

# Attendance patterns of Steller sea lions (*Eumetopias jubatus*) and their young during winter

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## Abstract

Winter attendance patterns of lactating Steller sea lions *Eumetopias jubatus* and their offspring were recorded during the late stages of nursing when the young were expected to move from milk to independent foraging. Trip duration and nursing visits to shore by 24 mothers with pups (7–9 months old) and six mothers with yearlings (19–21 months old) were noted during 600 h of observations (from 22 January to 1 April 1996) at a non-breeding haulout site in south-eastern Alaska. Pups and yearlings tended to stay on or near the haulout while their mothers were away and showed no signs of weaning during winter. Their average trips to sea were 43% shorter in duration than those of lactating females, suggesting that pups and yearlings make independent trips away from the haulout while their mothers forage. The winter attendance cycle of lactating females (consisting of one trip to sea and one visit on land) averaged about 3 days, with the mothers of pups spending an average of 15 h of this time onshore with their offspring. The winter attendance cycle of pups and yearlings averaged just over 2 days, with the immature sea lions spending an average of 22 h on shore. Foraging trips by mothers of yearlings were significantly longer than those by mothers of pups. However, there was no significant difference in the foraging times of mothers of male and female pups. Lactating females spent more time at sea during winter than during summer. The probability of sighting an individual on the winter haulout during daylight hours was 15% for lactating females and 40% for immature animals.

**Key words:** *Eumetopias jubatus*, Steller sea lion, behaviour, attendance, weaning, foraging, maternal investment, Alaska

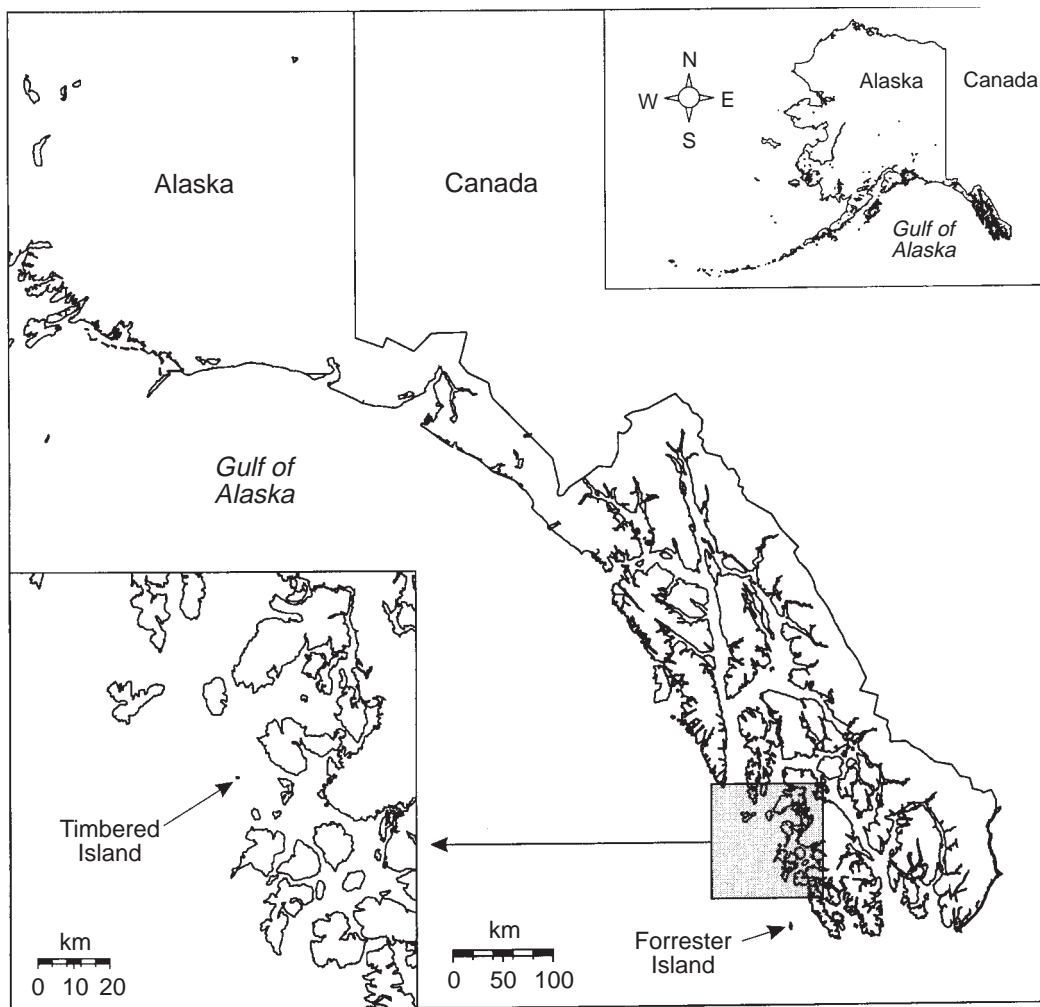
## INTRODUCTION

Unlike most phocids, lactating otariids must make intermittent trips to sea to feed (Gentry, 1970; Sandegren, 1970; Trillmich & Lechner, 1986; Merrick, 1987). This constant shift between time on shore with the pup and time spent at sea foraging is repeated throughout lactation and is referred to as the maternal attendance pattern. It is an important part of the otariid rearing strategy. Pinniped neonates must attain sufficient body weight and energy reserves prior to weaning to survive on their own. Otariid pups are mostly dependent upon the milk produced by their mother, although some may supplement milk with solid food as they near the time of weaning (Trillmich, 1986a,b).

