2	(8.7–27.0)
Lovushki	2005	31.7	(19.3–47.0)	6.5	(4.5–9.5)
	2006	19.0	(15.5–23.0)	6.5	(4.5–9.0)
	2007	18.2	(16.2–41.2)	7.5	(6.5–8.8)
	All years	19.5	(16.2–40.7)	7.0	(4.5–9.0)
Antsiferov	2005	35.5	(14.1–72.5)	13.2	(9.0–26.2)
	2006	40.8	(18.1–46.5)	9.6	(6.6–26.0)
	2007	24.0	(14.9–44.3)	10.5	(7.5–24.0)
	all years	37.1	(17.5–47.7)	11.0	(7.3–26.0)
Medny	2005	22.5	(15.6–45.0)	9.7	(5.8–15.7)
	2006	42.8	(19.4–85.4)	6.9	(4.5–16.1)
	2007	31.6	(13.4–73.8)	15.2	(10.3–48.1)
	All years	33.6	(15.8–67.3)	10.2	(5.5–24.0)
Yamsky	2007	28.5	(15.2–51.8)	19.9	(12.9–28.1)
Overall totals		25.5	(13.2–64.9)	9.0	(6.2–19.0)

= 0.026), with younger females spending about 8.75 days (*SD* = 2.0) nursing before their 1st foraging bout compared to 12.5 days (*SD* = 4.2) for older females. On other islands no significant relationships ($P > 0.05$) were found between age of the mother and PPP. However, when mean PPP was compared for older and younger females for each of 13 island–year combinations (of the 16 total island–year combination, 3 did not have females under 6 years of age), on 10 the PPP for older females was larger than the PPP for the youngest females, a significant result when compared to randomness (binomial(0.5, 13), $P = 0.046$).

Trip durations ranged from 3 to 72 h, with a global median of 9.0 h and interquartile range from 6.2 to 19.0 h (Table 2). The distribution of trip durations is right-skewed and multimodal (Fig. 4A), with a large peak at 5–12 h and a smaller peak at 20–29 h, reflecting trips that took place overnight and over a day and a night. Variation was considerable between individual females ($F_{186,1,403} = 3.73$, $P < 0.001$) and islands ($F_{4,1,585} = 24.80$, $P < 0.001$), but less so among years (Table 2). Trip durations were significantly ($P < 0.05$) shorter on Lovushki Islands than all other islands in all years (median 7.0 h), followed by Brat Chirpoev, Medny, and Antsiferov (between 9.0 and 11.0 h) with nonsignificant ($P > 0.05$) differences, and Raykoke and Yamsky Islands displaying the longest median trip durations (15.2 and 19.9 h, respectively). These basic patterns are generally consistent among most years, with the exception of an increase in median trip durations on Medny in 2007 and on Raykoke in 2006.

We performed an array of analyses fitting linear mixed effects models using island, year, mother’s age, and pup age as fixed effects, and grouping the data according to identification

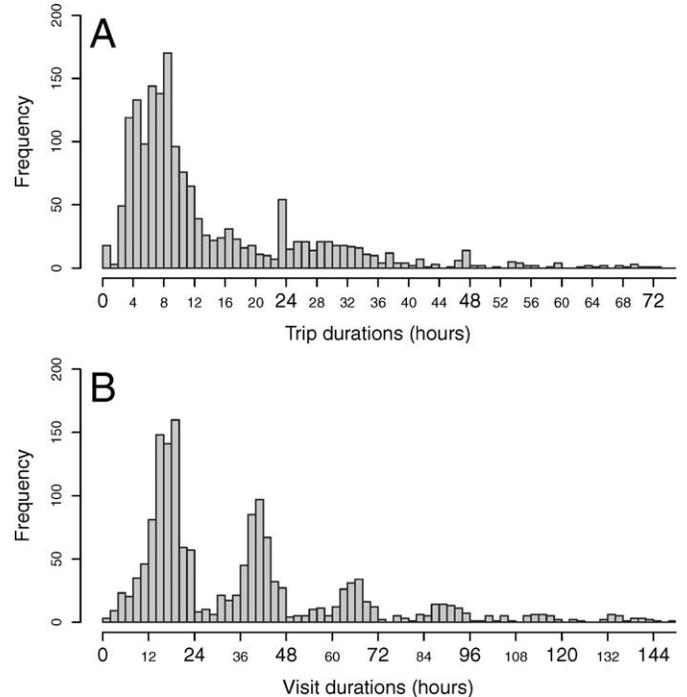


FIG. 4.—Histograms of A) trip durations and B) visit durations for all animals.

as the random effect. Model selection based on minimizing AIC suggested significant main and interaction effects among island, year, and mother’s age. Pup age was not a significant factor (Fig. 5A), indicating that trip durations do not change throughout the season.

