

Maternal attendance patterns of Steller sea lions (*Eumotopias jubatus*) on Russian rookeries

Eli Gurarie, Vladimir Burkanov, Alexey Altukhov, Evgeny Mamaev,
Peter Permyakov, Sergey Purto, Aleksey Trukhin, others?

May 12, 2008

Abstract

It has been suggested that food availability or nutritional stress has been a cause for Steller sea lion declines, and that the earliest life stages are the most vital for survival. In order to test these hypotheses, we conducted detailed observations of attendance patterns by adult females on reproductive rookeries. The study was conducted from 2005 to 2007 over the entire summer reproductive season on six major rookeries in Russian waters, including both stable and depleted populations. Branded and individually identifiable females were observed during the post-parturition period with special attention paid to presence and absence during the day and to departure and arrival times. Statistical analyses of the data suggest that the variability in attendance patterns is most likely attributable to the local quality of the foraging base. No evidence was obtained to relate attendance patterns to population status.

1 Introduction

Steller sea lions (*Eumetopias jubatus*) range along the North Pacific from northern Japan to California. The U.S. population has been subdivided into two stocks: the Western U.S. stock, which includes all animals west of 144° W, including all of the Aleutian islands, and the Eastern U.S. stock, including all animals east of 144° W, from south-eastern Alaska to California (NOAA SAR 2002). Consistent declines in populations since the first trend counts in Alaska in 1956-60 have led to the listing of the Western stock as “endangered” and the Eastern stock as “threatened” under the Endangered Species Act. An intense research effort has been underway to identify the causes of the population decline (Loughlin 1998). Though definite causes have proven difficult to indentify, a leading hypothesis has been food limitation due to overfishing (Merrick and Loughlin 1997) - [others?]

In Russia, Steller sea lions are found on the Commander Islands - the westernmost islands of the Aleutian chain, along the east coast of Kamchatka, along the Kuril islands,

on Sakhalin island and around the sea of Okhotsk. Recent genetic evidence together with branded animal resightings patterns indicate that the Kamchatka, Kuril, Sakhalin and Sea of Okhotsk populations constitute a separate Asian stock while the Commander Island population belongs to the Western stock (Baker et al 2005) (figure 1). Population trends in the Commander Island have mirrored Western population declines, with an estimated 86% drop since 1977 (Burkanov et al. 1991, Burkanov and Loughlin 2005), while the Kuril island populations appear to have stabilized since 1989 following a prolonged period of decline and are showing a recent increasing trend at about 2.3% growth per year (Burkanov and Loughlin 2005).

Unlike most phocids, lactating otariid females periodically leave their pups on the reproductive rookery and go on foraging trips, balancing a need to replenish energetic reserves at sea and provide milk for their offspring on shore. The relative durations and frequencies of foraging trips and on-shore visits is referred to as the maternal attendance pattern. In this context, a comparison of maternal attendance patterns can serve as a means of inferring the bioenergetic constraints on different populations (Gentry 1998, Brandon 2000, Trites and Porter 2002, Milette and Trites 2003). Nutritionally stressed populations might be expected to adjust their trip lengths as a response to food availability, spending more time at sea and less on land than stable populations (Trites and Porter 2002). This has been shown to be the case for several other species of otariid. Antartctic fur seals (*Arctocephalus gazella*), South American fur seals (*Arctocephalus australis*), Galapagos fur seals (*Arctocephalus galapagoensis*), northern fur seals (*Callorhinus ursinus*), and California sea lions (*Zalophus californianus*) have all been shown to make longer trips when prey is scarce, in particular during the 1983 El Niño (Boyd 1999, Trillmich 1986, Ono et al. 1987, Costa et al. 1989, DeLong and Antonelis 1991, Heath et al. 1991, Majluf 1991, Trillmich 1991, McCafferty et al. 1998).

Analogous studies on Steller sea lions have yielded contradictory results. Hood and Ono (1997) report that sea lions at Año Nuevo Island spent more time at sea than during a moderate 1992 El Niño event. On the other hand, Brandon (2000) notes that stressed populations in the Aleutian island exhibit shorter foraging trips than the stable population in Southeast Alaska. Similarly, Milette and Trites (2003) also compared a stable Southeastern Alaska population with a declining Western stock population and determined that foraging trips were shorter for the declining population than the stable population, contradicting the authors' expectations. The results indicate either that food limitation is not an appropriate hypothesis to explain decline or that the variability between locations is greater than adaptive behavioral variation.

Most of the studies to date have focused on radio-telemetry studies, which have the advantage of providing highly accurate data. However, these studies are costly and can

be difficult to implement especially on full grown adults that can not easily be captured and for the use of tranquilizers can be risky. It is therefore difficult to obtain a statistically significant number of individuals for large scale comparisons. Observational studies on large numbers of marked animals are less accurate but provide a few greater amount of data. In Russia, animals 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. Because of the long-term nature of the branding project in Russian waters, we have access to a large, multi-year dataset and complete knowledge on the origin, age and resight history of many animals.

It is our primary intent in this report to explore maternal attendance patterns based on data obtained during three reproductive seasons, from 2005 to 2007, on five rookeries in the Asian stock, where the population is stable or increasing (four rookeries on the Kuril islands and one in the northeast Sea of Okhotsk) and on one rookery belonging to the Western stock, where the population is depleted. These six rookeries account for more than half of all Steller sea lions reproducing in Russian waters. A comparison of behaviors on these islands can yield some indirect site-specific knowledge about the respective forage bases and shed light on some of the sources of variability in attendance behavior. Furthermore, the results can be compared over a wide range to results obtained elsewhere in the sea lions' range.

2 Study sites and branding effort

The data presented in this article was obtained at six reproductive rookeries. Four of the rookeries are on the Kuril islands and belong to the Asian stock, ranging from the southernmost Brat Chirpoy in the mid-Kuril Islands, to the northernmost Anstiferov, off the coast of Paramushir Island (see figure 1). The last rookery is on the Commander islands and has been shown to belong genetically to the Western Aleutian stock. Here we briefly describe the geography and observation conditions of these rookeries and the observation effort, moving from the southernmost to northernmost rookeries.