Steller sea lions *Eumetopias jubatus* are born during the summer (late May to early July). Most pups wean before their first birthday, but some may continue to nurse for longer. The first winter following birth is believed to be a critical stage in the life history of young Steller sea lions and may be the key to understanding the population decline that has occurred in most parts of Alaska (York, 1994; Trites & Larkin, 1996; Merrick & Loughlin, 1997). Unfortunately little is known about the life history of Steller sea lions during winter.

The primary motivation for our study was to document the attendance patterns (time at sea and time on shore) of lactating Steller sea lions and their young during winter. We sought to fill in an important missing piece of the Steller sea lion life history that many feel is critical to resolving the population decline. We particularly wanted to document the weaning process and determine whether mothers and pups make independent

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**Fig. 1.** Map of the Gulf of Alaska showing Timbered Island in south-eastern Alaska ( $133^{\circ} 48' \text{ W}$ ,  $55^{\circ} 41' 45'' \text{ N}$ ), and Forrester Island where the animals observed were branded when 1 month old.

trips to sea. Weaning is a process that includes many complex behaviours (parent–offspring conflict, changes in the rate and length of suckling bouts, abandonment, etc.). We documented changes in time on shore and at sea, and watched for abandonment as indicators of weaning.

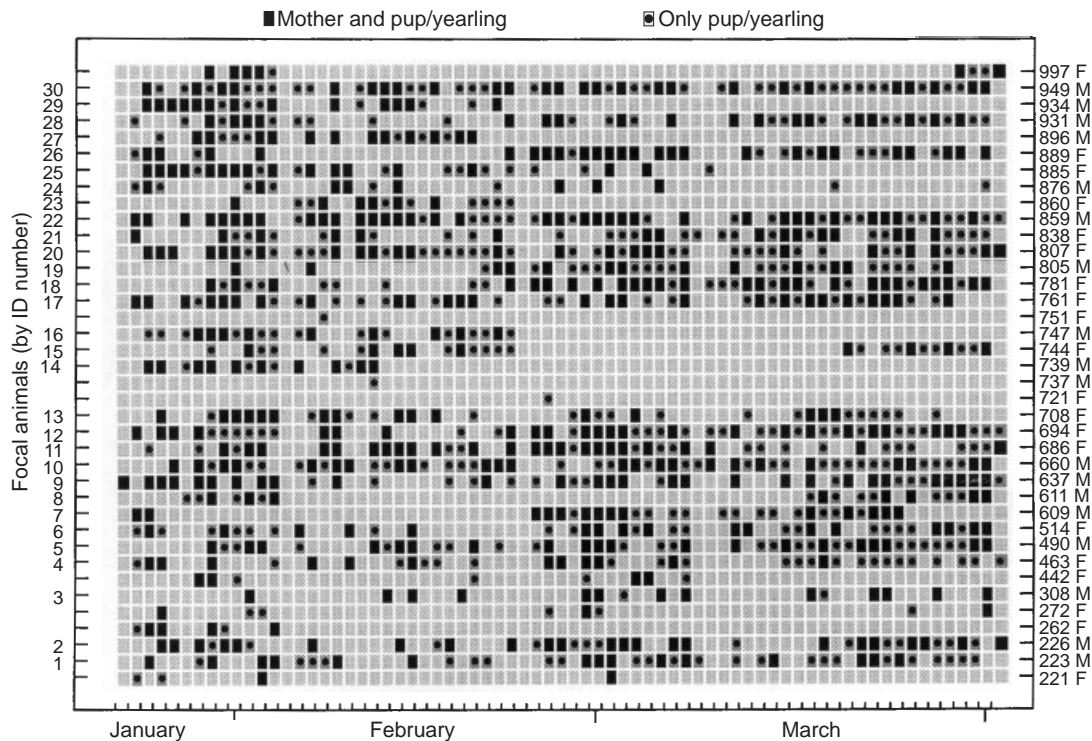
Our study also afforded us the opportunity to evaluate maternal investment relative to age and sex of offspring. We estimated the amount of time mothers and young spent on shore and at sea, and compared their winter (January–March) haulout patterns with similar data available from summer observations (June–August). Foraging trip duration and time on shore were also used as measures of maternal investment to test two hypotheses: (1) that mothers of male offspring spend more time at sea than do mothers of female offspring to provide for the greater nutritional needs of the larger males; (2) that mothers of yearlings (age 1–2 years) make longer foraging trips than females with pups (age 6–9 months). Both of these strategies, if used, might offset the cost of rearing larger and more demanding immature animals.