In the complete mixed-effects interaction model, the main effect of mother’s age on trip duration was marginally nonsignificant ($0.05 < P < 0.10$), with younger mothers (4–5 years) displaying a longer median trip duration than older mothers, with marginal nonsignificance (median 13 h and 8.9 h, respectively; $F_{1,1,499} = 3.115$, $P < 0.078$). When analyzed separately, this difference was significant on Brat Chirpoev ($F_{1,304} = 4.36$, $P = 0.038$) and marginally nonsignificant on Antsiferov ($F_{1,192} = 3.48$, $P = 0.063$). On the other islands we found no significant difference in trip duration by mother’s age.

The median visit duration was 25.5 h, with an interquartile range between 13.2 and 64.9 h (Table 2). Visit duration had a more markedly multimodal distribution than trip durations, with peaks separated by 24 h intervals (Fig. 4B). Visit durations similarly varied widely among individuals, islands, and years (Table 2), with a strong island–year interaction effect ($F_{8,1,449} = 5.55$, $P < 0.001$). Lovushki onshore visit durations were consistently shorter than any others ($P < 0.001$), whereas the remaining rookeries were grouped. A few significant interannual changes were observed. For example, for Lovushki median visit durations fell from 31.7 to 19.0 h between 2005 and 2006.

Unlike for trips, pup age was a highly significant explanatory factor for visit durations ($F_{1,1,574} = 176.70$, $P < 0.001$), which shortened as the season progressed and the