2.1 Kuril Islands

Of the roughly 16 thousand sea lions in Russia, roughly eight thousand (50%) belong to the Kuril Island population (Burkanov and Loughlin 2005). There is considerable movement of sea lions between the Kuril islands and between rookeries further north and west in the Okhotsk sea, but rare movements to Eastern Kamchatka and extremely exchange with the Commander Islands. Observers were stationed at rookeries from May 25-26 through July 15-21 all three years, making dawn to dusk observations from blinds. This time period

captured nearly all the parturition events on the rookeries, and the nursing of pups until almost all could swim. Near the end of this period, some females left the rookery entirely with their pup.

2.1.1 Brat Chirpoev

Chirpoy and Brat Chirpoev (Russian: Chirpoy's brother) (46.5° N 150.8° E) are twin volcanic islands located between Simushir and Urup in the southern group of the Kuril Island Chain. The rookery is located in the middle of the southwestern edge on a flat, gently sloping lava flow. During high tide and surf, about 30% of the rookery is submerged. The observation booth is located at the top of a cliff perfectly overlooking the entire rookery. The Brat Chirpoev rookery is the second largest (after Lovushki) of the Kuril Island rookeries where observations were performed, and third in size on all the Kuril Islands with 350-400 pups born each season in the years of observation. Since 1989, 876 pups have been branded on Brat Chirpoev, with the Russian letter "B".

2.1.2 Raykoke

Raykoke Island (50.2° N 153.2° E) is a small circular volcanic island 18 km north of the much larger Matua in the central Kuril Islands. The rookery is located on a lava flow on the western end of the island. An observation blind is located some X m above the rookery on a steep hill overlooking the rookery. Approximately 200 pups are born annually on Raykoke, making it, along with Antsiferov, one of the two smaller Kuril Island rookeries. Since 1989, 877 pups have been branded on Raykoke, such that the age of branded animals ranges from 1 to 18 years. The branding code on Raykoke is "P", corresponding to the cyrillic "R".

2.1.3 Dolgaya Rock, Lovushki Islands

Lovushki Islands (48.3° N, 153.8° E) are the exposed edge of a sinking caldera representing four separate rocks and numerous reefs some 45 km ENE of Raykoke. The observations were conducted on Dolgaya Rock, one of the larger islands, about X m long, with a maximum elevation of 30 m. The reproductive rookery takes up almost the entire circumference of the rock. With an annual pup production of around 500 pups it is together with Srednyoga, one of the two largest Steller sea lion rookeries. Since 1989, 877 sea lion pups have been branded on Dolgaya Rock, with branding code "JI" or cyrillic "L".

Dolgaya Rock is also the site of one of the larger fur seal rookeries on the Kuril islands, with about 10,000 pups counted in 2005 and 2006 (?).

2.1.4 Antsiferov

Antsiferov Island (50.2°N 153.2°E) is a circular volcanic island about 18 km west of the southern end of the much larger Paramushir in the northern Kuril Islands. The rookery is located on a lava flow on the southern end of the island, with an observation blind located on a steep hill some X m above the rookery. The topography of the rookery is dominated by a large cliff rising in the middle, such that one third of the rookery is obscured. Consequently, analysis is restricted to animals residing on those sections of the rookery that are clearly visible from the booth.

In the years of observation, between 200 and 300 pups were born annually on Antsiferov. Since 1996, 750 pups have been branded on Antsiferov with branding code “Y”.

2.2 North Sea of Okhotsk: Yamsky Islands

The north Sea of Okhotsk Steller sea lion population (about 30% of Russian SSL’s) reproduces primarily on two major rookeries: Iony Island in the northwest Sea of Okhotsk produces over 1000 pups per year, and Yamsky Islands produces about 400 pups. The majority of exchange in the north occurs between these islands, although Kuril island animals are regularly sighted. Branding has been taking place on Iony Island since 1997 and on Yamsky Islands since 2000. The first dedicated maternal attendance observation effort was initiated on Yamsky Island in 2007.

Yamsky Islands (59.3°N 155.5°E) are located in the northeasternmost region of the Sea of Okhotsk, at the mouth of Shelikhov Bay. The rookery is located on Matykil Island, which is oriented east-west, about 4.6 km long and 1.6 km wide at the widest. It is marked by steep cliffs and a high sharp ridge with a maximum elevation about 360 m. It is the northernmost rookery in Russia and among the most northern reproductive sites in the world. When the sea lions arrive in May, the island is often surrounded by ice floes, through the active currents in the opening of the Shelikhov bay help maintain open water. The sea is typically clear of ice by the first week of June.

In 2007, three observers were stationed on Yamsky island from June 1 to July 25. Observations were performed from a blind some 40 m above the rookery throughout daylight hours.

2.3 Commander Islands: Medny Island

The two Commander islands, Medny (or Copper Island) and Bering are the westernmost links in the Aleutian chain. The sealions populating these islands belong to the Western stock but travel regularly to eastern coast of Kamchatka. Medny island (52° N, 168° E), the smaller of the two Commander islands, is about 50 km long, about 6 km wide at its widest

and oriented in an almost exactly northwest-southeast direction. The central plateau is grassy, reaches a maximum elevation about 310 m, and is marked by steep, cliffy descents to the rocky-gravelly beaches.

The Steller sea lion rookery is located on Yugo-Vostochny (Russian: “Southeastern”) Cape and takes up a X km strip of gravel or rocky beach at the southeasterly tip of the island and overlaps with a large northern fur seal rookery that can produce over 30,000 pups (Chelnokov 1983). The total number of non-pup adult sealions on Medny has fallen 86% since 1977 (Loughlin et al. 1992, Burkanov and Loughlin 2005). The numbers appear to have stabilized at a depressed level in recent years (Burkanov and Loughlin 2005, ?).

Since 1996, 721 pups have been branded on Medny island, such that the age of identifiable Medny-born animals ranges from 1 to 11 years. The rookery-identifying letter code is “M”. Observers were stationed on Medny island, from May 22-25 through August 14-17 in 2005 through 2007. Observations are performed from two observation points located X and X m above sea level on the cliffs overlooking the beach. This is the longest observation period among the six rookeries and encompasses the entire range of parturition dates and well into the post-reproductive break-up of the rookery.

