STELLER WATCH: TIMING OF WEANING AND SEASONAL PATTERNS IN NUMBERS AND ACTIVITIES OF STELLER SEA LIONS (*EUMETOPIAS JUBATUS*) AT A YEAR-ROUND HAULOUT SITE IN SOUTHEAST ALASKA

by

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Abstract

Variability in length of lactation and maternal association allows otariids flexibility to buffer their young against changes in nutrition. It also increases the chance of their young surviving to sexual maturity, which is particularly important in a declining species such as Steller sea lions (*Eumetopias jubatus*). Timing of weaning is a critically important event in mammalian development that can affect subsequent aspects of an animal’s adult life, and may hold the key to understanding the population dynamics of Steller sea lions. Unfortunately no studies have yet fully documented the behavioural ecology of Steller sea lions outside of the breeding season.

The goal of my study was to document suckling behaviour over 13 consecutive months to determine the timing of weaning for male and female Steller sea lions under three years of age at Southwest Brothers Island, Southeast Alaska (July 2004 – July 2005). I also wanted to ascertain the haulout patterns and activity levels of the colony in relation to season, prey availability, time of day, and weather. Finally, I sought to evaluate the feasibility of using an automated, time-lapse camera system to monitor sea lions and its potential for future use.

Male Steller sea lions were found to suckle longer than females, with a greater proportion of males than females suckling at one year. Time spent suckling declined with age suggesting that the animals became more independent as they grew older, most likely as they increased their ability to forage successfully on their own. Male sea lions that remained with their mother for longer than one year may have had reduced exposure to predation, and obtained more calories with less energy expenditure from milk, compared to females that became nutritionally independent sooner. As a result, this may provide males with a chance to grow as big as possible, as fast as possible, and increase their ability to hold a territory and have access to mates later in life.

The number of sea lions onshore at Southwest Brothers Island was influenced by weather on a daily time-scale, but also displayed seasonal changes that may have been related to prey availability and the timing of breeding. The colony abandoned the island mid-March to mid-April, coinciding with the herring spawn and eulachon runs, which are high-fat species and spatio-temporally predictable prey. High daily variability in numbers of animals at Southwest Brothers likely reflected movement of animals to and from other nearby haulouts. Activity levels varied throughout the year, with proportionally more animals resting in the summer and more animals engaged in low activities in the winter. This suggests a higher behavioural expenditure of energy in the winter, contributing to their need for high quality nutrition.

June and July is an optimum time to assess sea lion numbers due to the high number of animals onshore at that time and a greater predictability in sea lion behaviour. The counts obtained from the automated time-lapse camera system's digital images correlated with counts obtained from direct observation (r^2 = 0.99). The direct counts were on average 22% greater than the digital images. While direct observation is the best method for obtaining a greater variety of data, the camera systems have a good potential to be used to monitor Steller sea lions and other species when researchers cannot be physically present.

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Chapter 1: General introduction: Weaning behaviour and haulout patterns of a colony of Steller sea lions in an increasing population

Weaning behaviour

Many elements of the weaning process, such as the role of the mother or offspring in initiating weaning, are poorly understood despite the critical importance of this event in mammalian development and its affect on subsequent aspects of the animal's adult life (Counsilman & Lim, 1984; Martin, 1984). Female otariids have a flexible period of lactation and can forgo pupping in favour of nursing their current offspring for an additional one or two years. Part of this flexibility arises from the mother's ability to alternate foraging trips at sea with nursing sessions on land throughout the offspring's period of dependence.

The majority of otariid species have been observed nursing juvenile offspring (i.e. > one year) at some point in time (Bonner, 1984), but none have been seen to successfully raise two at the same time. Energetic constraints likely explain why a Steller sea lion mother does not rear two offspring simultaneously (Winship, Trites & Rosen, 2002). Most Steller sea lions are believed to wean sometime before their first birthday (Pitcher & Calkins, 1981). Females that give birth while nursing a juvenile tend to reject the newborn pup in favour of the older sibling (Sandegren, 1970). Anecdotal field reports have noted older Steller sea lions nursing, sometimes up to four years of age (Sandegren, 1970; Porter, 1997), although no attempt has been made to quantify the proportion of the population these animals represent.

The decline of Steller sea lions in the Gulf of Alaska and Aleutian Islands is thought by some to be caused by a high mortality of juveniles at the time of weaning (York, 1994). An alternative hypothesis is that the population decline reflects an extended period of nursing and a corresponding drop in birth rates (Trites *et al.*, 2006). Both hypotheses are contingent on the weaning process, which is poorly understood in Steller sea lions.

Despite the decline in the global population of Steller sea lions (Merrick, Loughlin & Calkins, 1987), the eastern population of Steller sea lions has been increasing since the 1950s when population surveys began. Trends show that the current population is larger than the historical pre-decline abundance level (Trites & Larkin, 1996). For the past 25 years, the eastern population has been increasing by an average rate of 3.1% per annum with no sign of slowing (Pitcher *et al.*, in press). This rate of increase is still well below the theoretical maximum intrinsic rate of increase for pinnipeds, suggesting that other factors may limit the population growth rate (Pitcher *et al.*, in press). It has been proposed that increased juvenile mortality may be a source of the overall species decline which would have a profound effect on population trajectories (York, 1994). However, estimating population trends becomes complicated if high proportions of animals are not weaning before each breeding season as previously thought and instead extend their nursing time.

Factors that may influence extended lactation in pinnipeds, such as food availability, have not been thoroughly investigated. Consideration of circumstances in which extended lactation occurs will aid in gaining an understanding of population dynamics. In particular, determining when Steller sea lions wean in an increasing population may provide insights into the decline of the western population in the Gulf of Alaska and Aleutian Islands.

My study sought to document the timing of weaning and period of nursing by observing Steller sea lions for 13 consecutive months at a haulout in Southeast Alaska (Fig.1.1) where the population has been increasing at a rate of 3.1% per annum (Pitcher *et al.*, in press). Observing a presumed healthy population was believed to offer insight into a critical component of Steller sea lion life history.

I investigated weaning behaviour in relation to offspring age and sex by recording time spent suckling and termination of suckling bouts. I also evaluated Trivers' (1974) theory of parent-offspring conflict by recording all aggressive and passive interactions between mother and offspring during suckling bouts. There has been widespread debate over Trivers' theory (Bateson, 1994; Godfray, 1995) primarily due to conflicting results from previous studies which indicated little to no evidence for increased parent-offspring aggression related to weaning (Martin, 1986; Jensen & Recén, 1989; Packard, Mech & Ream, 1992; Malm & Jensen, 1997).

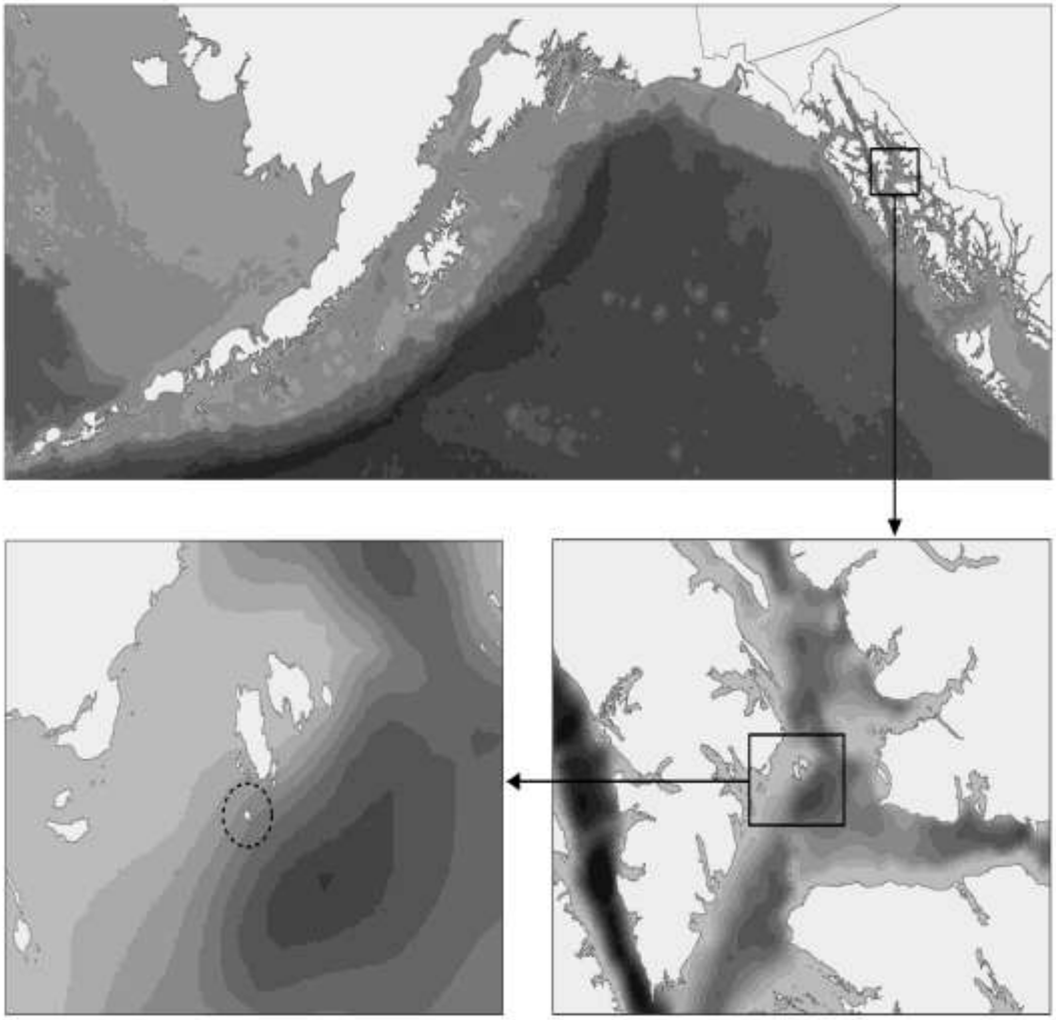

Figure 1.1. Location of Southwest Brothers Island behavioural study site (57°15’N, 133°55’W).

Haulout patterns

In addition to documenting the weaning process, a year-long field study also afforded an opportunity to investigate some general assumptions regarding site fidelity, haulout composition, and seasonal activity patterns throughout the year. The time a pinniped spends hauled out on land or foraging at sea has been associated with a number influences including prey availability, predator avoidance, thermoregulation, social activity, and weather effects (Milinski & Heller, 1978; Trillmich & Mohren, 1981; Schneider & Payne, 1983; Gentry & Kooyman, 1986; Costa, Croxall & Duck, 1989; Watts, 1992; Moulton *et al.*, 2002; Nordstrom, 2002; Kucey, 2005; Soto, Trites & Arias-Schreiber, 2006). Obtaining an understanding of individual behaviour provides better insight into community level behavioural strategies. I therefore examined the haulout patterns and activity levels of Steller sea lions in relation to environmental factors and season.

Automated time-lapse camera systems

Observations of weaning behaviour and haulout patterns are generally done during the breeding season by directly observing animals from blinds using binoculars. An alternative approach is to use camera systems that are often used to monitor wildlife and aid in conducting population surveys. Cameras provide a means to obtain information about a great number of animals over a wide-ranging area and throughout all seasons, but require validation before being widely used. I therefore ran two camera systems that took digital images of the colony once per hour throughout the year to assess the accuracy of a local time-lapse camera system. Simultaneous direct counts were also made of the colony. To assess the accuracy of this system, I later compared the digital counts with direct counts and created a correction factor to account for animals missed in the digital images.

Overview

The goals of my thesis were to 1) determine the timing of weaning and suckling behaviour of male and female immature Steller sea lions between four months and three years old; 2) examine seasonal and daily haulout patterns and activity levels of the animals; and 3) evaluate the effectiveness in obtaining counts using an automated time-lapse camera system compared to direct observation.

My thesis is divided into three main chapters. Chapter 2 examines several aspects of weaning behaviour such as time spent suckling, parent-offspring conflict, and whether mother or offspring terminated the suckling bout. Chapter 3 investigates the haulout behaviour of the sea lions seasonally over the course of one year, paying particular attention to changes in proportion of age/sex classes by season, changes in activity levels, and the influence of weather variables on the number of sea lions hauled out through the year. Chapter 4 evaluates the use of an automated time-lapse camera system with respect to accuracy compared to direct counts and ease of use, and provides recommendations for future use in field studies and population monitoring.

The three primary chapters were written as independent manuscripts intended for publication in the primary literature. As such there is some redundancy as they are all based on the same study methodology, site, and time period.

All field research was conducted under the U.S. Marine Mammal Permit #715-1457 and the University of British Columbia’s Animal Care certificate, Protocol number: A04-0097.

Chapter 2 : Mama’s boys and independent females: Sex-biased weaning behaviour in a sexually dimorphic species, the Steller sea lion

Introduction

Many elements of the weaning process, such as the role of the mother or offspring in initiating weaning, are poorly understood despite the importance of this critical event in mammalian development (Counsilman & Lim, 1984). The timing of weaning, which is the end of parental care and transition to nutritional independence, is believed to affect subsequent aspects of the animal’s adult life (such as survival and reproductive output), and may significantly affect the population dynamics of species that have variable extended periods of nursing (i.e. >1 year). Many studies have examined cumulative maternal investment and the role of the mother in initiating weaning (e.g., Ono, Boness & Oftedal, 1987; Higgins *et al.*, 1988; Trillmich, 1990; Lee, Majluf & Gordon, 1991; Festa-Bianchet & Jorgenson, 1998; Trites & Porter, 2002; Milette & Trites, 2003). Generally, studies of weaning behaviour have focused on domestic animals and small terrestrial populations (e.g. Martin, 1986; Jensen & Recén, 1989; Packard, Mech & Ream, 1992; Malm & Jensen, 1996; Malm & Jensen, 1997). Few studies have investigated the exact time of weaning and behavioural interactions between mother and offspring in pinnipeds due to the difficulties involved with studying extended lactation and identifying individual pairs in wild populations (Higgins & Gass, 1993; Rosen & Renouf, 1993; Trites *et al.*, 2006).