## METHODS

### Study area

Steller sea lions were observed from 22 January to 1 April 1996, on Timbered Island ( $133^{\circ} 48' \text{ W}$ ,  $55^{\circ} 41' 45'' \text{ N}$ ) in south-eastern Alaska (Fig. 1). This island is a non-breeding haulout site. It is round, 1.0 ha, 150 m wide, and has a maximum elevation of 38 m. Three sides of the island are exposed to the Gulf of Alaska; the other faces Prince of Wales Island. The sea lions haul out along the edges of the main island and on 2 low, exposed rocks 30 m offshore that are awash during stormy weather and high tides. Observations were performed from elevated blinds with clear, unobstructed views of the 2 main haulout sites.

Timbered Island was selected as a typical Steller sea lion winter haulout based on historical accounts and annual aerial count data, which indicated that a high number of mature and immature animals were present during past winters (Alaska Department of Fish and Game, unpub. census data). The site was also selected



**Fig. 2.** Daily attendance of lactating females and their dependent offspring. The Y-axis identifies the individuals sighted at the haulout by brand (all animals sighted) and ID (those used for analysis). Yearlings had brands 201–599 and pups had 600–998. The letter at the end of each brand number (which was not part of the brand) identifies sex of the immature animal (M, male, F, female). Immatures sighted at least once during the day were scored as present (grey boxes with dot). Black boxes indicate that both the immature/mother pair was present at least once during the day. Note that no animals were onshore on 4 February when 3–5 m waves broke over the haulout, and that animals could not be seen during the blizzard of 23 February when visibility was reduced to zero.

for ease of observation, as well as for safety and logistical considerations.

### Data collection

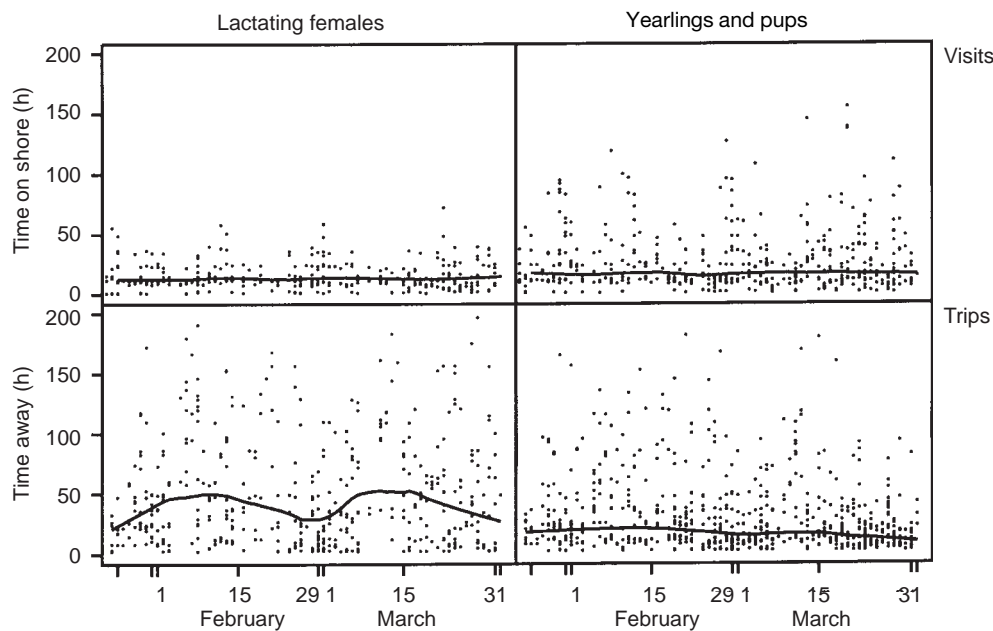
Time ashore and at sea were determined by the presence or absence of sea lions at the haulout during daily observations. Since few lactating females could be identified individually, they were only counted as present when seen with recognizable dependent offspring. A number of the pups and yearlings at our study site were branded in 1994 and 1995 on Forrester Island (1 of 3 breeding sites in south-eastern Alaska, and located about 100 km south of Timbered Island, Fig. 1). They were branded when 1 month old (with a letter and 3 digits) by the Alaska Department of Fish and Game (ADF&G). All data were thus collected using the marked pups and yearlings. Mature females were scored as away if they were not observed on the haulout with their pup or yearling during daily observations. The behaviour and association of branded immature sea lions (pups and yearlings) were noted every 15 min using focal sampling. Behavioural observations were restricted to daylight hours (maximum 06:00–20:00, average 08:00–16:30) and included 600 h of observations over 70 days ( $\bar{x} = 8.6$  h per day,  $SE = 0.34$ ). Observations

were made every day, except 23 February when a blizzard reduced visibility to zero (see Fig. 2).