3 Methods

3.1 Raw Data Collection

The standard methodology for observers on all islands was to be present in the blinds from dawn to dusk. All branded and naturally marked animals were photographed daily with digital cameras through telescopes. During the morning and evening hours, the rookery was scanned visually and every half-hour the presence or absence of every branded or naturally marked reproductive female was noted. The frequency of all-rookery scans was reduced to once an 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 (AT) and departure times (DT) of certain focal females (FF). Focal females were those adult females that were either branded or with distinctive natural markings that gave birth in sections of the rookery that were well-observed from the blinds. Naturally marked animals usually had large traumas such as collars from net entanglement and large sections of missing skin which make them as similarly identifiable and visible as branded animals. Parturition, nursing, copulation and occasional deaths were noted wherever possible.

Often, exact AT and DT of an animal were unobservable. Most commonly this was because they occurred during nighttime hours. In these cases, arrivals or departures were arbitrarily assigned to the midpoint of the non-observation period, usually 2:30 am. In other

cases, observers were asked to make estimates of AT and DT based on other constraints. This was possible when, for example, an animal's pelage is still wet when it is observed in the mornings, allowing for an estimate of arrival within a 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 AT and DT in these cases were recorded as "Estimates".

The collected AT and DT were used to calculate visit (VD) and trip durations (TD). In those cases when even an estimate of arrival and departures was impossible, the corresponding VD and TD estimates were excluded from the analysis.

In order to improve the effectiveness of this method, the observers worked on alternating 24 hour cycles from midday to midday, such that the observer was familiar with the animals that departed in the evenings and could recognize whether an animal returned on the following morning. The arrival and departure time estimation methodology are broadly consistent with those used by (Higgins et al. 1988) in their studies of maternal attendance patterns on Año Nuevo Island and by (Trites and Porter 2002) on Alaska haulouts in winter.

3.1.1 Possible biases

Trip durations (TD) might be slightly underestimated by the conservative approach to guessing arrival and departure times, in contrast to the possible overestimation of trip lengths in Higgins et al. (1988). Because the algorithm that fixed departure and arrival times from a combination of the observed haul-out and departure data and the attendance tables, any biases may exist should be consistent between all animals. Thus, though absolute estimates of trip and visit lengths may be biased, the estimates should be useful for making relative comparisons. Because observers vary in their experience and make-up on the islands and between years. Also, while we encouraged observers to be relatively conservative The greatest potential drawback of the visual observation method was the inability to make observations at night, roughly 10:30 to 5:30. Most departures occur at dusk and significant portion of arrivals occur at night. While radio tagging studies such as Brandon (2000) and Milette and Trites (2003) indicate that relatively few trips last less than 6 hours, the possibility that we miss entire trips that occur during the night cannot be excluded.

3.2 Statistical Analyses

For consistency between the attendance observation logs, we restricted the data for analysis as follows:

- Only the period within 30 days after parturition were considered to account for different observation periods on the different island and to minimize the chance that a

female moves with the pup off of the main reproductive rookery, which we observed to occur sometimes as soon as 40 days after birth.

- Those animals that were observed for less than 10 days were excluded from the analysis.
- Attendance data was analyzed only for dates before branding. Because of the disturbance of the branding operation, which occurred on June 28 in 2006 on Medny and in between July 1-16 on the Kuril Island in 2005 and 2007. Since all adults are chased off the rookery during branding, and several mothers leave shortly thereafter with their pups, attendance patterns can be significantly affected.

We used the logged arrival and departure times and parturition dates to obtain several variables of interest: The inter-parturition period (IPP), defined as the period between parturition and the first departure; the trip and visit durations (TD and VD); the total attendance cycle (AC), defined as the time between consecutive departures; and the proportion of time (P) spent on the rookery. VD, AC and P were defined after the first trip, since the IPP is always much greater than subsequent visit periods.

Analyses were performed using linear regressions and analysis of variance (ANOVA) using island (*I*) and year (*Y*) as discrete factors and age of pup in days (*D*) as continuous covariates. Mother's ages were subdivided into three discrete groups: "Young" (4-5 years old), "Medium" (5-10 years) and "Old" (greater than 10 years) and analyzed as a discrete factor. For multiple paired comparisons, standard least squared difference t-tests were performed with Bonferroni adjustments on the alpha level (Zar 1999).

Analysis of proportion of time spent on the rookery p was performed using a binomial model with a logit link (Zar 1999).

Inter-parturition time were distributed normally, the trip and visit length durations distributions were right-skewed and showed heavy tails. Therefore, analyses were performed on log-transformations of these data, and we report medians and confidence intervals derived from the transformed response.

In analyzing trip and visit durations, the data on each individual is treated as a repeated measure to account for the fact that each individual takes several trips. We used a linear mixed effects (lme) model to take the correlation of an individual's response into account (Verbeke and Molenberghs 2000). The linear mixed effects model permits a separation of linear factorial relationships from the "random effect" (in our case, animal ID), which is essentially a nuisance parameter.

Because there are different numbers of animals per island per year and different number of trips per animal, the data is unbalanced. Consequently, we used Akaike's information criterion (AIC) to assess models rather than F-tests on sums of squares (Oehlert 2000).

All analyses were performed using the R statistical software package.

It should be noted that since this was a long-term observational study rather than a designed experiment, all analysis techniques are used as guides to identify significant differences and influential factors, rather than parameterize a “complete” statistical model.

4 Results

A total of 280 nursing females were included in the analysis, an average of 18 per island per year (Table 1). Of these, 252 were branded i.e. of known age. The ages of the females varied from four to 18 years, with average ages ranging from 5.6 years on Yamsky Island to 10.4 years on Lovushki Island in 2007, reflecting the branding history on these islands. Figure 2 presents the attendance data analyzed for two well-contrasted islands: Yamsky in 2007 and Lovushki in 2006, illustrating the considerable variation between islands, years and individuals in all the variables of interest. The statistical analyses are used as guides to help quantify these differences.