Unlike most phocids (the ‘true seals’), otariids (fur seals and sea lions) have flexible periods of maternal care because they do not have the body reserves to completely nourish their pups and must conduct periodic foraging trips to replenish their fat stores throughout the entire lactation period (Schulz & Bowen, 2004). As such, females may suckle their young until shortly before they give birth again. Nine of the fifteen species of otariids show flexibility in individual maternal investment strategies and have been observed nursing offspring past their first birthday (Bonner, 1984). Three species that do not suckle yearlings are migratory (Northern fur seal *Callorhinus ursinus*, Subantarctic fur seal *Arctocephalus tropicalis*, and Antarctic fur seal *Arctocephalus gazella*). Pups from the previous season are not present on the rookeries of New Zealand fur seals *Arctocephalus forsteri* and there are incomplete data for two species (Guadalupe fur seal *Arctocephalus townsendi* and Juan Fernandez fur seal *Arctocephalus philippii*). Bonner (1984) suggested the flexible lactation time may contribute to the complex social structure of otariids. The greater sociability and generally larger size of otariids may result in terrestrial predators posing less of a threat than they do for some phocids and therefore reduce pressure to wean quickly. Whether the mother or offspring finally determines the end of maternal care is uncertain.

Trivers' (1974) theory of parent-offspring conflict proposed there would be 'disagreement' over the amount of resources transferred to the offspring as termination of parental care approached. If acquiring more resources gives the offspring an advantage in terms of lifetime reproductive success, the offspring is expected to demand more resources than the mother is selected to give. However a mother's own health and future reproductive success may be jeopardized if she continues to provide increasing amounts of nutrition. This conflict led Trivers to suggest that a measure of behavioural conflict between the mother and offspring would indicate the approach to weaning. This conflict over when to wean would likely be exhibited as an increase in aggression of the mother toward the young and an increase in unsuccessful suckling attempts by the young animal. To date, few mammalian studies have investigated the role of the offspring in weaning itself (Malm & Jensen, 1997), and only one study has thoroughly investigated the role of the offspring in weaning itself among otariids (Hasse, 2004).

The sex-biased investment theory further suggests that differences may be observed between male and female offspring during weaning (Trivers & Willard, 1973; Maynard Smith, 1980; Clutton-Brock, Albon & Guinness, 1981). This theory has been extensively debated (Clutton-Brock & Iason, 1986; Leimar, 1996; Hewison & Gaillard, 1999; Brown, 2001) and has become the basis for a number of ecological arguments (Cappozzo, Campagna & Monserrat, 1991; Kretzmann, Costa & Le Boeuf, 1993; Birgersson, Tillbom & Ekvall, 1998). In a sexually dimorphic species, a large body size in males is presumed to confer a reproductive advantage that manifests itself in a higher lifetime reproductive output. Males can sire many young per breeding season while females will always be limited to one at a time. Thus, adult females in good body condition should invest more heavily in male offspring over female offspring, while females in poor condition should invest in a female offspring rather than produce an average male (Trivers & Willard, 1973).

Steller sea lions have long been recognized as one of the most extreme sexually dimorphic otariids that displays considerable variability in the age of weaning. Male pups are known to be larger on average at birth than female pups (Merrick *et al.*, 1995; Brandon *et al.*, 2005), with mature males attaining sizes that are on average 1.3 times longer and approximately 2.4 times heavier than females (Winship, Trites & Calkins, 2001). Field observations of Steller sea lions have noted that some immature animals remain with their mother and continue to suckle for longer than one year (Pitcher & Calkins, 1981; Porter, 1997). If a female continues to nurse her young for an additional year, there are fewer pups in that year's cohort of animals. Despite the implications of extended lactation on population dynamics, only one study has so far attempted to document the timing of weaning in Steller sea lions (Trites *et al.*, 2006).

Trites *et al.* (2006) tested a widely held view that Steller sea lions weaned during winter (Jan – Mar). Piecing together a melange of eight sets of behavioural observations recorded during the late 1990s from four haulout sites (one in Southeast Alaska and three in the Gulf of Alaska) over four years and three seasons (winter, spring, and summer), they concluded that Steller sea lions weaned near their first, second, or third birthdays (June). They also concluded that most immature males during the late 1990s were weaning at age two, with about half of the females weaning at age one, and the rest at age two. Mark-resight models of marked animals in Southeast Alaska (2000 – 2004) suggest that most animals may now be weaning at two years (K. Pitcher, unpublished, ADF&G).

My study was designed to overcome the short-comings of the meta-analysis reported by Trites *et al.* (2006) by continuously observing the weaning behaviour of Steller sea lions at a year-round haulout for 13 consecutive months. I sought to more precisely document the weaning process and quantify the proportion of sea lions weaning at one, two, and three years of age as population growth in Southeast Alaska continues (Pitcher *et al.*, in press). The extreme case of sexual dimorphism among Steller sea lions also afforded an opportunity to determine whether sex-biased behavioural differences exist among young animals during this stage of ontogeny. I aimed to determine the proportion of animals suckling at one, two, and three years of age, and whether there were differences between the sexes in the time spent with their mothers throughout the year. Finally, I investigated whether there was observable behavioural evidence of the mother or offspring initiating the weaning process.

Study site

My study was conducted from 6 July 2004 – 31 July 2005 in Frederick Sound, Southeast Alaska on Southwest Brothers Island (57°15’N, 133°55’W) where a colony of Steller sea lions consisting of both sexes and all age classes hauls out year-round (Fig. 1.1).

Observations were conducted with the aid of spotting scopes and an unobstructed view from a hidden blind 125 m from the haulout. This study site was selected based on historical accounts and annual aerial census data, which indicated that high numbers of animals from both sexes and all age classes were present year-round. The site was also home to a number of animals that had been branded at breeding sites in Southeast Alaska with a letter and three digits when they were approximately one month old by the Alaska Department of Fish and Game (ADF&G, 1996; Merrick, Loughlin & Calkins, 1996), which provided over 280 uniquely identifiable individuals of known sex ranging in age between four months and eleven years during our study.

Methods

Direct observations were conducted from 08:00 to 16:00 h each day and resulted in over 2,800 hours of observations over 13 months. The behaviour of all branded individuals and the identity of their nearest neighbour was recorded every 15 minutes using instantaneous focal scan sampling (Appendix 1) (Altmann, 1974; Martin & Bateson, 1993). Behaviours recorded were resting, low active, playing, swimming, locomotion, aggression, vocalization and suckling (Appendix 2). Behaviours that did not fit into one of these categories were scored as ‘other’. Behaviours that could not be clearly observed were noted as obscured. Suckling was defined as head positioned by teat or actively searching for a nipple.

The nearest neighbour to the focal animal was defined as the closest animal within one adult female body length (~2m). The nearest neighbours allowed me to compare time the young animal spent with its mother compared to all other animals and whether it changed over the year. Nearest neighbours were identified by age class as pups, juveniles, adult females, sub-adult males (SAMs), bulls, or mothers. If the focal animal was more than one adult female body length from all other animals, it was recorded as alone. If several animals were equidistant to the focal, then the nearest neighbour was marked as ‘other’. The mother of the focal animal could only be designated as such if suckling behaviour was observed. This strict definition was used to eliminate the possibility of misidentifying an animal as being with its mother if it was simply near another adult female. Except in rare instances, adult females provide milk only to their biological young and not to other pups or juveniles (Porter & Trites, 2004; Maniscalco *et al.*, in press).

One advantage of using branded individuals as focal animals was that I could be confident of the animal’s identity throughout the entire year and amongst several observers. Additionally, observers were ‘blind’ to the sex of the animal during observations so no unintentional bias could be introduced. I began classifying the 2004 pups as juveniles (age one – three years) on June 4, the median birthing date of the pups from the Forrester Island complex where the majority of the focal animals were branded (Pitcher *et al.*, 2001).

Beginning in February, I recorded whether the offspring or the mother ended the suckling bout. Suckling bouts were defined to end when either the mother or offspring physically left the immediate area (~2m) because that signified the end of the opportunity to suckle while they were associated. Additionally, I recorded whether each interaction between mother and offspring was ‘passive’ or ‘aggressive’. Direct interactions such as biting or loud vocalizations were considered aggressive, as were indirect interactions such as the mother lying on her stomach or rolling over to prevent access to teats. Passive suckling interactions included all other behaviours such as resting and low active behaviours.

All occurrences of abortions were recorded, in addition to all other disturbances (Appendix 3). Events were classified as aircraft, vessel, bird, whale, unknown, and other. Reaction of the animals to events was classified into three categories: detection, alarmed and disturbed. ‘Detection’ was scored if one or more animals raised their head and oriented it toward the potential disturbance. ‘Alarmed’ was scored if one or more animals moved from their resting area but did not enter the water. ‘Disturbed’ was scored if more than one animal entered the water.

Data analysis

Abundant movements of sea lions to and from my study site limited the consistency of individuals observed. No individual animal was present throughout the entire year. Sample size was also sometimes low due to unexpected seasonal movements that limited the number of animals present during parts of the year. There also tended to be more branded juvenile males present than females. I therefore compared proportions instead of numbers for all statistical analyses.

Only animals that were observed at least 10 times per month were included in the statistical analyses to ensure that animals were not misclassified as non-suckling animals due to insufficient observations (Trites *et al.*, 2006). Seven animals were identified as suckling following months when they were scored as non-sucklers. It is unlikely these animals had weaned and then subsequently ‘unweaned’. Such animals were therefore re-scored as sucklers for the previous months.

I calculated the proportion of suckling to non-suckling animals in each age category by month. Percentages were arcsine-transformed and compared using analysis of variance with Tukey tests to determine when and where differences in suckling behaviour were significant (Zar, 1996). I compared immature males and females by month using a paired t-test. An analysis of variance was performed separately on males and females with age in years as the independent variable and the proportion of branded animals that were observed suckling as the dependent variable. I also compared how suckling behaviour and timing of weaning varied by age class and season.

The proportion of time that the immature animals engaged in suckling behaviour was determined as a function of 1) time spent on shore, and 2) time spent onshore with their mother (Trites *et al.*, 2006). This second method allowed actual time in suckling behaviour with mother to be compared with available opportunity. Only those animals seen suckling at least once were included in the analysis to exclude weaned immature animals and animals that only made a brief appearance at the haulout. Each observed animal contributed a single mean time spent in suckling behaviour for the entire year for his or her corresponding age class. Percentages were arcsine-transformed and analyzed by age class and season using a 2-way ANOVA, and Tukey-Kramer tests were used to determine when and where time in suckling behaviour differed (Zar, 1996). Interactions between mother and offspring during nursing and at the end of a suckling bout were compared using a Chi-squared test with a Yates continuity correction. All statistical tests were performed using S-PLUS (2000).

Results

Proportion of animals engaged in suckling behaviour & the influence of season

Significant differences were noted among age classes in the proportions of males ($F_{2,24} = 39.24$, $p < 0.0001$) and females ($F_{2,26} = 5.29$, $p = 0.01$) engaged in suckling behavior (Fig. 2.1. Among females, proportions of suckling pups and yearlings did not differ significantly, nor was there a difference between the proportions of yearlings and two-year olds observed suckling (Tukey test). However, female pups and two-year olds did differ significantly. In contrast, males showed significant difference between the proportion of pups, yearlings, and two-year olds engaged in suckling behaviour (Tukey test).

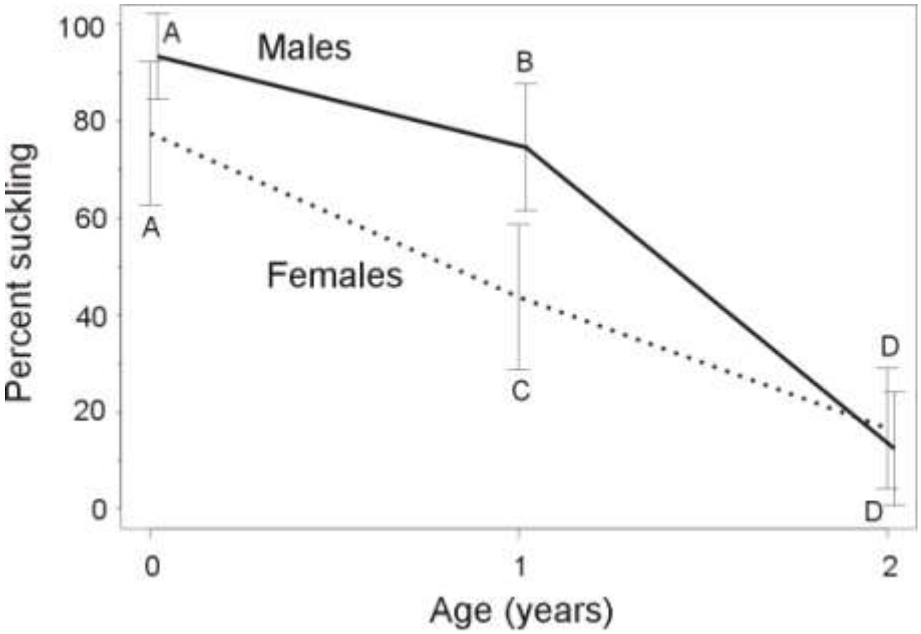

Figure 2.1. Percent of branded animals observed suckling at Southwest Brothers Island by age and sex in 2004/2005. Capital letters indicate statistical significance for each age class. No statistical significance was found for male and female pups and two-year olds. Male and female one-year olds are statistically different. Bars represent standard error.

No significant difference was noted between males and females when the sexes were compared by age class for pups or two-year olds but a significant difference was found between males and females at one year (Fig. 2.1, paired t-tests, p = 0.04). Less than 100% of pups were observed suckling, possibly due to observer error or because some pups visited our study site without their mothers. Additionally, some pups were observed only during the spring and may have been weaned already. The implication of this is that similar error must be assumed in the proportions of yearling and two-year old age classes observed suckling, such that the estimated proportion of animals suckling are likely underestimated.

The proportion of branded animals engaged in suckling behaviour declined during late spring and early summer around their birthday (Fig. 2.2 B,C). Fewer pups and yearlings were observed suckling in the spring. Examining composition by month showed that males were more consistently observed than females (Fig. 2.2 A, Table 2.1).