### Data analysis

Steller sea lions present at dusk and dawn were assumed to have spent the night on the haulout. Similarly, animals absent at dusk and the following dawn were assumed to have been away all night. We also assumed that dry animals noted within the first 3 h of beginning daily observations had spent the night on the haulout. Such a distinction could not be made however during infrequent heavy rains. When focal animals were first seen at the start of observations in the morning, or last seen at the end of the day, the mid-point during the night (between the end and start of observations) was calculated as the departure or arrival time. It was not possible to exclude the chance that individuals were hauled out at other sites, although previous work done with satellite telemetry has shown adult females rarely haul out on multiple sites during foraging trips (ADF&G unpubl. data; Merrick & Loughlin, 1997).

We defined visits (time on shore) to be  $\geq 1$  h, and trips (time spent away from the haulout) to be  $> 2.5$  h and  $< 200$  h. Short trips ( $\leq 2.5$  h) often consisted of animals rafting or swimming near shore for short



**Fig. 3.** Length of time spent on shore (visits) and away from the haulout (trips) by lactating females and their dependent young (yearlings and pups combined). Data from pups and yearlings were combined because no significant differences were detected between the trends of the two age categories. Each data point indicates the duration of a single trip or visit by time of month. The data were fitted with locally weighted regressions (loess,  $f = 0.33$ ).

periods (pers. obs.). This is consistent with summer studies at other sites in Alaska that used VHF telemetry and noted gaps in the frequency distributions of the signal record that were indicative of non-foraging activity. Higgins (1984) studied Steller sea lions in California and found no foraging trips lasting  $< 8$  h. We examined the distribution of trips we recorded, and assumed those animals with trips  $> 200$  h made an unrecorded visit to the haulout, or had moved to another site for an extended period. We also assumed that those with trips  $\leq 2.5$  h were obscured for a short period and incorrectly noted as 'absent' when they were actually present on land or in the water adjacent to the haulout. Hence, only trips  $> 2.5$  h and  $< 200$  h were included in our analyses. Average trip duration was calculated for each mother and her offspring, such that each animal contributed only a single value (their mean) to the grand mean estimate of trip duration (for all lactating females or all immatures combined).

We calculated the probability of mothers and immatures being present on land during daylight hours as the number of hours they were seen, divided by the total number of hours observed. We used an attendance matrix (a plot showing presence and absence of animals) to determine the overall period of residency given that some animals were present during the entire study, while others abandoned the site after a few weeks, or returned and became regular users of the site at the end of the study. Thus, the denominator (total number of hours observed) was adjusted to reflect the period of time each animal was deemed to be resident at our study site.

## RESULTS

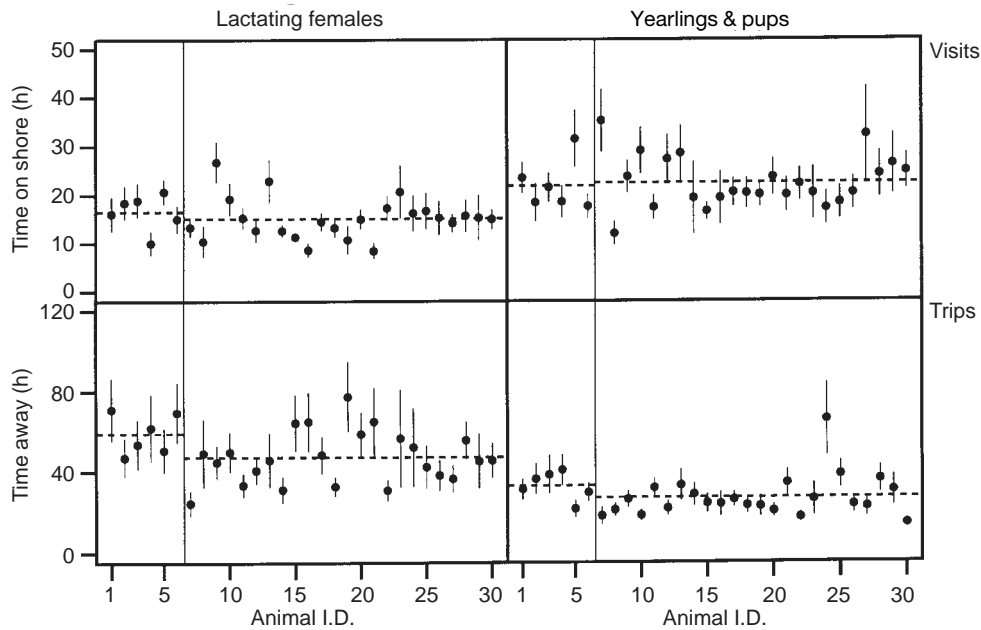
The haulout at Timbered Island was used by an average of  $224 \pm 14.0$  (SE) Steller sea lions per day during the winter months, and consisted of pups and yearlings ( $58.6 \pm 1.0\%$ ), mature females ( $39.5 \pm 1.0\%$ ), and bulls and sub-adult males ( $1.9 \pm 0.2\%$ ). Weather, tide and unknown factors caused numbers to fluctuate from zero to 569 but there was no discernable trend in numbers using the Timbered Island haulout from 22 January to 1 April (c.f. Porter, 1997). Some of the branded pups and yearlings regularly hauled out at Timbered Island during the winter months, while others used this haulout for short periods, or made only a brief visit (Fig. 2). Our estimates of time on shore and time away were calculated for the animals we deemed to be resident, and for the blocks of time that they consistently used the haulout (Fig. 3).