4.1 Inter-parturition period (IPP)

IPP (total mean 12.4 days, s.e. 4.5) varied significantly between islands and individuals ($p \ll .001$) but not between years ($p = 0.57$) (table 1, figure 3), with Yamsky Island animals displaying the lowest (10.3, s.d. 4.24) with Medny Island displaying the highest mean (14.1, s.d. 5.43). A multiple comparison test (Tukey honest significant difference) suggests that the other islands are not significantly different from these extremes. On Chirpoev and Yamsky islands, IPP showed a significant dependence ($p < 0.01$) on mother’s age, with the youngest females spending on average 8.75 days (se 2.0) compared to 12.5 days (se 4.2) for older females. On other islands there was no detectable relationship between Age and IPP.

4.2 Trip durations

Trip durations ranged from 3 to 72 hours, with global median value of 9.0 hours and inter-quartile range from 6.2 to 19 hours. The distribution of trip durations is right-skewed and multimodal, with a large peak at 5-12 hours, a smaller peak at 20-29 hours, and a smaller one at 40-48 hours, reflecting trips that took place overnight, over a day and a night, and two day trips respectively.

Variation was considerable between individual females and islands (mle ANOVA p -values all $\ll 0.001$), but less so between years (figure 3 B, table 2). Lovushki island consistently displayed the shortest trips in all years (median 7.0 hours), followed by Chirpoev, Medny and Antsiferov (between 9.0 and 11.0 hours) and Raykoke and Yamsky island displaying dramatically longer trip durations (16 and 19 hours). Multiple paired comparisons (Tukey’s

HSD) suggests the following grouping structure: (Lr)-(Br, M, Y)-(P, Yar). These basic patterns are roughly consistent between most years, with the exception of a dramatic increase in median Medny trip durations in 2007 and Raykoke trip durations 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 ID as the random effect. The most parsimonious model based on minimizing the AIC suggest that there significant main and interaction effects between Island, Years and Mother's age. Pup Age was not deemed to be a signifant factor, suggesting that trip durations remain roughly constant throughout the season.

Younger mothers (4-5 years) showed longer trips on average (13 hours compared to 8-9.5 hours for older mothers), but this difference was only significant on Raykoke, Medny and Antsiferov islands; elsewhere there was no effect.

4.3 Visit durations

The median visit duration is 30 hours, with an inter-quartile range between 16.5 and 45.4 hours.

Visit durations similarly varied widely between individuals, islands and years (figure 3 B, table 2), with a strong island-year interaction effect. There were several significant changes in 2006. Notably, Lovushki Island females whose median visit duration was among the highest in 2005 fell at 45 to 24.3 hours (CI:11,54) while Raykoke visit durations shot up to 43 hours (CI: 20, 91). The final grouping structure in 2006 is: (*Lr*), (*M*, [*Br*], *Y*, *P*)

Unlike trip duration, pup age was generally a much more significant explanatory factor for visit duration which tended to get shorter as the season progresses (figure 4). While the exact value for the regression varied between islands, an average visitation period will last on average 44 hours 10 days after birth and drop to about day 18 hours 30 days after birth.

Age of mother had a effect ($p = 0.03$) on visit durations on Brat Chirpoev and Antsiferov, in both cases young females median visit duration is about 27 hours compared to 33 hours for older females. This relationship was consistent between years. Elsewhere, there were no significant relationships.

4.4 Proportion of time spent on land (P)

Proportion of time spend on land (P) was calculated after the first trip for each sea lion. The overall median was 0.75, with island medians differing significantly from 0.63 on Yamsky and Raykoke to 0.80 and 0.81 on Brat Chirpoev and Lovushki. There was a highly significant increase in P as a function of the age of the mothers ($p \ll 0.01$): Youngest mothers spend on average around 30% of their time foraging, while females 6 year and older spent on average 22% of their time foraging, with no significant differences between the oldest and middle

aged females (6-10 years old). On Medny Island in 2007 and on Raykoke Island in 2006, P was significantly lower than in other years. Otherwise, the values remained consistent on each island between years (Tukey's HSD).

5 Discussion

Stellar sea lions on Russian rookeries followed behavioral patterns that have been well documented elsewhere (Ono et al. 1987, Higgins et al. 1988, Costa et al. 1989, Hood and Ono 1997, Brandon 2000, Trites and Porter 2002), hauling out usually 1-3 days before giving birth, nursing for one to two weeks without leaving the rookery and typically copulating before taking a first trip. The inter-parturition period is followed by a period of foraging trips and returns to the rookery ranging from several hours to several days. General activity on the rookeries is highest in the evenings, about an hour before and after dusk, when most of the departures occurred and in the mornings, when most of the arrivals occur.

Inter-parturition periods can be considered to be a index of maternal fitness before arriving at the rookery. This is corroborated by the observation that younger, smaller, presumably less fit females have significantly shorter IPP's than older females. There was little consistent variability between the islands as the bulk of the IPP's ranged between nine and 16 days. However, there were some significant differences between years on single islands (increasing on Madny and Antsiferov). This suggests that there might be significant interannual variation during the winter, though this is also confounded by the fact that the average age of branded females is increasing annually.

The total attendance cycle of nursing females shortens with pup age. This occurs primarily because of decreasing visit durations, while trip durations remain constant. This indicates that in order to fulfill the increasing nutritional need of the pups, females must make trips more frequently rather than take longer trips, suggests that the amount of energy obtained in a trip and perhaps the net distance of a trip remain relatively constant throughout the season, but that in order to meet the increasing energetic demand of growing pups, the frequency of trips has to increase. This pattern was consistent across all islands.