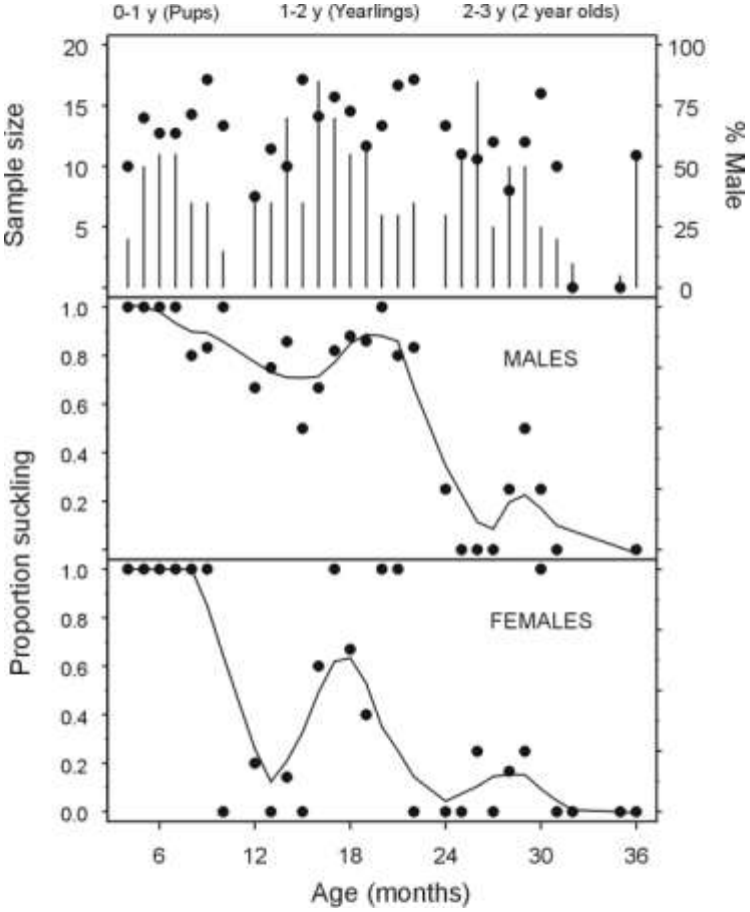

Figure 2.2. Sample size and proportion of animals suckling by sex at Southwest Brothers Island each month. (A) Sample size (vertical bars) and the proportion of young males observed (circles). (B, C) Proportion of all branded animals observed suckling that were male and female. Increases in proportions of suckling yearlings and two-year olds following the breeding season is presumed to reflect the return of mothers to the haulout with their dependent offspring. A loess curve illustrates suckling trends (Loess $f = 0.25$).

Table 2.1. Proportion of branded animals observed suckling each month by sex, sample size, and percent of sample size that were male.

Age	Month of	Females			Males			Total	%
(months)	observation	Mean	SE	*n*	Mean	SE	*n*	N	males
4	Sep	1.00	0.00	2	1.00	0.00	2	4	50
5	Oct	1.00	0.00	3	1.00	0.00	7	10	70
6	Nov	1.00	0.00	4	1.00	0.00	7	11	64
7	Dec	1.00	0.00	4	1.00	0.00	7	11	64
8	Jan	1.00	0.00	2	0.80	0.08	5	7	71
9	Feb	1.00	0.00	1	1.00	0.00	6	7	86
10	Mar	0.00	0.00	1	1.00	0.00	2	3	67
11	Apr	-	-	0	-	-	0	0	-
12	May	0.20	0.08	5	0.67	0.16	3	8	38
13	Jun	0.00	0.00	3	0.75	0.11	4	7	57
14	Jul	0.14	0.05	7	0.86	0.05	7	14	50
15	Aug	0.00	0.00	1	0.50	0.08	6	7	86
16	Sep	0.60	0.10	5	0.67	0.04	12	17	71
17	Oct	1.00	0.00	3	0.82	0.04	11	14	79
18	Nov	0.67	0.16	3	0.88	0.04	8	11	73
19	Dec	0.40	0.10	5	0.86	0.05	7	12	58
20	Jan	1.00	0.00	2	1.00	0.00	4	6	67
21	Feb	1.00	0.00	1	0.80	0.08	5	6	83
22	Mar	0.00	0.00	1	0.83	0.06	6	7	86
23	Apr	-	-	0	-	-	0	0	-
24	May	0.00	0.00	2	0.25	0.11	4	6	67
25	Jun	0.00	0.00	5	0.00	0.00	6	11	55
26	Jul	0.25	0.05	8	0.00	0.00	9	17	53
27	Aug	0.00	0.00	2	0.00	0.00	3	5	60
28	Sep	0.17	0.06	6	0.25	0.11	4	10	40
29	Oct	0.25	0.11	4	0.50	0.08	6	10	60
30	Nov	1.00	0.00	1	0.25	0.11	4	5	80
31	Dec	0.00	0.00	2	0.00	0.00	2	4	50
32	Jan	0.00	0.00	2	-	-	0	2	0
33	Feb	-	-	0	-	-	0	0	-
34	Mar	-	-	0	-	-	0	0	-
35	Apr	0.00	0.00	1	-	-	0	1	0
36	May	0.00	0.00	5	0.00	0.00	6	11	55

Table 2.2. Proportion of branded Steller sea lion pups, yearlings, and two-year olds that were observed suckling each season.

Season	Pups			Yearlings			Two-year olds		
	%	SE	*n*	%	SE	*n*	%	SE	*n*
Summer	-			46.43	9.42	28	6.06	4.15	33
Autumn	100.00	0.00	25	76.19	6.57	42	32.00	9.33	25
Winter	96.00	3.92	25	79.17	8.29	24	0.00	0.00	6
Spring	45.45	15.01	11	46.15	13.83	13	0.00	0.00	12

Calculating proportions of suckling animals by age class and season (summer – June, July, August; autumn – September, October, November; winter – December, January, February; and spring – March, April, May), a 2-way ANOVA showed a significant effect of age class ($F_{2,18} = 67.21$, $p < 0.001$) and season ($F_{3,18} = 21.77$, $p < 0.001$) but no interaction between the two ($F_{5,18} = 2.73$, $p > 0.05$) (Table 2.2). Differences were noted among the proportions of pups, yearlings and two-year olds observed suckling (Tukey test). A Tukey test further indicated a difference between all seasons except during autumn and winter, and between spring and summer.

No two-year olds were observed suckling after the autumn, and only about half the pups observed in the spring continued to suckle. Data were not available for pups during summer when they were born on rookeries. Pups were first observed at my study site at the end of August when they were brought by their mothers.

Time spent suckling & the influence of season

Mean time engaged in suckling behaviour as a function of time spent with their mother decreased with age (pups – 56%, yearlings – 51%, and two-year olds – 39%), but the decline was not statistically significant (Table 2.3).

Table 2.3. Proportion of time branded Steller sea lions were observed suckling as a function of time present with their mother and of total time hauled out over the year and by season. None of the apparent differences by age class over the year or by season were statistically significant except yearlings with mother in spring and summer.

		Pups			Yearlings			Two-year olds		
		% time	SE	*n*	% time	SE	*n*	% time	SE	*n*
With Mother	year	55.88	1.54	14	50.92	1.42	15	39.29	3.49	4
	summer	-			45.54	3.33	7	43.48	7.31	2
	autumn	57.40	2.34	12	48.75	1.98	11	38.00	3.96	4
	winter	53.25	3.29	8	55.02	2.74	8	-		
	spring	62.00	4.85	3	74.07	5.96	3	-		
Total Time	year	15.94	0.57	16	15.39	0.55	18	12.61	1.29	7
	summer	-			22.78	1.95	9	13.79	2.86	2
	autumn	13.81	0.80	15	14.54	0.74	14	12.28	1.44	6
	winter	16.97	0.85	11	12.85	0.89	9	-		
	spring	22.30	2.42	4	27.17	3.28	5	-		

Analyzing time spent suckling as a function of time the young animals were present with their mother using a 2-way ANOVA showed no significant effect of age or an interaction between age and season (Table 2.3, $p > 0.05$). However, there was an effect of season ($F_{3,50} = 3.38$, $p = 0.03$). A Tukey test showed the effect due to the difference between spring and summer. Analyzing time spent suckling as a function of total time spent hauled out using a 2-way ANOVA revealed no significant difference between the age classes and seasons — nor was any interaction noted between age and season (Table 2.3, $p > 0.05$).

Analyzing time spent with mother as a function of time spent hauled out revealed no significant difference over the year for each age class ($p > 0.05$), indicating time spent with mother did not decline significantly over the year.

Parent-offspring conflict

A significant percentage (98.9%) of the 280 interactions recorded between mothers and offspring were passive, with the mothers allowing the offspring to suckle with no hindrance ($\chi_1^2 = 267.9$, $p < 0.001$) while the remaining few interactions were recorded as aggressive. The aggressive encounters recorded did not prevent the offspring from suckling, and the offspring was observed suckling directly after the aggressive encounter.

Offspring terminated the suckling bout by physically leaving the mother in the majority of situations observed (91.3%, χ_1^2 = 15.5, $p < 0.001$) — even though the teat was still available. Terminations of suckling bouts were recorded 23 times and were generally difficult to witness due to the high number of animals hauled out and the frequent disturbances by eagles looking for aborted fetuses. Females left the area before their offspring on only 2 of the 23 documented terminations. No aggressive interactions occurred — rather the females simply got up and entered the water.

Reproductive failure — abortions

Eight abortions were witnessed on land over the months of January, February, and March when the fetus would have been about three to five months developed. Abortions that occurred overnight were usually detected in the morning by the presence of blood and tissue. However, we have no information on the proportion of abortions that may have occurred in the water. Steller sea lions regularly travel to more than one haulout, which makes it difficult to estimate reproductive failure at a population-level or even at a community-level.

Eagle disturbances increased during the months of December – March, ranging from 17 – 30 per month (Fig. 2.3) and constituted 84% of all bird disturbances and 78% of all disturbances combined (vessels, killer whales, unknown, and aircraft). Eagle disturbances from December – March were associated with eagles flying low and landing on the haulout searching for aborted fetuses and associated placentas. Eagle disturbances in May – July were associated with eagles flying to and from their nest and loud territory disputes.

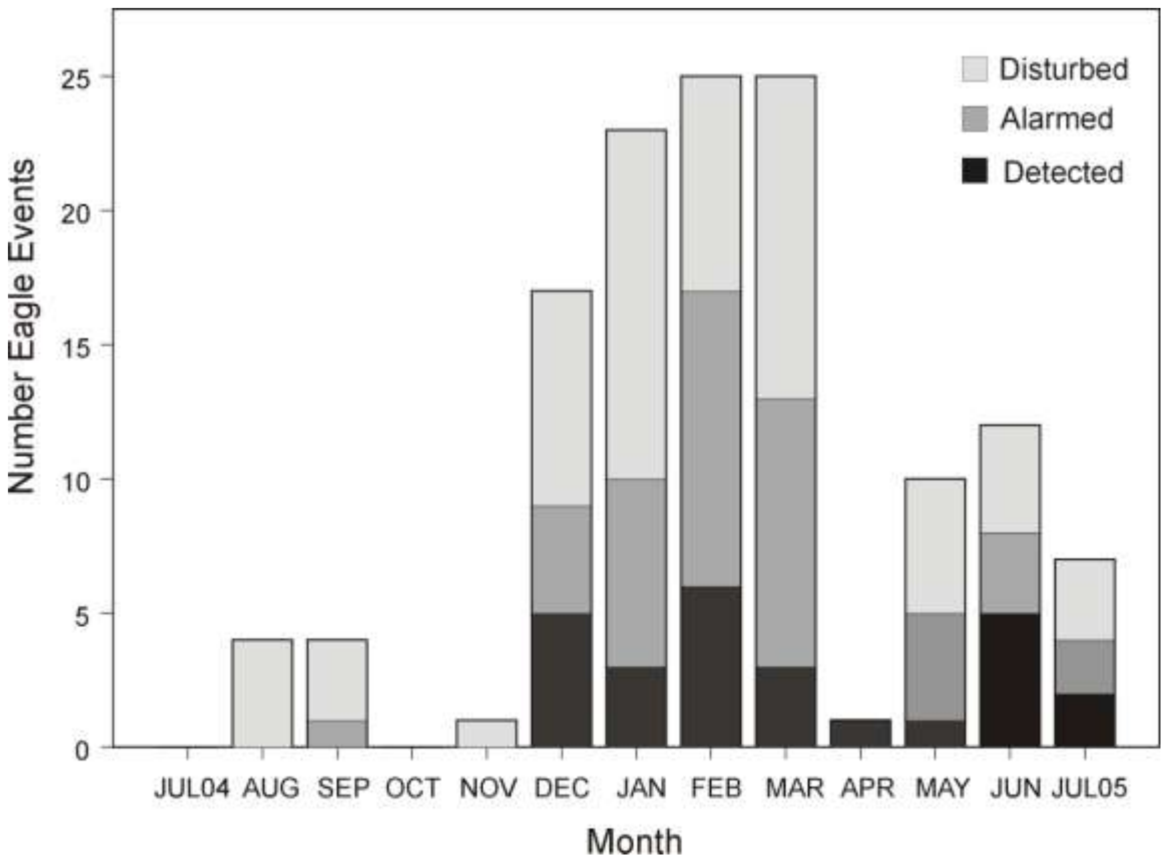

Figure 2.3. Number of eagle events per month from July 04 — July 05 that caused Steller sea lions to react. Reaction of animals was classified as 'Detected', 'Alarmed', or 'Disturbed'. Note that few sea lions were present on the haulout in April.

Discussion

Conducting direct behavioural observations of Steller sea lions at one site for 13 continuous months showed many animals were dependent on their mother until their third year of life, with a high proportion of suckling yearlings and a propensity for males to stay longer than females with their mothers. No significant conflicts were observed between mothers and offspring, and no significant reductions in suckling times was recorded, suggesting that time of year, rather than age, was a stronger determinant for weaning of pups and yearlings.

Biases

My results must be interpreted in light of the limitations associated with the methods used to measure the weaning process, as well as the variables that I was not able to measure such as suckling ability of the offspring, motivation for suckling, experience and physiology of the mother, her ability to release milk, non-nutritive suckling, and variation in milk composition (see Cameron, 1998, for a full review). Suckling observed during the daytime might also not be an accurate reflection of what occurs at night. However, such limitations should not impinge upon my general conclusions given that my study used behavioural association with the mother as an indicator of dependence, and my questions were not related to motivation or actual energy transfer.