Daily attendance of 38 mature females and their dependent offspring observed from 22 January to 1 April 1996 are shown in the attendance matrix (Fig. 2). Of the 38 immature Steller sea lions, six yearlings and 24 pups were observed frequently enough for statistical analysis (i.e. observed for  $> 10$  days, as shown in Fig. 2).

The distribution of trip durations showed distinct upper and lower cut-off points with very few data points at either extreme (Fig. 3). Average trips by mothers with yearlings (Table 1, Fig. 4) lasted 2.5 days and were significantly longer than the 2.0 days averaged by mothers with pups ( $t_{28} = 2.06$ ,  $P = 0.049$ ). In contrast, the average duration that dependent immatures spent

**Table 1.** Mean attendance cycles (consisting of one trip to sea and one visit onshore) of pups, yearlings and their mothers during winter.

Time (h)	Mothers of						Immatures					
	Pups			Yearlings			Pups			Yearling		
	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>
On shore	15.08	0.87	24	16.56	1.54	6	22.44	1.09	24	21.88	2.13	6
At sea	47.20	2.65	24	58.96	4.08	6	26.82	2.11	24	32.88	2.87	6
Total	62.28			75.52			49.26			54.76		

**Fig. 4.** Mean length of time spent on shore (visits) and away from the haulout (trips) by lactating females and their dependent young (yearlings, 1–6; pups, 7–30). Individual means are shown  $\pm 1$  standard error and the grand mean for each age category is shown by the dashed lines.

away from the haulout was 1.1 days for pups and 1.4 days for yearlings (Table 1). Mothers with male pups (<1 y) were away for an average of 2.0 days ( $=48.0 \pm 4.1$  h SE,  $n=12$ ) compared to 1.9 days ( $=46.4 \pm 3.5$  h,  $n=12$ ) for those with females, but the difference was not statistically significant ( $t_{22}=0.30$ ,  $P=0.77$ ).

The amount of time that mothers spent on foraging trips varied considerably between and within individuals (Figs 3 & 4). Trip durations of pups and yearlings also varied considerably, but were 21.5 h shorter on average than those of lactating females (Table 1, paired  $t_{29}=7.94$ ,  $P<0.001$ ) and showed a slight, but significant decline in mean time spent away from the haulout over the winter months (Fig. 3,  $F_{1,929}=39.01$ ,  $P<0.001$ ). In contrast to the seasonal changes in trip durations, time spent on shore by mothers and young remained relatively constant over the winter months (Fig. 3). However, there was considerably less variability in the durations of visits by mothers compared to those of their young (Fig. 3).

Mothers spent an average of 15.4 h on shore between

trips to sea ( $n=30$ , SE=0.76, range 8.5–26.8 h; Fig. 4). In contrast, their dependent young spent an average of 22.3 h on shore ( $n=30$ , SE=0.95, range 12.0–35.2 h; Fig. 4). Differences in the lengths of time mothers spent onshore with pups versus yearlings, or with male versus female offspring were not statistically significant.

The winter attendance cycle averaged about 3 days for lactating females (i.e. 65.0 h = 49.6 h away + 15.4 h on shore;  $n=30$ ) and just over 2 days for pups and yearlings (i.e. 50.3 h = 28.0 h away + 22.3 h on shore;  $n=30$ ). Lactating females thus spent an average of 24% of their time on shore, compared to 44% for their young. The probability of sighting a lactating female during daylight hours was  $14.9 \pm 1.1\%$  SE ( $n=30$ ). This is about half the value that was expected (i.e. 24%) based on attendance patterns. These two probabilities should have been the same if the mothers behaved similarly at night and during the day. The discrepancy suggests a diurnal pattern in haulout behaviour of lactating females.

Numbers of pups and yearlings arriving and departing ( $n=926$  visits) were evenly distributed between

night (17:00 and 09:00) and day (09:00 and 17:00) (i.e. 50% of arrivals and departures occurred overnight, and 50% occurred during the day). Arrivals of lactating females ( $n = 534$  visits) were also evenly distributed between night and day. However, twice as many mothers left the haulout during the day than during the night (i.e. 34% of departures occurred overnight and 66% occurred between 09:00 and 17:00).

The probability of sighting an immature animal on shore during daylight hours was  $40.7 \pm 2.4\%$  SE ( $n = 30$ ), and was close to the 44% that was expected based on estimated cycle times. The probability of sighting immature sea lions was about three times higher than the probability of sighting mothers on shore. Mothers had a 24% probability of being on shore, and made longer feeding trips than their young. This difference and the observation that mothers were absent from the haulout for significantly longer periods than their offspring suggest that dependent young possibly made independent trips to nearby areas during their mothers' absence, and is consistent with our observation that most pups and yearlings stayed on or near the haulout while their mothers were away.