There was considerable variability in both frequency and duration of foraging trips between islands and individuals, and to a lesser extent between years. The island with the shortest trips and the highest proportion of time spent on land was Lovushki, where females typically left late in the evening and would be back on the rookery nursing by the following morning. These patterns suggest that the foraging base near Lovushki is abundant and nearby, a suggestion supported perhaps by the fact that Lovushki is one of the biggest rookeries on the Kuril Islands and home to the largest reproductive groups of Northern fur seals as well. This might be related to its location closer to the edge of the Okhotsk continental shelf and the corresponding highly productive upwelling zone. In

contrast, mothers on neighboring Raykoke Island consistently showed significantly longer trips, many returning late in the morning or even being absent for more than a day. This, despite the fact that Raykoke is located only 45 km away to the west and that there is high exchange of reproductive animals between these two rookeries (Gurarie *pers. comm.*). This result suggests that the spatial variability in foraging base quality can be extremely fine-scaled.

Southernmost Brat Chirpoev mothers exhibited a more Lovushki-like pattern, with shorter trips and very high percentage of time spent on land. The northernmost Kuril island, Antsiferov, reflected the longer trip durations displayed on Raykoke. It is notable that Brat Chirpoev is second in size to Lovushki, suggesting that the largest rookeries are located at particularly optimal locations for foraging. These variations occur within the Kuril islands on locations where the populations are stable or increasing and where there is considerable exchange of animals. Medny island, where the populations are severely depleted, displayed roughly intermediate values for trip durations and proportion of time spent on the rookery. There is no evidence that food availability as reflected by attendance patterns can be easily related to population levels on Medny Island.

Yamsky island, located in the far northern Sea of Okhotsk, displayed the most consistently longest foraging trips, often leaving in the very early evening and spending more than one night at sea. Yamsky is the only study site located far from a continental shelf, located in the shallow North Sea of Okhotsk where the high productivity is associated with high inflows of fresh water in the estuaries and bays. It is likely that the distinctly different attendance patterns observed on Yamsky island is related to a fundamentally different foraging strategy based on identifying more localized and concentrated sites of forage, such as Pacific herring (*Clupea pallasii pallasii*) spawning grounds or the mouths of salmon spawning (*Onchorrhynchus* spp.) rivers.

Our study is the first that has demonstrated a consistent and statistically significant difference between the initial fitness and subsequent foraging behavior between younger and older Steller sea lion females.

In order to more fully interpret observed attendance patterns, more needs to be known about the distribution of various prey species in the waters surrounding the rookeries and the diet of the animals. Relating the attendance patterns over these three years to eventual estimates of pup survival will contribute insight into the sensitivity of survival on the earliest life stages of the pups.

6 Summary

Non-invasive, visual observation efforts can yield high-volume data with great detail at relatively low cost and no risk to animals. The variability in attendance patterns between

geographically disperse rookeries is attributable to geographic variation in the foraging base, which can be very fine-scaled. Younger mothers are quantifiably less fit than older mothers. Analysis of attendance patterns does not provide any evidence in support of food-limitation as an explanation of population decline.

7 Acknowledgments

Gratitude is extended to everyone who contributed to collecting data in the field, especially Roman Belobrovich, Alexei Kondratyuk, Aleksei Chetvergov, Svetlana X, Masha X, и т.д. Thanks to Katie Grieve for useful discussions on statistical analysis. The research was funded by NOAA Grant # xxxxx. All work on rookeries was conducted under permits issued annually by Russian permitting agencies.

References

- I. L. Boyd. Foraging and provisioning in Antarctic fur seals: interannual variability in time-energy budgets. *Behavioral Ecology*, 10(2):198–208, 1999.
- E. A. A. Brandon. *Maternal Investment in Steller Sea Lions in Alaska*. PhD thesis, Texas A&M University, 2000.
- V. N. Burkanov and T. R. Loughlin. Distribution and abundance of Steller sea lions, *Eumetopias jubatus*, on the Asian Coast, 1720’s-2005. *Marine Fisheries Review*, 67:1–62, 2005.
- V. N. Burkanov, A. R. Semenov, and V. V. Vertiankin. Counts of Steller sea lions at Kamchatka and the Commander Islands, USSR. AFSC Processed Report 91-13, Department of Commerce, Seattle, WA, 1991.
- D. P. Costa, J. P. Croxall, and C. D. Duck. Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology*, 70(3):596–606, 1989.
- R. L. DeLong and G. A. Antonelis. Effects of the 1982-83 El Niño on several population parameters and diet of California sea lions on the California Channel Islands. In F. Trillmich and K. A. Ono, editors, *Pinnipeds and El Niño: responses to environmental stress*, pages 166–172. Springer-Verlag, Berlin, 1991.
- R. Gentry. *Behavior and Ecology of the Northern Fur Seal*. Princeton University Press, 1998.

- C. B. Heath, K. A. Ono, D. J. Boness, and J. M. Francis. The influence of El Niño on female attendance patterns in the California sea lion. In F. Trillmich and K.A. Ono, editors, *Pinnipeds and El Niño: responses to environmental stress*, pages 138–145. Springer-Verlag, Berlin, 1991.
- L. V. Higgins, D. P. Costa, A. C. Huntley, and B. J. LeBoeuf. Behavioral and physiological measurements of maternal investment in the Steller sea lion, *Eumetopias jubatus*. *Marine Mammal Science*, 4(1):44–58, 1988.
- W. R. Hood and K. A. Ono. Variation in maternal attendance patterns and pup behaviour in a declining population of Steller sea lions (*Eumetopias jubatus*). *Canadian Journal of Zoology*, 75(8):1241–1246, 1997.
- T. R. Loughlin. The Steller sea lion: a declining species. *Biosphere Conservation*, 1(2): 91–98, 1998.
- T.R. Loughlin, A.S. Perlov, and V.A. Vladimirov. Range-wide survey and estimation of total number of Steller sea lions in 1989. *Marine Mammal Science*, 83(3):220–239, 1992.
- P. Majluf. En Niño effects on pinnipeds in Peru. In Fritz Trillmich and Kathryn A. Ono, editors, *Pinnipeds and El Niño: responses to environmental stress*, pages 55–65. Springer-Verlag, Berlin, 1991.
- D. J. McCafferty, I. L. Boyd, T. R. Walker, and R. L. Taylor. Foraging responses of Antarctic fur seals to changes in the marine environment. *Marine Ecology Progress Series*, 166:285–299, 1998.
- R. L. Merrick and T. R. Loughlin. Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. *Canadian Journal of Zoology*, 75(5):776–786, 1997.
- L. L. Milette and A. W. Trites. Maternal attendance patterns of Steller sea lions (*Eumetopias jubatus*) from stable and declining populations in Alaska. *Canadian Journal of Zoology*, 81:340–348, 2003.
- G.W. Oehlert. *Design and Analysis of Experiments*. W.H. Freeman and Company, New York, 2000.
- K. A. Ono, D. J. Boness, and O. T. Oftedal. The effect of a natural environmental disturbance on maternal investment and pup behavior in the California sea lion. *Behavioral Ecology*, 21(2):109–118, 1987.
- F. Trillmich. Attendance behavior of Galapagos fur seals. In R.L. Gentry and G.L. Kooyman, editors, *Fur Seals: Maternal Strategies on Land and at Sea*, pages 168–185. Princeton University Press, Princeton, NJ, 1986.