Male versus female

The proportion of young males I observed suckling was more variable than that of the females (compare Figs. 2.2B and 2.2C). This might reflect males being more active than the females, which would have resulted in them being recorded at the haulout for a shorter duration or a greater likelihood of being missed all together. The peaks in proportions of individuals suckling in Fig. 2.2B and especially 2.2C likely reflect the return of mothers from rookeries with their dependent one- and two-year olds at the end of summer.

Proportionally more males than females were observed suckling as they approached their first birthdays (Fig. 2.2), suggesting that females tended to wean earlier than males. Males may have stayed longer because their energy needs were higher than females, and they could not obtain sufficient energy from foraging on their own (Trites *et al.*, 2006). The apparent longer-term association between mothers and sons may have provided males with more time to learn to forage, more calories with less energy expenditure for increased growth, and may have reduced their exposure to predation. Testosterone may further allow males to assimilate the energy in milk more efficiently than females (Glucksman, 1981; Kretzmann, Costa & Le Boeuf, 1993), which would mean that even a small amount of milk would provide a greater benefit to males.

Differences in the way that males and females allocate energy towards growth have been reported for Australian fur seals (*Arctocephalus pusillus doriferus*) and Antarctic fur seals (*Arctocephalus gazella*) (Arnould, Boyd & Socha, 1996; Guinet, Lea & Goldsworthy, 2000; Arnould & Hindell, 2002). It appears that males preferentially allocate energy toward building lean body mass, while females allocate more energy towards the buildup of lipid stores. On average, males of both species have higher weights than females even though males and females consume similar amounts of milk (Arnould, Boyd & Socha, 1996; Arnould & Hindell, 2002). This suggests there is little, if any, apparent difference in maternal investment with regards to nutrition — although some have cited the observations of males being heavier than females as evidence of sex-biased maternal investment (Trillmich, 1986; Cappozzo, Campagna & Monserrat, 1991).

The sex-specific difference in how young fur seals allocate energy suggests that females will have proportionally more lipid stores than males at the time of nutritional independence. This in turn might result in a differential tolerance to environmental variation. A young female that has difficulty finding or obtaining food will catabolize her greater lipid stores, which provide twice the energy of protein catabolism (Randall, Burggren & French, 1997) and therefore could increase her chances of survival. Males may pay higher thermoregulatory costs during activities such as swimming because they have proportionally less lipid for energy storage. The differences in growth strategies between males and females may further mean that it is more beneficial for males to stay with their mother for as long as possible to supplement their diet, enhance their growth, and buffer against environmental variation. The fact that Steller sea lions are the most dimorphic otariid species (with male pups being larger on average than females at birth [Winship, Trites & Calkins, 2001; Brandon *et al.*, 2005]) may also mean that this male strategy has been selected to obtain the added resources they require to grow to such a large size.

Parent-offspring conflict

Bioenergetic models estimate that a nursing female Steller sea lion would require 70% more food than a non-nursing female if her young were completely dependent on her for nutrition (Winship, Trites & Rosen, 2002). The lack of observed aggression between mother and offspring suggests the young obtained adequate nutrition either from the milk alone, or by supplementing their milk intake with solid food. The absence of conflict between the two in my study suggests that the mother and young obtained the nutrition that each required such that there was no 'disagreement' over allocation of limited resources as predicted by Trivers (1974).

A variety of animals have demonstrated little to no evidence of maternal aggression or indirect behavioural conflict between mothers and dependent young around the time of weaning (e.g. cats: Martin, 1986; pigs: Jensen & Recén, 1989; arctic wolves: Packard, Mech & Ream, 1992; dogs: Malm & Jensen, 1997). Offspring of such species have generally been observed to terminate suckling bouts as opposed to their mother ending them, indicating that opportunity to suckle was not a limiting factor. In the case of young sea lions, those that had stomachs full of milk and/or solid food would have had less motivation to stay for more suckling opportunities. Observations of New Zealand fur seals have shown that pups terminate the suckling bouts the majority of the time (Hasse, 2004). Similarly, anecdotal observations from Porter's (1997) winter study on Steller sea lions revealed offspring leaving the mother more often during nursing bouts. I also found no evidence for increases in parent-offspring conflict in the Steller sea lion to occur as the time to the next breeding season approached. Nor did I note any decrease in access to mother's teats and suckling opportunities as the amount of time spent with their mother did not decrease over the year. It therefore seems that Steller sea lion offspring wean themselves.

Further evidence that Steller sea lions wean themselves comes from the observed difference in timing of weaning of males and females. Mothers are unlikely to be aware of the sex of their offspring and preferentially decide to wean females early and keep males for an extra year. It seems more probable that males elect to stay with their mothers because they can more readily meet their daily energy needs from milk rather than from fish and cephalopds.

When to wean?

Part of deciding when to begin taking solid food, how much to take, and when to cease suckling completely is related to the relative cost-benefit ratio associated with suckling versus obtaining and digesting solid food (Jensen & Recén, 1989; Malm & Jensen, 1996). Animals may begin to forage on their own to fulfill their growing caloric needs if milk does not provide the required nutrition and calories. Compensating with solid food has been predicted to occur in pinnipeds, primates, and ungulates when the offspring reach 2.1 times their birth mass with weaning predicted to occur when they reach 4.0 times their birth mass (Lee, Majluf & Gordon, 1991). Applying standardized growth curves (Winship, Trites & Calkins, 2001) suggests that male Steller sea lions should start to wean when they are 46 kg (2.8 months old) and be fully weaned when they are 88 kg (7.7 months old) — and that females should start to wean when they are 42 kg (3.8 months old) and be fully weaned when they are 80 kg (10.4 months old). Contrary to the theoretical predictions, males weaning on their birthdays are on average 5.7 times their birth weight at one year, 7.0 times at two years and 8.6 times at three years, while females that wean on their birthdays are an average of 4.5 times their birth weight at one year, 6.4 times at two years, and 7.8 times at three years. Thus there is considerable disparity between the theoretical limits and the field observations.

At one year of age, male yearlings require 15.0 ± 3.8 kg of prey on a mixed diet of fish species, while females require 11.0 ± 2.7 kg (Winship, Trites & Rosen, 2002). Expressed as a percentage of body weight, male yearlings require about 12 ± 3% of their body weight per day, while females require 13 ± 3%. At two years, energy requirements relative to body mass per day on a diet of mixed species drop to 11 ± 2% for males and females but increase in kilograms to 16.9 ± 3.1 kg and 14.1 ± 2.6 kg respectively. A further decrease occurs at age three: 9 ± 2% for males and 10 ± 2% for females (increase of 17.0 ± 3.8 kg and 15.6 ± 3.1 kg respectively). Rosen and Trites (2004) estimate that the maximum average amount of food a yearling sea lion can consume is equivalent to 14–16% of their body mass and that young animals may not be able to meet their daily energy needs if they were to consume primarily low energy prey species. They hypothesize that even consuming moderately energy dense prey, juveniles are living energetically on the edge. By prolonging weaning and providing her offspring with milk during this time, the adult female may buffer her young against nutritional hardship. The greater relative energy needs of males may move them closer to the energetic edge and may explain why more males than females elect to stay with their mothers for an extra year.

Lactation is regarded as the most expensive aspect of maternal care (Gittleman & Thompson, 1988) and is a period that mothers may wish to limit despite the clear benefits for young animals to obtain more milk. However, Pond (1977) pointed out that extended lactation might be preferred over extended gestation for species whose food sources are scattered and of low nutritional content. A longer lactation period should also be preferred if the mother must travel long distances to obtain prey, and if the species must rely heavily on speed and agility to capture prey and elude predators (Pond, 1977).

Extending lactation beyond the next breeding season is not a rare event among the otariids and can impact their future reproductive success. For example, 29% of mature Australian sea lions (*Neophoca cinerea*) were observed in one study to not pup each breeding season, and opted to nurse their juvenile until the next breeding season (Higgins & Gass, 1993). The Galápagos fur seal (*Arctocephalus galapagoensis*) observed in another study with a dependent yearling or two-year old was less likely to give birth than those females without dependent young (Trillmich, 1986). In contrast, Maniscalco *et al.* (2005) found Steller sea lions that did not pup or had lost their pup were less likely to give birth the following season.

Extended lactation also occurs among terrestrial species. For example, observations of red deer suggest that mothers that did not conceive would continue to nurse their young calf the following breeding period, whereas she would likely wean the calf before she gave birth if she did conceive (Clutton-Brock, Guiness & Albon, 1982).

Time spent in suckling behaviour did not change significantly over the year, suggesting that time of year was a stronger driving factor in determining the final stage of weaning in Steller sea lions than was age of the animal. This is consistent with the observations of Raum-Suryan *et al.* (2004). I observed a sharp decline in the proportion of animals suckling when 12 and 24 months old (Fig. 2.2B,C) suggesting that animals suckled the entire year until their next birthday. Two-year olds (>24 months) were an exception and were not observed suckling beyond autumn when 28 months old. This suggests the two-year olds may have been completely independent by this time.

Mothers that will produce another pup while still nursing an offspring from a previous year might abandon the yearling just before they return to the rookery to give birth. Immature animals that accompany their mothers to rookeries may be forced to wean or the yearling may out-compete their new sibling. The limited information available on the behaviour of juveniles at the rookeries indicates that many of the females were accompanied by nursing juveniles and that females that lost their pup were re-joined by their juvenile — and that pups were occasionally rejected in favour of the juvenile (Sandegren, 1970).

Population dynamics

An accurate estimate of the proportion of the breeding population producing pups is key to assessing population trajectories. My study has shown that sea lions at the Southwest Brothers haulout were suckling up to age three but that most were weaned by age two. If this site is representative of the larger population in Southeast Alaska, many females are not having new pups each year (possibly due to reproductive failure as shown by the observed abortions) and may be nursing their current young longer (possibly to buffer them against environmental fluctuations).

The eastern population of Steller sea lions has been increasing since the 1950s when surveys began and trends show that the current population is the highest recorded (Trites & Larkin, 1996). For the past 25 years, the eastern population has increased at an average rate of 3.1% per annum as new rookeries have been established with some influx of animals from the Gulf of Alaska (Pitcher *et al.*, in press). This rate of increase is still well below the theoretical maximum intrinsic rate of increase for pinnipeds, suggesting that other factors may limit population growth (Pitcher *et al.*, in press). Increased juvenile mortality has been suggested as a source of the overall species decline, which would have a profound effect on population trajectories (York, 1994; Trites & Donnelly, 2003). However, the low numbers of juveniles in the population could also be explained if these animals were simply not being born due to their mothers continuing to nurse their juvenile and a high rate of reproductive failure (Trites *et al.*, 2006). Additionally, about 45% of the population do not travel to rookeries (Trites & Larkin, 1996) and not all females that remain at the haulouts have dependent young.

Identifying the factors that extend lactation and weaning help to decipher the dynamics of Steller sea lion populations. Results from my study also provide baseline data for comparison with future trends and with other populations. My data indicate that many females are nursing juveniles and are not raising a new pup each year. This factor needs to be considered when estimating future population trends.

Future studies should investigate the causes of reproductive failure and why the sex differences in weaning behaviour exist. In addition, weaning of juveniles at the rookery should be investigated, and the proportion of females that do not invest in raising offspring each year should be determined. Finally, a concerted effort should be made to determine these parameters in both increasing and decreasing populations to fully assess the role that delayed age at weaning has played in the decline and lack of recovery of sea lions in the Gulf of Alaska and Aleutian Islands.

Summary

Behavioural observations related to weaning of Steller sea lions (*Eumetopias jubatus*) were recorded for 13 consecutive months (July 2004 – July 2005) at Southwest Brothers Island in Southeast Alaska to 1) document the age at weaning, 2) establish whether parent-offspring conflict influenced the timing of weaning, and 3) determine whether there was sex-biased investment by mothers. Recorded observations included proportions of known-aged animals suckling, antagonistic behaviours between mothers and their young, and frequency of observed abortions. My observations were the first to be made over an entire year and revealed a high number of late-term abortions associated with a high proportion of young continuing to suckle beyond their first birthday. The proportion of males (75%) compared to females (44%) observed suckling at one year old suggests that most females were weaned just before their first birthday, while males were not weaned until just before their second birthday. The insignificant level of conflict between mother and offspring and the observation that offspring tended to end all suckling bouts, suggests considerable responsibility for self-weaning. All noted abortions occurred during the winter months when the fetus was approximately three to five months developed. Providing milk for an additional year presumably enhances the chance of the juveniles surviving to sexual maturity. Having fewer, but healthier pups, may increase the lifetime reproductive fitness of the adult female. Approximately half of female Steller sea lions in Southeast Alaska may thus be giving birth biennially rather than annually as previously thought. Such a reduction in birth rates could significantly curtail population growth and have a profound effect on estimated population trajectories.

Chapter 3 : Year-long observations of haulout patterns and activity levels of Steller sea lions at a year-round haulout site in Southeast Alaska

Introduction

The time that pinnipeds alternate between foraging at sea and resting and socializing onshore can be related to a variety of factors including prey availability, predator avoidance, thermoregulation, and social activity (Milinski & Heller, 1978; Trillmich & Mohren, 1981; Gentry & Kooyman, 1986; Costa, Croxall & Duck, 1989; Watts, 1992; Moulton *et al.*, 2002; Nordstrom, 2002; Soto, Trites & Arias-Schreiber, 2006). Environmental covariates such as wind chill, intensity of solar radiation, cloud cover, precipitation, and tide have also been associated with numbers of pinnipeds onshore (Schneider & Payne, 1983; Watts, 1992; Rogers & Bryden, 1997; Reder *et al.*, 2003; Kucey, 2005). Understanding the variables that influence haulout patterns is useful for gaining insight into how animals respond to environmental conditions in relation to life-history challenges (Trites & Antonelis, 1994; Sepúlveda, Oliva & Palma, 2001), energetic requirements (Trillmich & Kooyman, 2001), and the effects of disturbance on Steller sea lion numbers and behaviours (Allen *et al.*, 1984; Kucey, 2005). Understanding how animals respond to climate is also needed to conduct census counts at appropriate times using suitable correction factors that account for the animals not present (Porter, 1997; Frost, Lowry & Ver Hoef, 1999; Small, Pendleton & Pitcher, 2003).

Careful monitoring is crucial to the future and management of Steller sea lions (*Eumetopias jubatus*) which have declined globally by over 85% since the late 1970s (Merrick, Loughlin & Calkins, 1987; Trites & Larkin, 1996; Calkins *et al.*, 1999). Population surveys provide insight into broad-scale sea lion population trends. However, fine-scale monitoring provides a further understanding into community level behavioural strategies, which may influence population dynamics.