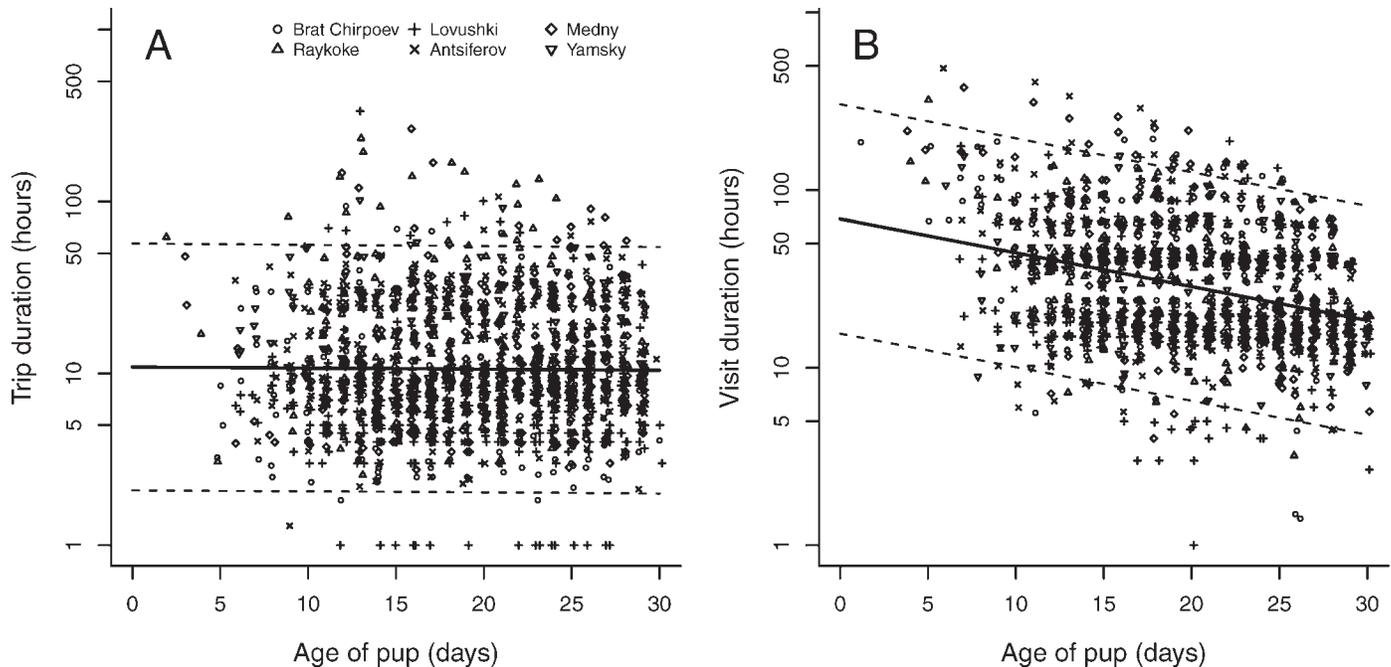


FIG. 5.—A) Foraging trip duration and B) onshore visit duration plotted against pup age. The thick line and the dotted lines represent the linear regression and 95% prediction interval, respectively.

pups aged (Fig. 5B). The model predicted a median visit duration of 44 h 10 days after birth, dropping to about 18 h 30 days after birth, although the exact values of the regression estimates varied among islands.

Age of mother had much less explanatory power for visit durations than for trip, with no significant main-effect differences ($F_{1,1,173} = 1.80$, $P = 0.18$). Analyzed separately, on Brat Chirpoev and Antsiferov Islands, the visit durations for the younger females (4–5 years) were significantly shorter (Brat Chirpoev: 21.3 and 39.25 h for younger and older females, respectively; $F_{1,304} = 5.68$, $P = 0.018$; Antsiferov: 22.1 and 38.4 h; $F_{1,255} = 4.01$, $P = 0.046$). This pattern was consistent among years.

The overall median proportion of time spent on land (P) was 0.74, with medians differing significantly among islands, from 0.59 on Yamsky and Raykoke to 0.84 on Brat Chirpoev and Lovushki ($F_{5,189} = 7.88$, $P < 0.001$; Table 1). A highly significant increase in P results when younger mothers are compared with older mothers ($F_{1,201} = 5.277$, $P = 0.022$). The youngest mothers spent on average 0.65 (95% confidence interval [95% CI] = 0.45–0.86) of their time on land, compared to 0.76 (95% CI = 0.58–0.89) for females ≥ 6 years old. Year was not a significant main effect ($F_{1,226} = 2.37$, $P = 0.12$). Among the Kuril Islands exclusively we found a significant linear response to accessible depths, defined as proportion of area < 100 m deep within 20 km of the rookery ($F_{1,205} = 8.205$, $P = 0.005$; Fig. 6). Approximately 5% more time was spent on the Kuril Islands rookeries for every 10% more accessible depth. Almost all of the differences between the Kuril Islands were explained by accessible depths, and the AIC of a model with island as a fixed-effect factor was lower

than the AIC of a model with bathymetry as a linear covariate (504.5 versus 509.2).

Meta-analysis.—Across all rookeries in Russia PPP values are longer than those reported for this species throughout its range (Table 3). The greatest differences are with those reported on Año Nuevo rookery in California ($\bar{X} = 3.2$ –6.7 days compared to 10–16 days). PPP values on rookeries in Alaska where they have been reported, on Sugarloaf, Forrester (Milette and Trites 2003), and Chiswell (Maniscalco et al. 2006) rookeries, fall between those from California and Russia, although they overlap with the shorter range in Russia.

Visit durations on Russian rookeries were consistently and significantly longer on all islands (medians from 25 to 35 h, means from 30 to 53 h) than on rookeries in Alaska and California, which range from 20 to 25 h (Table 4). Visit duration was the least variable attendance index, with a range encompassing a factor of ≤ 2 compared to the 7-fold difference in trip duration.

Trip durations were the most variable of the attendance pattern indices across the sea lion range. Trip durations were shortest (< 10 h median) in the central Kuril Islands (Lovushki and Brat Chirpoev) and in the central Aleutian Islands (Seguam), and longest (up to a mean of 50 h) in California (Table 3). The broad range of means in Russia (from 10 to 25 h) was comparable to the range of means in Alaska (7–26 h).

The proportion of time spent onshore (P) was higher in our observations (range-wide median 74%) than in comparable studies. Most studies do not report values of P explicitly; however, they can be estimated from reported values of trip and visit durations. Thus, on Año Nuevo Island Higgins et al.