- F. Trillmich. The effects of El Niño on pinniped populations in the eastern Pacific. In F. Trillmich and K.A. Ono, editors, *Pinnipeds and El Niño: responses to environmental stress*, pages 247–270. Springer-Verlag, Berlin, 1991.
- A. W. Trites and B. T. Porter. Attendance patterns of Steller sea lions (*Eumetopias jubatus*) and their young during winter. *Journal of Zoology*, 256:547–556, 2002.
- G. Verbeke and G. Molenberghs. *Linear Mixed Models for Longitudinal Data*. Springer, New York, 2000.
- J.H. Zar. *Biostatistical Analysis. 4th Edition.* . Prentice-Hall, Inc., Upper Saddle River, NJ., 1999.

8 Figures

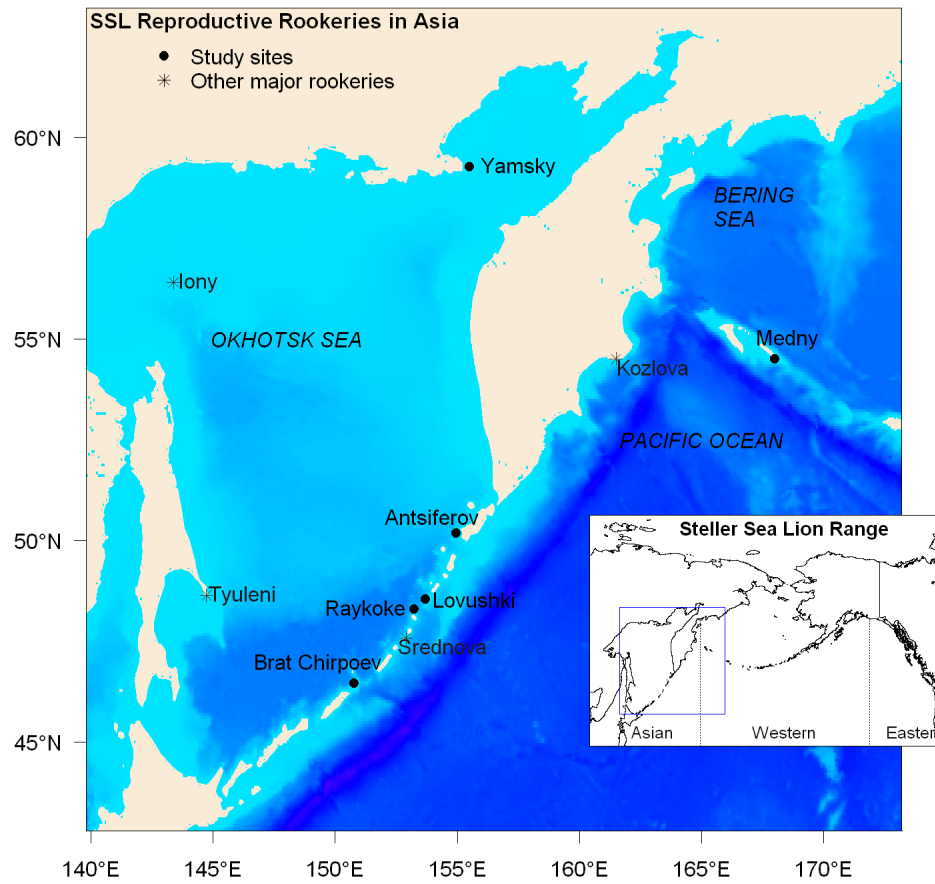


Figure 1: Map of reproductive Steller sea lion rookeries in Russia with bathymetry. Darker colors represent deeper waters. The dots represent those sites where maternal attendance data was collected. Crosses identify major reproductive rookeries where animals are branded, but where data on attendance patterns was not collected.