Steller sea lions use two types of terrestrial sites: haulouts and rookeries. Haulouts are primarily non-breeding, year-round sites, whereas rookeries are used only during the summer breeding season to give birth, nurse young, and mate. Most behavioural studies have been conducted at rookeries (Sandegren, 1970; Gentry, 1974; Merrick & Loughlin, 1997; Milette & Trites, 2003) in contrast to year-round haulouts that have seldom been studied (Porter, 1997; Kucey, 2005) and have never been directly observed for an entire year. Behaviour of animals at haulouts may provide essential insight and clues into the Steller sea lion decline.

I monitored a Steller sea lion haulout constantly for a year to determine the degree of site fidelity, haulout composition, and seasonal activity patterns. Mature females have generally been believed to leave haulouts to travel to the rookeries to give birth during the summer, and return with their pups in the fall. Numbers of juveniles, sub-adult males (SAMs) and adult males (bulls) are generally believed to remain relatively constant throughout the year. I sought to test these assumptions, as well as determine the influence of environmental factors on haulout patterns and activity levels of Steller sea lions. Previous studies have examined the effect of different covariates on the number of sea lions hauled out (Porter, 1997; Kucey, 2005), but none of these studies had detailed information about weather, relying instead on modified Beaufort scales.

Studies investigating haulout patterns of pinnipeds have often been restricted in space and time and therefore only collect a narrow range of information. My study was designed to observe sea lions over thirteen consecutive months to determine the finer effects of covariates on numbers of sea lions hauled out as well as the activity level of each age/sex class and their response to environmental factors, time of the year, and seasonal prey availability.

Methods

My study was conducted from 6 July 2004 – 31 July 2005 in Frederick Sound on Southwest Brothers Island, Southeast Alaska (57°15’N, 133°55’W), where a colony of Steller sea lions consisting of both sexes and all age classes hauls out year-round (Fig. 1.1). This is one of the largest haulouts used by Steller sea lions in Southeast Alaska and was considered to be representative of other sites used throughout the year. Observations were conducted with the aid of spotting scopes and an unobstructed view from a hidden blind 125 m from the haulout.

Over 2,800 hours of direct observations were conducted from 08:00 to 16:00 h each day over the study period (the shortest period of daylight, which ensured a consistent observation period throughout the year). One observer collected data at a time, with 5 observers participating over the 13-month study. Each observer was trained in the lab and the field prior to data collection to standardize the identification of age classes and activity categories between observers. All visible pups (<1 year), juveniles (1–3 years), adult females, SAMs, and bulls were counted from the blind every 30 minutes and data recorded included total number of animals and number of animals in each activity category (Appendix 3). Activity categories noted for each age/sex class were either active (moving, playing, aggressive displays, intense vocalization, male copulation), low active (small head movements, low level vocalizations, sitting up with eyes open, scratching and grooming, female copulation, nursing), resting (lying down, sleeping, sitting up with eyes closed), or suckling (suckling or searching for nipple).

A Davis Vantage Pro weather station (model #6320C) collected detailed weather on the hour and calculated apparent temperature indices (Appendix 4). As a precaution against technical failure, weather was also estimated three times daily (at 08:00, 12:00, and 16:00 h) using a modified Beaufort scale similar to that used by Porter (1997) and Kucey (2005) (Appendix 5). Data from the weather station was downloaded weekly to a laptop computer.

Data analysis

Age/sex composition on the haulout

Proportions were arcsine-transformed and analyzed using an analysis of variance and a chi-square test for multiple proportions (S-PLUS 2000) to compare the proportion of sea lions hauled out by age/sex class. Proportions of pups, juveniles, adult females, SAMs and bulls were analyzed separately to determine if their presence on the haulout varied by season.

Haulout trends

Generalized linear models are commonly used to assess haulout trends over time (Calkins *et al.*, 1999; Frost, Lowry & Ver Hoef, 1999; Small, Pendleton & Pitcher, 2003) and the effects of environmental variables (Gurnell, 1996; Kucey, 2005). I used a maximum likelihood generalized linear model (S-PLUS 2000) to investigate the effect that different covariates had on the number of sea lions hauled out at my site. Variables investigated included heat index, temperature, wind chill, humidity, rain, rain rate, and THSW index (temperature/humidity/sun/wind). The generalized linear models were applied to daily averages of weather variables and counts.

Age/sex class and activity state

A daily mean for each activity state (active, low active, resting, and suckling) was calculated for the animals hauled out on shore by each age/sex class.

Results

General trends

Daily mean numbers of animals hauled out at the haulout varied greatly throughout the year, from a minimum of zero animals in spring to a maximum of approximately 350 in summer and fall (Fig. 3.1A).

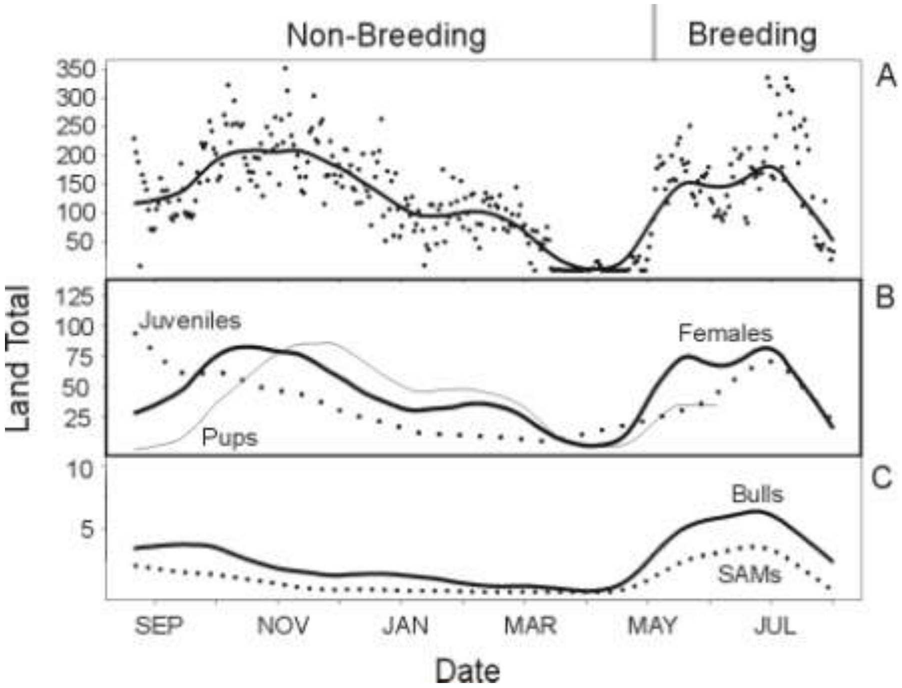

Figure 3.1. Mean daily number of animals hauled out from August 04 – 05. A) total animals B) pups, juveniles, and females C) SAMs and bulls. Data were smoothed with a loess curve (*f* = 0.25).

The haulout was temporarily abandoned gradually in mid-March 2005 for no apparent reason. Sea lions slowly began to return in mid-April and were back to their pre-abandonment (October – December) numbers by early May. Numbers increased again through June until the beginning of July 2005 at which point the animals began moving to the other side of Southwest Brothers Island. This shift in movement of animals to the opposite side of the island was observed in both years (i.e. July 2004 and 2005). Overall, sea lions at Southwest Brothers were most abundant from May – December, at medium density from January – mid-March, and absent from mid-March – May. Considerable variability was noted in numbers on shore from one day to the next (Fig. 3.1A).

Plotting the number of animals hauled out by age class revealed that trends for pups tended to lag behind those of adult females in the fall (Fig. 3.1B). Both age groups tended to increase until the early autumn (October/November) reflecting their joint return from the summer rookeries. Juveniles were present in their highest numbers during summer, and declined steadily throughout the autumn and winter, possibly reflecting the greater tendency for juveniles to disperse (Raum-Suryan *et al.*, 2002). SAMs and bulls were present at consistently low numbers throughout the year and were most abundant during summer (Fig. 3.1C).

Age/sex class composition by season

A 2-way ANOVA revealed a significant effect of age/sex class ($F_{4,2} = 607.87$, $p < 0.01$) and an interaction between season and age/sex class ($F_{15,2} = 63.89$, $p = 0.02$). The proportion of each age/sex class hauled out differed significantly by season at Southwest Brothers Island for pups ($\chi^2_4 = 38.42$, $p < 0.001$) and juveniles ($\chi^2_4 = 14.51$, $p < 0.01$) but not for females ($\chi^2_4 = 1.12$, $p > 0.05$), sub-adult males ($\chi^2_4 = 3.69$, $p > 0.05$), or bulls ($\chi^2_4 = 2.79$, $p > 0.05$) (Fig. 3.2).

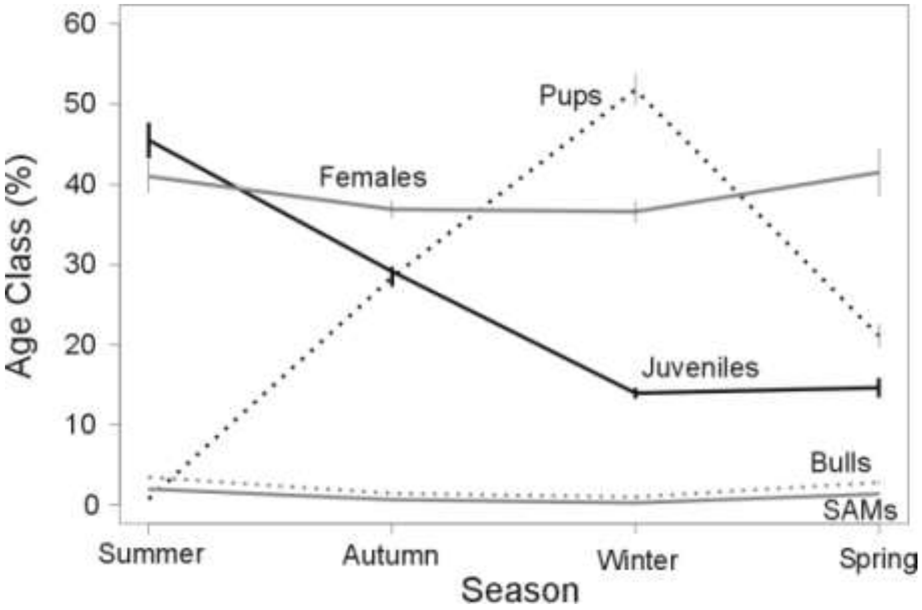

Figure 3.2. Average seasonal proportions and standard error of each age/sex class hauled out at Southwest Brothers Island, Alaska from July 04 – August 05.

Site Fidelity

Numerous marked focal animals visited Southwest Brothers throughout the year — 141 immature (age 0-3), 54 adult females, and 66 males. 98% of marked males, 94% of females, and 89% of immature animals were observed less than six months total. This reflected differences in their overall fidelity to this site — immature (1 – 11 months), females (1 – 7 months), and males (1 – 7 months) (Figure 3.3). The number of consecutive months the animals were seen varied with each class.

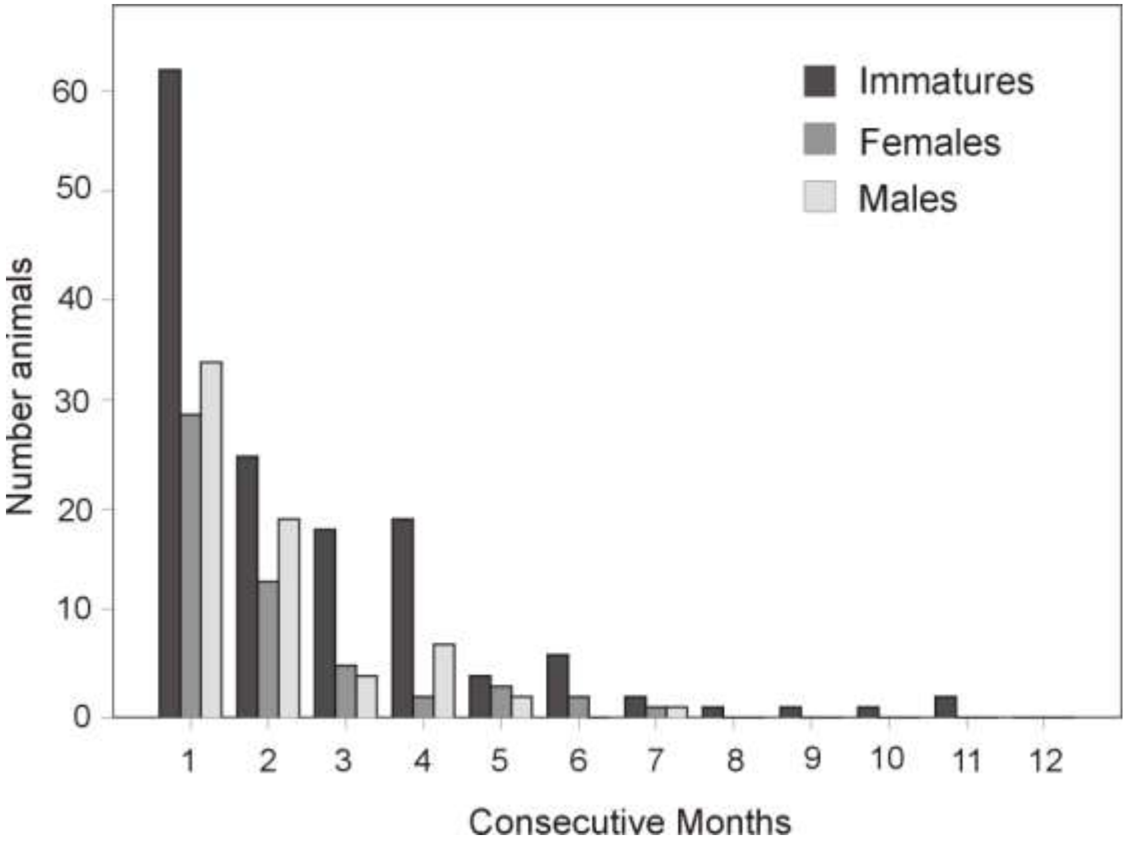

Figure 3.3. Number of marked animals observed at Southwest Brothers Island during consecutive months. The majority of animals were present for only one month at a time.