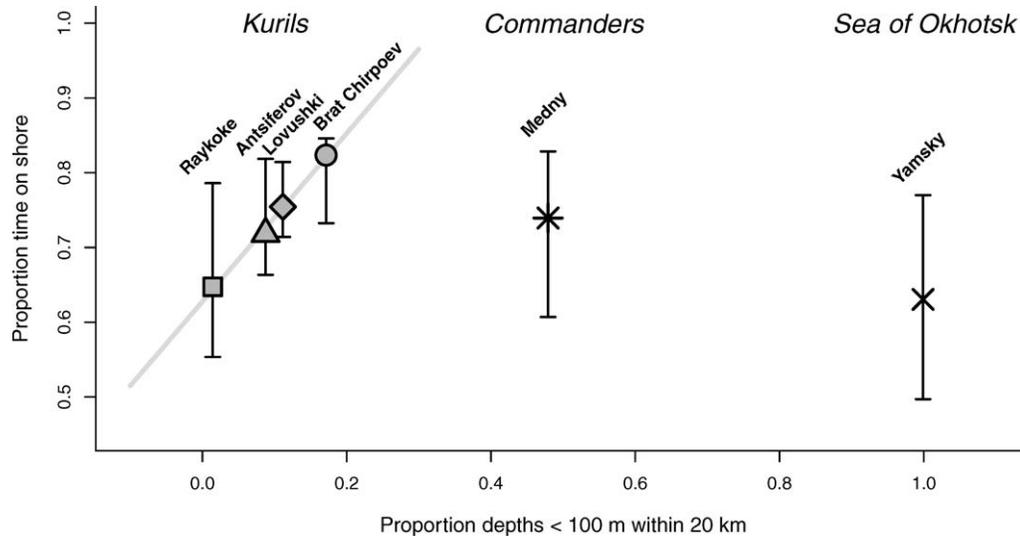


FIG. 6.—Proportion of time spent on shore versus an index of accessible depths, defined as proportion of the area <100 m in depth within 20 km of the rookery. Bars represent the interquartile range for all pooled data. The gray line is a linear regression for the Kuril Islands.

(1988) reported visit durations of 22.6 ± 9.5 h and trip durations of 37 ± 19 h, leading to an approximate median proportion of time onshore of $40\% \pm 17\%$. Brandon (2000) reported values ranging from $49\% \pm 17\%$ on Lowrie Island in Southeast Alaska to more comparable values of $76\% \pm 24\%$ on the Aleutian Islands.

Diet analysis.—Based on percent frequency of occurrence, the 3 main prey items identified in scats were Pacific salmon (*Oncorhynchus* spp.), pollock (*Theragra chalcogramma*), and

Atka mackerel (*Pleurogrammus monopterygius*), with Pacific herring (*Clupea pallasii*) and northern smoothtongue (*Leuroglossus schmidti*) within the top 3 prey items on some islands (Table 4). Considerable variability existed among the islands, with Atka mackerel predominating on Lovushki (Waite 2010; Waite and Burkanov 2006) and, with a smaller margin, on Brat Chirpoev. Pollock was the main prey item by a wide margin on Yamsky. On Antsiferov salmon, pollock, and Atka mackerel were represented in the scats in approximately equal

TABLE 3.—Measurements of 3 major attendance pattern indexes of lactating Steller sea lions across the North Pacific, ordered approximately from west to east. The sources are: A, this study; B, Brandon (2000); C, Merrick and Loughlin (1997); D, Milette and Trites (2003); E, Maniscalco et al. (2006); F, Sandegren (1970); G, Rehberg et al. (2009); H, Hood and Ono (1997); and I, Higgins et al. (1988). For all studies but the current study all visit duration (VD) and trip duration (TD) data are reported as means. For this study medians and means (separated by a slash) are reported to facilitate comparisons between studies. PPP, postpartum period; obs., observations; VHF, very high frequency.