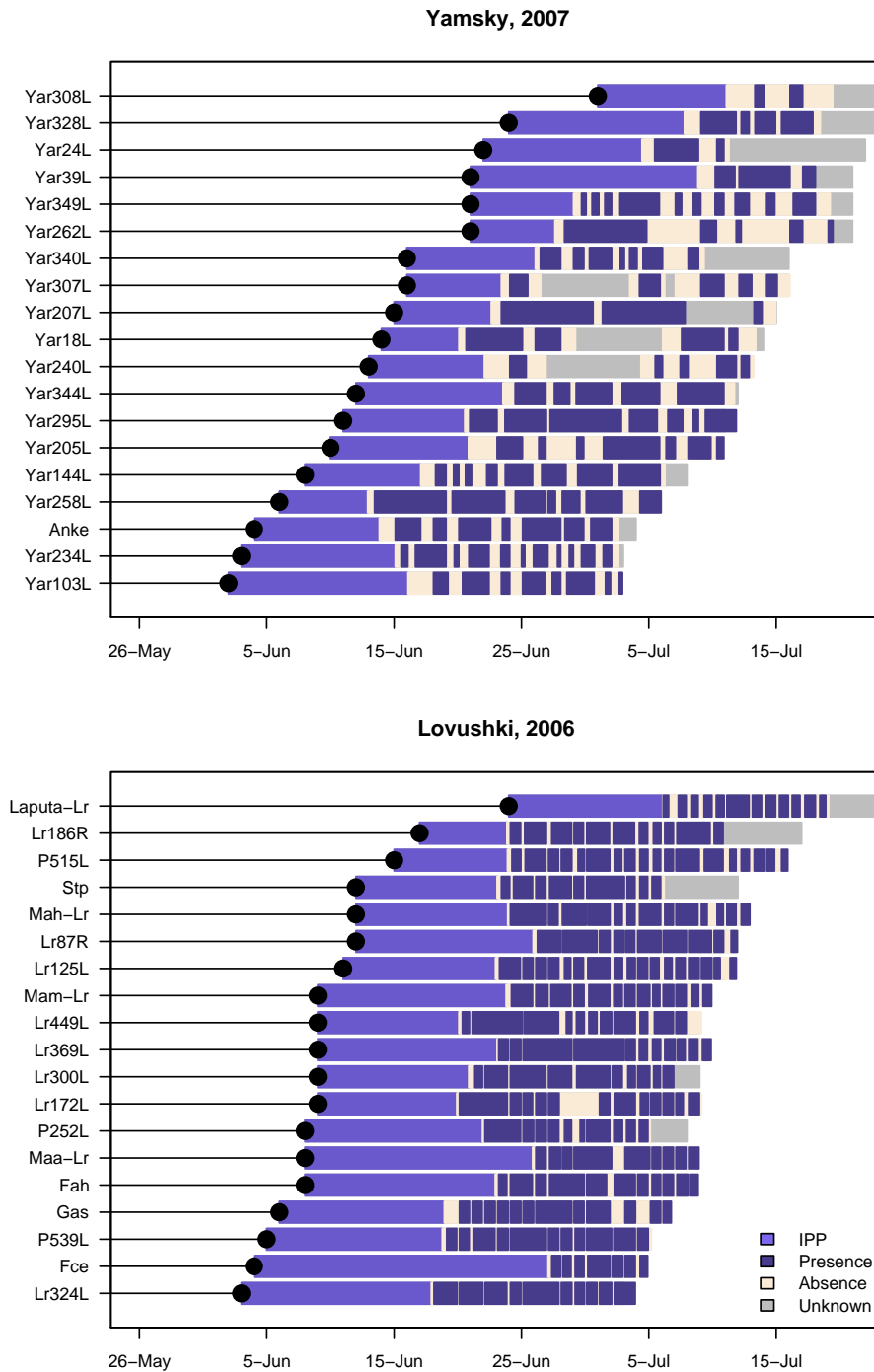


Figure 2: Examples of attendance patterns obtained on nursing females on (A) Yamsky Island in 2007 and (B) Lovushki Island in 2006. Females are identified according to their brands, plastic tag number or natural markings on the *y*-axis. The black dots represent the parturition dates for the females. Blue bands represent presence, with the lighter blue bands representing the period before the first trip (IPP), while pink bands represent absence. Grey represents omitted observations because either arrival or departure times could not be determined.

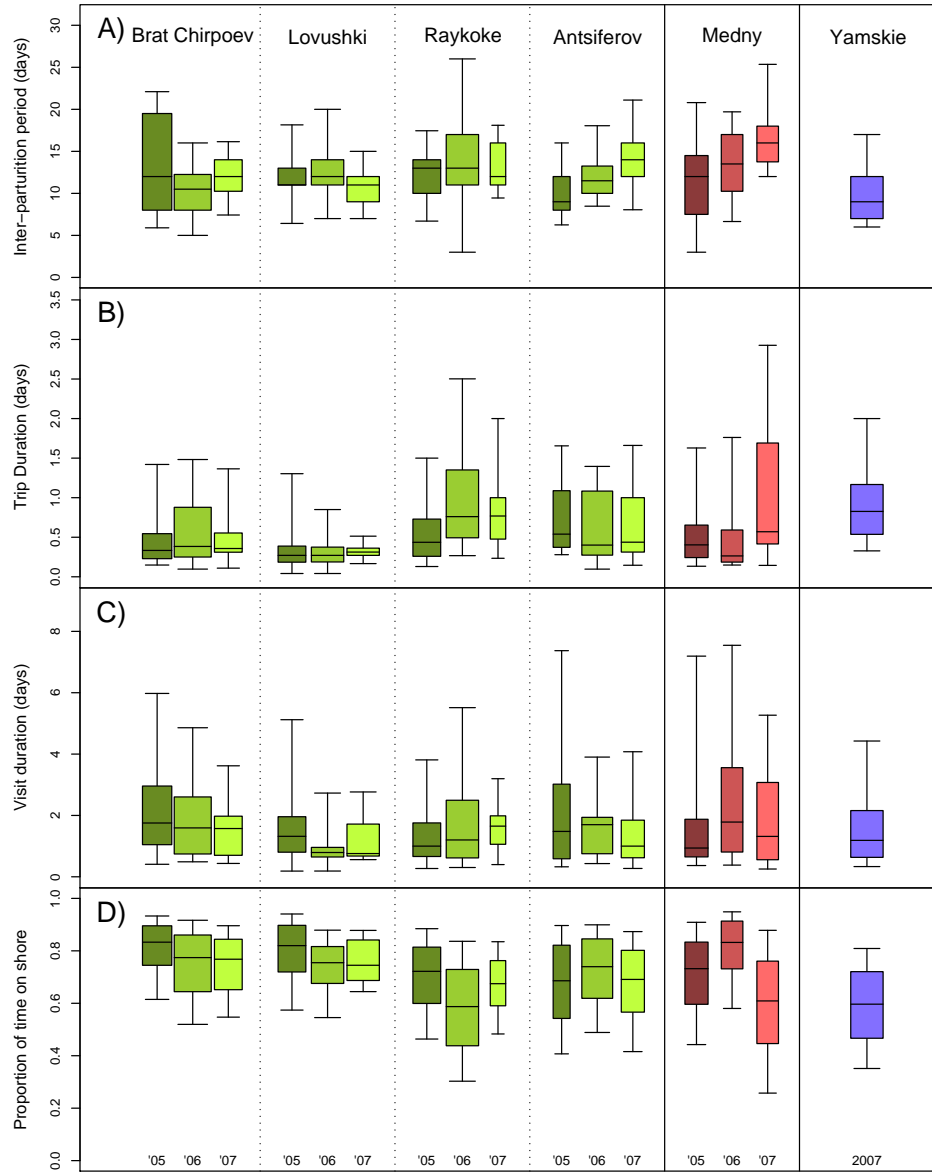


Figure 3: Boxplots of (A) inter-parturition periods (IPP), (B) and (C) trip and visit durations, and (D) presence probabilities on all six islands. The width of the boxes is proportional to the number of observed females per island.