## DISCUSSION

We estimated that the average attendance cycle (time on shore and time at sea) was about 3 days for lactating females, and just over 2 days for pups and yearlings. Average time on or near shore was about 1 day for pups and yearlings and 16 h for their mothers. However, these are mean times and hide the fact that there was considerable variability (particularly in time spent at sea) between and within individuals (Figs 3 & 4). In the case of lactating females, some of the differences in trip durations may reflect differences in the availability of prey or in the age, physical condition, or ability of the females to locate and capture prey. Some females may also have preferred prey, preferred foraging areas, or fixed foraging strategies.

One of the shortcomings of our estimates of trip and visit durations is that we were unable to observe animals during the long winter nights and might have errors as large as  $\pm 8$  h if animals arrived or departed overnight. An alternative means of estimating the attendance cycle is by satellite telemetry or VHF radio tags glued to the animals' fur. However, telemetry techniques may affect normal foraging behaviour (Walker & Boveng, 1995), and have so far been difficult to apply in large numbers to Steller sea lions.

The few studies that have compared attendance patterns of other pinniped species calculated from radio telemetry and visual observations have yielded estimates that differ by as little as 3.4% and by as much as 77.0% (Boyd, Lunn & Barton, 1991; Goldsworthy, 1992; Higgins & Gass, 1993). However, there has been no consistent pattern among the various estimates of trip durations and shore visits to determine which of the techniques is biased or by how much. Ideally both

techniques should be applied concurrently in future behavioral studies of Steller sea lions to refine our estimates of attendance times. However, the choice of technique does not affect our conclusion that dependent Steller sea lions have shorter attendance cycles than their mothers.

A second shortcoming of our study is that we relied on identifying lactating females by their behavioural association with a branded pup or yearling. Thus, it is possible that the time that lactating females spent on shore could be underestimated and the time away overestimated given that pups may wander away from their mothers after suckling and return to them hours later when hungry again. However, we do not believe this is a significant source of bias given that four of the mothers of branded pups (F308, F490, F611 and F931) were recognizable from natural markings (fungal patches and scars) and had similar attendance patterns to those of the other females (shore visits  $t_{28} = 0.55$ ,  $P = 0.59$ ; trip lengths  $t_{28} = 0.44$ ,  $P = 0.66$ ).

## Differential investment

In theory, the higher energetic demands of larger offspring compared to smaller offspring should be reflected in the amount of time mothers spend at sea, and on shore. A mother (10 years old and pregnant) nursing a pup 7–9 months old must consume approximately 85% more food than one without a pup (95% for males, 74% for females), while a mother nursing a yearling (19–21 months old) requires approximately 115% more food (Winship, Trites & Rosen, in press). Thus, we expected that mothers of male offspring would spend more time at sea than would mothers of female offspring to provide for the greater nutritional needs of the larger males. Similarly, we expected that mothers of yearlings would take longer foraging trips than females with pups to offset the cost of rearing the larger and more demanding immature animals. Further support for this expectation comes from the correlation between the duration of maternal foraging trips by Antarctic fur seals and the amount of milk consumed by pups (Arnould & Boyd, 1995), and by the correlation between the duration of the attendance cycle and the growth of offspring (Goldsworthy, 1995).

In Steller sea lions, we did not find any difference in the amount of time females spent on shore with their offspring, but did find that the average trips of mothers with yearlings (2.5 days) were significantly longer than the 2-day trips averaged by mothers with pups. However, we did not find any significant difference in the average trip times for mothers with male (48.0 h) or female (46.4 h) pups. Studies of other pinniped species, such as Australian sea lions (Higgins, 1990) and Galapagos sea lions (Trillmich, 1986b) have also failed to note statistically significant differences in time associated with raising male and female pups. This may reflect the high variability of the trip times and the relatively small numbers of animals observed. Differ-

ences in foraging times may also not be a good indication of differential investment given that longer foraging times result in longer fasting periods for their young, which may balance out any net gain of a longer foraging trip (Arnould, Boyd & Socha, 1996). Furthermore, it is possible that mothers invest the same amount of resources in a pup regardless of sex, but that male and female pups partition their resources differently between body composition and growth rates (Guinet, Lea & Goldsworthy, 2000).

### Summer vs winter attendance

Lactating Steller sea lions appear to spend about the same amount of time on shore with their young in summer and winter. Estimates of average shore visits range from 19 to 27 h in summer (Merrick & Loughlin, 1997; Milette, 1999) and 15 to 23 h in winter (Table 1; Merrick & Loughlin, 1997). However, time spent at sea was greater in winter than in summer.

Summer foraging trips by lactating Steller sea lions tending neonates on rookeries averaged between 0.8 and 1.9 days (Gentry, 1970; Sandegren, 1970; Merrick, 1987; Higgins *et al.*, 1988; Swain, 1996; Merrick & Loughlin, 1997; Milette, 1999). This is shorter than our finding of 2.1 days in winter. Merrick & Loughlin estimated that the average trip was considerably longer in winter (i.e. 8.5 days), but their estimate was for five adult females of which three were presumably not nursing dependent offspring. Adult females that are not restrained by caring for pups possibly make extended trips as has been shown by Melin (1995) for California sea lions.