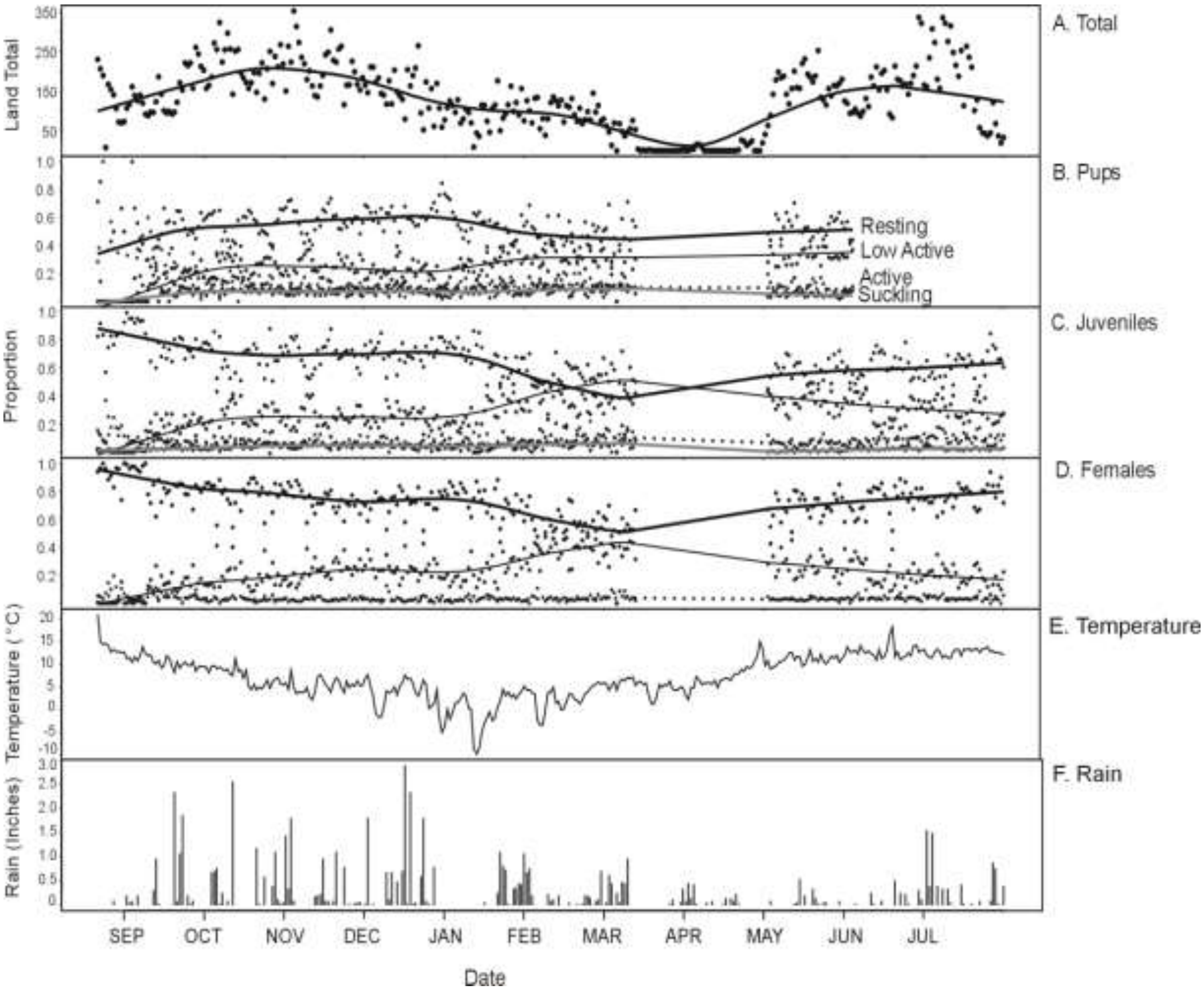

Figure 3.4. Mean daily proportion of animals in each activity class, and mean temperature and rainfall. A) Total sea lions, B) Pups, C) Juveniles, D) Adult females, E) Temperature, F) Rain. Activity was classified as resting (thick line), low active (thin line), active (dotted line), and suckling (grey line). Data were smoothed with a loess curve (f = 0.25).

Activity states

Seasonal behaviour patterns were generally similar among pups, juveniles, and adult females (Fig. 3.3B,C, and D) despite seasonal changes in weather (Fig. 3.3E,F) and numbers onshore (Fig. 3.3A).

Low active behaviours such as sitting with eyes open, head movements, and low vocalizations tended to increase with the onset of winter, while the proportion of time spent resting decreased. Little seasonal change was noted throughout the year in the frequencies of active behaviours such as moving, biting, and loud vocalizations. Pups suckled consistently throughout the year until their birthdays in early June (Fig. 3.3B-assumed median pupping date of June 4 at the Forrester complex where most of our branded animals were born [Pitcher *et al.*, 2001]), at which point they were classified as juveniles. A smaller proportion of juveniles suckled compared to pups, with a higher frequency of juveniles suckling in the winter than in summer (Fig. 3.3C). Adult females increased the proportion of time they engaged in low active behaviours and decreased their resting behaviours through the autumn and into the winter (Fig. 3.3D). However, they reversed this trend from spring through summer (Fig. 3.3D).

Air temperatures ranged from a low of -10°C in January to a high of 21°C in August, with a grand average of 8°C for the year (Fig. 3.3E). Rainfall totaled 1660 inches for the year with the wettest month in December (369 inches) and the driest in August (23.6 inches). Combining air temperature, atmospheric pressure, and wind speeds to calculate humidity, windchill, heat index, and THSW index (i.e. the weather perceived by the sea lions) showed positive correlations with numbers of animals hauled out over the year (Table 3.1). Daily rainfall and rain rate were the only variables that were not significant predictors of numbers of sea lions hauled out over the year (Table 3.1). However, analysis by season revealed both rain and rain rate to be significant factors in the summer (Table 3.2). Temperature and indices related to temperature were significant in winter and spring (Table 3.2).

Table 3.1. Covariates affecting the number of sea lions hauled out from July 2004 – July 2005. Intercepts and variable coefficients of the generalized linear models for each respective covariate on the response variable of number of sea lions hauled out (n = 343). Significant coefficients are shown in bold.

Covariate	Intercept	Variable Coefficient
THSW Index	4.71	**0.025**
Rain	4.86	0.007
Rain Rate	4.86	-0.001
Temperature	4.62	**0.031**
Humidity	3.75	**0.014**
Wind Chill	4.72	**0.023**
Heat Index	4.61	**0.033**

Table 3.2. Covariates affecting the number of sea lions hauled out each season from July 2004 – July 2005. Variable coefficients of the generalized linear models for each respective covariate on the response variable of number of sea lions hauled out. Significant coefficients are shown in bold.

Covariate	Autumn	Winter	Spring	Summer
THSW Index	-0.04	**0.05**	**0.30**	-0.14
Rain	-0.10	-0.10	-1.16	**0.27**
Rain Rate	-0.04	0.00	-0.05	**0.07**
Temperature	-0.05	**0.05**	**0.15**	-0.18
Humidity	**0.01**	**0.00**	0.00	0.03
Wind Chill	-0.04	**0.05**	**0.13**	-0.17
Heat Index	-0.05	**0.05**	**0.18**	-0.17

Time of day

Considerable daily variability was noted in numbers of animals hauled out throughout any given day. Standard error in mean daily counts ranged from 0.18 to 37.00 for the entire year. The greatest variability in hourly counts occurred in June (109–368 sea lions), and the least in March; however there was no seasonal trend in daily variability in numbers onshore. No distinguishable yearly or seasonal diurnal pattern was detectable during the hours of 08:00 and 16:00 at this site, consistent with previous site-specific results (Kucey, 2005).

Discussion

Southwest Brothers Island was chosen as a representative year-round Steller sea lion haulout site where animals could be observed for 365 consecutive days to document seasonal changes in sea lion behaviours and numbers that have bearing on assessing population status. It is one of nearly 600 haulouts used by sea lions throughout their range (283 in Southeast Alaska), and is the first to be observed for a consecutive 13 months. Some of the conclusions drawn are likely specific to Southwest Brothers (i.e., abandonment in mid-March and movement in July), while other observations can likely be applied range wide (i.e., variability of numbers onshore and the effect of weather on sea lion behavior).

Although classified as a year-round haulout, there was considerable seasonal variation in numbers of sea lions that used the Southwest Brothers haulout, including a period of time when sea lions abandoned it altogether. In all likelihood other Alaskan haulouts that are classified as year-round use sites are also equally dynamic with numbers generally declining as the summer breeding season approaches, and increasing again in the fall as adult females return with their newborn pups.

Censusing Steller sea lions

Estimating population size of Steller sea lions is a core component of population management that requires knowing when to census and what factors can influence the numbers observed onshore. Observations from Southwest Brothers suggest time of day and prevailing weather conditions had little effect on sea lion numbers, but that seasonal shifts in sea lion distribution were most significant. Maximum numbers of sea lions tended to be on shore during the breeding season (i.e. June) making this an optimum time to count — and is when the majority of censuses take place (Loughlin, Perlov & Vladimirov, 1992; Fritz & Stinchcomb, 2005). A second period of relative stability in sea lion numbers was noted during winter (February), during which time a greater proportion of animals were likely at sea feeding. The reduction in numbers on shore during winter points to the need to apply appropriate correction factors to estimate total population size and account for missing animals.

Current surveys take place during the breeding season on rookeries and haulouts using a variety of methods, depending on the location (aerial, land, or boat-based) (Loughlin, Perlov & Vladimirov, 1992). Correction factors for numbers of animals missed during the survey have been estimated based on life-tables and mathematical models (Trites & Larkin, 1996), however, trends in the size of the population are commonly determined by using counts of pups and non-pups over time by consistently surveying specific 'trend' sites (Fritz & Stinchcomb, 2005). Numbers of sea lions at haulouts are more variable than numbers at rookeries, and site-specific variability is considerable (Kucey, 2005). It may be that trend sites are more informative than range-wide correction factors to determine the health of the global population until site-specific correction factors can be determined.

Haulout behaviour at Southwest Brothers

The temporary abandonment of Southwest Brothers Island in mid-February was unexpected and may have been related to the seasonal availability of prey that was outside the normal foraging range of my study animals. Most pinnipeds use terrestrial sites outside of the breeding season to rest, moult, nurse and/or conserve energy (Thompson, 1989; Thompson *et al.*, 1989). In the case of Steller sea lions, haulout sites are believed to be situated close to waters that are relatively shallow and well-mixed, with higher average tidal speeds and less-steep bottom slopes (Ban, 2005). To have animals abandon a regularly used site presumably reflects a deliberate foraging strategy rather than a random, opportunistic event.

Steller sea lions are known to target prey that are in dense spawning or migrating groups such as Pacific herring (*Clupea harengus pallasi*), cod (*Gadus macrocephalus*), salmon, sandlance (*Ammodytes hexapterus*), and eulachon (*Thaleichthys pacificus* Girad) (Sinclair & Zeppelin, 2002; Sigler, Womble & Vollenweider, 2004). Eulachon have an unusually high energy content, spatio-temporal predictability, and accessibility (40–150m depth), and are thought to be an important seasonal prey item for Steller sea lions (Sinclair & Zeppelin, 2002; Sigler, Womble & Vollenweider, 2004) at a critical time of the year when energy demands are the highest such as winter (Winship, Trites & Rosen, 2002; Kumagai, Rosen & Trites, 2006).

Eulachon are abundant in most major drainages from Southeast Alaska and generally spawn from March to May (Womble *et al.*, 2005), and may be what drew sea lions away in mid-March. Along these lines, it is noteworthy that over 1000 animals were reported in Lynn Canal in late March (L. Jemison, ADF&G, pers comm), when both the herring spawn and eulachon runs generally occur (Sigler, Womble & Vollenweider, 2004; Gende & Sigler, 2006). It is also noteworthy that other predators including harbour seals and seabirds aggregate around eulachon runs (Marston, Willson & Gende, 2002) and that high variations of harbour seals hauled out at different sites throughout the year is believed to be related to the presence of eulachon smelt (Thompson, 1989). Eulachon spawning runs are known to draw significant aggregations of Steller sea lions in Southeast Alaska and may increase the energy intake of sea lions by as much as 90% (Sigler, Womble & Vollenweider, 2004).

The second unexpected change in sea lion numbers occurred during July 2004 and July 2005, when animals slowly shifted to hauling out on the opposite side of the island. This new haulout area featured a west-facing, shallow-sloping gravel beach, and was in sharp contrast to the jagged rocks and steep slope of their main haulout site. The new site appeared to provide ample room for the juveniles to interact with each other and the SAMs, which may have facilitated play, an essential part of the life-history learning process. Play is a way of learning specific behavioural patterns for later adult life such as territory defense and fighting bouts, and may allow for a greater behavioural flexibility later in life (Gentry, 1974).

The first year the sea lions exhibited this shift in local site fidelity, I assumed there were some unusual cause or motivation, but the following year, approximately a week later, they began to move again. There were no major disturbances or severe weather observed at the main site and the sea lions moved over gradually, with the bulls and SAMs hauling out first, followed slowly by the rest of the colony. The shift in animal abundance from the main haulout parallels to some extent the shift in breeding animals from rookeries to nearby haulouts. Mature bulls have been noted to hold territories at haulouts during summer and have been observed to copulate with females (Coombs & Trites, 2006) and similar behaviour was noted at Southwest Brothers. Thus it is conceivable that the breakdown of the main haulout might have reflected the movement away from the territorial males towards immature males and less aggressive interactions. Sea lions are a gregarious species and preferentially haul out together (Gentry, 1970), which may explain the gradual movement to the other site — the more animals that hauled out, the increased likelihood that others would haul out there too.