	Rookery	Area	PPP (days)	VD (h)	TD (h)	Comments	Source
1	Yamsky	Northern Sea of Okhotsk	10.3	29.3/40.1	19.8/23.3	2005–2007, visual obs.	A
2	Brat Chirpoev	Kuril Islands	12	36.2/45.7	9.8/13.3	2005–2007, visual obs.	A
3	Raykoke	Kuril Islands	13.3	30.8/40.1	17.7/24.9	2005–2007, visual obs.	A
4	Lovushki	Kuril Islands	11.8	25.6/30.8	7.2/10.0	2005–2007, visual obs.	A
5	Antsiferov	Kuril Islands	12.2	32.7/46.1	13.0/16.4	2005–2007, visual obs.	A
6	Medny	Commander Islands	14.1	34.3/52.6	13.9/20.0	2005–2007, visual obs.	A
7	Seguam	Aleutian Islands	—	23.5	7.1	1997, VHF tags	B
8	Ugamak	Aleutian Islands	—	18	25	1990–1993, VHF tags	C
9	Chirikoff	Gulf of Alaska	—	20.7	11.2	1997, VHF tags	B
10	Western Gulf of Alaska	Gulf of Alaska	—	18	18	1990–1993, satellite tags	C
11	Sugarloaf	Gulf of Alaska	9.9	27	19.5	1994–1995, visual obs.	D
12	Marmot	Gulf of Alaska	—	19	21	1990–1993, VHF tags	C
13	Chiswell	Gulf of Alaska	10.7	22.5	16.5	2002–2004, video based visual	E
14	Lewis	Gulf of Alaska	9	17	16.7	1967–1968, visual obs.	F
15	Fish	Gulf of Alaska	—	25.2	19.4	1997, VHF tags	B
16	Hazy and Forrester	Southeast Alaska	—	20.8	20.8	1992–1993, satellite tags	G
17	Forrester	Southeast Alaska	7.9	22.6	24.9	1994–1995, visual obs.	D
18	Forrester	Southeast Alaska	—	22.3	25.6	1997, VHF tags	B
19	Año Nuevo	California	3.2	20.8	21.8	1973, visual obs., El Niño	H
20	Año Nuevo	California	6.7	21	36	1983, visual obs., El Niño	I
21	Año Nuevo	California	5.8	20.4	50.2	1992, visual obs., El Niño	H

TABLE 4.—Summary of bathymetry and diet on Russian Steller sea lion study sites. The diet data are percent frequency of occurrence of each prey species in the scat samples. *n* refers to the number of samples collected.

Rookery	Bathymetry		Year of collection	<i>n</i>	Diet				
	Proportion of waters <100 m within 10 km	Proportion of waters <100 m within 20 km			Salmon	Pollock	Herring	Northern smoothtongue	Atka mackerel
Yamsky	1.00	1.00	2004	41	20	80	22		
Brat Chirpoev	0.21	0.17	2003	68	62	31			72
Raykoke	0.05	0.14	2003	58	71			56	69
Lovushki ^a	0.27	0.11	2003, 2005, 2007, 2008	271	20	20			86
Antsiferov	0.08	0.09	2003	121	58	66			46
Medny	0.88	0.48	—	—	—	—	—	—	—

^a Data from Waite (2010) and Waite and Burkanov (2006).

percentages, and Raykoke was the only island where salmon was the most frequently observed prey item and where northern smoothtongue also was prevalent.

DISCUSSION

Steller sea lions on Russian rookeries exhibited attendance patterns that were broadly similar to those documented in other areas (Brandon 2000; Higgins et al. 1988; Hood and Ono 1997; Maniscalco et al. 2006; Merrick and Loughlin 1997; Milette and Trites 2003). Animals hauled out approximately 1–3 days before giving birth, nursed for 1–2 weeks without leaving the rookery, and typically copulated before taking their 1st foraging trip. The PPP was followed by a series of foraging trips and returns to the rookery to feed their pup, trips which ranged from several hours to 3 days. As shown earlier (Altukhov et al. 2008), Steller sea lions demonstrated a strong and consistent diurnal behavior pattern on all Russian rookeries; activity on the rookeries was greatest in the evenings, and most foraging trip departures occurred about an hour before or after dusk, with arrivals occurring in the morning.

Although intensive, multiyear visual observations over a wide range can provide large sample sizes, the potential exists for introduced biases. In our study observers varied widely in their experience and composition among the islands and between years, especially on Medny and Antsiferov islands. Furthermore, trip durations might be underestimated slightly by assigning a fixed arrival and departure time when not visually observed, and a small possibility exists that entire trips during darkness were missed.

When all data in our study were pooled, older mothers (>6 years old) took significantly shorter foraging trips than younger mothers (4–5 years old). This is likely due to older mothers being more experienced at searching for and finding food, or by physiological limitations on the diving ability of smaller females. The diving limitation hypothesis also is consistent with the observation that trip durations are most dependent on age on Raykoke and on Antsiferov, where less-proximate shallow habitat existed than on Lovushki and Brat Chirpoev. Along with longer trip durations, younger females

also exhibited significantly shorter median visit durations. This is explained either by younger inexperienced females having less time to attend to their pups because of longer foraging trips or that their accumulated resources are depleted more quickly by nursing. These patterns are likely to be reflected in lower physical condition and survival rates of pups of mothers <6 years old. Finally, the observation that the youngest females, which presumably have fewer overwintering reserves, have significantly shorter PPPs than older females on several islands suggests that PPP can serve as an index of the physical condition of returning females.