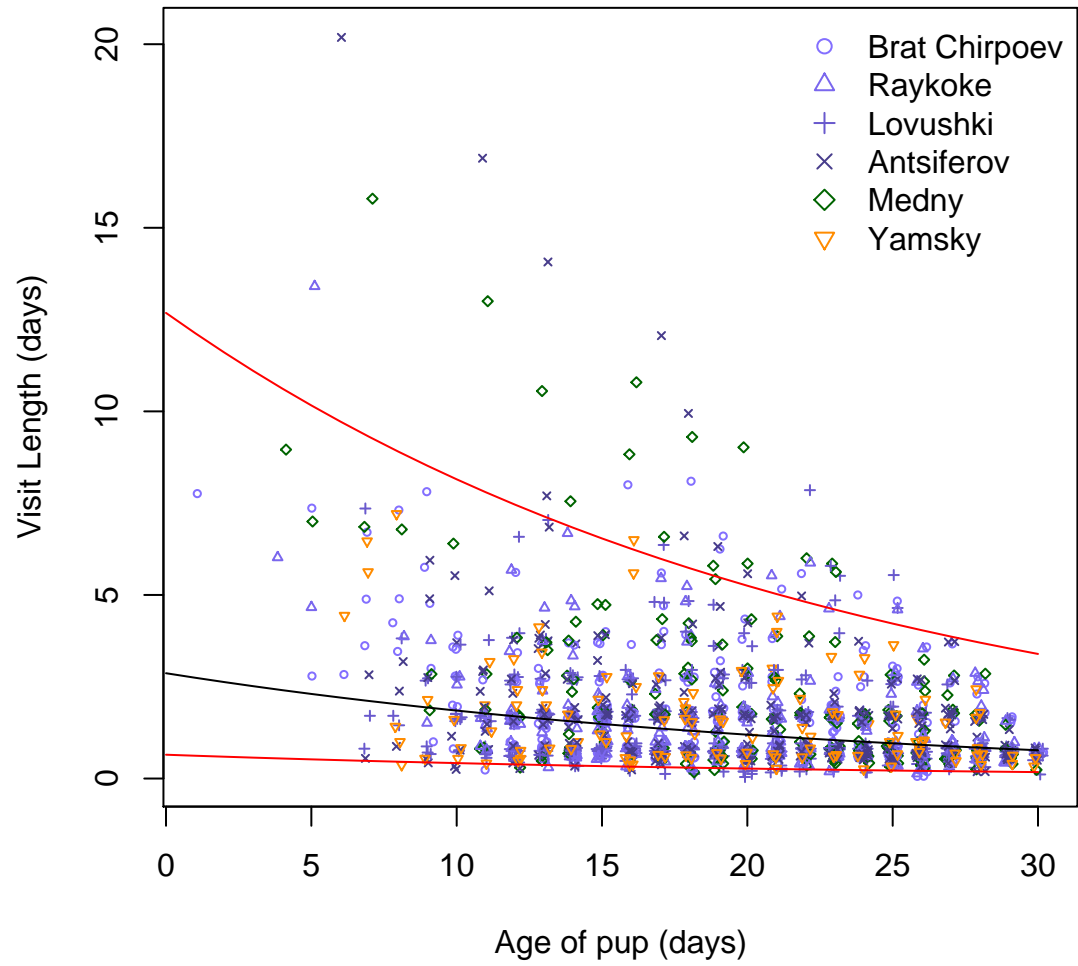


Figure 4: Visit durations (log scale) against age of pup. Red lines are 95% confidence intervals.

9 Tables

Table 1: Table of inter-parturition and probability presence summary statistics. The 68% confidence interval is analogous to one standard deviation from the mean for the logit transformed probability data.

Island	Year	N females	n trips	n visits	IPP (days)	s.e.	P (95% C.I.)
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)

Table 2: Table of Visit and Trip duration statistics on all islands and all years.

Island	Year	VD (hours)	(95% C.I.)	TD (hours)	(95% C.I.)
Brat Chirpoev	2005	44.0	(20.2, 95.6)	9.24	(4.68, 18.2)
	2006	34.1	(16.3, 71.4)	10.06	(4.44, 22.8)
	2007	30.5	(14.4, 64.5)	9.96	(4.64, 21.3)
Raykoke	2005	27.1	(13.0, 56.4)	10.93	(5.15, 23.2)
	2006	29.4	(11.7, 73.3)	24.04	(9.88, 58.4)
	2007	35.8	(20.5, 62.5)	18.08	(8.91, 36.7)
Lovushki	2005	30.4	(12.5, 74.0)	7.00	(2.74, 17.8)
	2006	19.9	(10.6, 37.3)	6.65	(3.35, 13.2)
	2007	26.5	(14.5, 48.1)	7.95	(4.64, 13.6)
Antsiferov	2005	35.7	(12.6, 101.1)	15.35	(8.10, 29.0)
	2006	34.1	(17.3, 67.0)	11.49	(5.21, 25.3)
	2007	28.2	(12.5, 63.5)	12.25	(5.78, 25.9)
Medny	2005	29.9	(12.2, 73.3)	10.66	(4.74, 23.9)
	2006	42.0	(16.3, 108.4)	9.22	(3.60, 23.5)
	2007	30.9	(11.4, 84.0)	21.71	(7.93, 59.4)
Yamsky	2007	29.3	(13.3, 64.9)	19.75	(11.29, 34.5)