A number of pinniped species have shown diurnal patterns in numbers on shore thought to be associated with foraging and air temperature (i.e., Thompson, 1989 - *Phoca vitulina*; Lydersen, 1991 - *Phoca hispida*; Bengtson & Stewart, 1992 - *Lobodon carcinophagus*; Horning & Trillmich, 1999 - *Artocephalus galapagoensis*; Soto, Trites & Arias-Schreiber, 2006 - *Otaria flavescens*). In contrast, studies of other species have not found any evidence of diurnal foraging patterns (i.e. ringed seals- Born, Teilmann & Riget, 2002), with dives occurring at all times of the day and night (i.e. Australian fur seal- Hindell & Pemberton, 1997). Some studies have found daily haulout patterns which suggest the cycle of arrival and departures observed is indicative of Steller sea lions foraging at night (Sandegren, 1970; Withrow, 1982). Kucey (2005) found mixed results, with time of day significantly influencing the number of sea lions hauled out at some sites, but not others. However, only a weak trend was found at Southwest Brothers during daylight hours (08:00 – 16:00), even during winter when daylight was restricted to this period. Numbers of animals hauled out at each hour of the observed day did not differ over the year or by season, indicating no diurnal pattern, which might be indicative of a diversity of prey at all times.

The high thermoconductivity of water (which is 25x that of air, [Berta & Sumich, 1999]) means that thermoregulation is a particular challenge for warm-blooded animals inhabiting the ocean. The challenge for pinnipeds in particular is to conserve heat in the water and dissipate heat in air. Time of day, intensity of solar radiation, wind chill, cloud cover, and precipitation all play a role in perceived ambient temperature and have been found to correlate with the number of pinnipeds hauled out on various occasions (Porter, 1997; Reder *et al.*, 2003). Studies of pinnipeds have found differing results on the effect of weather on the number of animals hauled out, at times finding no correlations (Grellier, Thompson & Corpe, 1996).

In general the effect of weather on pinnipeds appears to be site and latitude specific. At low latitudes, warm, dry, calm weather appears to have the greatest influence (Schneider & Payne, 1983; Reder *et al.*, 2003), while haulout behaviour at high latitudes generally correlates negatively with wind-chill index, and numbers hauled out correlate with mid-day when the temperature tends to be the warmest (Lake, Burton & Hindell, 1997; Rogers & Bryden, 1997; Moulton *et al.*, 2002; Reder *et al.*, 2003). Haulout behaviour appears to be species and site specific, which could complicate wide-ranging population surveys. The highest numbers of animals were present at Southwest Brothers Island in the summer months, which was also the warmest weather.

Proportions of animals engaged in low active behaviours increased during the winter while the proportion in resting behaviours decreased dramatically for females and juveniles, with pups displaying a similar but weaker trend. Weather conditions were more extreme in winter than in the summer, and the animals appeared to be bothered by sudden changes in weather conditions, as anecdotally reported in previous studies (i.e., Sandegren, 1970; Withrow, 1982; Porter, 1997). Summer was the driest season and sea lions numbers were affected by rain and rate of rainfall at this time. Major disturbances due primarily to eagles looking for aborted fetuses and associated placentas occurred almost daily during the winter (Fig. 2.3). The constant disturbances from eagles caused major behavioural changes on the haulout, often causing animals to be more restless and vigilant.

Diurnal cycles and weather can often be trumped by more pressing behavioural requirements such as a female's need to nurse her young, and for her young to suckle in a safe place (Allen *et al.*, 1984; Thompson *et al.*, 1989; Lake, Burton & Hindell, 1997). During the worst weather when the haulout was covered in ice, the few animals hauled out were often female-pup nursing pairs. Haulout patterns of pinnipeds are often seasonal and can be correlated with reproductive stage or other life-history stages such as molting (Thompson *et al.*, 1989) and may vary with age class (Härkönen, Hårding & Lunneryd, 1999). For example, male and non-breeding female harbour seals spend longer periods of time ashore during the molt than females who have just pupped and are motivated to regain fat stores (Thompson *et al.*, 1989).

Inter- and intra-specific variability in haulout patterns can be considerable (Godsell, 1988; Thompson *et al.*, 1989; Born, Teilmann & Riget, 2002). Some animals will always be away from the haulout foraging, travelling, rafting, or playing. Different age and sex classes often have different behaviours, which may make them more or less likely to be observed (McLaren & Smith, 1985; Härkönen, Hårding & Lunneryd, 1999; Reder *et al.*, 2003).

Numbers of Steller sea lions found on shore are influenced by a multitude of factors at various times of the year and in differing ways. At this particular site, which was previously thought to be a year-round haulout, I discovered the animals abandoned it possibly in favour of a seasonally available, high fat prey. In contrast to the predictable haulout patterns at rookeries that reflect strong site fidelity and the presence of females with dependent pups and bulls maintaining breeding territories (Gentry, 1970; Sandegren, 1970), winter haulouts are more unpredictable, possibly due to seasonal access to prey and a more flexible relationship with dependent offspring (Porter, 1997). Site-fidelity at this site varied with each class of animals, the immature animals exhibiting the strongest fidelity, followed by females and lastly males, most likely due to a combination of dependence and other accessible sites nearby.

The local movement around the island was particularly surprising and the topographic features were the only obvious differences between the two locations on the small island. The weather predictors justify the timing of annual aerial surveys during summer and also showed that the level of detail on weather factors may not in fact be required. The animals appeared to spend proportionally more time in low active behaviours than resting during the winter compared with the rest of the year, which may have implications for nutritional requirements.

Summary

Numbers and behaviours of Steller sea lions were documented for 13 consecutive months (July 2004 – 2005) at Southwest Brothers Island in Southeast Alaska to test general assumptions about seasonal haulout patterns and the effects of weather on census counts. Proportions of females, sub-adult males (SAMs), and bulls on shore did not change significantly by season, unlike the proportions of pups and juveniles. Contrary to assumptions that the haulout was used ‘year-round’, animals abandoned the island in spring and preferentially hauled out on the opposite side of the island during both summers of observation. Abandonment of the haulout was correlated with the timing of the herring spawn and eulachon run, but movement of sea lions to the other local site could not be explained. Activity of animals on shore (active, low active, and resting) varied by season, with animals in general displaying more activity in the winter than the summer, which in turn correlated with increased disturbances and extreme weather. Generalized linear models showed that all indices of weather (THSW index, temperature, humidity, wind chill, and heat index) influenced the number of animals hauled out over the year, except for rainfall. No diurnal haulout pattern was noted at this site, over the year or by season. Winter haulout patterns are less predictable than at other times of year due to a combination of factors including weather, disturbance, seasonal prey availability, and possibly more flexible attendance patterns of mother-offspring pairs. Surveying animals during the breeding season, in the summer months may be the most effective way to get accurate population estimates because the highest numbers of animals are onshore. Although my study was only conducted at one haulout site, results are likely applicable to other haulout sites as Steller sea lion haulouts share many commonalties.

Chapter 4 : Steller Watch: Evaluation of an automated time-lapse camera system in relation to direct observation of a gregarious pinniped species, the Steller sea lion

Introduction

Cameras have long been used to monitor wildlife in the field, and circumvent the need for placing observers in remote and sometimes hostile conditions. Aerial photographs have been commonly taken to monitor population trends in wide-ranging, large groups of animals such as Steller sea lions (*Eumetopias jubatus*) and California sea lions (*Zalophus californianus*), and are generally accepted to be a more accurate method of surveying animals than counting on land or from boats due to the topography of the haulout (animals obscured by crevices and odd angles), dense aggregations of animals, movement of highly gregarious species, disturbances, and movement of boats (Loughlin, Perlov & Vladimirov, 1992; Westlake, Perryman & Ono, 1997; Lowry, 1999). Video and time-lapse photography have also been used to evaluate movements of animals on time scales of hours and days (Allen *et al.*, 1984; Thompson & Harwood, 1990; Maniscalco *et al.*, in press). However, no system has yet been deployed to monitor sea lion numbers on rookeries and haulouts in remote locations over an extended period of time (weeks and months).

The goal of my study was to assess the accuracy and reliability of an automated time-lapse camera system developed by Scientific Fisheries Systems Inc., (Anchorage, Alaska), and determine whether it can be used for future research to monitor sites when researchers cannot be physically present. The Scientific Fisheries camera system offers the possibility of collecting census data and identifying marked animals on a longer more site-specific basis than can be presently gathered from aerial photographs. The system was designed to have minimum impact on the environment and the animals, and to sustain severe climate and interference from insects, birds, and mammals.

Methods and study site

The study was conducted from 6 July 2004 – 31 July 2005 in Frederick Sound on Southwest Brothers Island (57°15’N, 133°55’W), where a colony of Steller sea lions consisting of both sexes and all age classes hauls out year-round (Fig. 1.1). This haulout was selected based on historical accounts and annual aerial census data conducted by the Alaska Department of Fish and Game (ADF&G), which indicated that animals from both sexes and all age classes were present throughout the year. Direct counts were made with the aid of spotting scopes by observers sitting in a blind next to the cameras. Total counts of animals hauled out onshore were conducted every hour, on the hour, from 08:00 – 16:00 daily (Appendix 4).

Two camera systems were bolted to rock 125 m in front of the haulout, and were programmed to capture one image per hour, on the hour – coinciding with the direct counts (Fig. 4.1). The two camera systems consisted of Nikon CoolPix 5700 (5-megapixel) digital camera and a DigiSnap 2800 controller (Harbortronics, Gig Harbor, WA). They were encased in a splash proof box (NEMA 4X rated) containing moisture-absorption packets, and a 65Ah gel-cell battery powered the system which was recharged during daylight by a 10W single crystal solar panel (Fig. 4.2). The 125 m distance to the haulout did not allow a single camera to fully cover the haulout. The 5-megapixel cameras (Nikon CoolPix 5700) were replaced with 8-megapixel cameras (Nikon CoolPix 8700) in February 2005 to improve image resolution. This allowed the quality of images taken with these two cameras to be compared.

A night vision scope (Multi-Use Minimonocular NVG), manufactured by Insight Technology Incorporated, (NVM-000-A1/A2) was initially attached to one of the cameras in order to have a daytime system and a nighttime system. This would have allowed numbers of sea lions to be recorded on the haulout over a 24-hour period. After encountering significant trouble with the range of the night scope and the quality of the images, it was decided to simply have two daytime systems, allowing the two cameras to be angled in such a way that the entire range of the haulout was photographed.

Figure 4.1. Outside view of the automated time-lapse camera system on Southwest Brothers Island.

Each day, the operational status of the camera was verified by looking through the plexiglas window of the system to make sure the green light on the DigiSnap controller was blinking. This indicated that the system was working correctly and capturing an image each hour. Once per week, a laptop and USB connection were used to download the images. The images were then deleted from the camera's memory to allow for maximum storage capacity. Each camera had an 8 GB memory card that could record 4,032 images of normal jpeg compression. Cameras were programmed to take one picture per hour – 24 pictures per day.

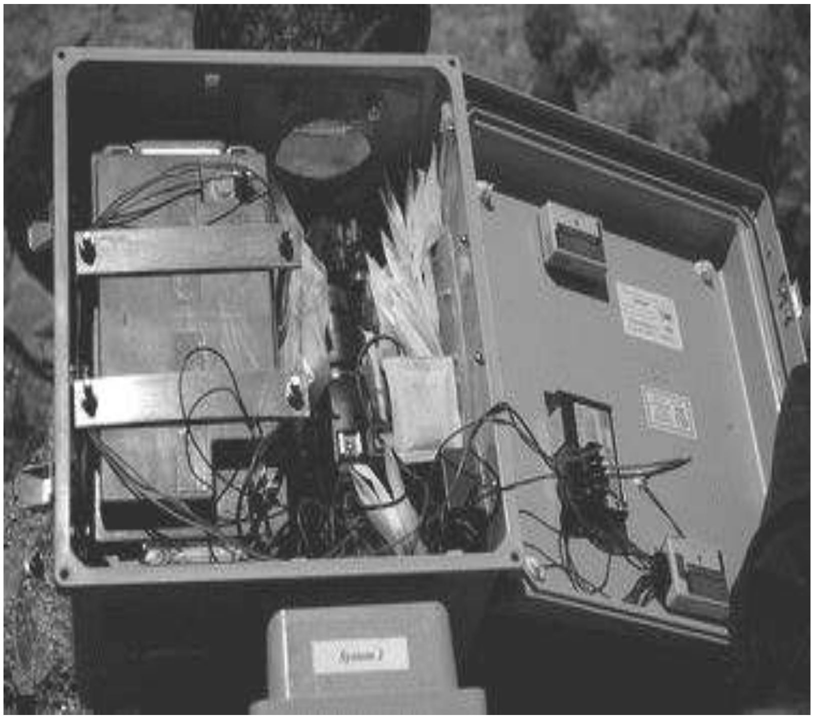

Figure 4.2. Inside of the automated time-lapse camera system on Southwest Brothers Island. The battery is on the left of the image, the camera and moisture absorption packets on the right.

The number of sea lions in each photo were subsequently counted on a computer screen using Adobe Photoshop 5.0. The images were magnified and a red mark was placed on each animal. Marks were counted to determine total animals present. Overlap between the two images was calculated and subtracted from the grand total. Due to the large quantity of data, I took counts from a select number of images to compare with the direct counts.

A two-sample paired t-test was used to check for significant differences in the means between counts obtained from direct observation and those obtained from the digital images. To analyze the accuracy of the system counts under optimal conditions, I excluded images that were of poor quality, where the images did not cover the entire haulout, and images where the overlap of time on the two systems was greater than five minutes. Analysis was conducted on the total number of images counted, on images obtained from the 5- and 8- megapixel cameras separately, and on images containing less than or greater than 50 animals respectively. The last analysis was done to account for disparity in the ability of the observer to count few or many animals. Finally, to test for an effect of experience counting and observing in the field, I compared the photo counts obtained from an experienced field counter with counts from an inexperienced counter.

Results and Discussion

System performance

Camera positioning in relation to the sun made a noticeable difference in picture clarity. For example, Camera 2 faced southeast and had clearer, "brighter" photos more often than Camera 1. Moisture/rain often accumulated on the outside of the camera box during or following bad weather and partially obscured animals on the haulout. However, all images were clear once the moisture dried.

Clarity and resolution of the 5-megapixel camera images were better at dawn, dusk, and early evening when contrast between the animals and haulout was better. There was good coverage per camera of the haulout and the images showed the overall spatial arrangement of the animals well. Nursing/suckling behaviours were sometimes distinguishable in the photographs.

In general, the resolution of the 5-megapixel camera was not fine enough to see all of the animals. This meant the images had to be magnified significantly, to the point that the animals in the photographs appeared as a collection of multi-coloured, grainy pixels. The sea lions were often difficult to distinguish from rock on heavily overcast or rainy days, when it was foggy or snowing, when the sun reflected off the water, rocks, and wet animals, when the sea lions were in shadows or in crevices, and when the animals were darkly coloured (i.e., wet or pre-moulted pups).