An intriguing pattern appears in the relationship between trip duration and visit duration as the pup ages. Despite a high degree of individual variability, no significant changes or trends were observed in trip length during maternal foraging over the first 30 days of a pup's life. This pattern was consistent across all rookeries and within each of the rookeries separately. Concurrently, a significant decline in visit length with pup age was observed across all rookeries, and within rookery, suggesting females spent progressively less time attending to their pups as the season progressed.

Seasonal increase in lengths of foraging trips are hypothesized to be related to increasing nutritional demands of the growing pup over time; larger, older pups suckle more milk and have greater energetic demands. Intuitively, one would expect the mother to spend more time at sea finding food as the pup grows. This hypothesis would be supported if prey were scarce, at which point increasing energetic demands would be reflected in greater amounts of time spent foraging. However, at our study sites, females made more frequent trips of the same (or relatively consistent) duration rather than longer trips. This suggests that trip duration could be dependent on the time required to transit a known distance to an abundant and reliable foraging area. The increasing energetic needs of the pup then are met by the female decreasing the time spent on the rookery and increasing the frequency of the trip durations as the season progresses. Although this strategy is dependent on local foraging conditions, in our study trip durations did not increase with pup age at a single rookery. This result suggests that many of the Russian rookeries are near spatially predictable and

sufficiently abundant sources of prey, at least within the first 30 days of pup life.

Trip durations tend to increase with pup age for many otariids (Boyd et al. 1991; David and Rand 1986; Gentry and Holt 1986) including Steller sea lions (Higgins et al. 1988), although all of these studies covered an observation period greater than the 30-day PPP in our study. On Sugarloaf and Lowrie islands in the Gulf of Alaska Milette and Trites (2003) reported that Steller sea lions increase their foraging trips by an average of 12 min per day, but visit durations decreased more rapidly, at 30 min per day, with no differences among islands. Thus, the frequency of trips in the Gulf of Alaska tended to increase as the season progressed, as in our study, despite the increase in trip duration. On Chiswell Island, also in the Gulf of Alaska, Maniscalco et al. (2006) described more dramatic long-term changes in trip duration, with a slight decrease in trip duration until 19 July and a subsequent rapid increase from about 10 to 60 h by mid-September. The longer-term balance of trips and visits on rookeries is clearly dynamic and likely related to the increased independence of pups as the rookery structure begins to collapse, underlining the relevance of our result to the earliest, most dependent period of pup development.

In general, the attendance patterns of sea lion females in Russia tended to be more favorable (longer PPP, higher P, shorter trip durations, and longer visit durations) than in other parts of the range of the sea lion. PPP can be considered an index of physical condition and quantity of energetic reserves before arriving at the rookery, as supported by comparisons of PPP between El Niño and non-El Niño years for other otariids (Trillmich 1991). These results suggest that lactating females on the Russian rookeries were in comparable or better condition than sea lions in the Gulf of Alaska and substantially better condition than those in California rookeries and could spend more time nursing their newborn pup. Visit durations, trip durations, and P, however, reflect local availability of resources during the reproductive period itself. Our results suggest that Kuril Islands and central Aleutian Islands sea lions generally have more abundant, consistent, and locally available resources than in sites in Southeast Alaska, California, and the northern Sea of Okhotsk.

Differences in attendance patterns within Russia did not generally correlate with population trends. The Kuril Islands rookeries had stable populations during our study despite widely variable attendance patterns. The low-density and increasing population on Yamsky Island, which might be expected to have the most favorable foraging conditions, displayed the least favorable attendance patterns in our study. On Medny Island, the only severely depressed population, most attendance patterns indices were intermediate. Similarly inconclusive relationships between attendance patterns and population status were found in Alaska (Andrews et al. 2002; Brandon 2000; Milette and Trites 2003), where attendance patterns in sites with the largest population declines appeared more favorable than at sites where populations were increasing.