Adult female Steller sea lions have been shown to forage over larger areas in winter compared to summer. Merrick & Loughlin (1997) found that, although winter trips were longer, mature females spent approximately the same amount of time per day actively searching for prey during both summer and winter. These observations suggest that food was not any more difficult to obtain, or less abundant during the winter. The observations also suggest that trip duration may indicate distance to the prey source and that foraging effort (diving for prey) may be more indicative of prey abundance. Some prey ordinarily consumed in summer (e.g. capelin, *Mallotus villosus*, and salmon, *Oncorhynchus* spp.) are more commonly found nearer to shore in summer than in winter. Several of these prey spawn near shore or do so anadromously during the summer. Consequently, they are likely to be more accessible near sea lion haulouts at that time.

In summer, Steller sea lions typically depart rookeries in the late evening and return over 24 h later around dawn (Withrow, 1982; Higgins, 1984; Merrick, 1995; Swain, 1996). In winter, our data suggest that 66% of lactating females departed during daylight hours, and that they returned with equal frequency during night and day. Such a difference between summer and winter timing may reflect a seasonal difference in prey sought, or in the relative lengths of daylight during the two

seasons. Steller sea lions are presumed to feed more often at night because the species of fish they prey upon move up the water column at night in search of food (Beamish, 1966; Harden Jones, 1968; Hansen, 1979) and would require less time and energy for sea lions to pursue near the surface than at depth during the day.

Lactating female Steller sea lions appear to spend a greater proportion of their time at sea during winter. Milette (1999) found lactating females spent an average of 41% of their time at sea during summer observations and more time at sea as the pup aged. The lactating females we observed at Timbered Island spent an average of 76% of their time at sea (which is similar to the 70% estimated by Higgins *et al.*, 1988, for late summer). Immature animals spent significantly shorter periods of their daily winter activity budget at sea, averaging between 37.5% (based on satellite telemetry – Merrick & Loughlin, 1997) and 56% (based on behavioural observations – Table 1). These results are similar to those reported by Melin (1995) for California sea lions (March–May: lactating females 75%, dependent pups 33%).

Mature females that are not providing for dependent offspring possibly have different foraging strategies than lactating females. Non-lactating California sea lions (Melin, 1995), northern fur seals (Gentry & Holt, 1986) and Steller sea lions (Merrick & Loughlin, 1997) appear to be more mobile and travel further and longer to forage than those with dependent offspring. Females with dependent offspring in the winter may not only have greater energy demands, but may also be limited in the distance they can travel away from the haulout. Therefore, lactation status of the female must be considered when comparing the foraging strategies of individual females.

### Seasonal foraging trends

We found no apparent seasonal change in the duration of foraging trips by lactating females from January 22 to April 1 (Fig. 3). However, their average trip duration was shorter towards the end of February and beginning of March compared to mid-February or mid-March (Fig. 3). Such changes might reflect a change in prey availability. Foraging theory predicts that the amount of time an animal devotes to capturing prey is related to individual metabolic needs and the availability of prey (Stephens & Krebs, 1986). This functional relationship is well documented for otariids (Costa, Croxall & Duck, 1989; Boyd & Arnobom, 1991; Trillmich & Ono, 1991; Boyd *et al.*, 1994). Thus, females should spend more time at sea if prey are less abundant, or more patchy during the winter to meet their metabolic needs (including those of their dependent offspring).

Studies of a number of different species of fur seals and sea lions have reported decreases (Higgins & Gass, 1993), increases (David & Rand, 1986; Doidge, McCann & Croxall, 1986; Gentry & Holt, 1986) and no apparent change in the duration of foraging trips by

lactating females (Melin, 1995). In the case of Steller sea lions, there is an apparent increase in the duration of foraging trips during early pup development (June–July) (Milette, 1999). Trip durations presumably continue to increase through the fall. However, we failed to find a progressive change in trip durations during winter (January–March). Merrick & Loughlin (1997) also found no apparent change in the duration of foraging trips by adult female Steller sea lions using satellite and VHF telemetry to measure winter foraging trips of mature Steller females with and without dependent offspring.

There are a number of possible explanations for why the foraging trips we recorded of Steller sea lions did not increase as expected over the winter months to meet the rising energetic demands of the growing young. One is that the lactating females adjusted the quality of their milk rather than trip duration. Another is that immature sea lions might have become more efficient at extracting milk from their mothers, as they grew older. However, neither of these possibilities has yet been investigated for Steller sea lions. Offspring may also obtain an increasing proportion of energy on their own if they begin to forage independently, although we did not observe this during our study (22 January to 1 April).