Many of the consistent differences in attendance pattern among islands can be explained by differences in diet and local bathymetry. For example, on the Kuril Islands the shortest trip durations were displayed by sea lions on Lovushki and Brat Chirpoev, where Atka mackerel were the more dominant components of the diet. Atka mackerel have relatively high energetic content and are a reliable source of food, because their spawning behavior in May–June involves nest-guarding behavior from males (McDermott and Lowe 1997; Zolotov 1993). On Lovushki and Brat Chirpoev, incidentally the 2 largest rookeries, Atka mackerel are exploited more readily and quickly due to the large amounts of relatively shallow and accessible depths enabling the sea lions to forage efficiently without moving far from the rookery. On Lovushki the proximity of the local foraging base was further corroborated with data from animal-borne video records, showing that Lovushki animals begin foraging on Atka mackerel aggregations almost immediately after entering the water (R. D. Andrews, University of Alaska, pers. comm.).

On Raykoke and Antsiferov, where trip durations were significantly longer, the amount of accessible shelf area and likely Atka mackerel habitat are more limited than on Lovushki and Brat Chirpoev. Animals from Antsiferov fed more predominantly on walleye pollock, a less energetically rich fish that occurs in ephemeral aggregations in the pelagic zone (Rosen and Trites 2000). Alternatively, animals from Antsiferov might have traveled to shallower waters near Paramushir Islands for more consistent benthic feeding on Atka mackerel. On Raykoke animals relied more heavily on similarly ephemeral aggregations of migrating Pacific salmon or likely traveled to the more shallow waters of Lovushki or neighboring Matua Island. These relationships might explain some differences in trip durations observed in Alaska. Just as on the Russian rookeries, those locations where Atka mackerel dominates in the prey analysis (e.g., Seguam) exhibit the shortest trip durations (under 10 h), but on those rookeries where animals relied more heavily on salmon and walleye pollock median trip durations were consistently above 10 h (Sinclair and Zeppelin 2002; Trites et al. 2007).

Perhaps the most vivid support for the importance of immediate local conditions is in a comparison between Raykoke and Lovushki islands. The 2 rookeries are only 50 km apart, have significant exchange of individuals, and their population fluctuations are identical (Burkanov 2009; Burkanov and Calkins 2008). However, the trip durations on Raykoke were, on average, twice as long as those on Lovushki.

Sea lions from Yamsky Island had the longest foraging trips within our study, often spending more than 1 night at sea, and the lowest median percentage of time spent on the rookery (59%). Yamsky is the only site in this study located well within the continental shelf, in the shallow northern Sea of Okhotsk. The foraging base for animals at this site is fundamentally different than on the Kuril Islands, dominated by Pacific herring, pollock, and spawning Pacific salmon (Waite and Burkanov 2006). All of these species form

aggregations, often related to seasonal spawning behavior, which can be very dynamic in time and space, potentially requiring longer travel and searching times for sea lions.

The qualitative relationship between attendance patterns and bathymetry is consistent with reported observations from Alaska (Brandon 2000; Merrick and Loughlin 1997; Milete and Trites 2003). In the Alaska locations where trip durations were lowest (Seguam and Chirikof) local bathymetric relief was highly structured, with large areas of shallow water and shelf breaks within 20 km of the rookery. In the areas where trip duration were longest (Ugamak, Sugarloaf, Fish, and Lowry) the bathymetry was more homogeneous, with shelf breaks more distant from the rookeries (greater than 40 km—General Bathymetric Chart of the Oceans 2003). A heterogeneous and structured bathymetry within 10–20 km of a rookery and shelf breaks can be important factors for explaining trip durations during the reproductive period.

The importance of immediate local conditions might lead us to conclude that comparisons of attendance patterns cannot be used to test the hypothesis that food limitation is related to population decline in a geographically dispersed population. Furthermore, the lack of any relationship might suggest that food limitation during the reproductive period in summer is not a key factor in population trends. However, this conclusion is tempered by several qualifications. The 3 years of observations reported here comprise a relatively short period of time compared to the reproductive cycle over which population effects might occur. Further, if attendance patterns do reflect an ecological process with population-level impacts, the impacts likely are limited to 1st-year survival. Additional possible processes, such as disease, predation, and movements among rookeries dilute the immediate impacts of summer foraging on population trends. To use attendance patterns to test the hypothesis that food limitation during the early postpartum period influences Steller sea lion population dynamics, one would need a longer-term study, encompassing significant changes in prey availability, together with good estimates of age-structured survival based on mark-recapture data.

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