### Weaning

A high mortality of juvenile Steller sea lions may explain the recent population declines in Alaska (NMFS, 1992; York, 1994). Juvenile sea lions are presumed to be susceptible to reduced food availability because young animals, especially newly weaned pups, are inexperienced foragers with limited ranges (Merrick, 1995). Young of the year Steller sea lions, with satellite recorders attached, had home ranges smaller than mature females (Merrick & Loughlin, 1997). Body size may preclude pups from successfully exploiting the deep foraging areas until they are older, or perhaps there is a learning component to foraging that takes time to develop. Young animals may thus be limited in what food is available to them (Merrick & Loughlin, 1997).

The attendance patterns we noted for immature Steller sea lions (pups and yearlings) suggest that dependent pups and yearlings do not accompany their mothers on feeding trips. Instead they appear to stay near the haulout or to make independent trips while their mothers are absent. Unfortunately the resolution of our behavioural observations is insufficient to rule out the possibility that immature Steller sea lions accompanied as many as one-third of their mother's foraging trips. However, attendance patterns of California sea lions measured with VHF tags showed that pups aged 6–8 months did not accompany their mothers to sea, but took short (1 day) trips away from the haulout while their mothers were away (Melin, 1995). In the light of these results, and the increased risk and energetic cost of a pup accompanying its mother, it

seems unlikely that dependent Steller sea lion pups and yearlings accompany their mothers on foraging trips.

Immature Steller sea lions possibly make a gradual transition from mother's milk to independent foraging. However, exactly when they begin to forage independently is not yet known. Our observations suggest that weaning does not occur during winter, but later in the spring (i.e. April–June). The pups and yearlings we observed from January to April did not increase the length of time they spent away from the haulout (Fig. 3), and none were abandoned by their mothers (Fig. 2). This does not mean that young sea lions could not supplement their milk diet with solid food during winter. However, dive profiles and trip durations, which are thought to reflect weaning status, are typically shallower and shorter for dependent immature animals compared to independent immature Steller sea lions (Swain & Calkins, 1997; Calkins *et al.*, 1999).

No studies have yet investigated the onset of solid food ingestion in Steller sea lions. However, California sea lion pups have been reported to ingest solid food at 7–10 months (Oftedal, Iverson & Boness, 1987; Melin, 1995). Steller sea lions may be similar, or they may not begin to ingest solid food until much older. There appears to be a nutritional or developmental necessity for Steller sea lion pups to remain dependent on their mothers to various degrees until near the end of their first or second year of life.

On several occasions we observed immature animals near the Timbered Island haulout with prey items on the surface, although it was unclear whether they had caught the live prey themselves, or if they had scavenged them. Most incidents involved thrashing at the surface and were similar to adult foraging behaviour in which large prey are brought to the surface and torn apart before being swallowed. The prey we could identify included octopus (*Octopus* spp.), lingcod (*Ophiodon elongatus*), and rock fish (*Sebastes* spp.). However, at no time did we observe any of the immatures swallow the prey that they held or played with in their mouths. Thus, it is conceivable that young Steller sea lions learn to dive and capture prey while away from the haulout, but do not consume what they capture. We have observed such behaviour in 9-month-old nursing pups at the Vancouver Aquarium Marine Science Centre, who could capture and kill live prey, but would not swallow them even when their milk intake was restricted.

The net benefit of shifting to an alternative resource (e.g. from milk to fish) must be the difference between the value of the resource and the cost of obtaining it. Thus, the timing of independence should be a function of the individual offspring's stage of development and the availability of alternative resources for replacing parental care. In this case, it is the availability of prey and the young animal's ability to locate and catch it. Maternal foraging activities may be hindered by the offspring if females must spend more time being vigilant, or consume food of lower quality in areas of reduced danger from predators (Sadler, 1969; Carl &



Robbins, 1988). Females are also restricted in their foraging range by the fasting ability of the offspring and the amount of resources they can carry (Broekhuizen & Masskamp, 1980; Gittleman, 1988; Gittleman & Thompson, 1988). It may therefore be more energetically efficient for the pup to remain at or near the haulout rather than accompanying its mother on foraging trips.

### Winter attendance cycle

In summary, the typical winter attendance pattern (January–March) of lactating females averaged about 3 days. Mothers with yearlings spent an average of 17 h on shore followed by 59 h at sea. This was longer than the average attendance pattern of mothers caring for pups, who spent 15 h on shore and 47 h away. The longer attendance cycle of mothers with yearlings may be biologically insignificant. However, it may reflect the maternal need to bring back more resources to older and larger offspring, or alternatively, may be part of the weaning process whereby mothers spend progressively more time away from the offspring as the young approach independence. Foraging trips were longer in winter than in summer. Pups were three times more likely to be seen on winter haulouts during daylight hours than were lactating females, and were absent from the haulout for an average of 27 h compared to mothers that were absent for an average of 47 h. This suggests that pups make independent trips to sea, but have a tendency to stay on or near the haulout to wait for their mothers. Steller sea lions are not known to suckle in the water and presumably fast for an average of 47–59 h until their mothers return to shore. Weaning was not observed during the winter and presumably occurs between April and the start of the pupping season in June as they near their first or second birthdays.

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