Pups were generally difficult to distinguish in the photographs, especially in early fall when they still had pre-molt dark fur and they were small enough to be obscured by other animals or the topography of the haulout. It was also sometimes difficult to distinguish one sea lion from another when they were in a densely packed, large group.

Suckling and nursing behaviours can be obscured in these situations. Moving sea lions appeared as smudges. Branded animals could occasionally be seen but were generally not legible, and flipper tags were indistinguishable at this resolution.

The images from the 8-megapixel camera were noticeably sharper and clearer and individual sea lions were easier to distinguish and required less magnification to be counted. Branded animals were also more easily distinguished and their numbers could sometimes be read if the branded animal was positioned optimally (at 90 degrees to the observer with left side visible). The 8-megapixel camera solved many of the problems presented by the 5-megapixel camera.

Daily checks of both systems to see that they were working revealed that the cameras were reliable for most of the time but occasionally stopped working. Instructions that were provided by Scientific Fisheries for maintaining and changing cameras were well written and comprehensive. The camera systems only lasting impact on the environment were the holes in the rock left by bolting the systems down. The casing itself was small and painted grey and was therefore camouflaged from tourists and other people on the water. They were completely waterproof and continued working even with a foot of snow piled on top of the solar panel and when buffeted by extremely high wind speeds. The moisture absorption packs that maintained a humidity-free environment inside in the systems were changed once in the year, and there was no interference with the images or the systems from insects, birds or small mammals.

At one point in the year the sea lions decided to haul out directly beneath the observation blind, and eventually came high enough up the rocks to lay next to (and on top of) the camera systems. As a result they inadvertently moved the camera boxes so the angle was entirely off. Future deployments of the cameras should therefore ensure that all bolts are tight enough to prevent movement once the systems are put in place and set to the desired angle. Another consideration is prevailing weather conditions while downloading images. High winds and rain made it difficult to shelter the computer, cords, and connections.

The camera systems stopped working on a number of occasions for no apparent reason. Restarting the system by pushing the re-boot button on the outside of the box was rarely successful, which meant manually re-booting the entire system. Manually re-booting worked well except that it could only be done when the weather was dry, because the entire system had to be opened. Re-booting the system often changed the programmed times for pictures to be taken by 5-10 minutes. Trying to coordinate the two camera systems to take their images at the same time was sometimes difficult, since any mistake meant waiting until the next hour to remove and re-program the cameras. Voltage data on the systems was collected to check if power might have caused the cameras to periodically stop, but did not offer an explanation. Nor did the times the systems stopped working correlate with light and weather conditions.

Comparison of counts

In general, counts made from the photograph were consistently lower than counts made by direct observation (Fig. 4.3). Gregarious species can be difficult to count from a still image, as shown by Allen *et al.* (1984) who used a film-based time-lapse camera system with an interval of one frame per minute and found that the camera was reliable for daily trends but was not a reliable indicator of the actual number of seals present. Direct observations have the benefit of being able to more easily identify behaviours and see shifting animals.

Table 4.1. Correction factors and standard error (%) for the 5- and 8-megapixel camera systems when numbers of animals were above 50 and between 1–50.

	Counts	SE	Counts	SE
Camera	< 50 & > 1		> 50	
5 mgpx	62.68	1.25	70.92	1.49
8 mgpx	70.70	2.90	77.76	0.62

Counts from direct observation and from photographs on both 5- and 8-megapixel cameras differed significantly ($p < 0.001$). While the 8-megapixel camera made the resolution better for counting the images, the difference between direct and image counts was still significant. Correction factors were determined for the camera counts when compared with the direct counts and were found to be quite good (Table 4.1). If cameras are set up at different sites, correction factors will have to be determined for each site according to the position of the system and topography of the haulout.

The correction factor between counts of the 8-megapixel camera was high with an $r^2 = 0.99$, suggesting the correction factor obtained would be consistently reliable (Figure 4.3).

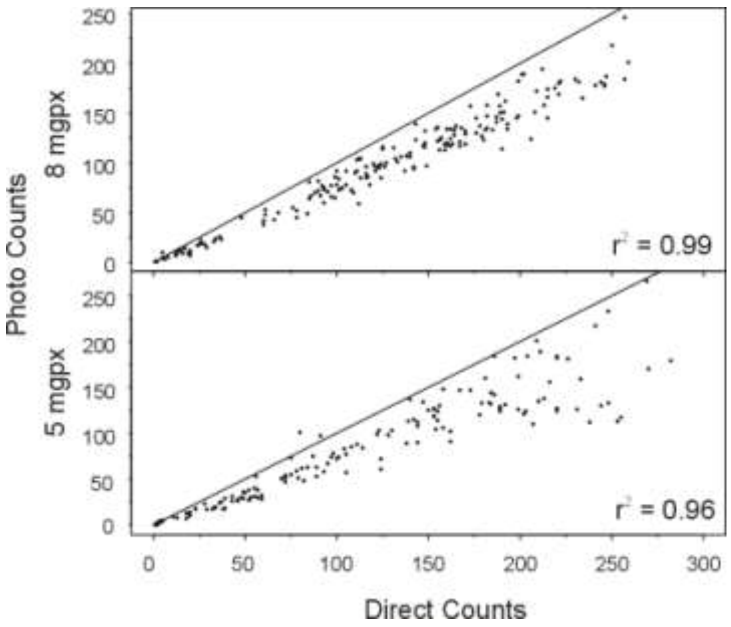

Figure 4.3. A comparison of counts taken from direct observation and counts obtained from 8 and 5 megapixel digital images.

There were no significant difference between the counts of the two inexperienced counters (P = 0.1861). However counts of sea lions in photographs made by a person who had previously observed sea lions in the wild were significantly higher than counts made by inexperienced counters. The inexperienced counters counted an average of 86% of the sea lions seen by the experienced field counter. Observers who have spent time in the field counting and recording sea lion behaviour have knowledge of the subtleties in sea lion shape and position, and are able to distinguish them from each other and their background. This suggests that experience must be taken into consideration when hiring researchers to count animals in photographs.

Time-lapse digital camera systems may be limited to answering specific questions about general trends in numbers and distributions and appear to be well suited for monitoring species where humans physically cannot observe and disturbance needs to be at a minimum, such as the cliff-side breeding nests of sea birds. They provide an index of abundance within a limited field of view. At my study site, Steller sea lions moved around the island on a consistent basis, often hauling out on tide-exposed rocks and areas other than the main site, and even at one point directly on top of the camera systems.

The systems I tested needed surveillance and monitoring to ensure they were running properly which may not be an acceptable limitation if they need to be left independently for long periods. A number of counts would have been missed if the camera systems had been relied on alone, and other types of information such as changes in behaviour, disturbances, predation attempts, re-sighted animals, and human interactions could not be extracted from the images.

Placement of the cameras is an important consideration when deploying automated systems. Distance to haulout must be considered with regards to resolution, clarity, and range of the image in relation to the type of information that is being gathered. An image taken above a haulout may be better than one pointed directly on, because the topography of the rocks would not interfere with visibility and the animals would not be hidden behind one another. However, the logistics of doing this for Steller sea lions are generally difficult and site specific, given that most haulout sites are on remote rocky outcroppings with no trees for mounting cameras (Ban, 2005). Getting the systems high enough to cover the entire space of the haulout can be equally challenging. Thus, each site will have a different set of advantages and limitations and would have to be assessed independently.

Sitting and watching animals directly in the wild is an integral part of formulating questions and gaining insight into life-history strategies. Human senses not only pick up sight, but also sound, smell and touch, which the mind can integrate to provide a more comprehensive, realistic understanding of the proximate causes of animal behaviour.

Cameras have clear economic benefits over the establishment of staffed field camps. However, the benefit of having a computerized system collecting information will often be out-weighed by the advantages of human eyes and a brain to think about the ‘why’ and ‘how’ questions that drive our curiosity and fuel our motivation for research.

Summary

The automated camera system, designed by Scientific Fisheries Systems Inc. was deployed from July 2004 – July 2005 on Southwest Brothers Island in Southeast Alaska to evaluate its potential to monitor sea lion numbers on rookeries and haulouts over extended periods, in remote locations. The system had no noticeable impact on the environment or the sea lions, and severe climate and interference from insects, birds, or mammals did not negatively affect it. Counts of animals from the digital images were consistently lower than direct counts by field biologists, and averaged approximately 78% of the direct counts under optimal conditions. The linear model of the two methods of counting animals suggested the correction factor would be consistently reliable ($r^2 = 0.99$). Counts from photographs reflected general site-use trends, but were not completely accurate representations of actual animal movement due to its limited scope. Specific data such as brand re-sights and individual behaviours such as suckling/nursing will still have to be gathered by direct observation. The camera systems may provide a novel approach in the future to fill in gaps in counts and monitor sites when researchers cannot be physically present.

Chapter 5 : General conclusions

The goals of my study were to document weaning behaviour in Steller sea lions, record site-fidelity in relation to seasonal haulout patterns and activity levels, and evaluate an automated time-lapse camera system as a means to monitor use of local haulouts of animals. In order to accomplish these goals, I conducted behavioural observations and counts at a colony of Steller sea lions in Southeast Alaska for 13 consecutive months. A weather station recorded hourly environmental variables and a time-lapse camera system photographed the haulout every hour.

Weaning behaviour

My study revealed a high proportion of animals suckling beyond their first and even second birthdays, with males showing a tendency to remain associated with their mother longer. I recorded no observable parent-offspring aggression and the offspring ended the suckling bout more frequently than the female. The results shown in Chapter 2 suggest that many females were not having a new pup each breeding season, opting instead to continue nursing their current offspring. This flexibility in length of lactation may reflect the sociability of this species and fluctuating prey resources, and may significantly affect the population dynamics of Steller sea lions.

Haulout behaviour

The haulout patterns and activity levels of the colony were investigated over 13 consecutive months. The proportion of pups and juveniles making up the colony varied significantly by season while proportions of females, SAMs, and bulls remained constant. All animals abandoned the site from mid-March to mid-April, when herring spawned and eulachon arrived at the mouths of rivers. These two species are energy dense prey and have a high spatio-temporal predictability. Over both summers of observation, the animals changed their local site and hauled out on the opposite side of the island, a topographically different area. No major disturbance was witnessed and the movement to the new site appeared gradual and deliberate. No simple explanation for this seasonal movement was apparent. Temperature and other indices were significant indicators of the number of animals hauled out onshore. No diurnal haulout pattern during daylight hours was found, in agreement with previous studies conducted at this site.

Automated time-lapse camera systems

I evaluated the efficacy and accuracy of the automated time-lapse camera systems when compared with direct counts. Even under optimal conditions, the counts of photographed sea lions were 22% lower on average than counts made in the field. The systems generally performed well when the weather was good, and the animals were hauled out in their normal location. The cameras provide a novel means for future studies to keep track of site-specific trends of animals when researchers cannot be physically present.

Strengths and weaknesses

Animals that live in a fluctuating environment need to adapt to constantly changing conditions that affect their abilities to find food, avoid predators, and obtain mates. Behaviour is one of the primary ways that animals adapt to the conditions they live in. Behavioural studies are often difficult to carry out due to the often subjective nature of categorizing what animals do. The behaviours and methods chosen and level of analysis will influence the interpretation of results. Data obtained from focal animals may not be entirely representative of the colony and correspondingly, the colony's behaviour may not be representative of the entire population of animals. In my study, not all animals hauled out at the site were visible from our observation point. I assumed that the animals within view were representative of the entire colony and that animals were not behaving differently at areas that could not be seen.

Despite difficulties in conducting behavioural studies, my research is the first study to conduct behavioural observations of one colony of Steller sea lions across all seasons consecutively for an entire year. This allowed me the opportunity to have consistency of site, observers, and animals. The animals were more mobile than expected. It was generally thought that there would be a core group of animals that would stay at the site consistently throughout the year, with others coming and going. Not only did the animals haul out at other areas and rocks around the island, but also data from our focal animals revealed different animals remained at the site for variable lengths of time. This most likely reflected seasonal availability of prey and the proximity of other haulouts to my study site.

Future studies

Research on weaning behaviour of otariids in the future would do well to use satellite tags to track the movement of female-offspring pairs. This information would clarify whether they forage together and potentially allow the exact time of permanent separation to be determined. Furthermore, behaviour at the rookeries during the breeding season should be thoroughly investigated with regards to female-juvenile-pup behaviour, mother-offspring conflict, reproductive failure/loss of pup resulting in extended lactation, and sex-biased behaviour to investigate the strategies of females that give birth to a new pup and have a dependent offspring present. Further studies could take place at other sites to determine the proportion of animals weaned at one and two years. Recommended length of future weaning studies is one month which would ensure observing the presence or absence of a mother with the young animal. Conducting a study before the breeding season may be inaccurate if weaning occurs at the rookery or if the mother lost her pup early on and resumed nursing her previous dependent. October is the time when most animals have returned from summer breeding rookeries to winter haulouts. Therefore, observing sea lions at this time would give confidence of whether the young animal was independent or not.

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Appendix 1. Focal animal scans data sheets

FOCAL ANIMAL SCANS   STELLER WATCH

Michelle Marcotte

SW BROTHERS ISLAND 2004-2005

DATE (DD/MM/YY):

OBSERVER:

First number- behaviour, Second number- association

TIME	8:05	8:20	8:35	8:50	9:05	9:20	9:35	9:50	10:05	10:20	10:35	10:50	11:05	11:20	11:35	11:50
ANIMAL ID																

FOCAL ANIMAL SCANS STELLER WATCH

Michelle Marcotte

SW BROTHERS ISLAND 2004-2005

DATE (DD/MM/YY):

OBSERVER:

First number- behaviour, Second number- association

TIME	12:05	12:20	12:35	12:50	13:05	13:20	13:35	13:50	14:05	14:20	14:35	14:50	15:05	15:20	15:35	15:50	16:05
ANIMAL ID																	

Appendix 2. Animal behavioural codes at Southwest Brothers Island

GROUP BEHAVIOUR SCANS

ACTIVE (A) = moving, playing, aggressive displays, intense vocalization, male copulation

RESTING (R) = lying down, sleeping, sitting up with head pointed to sky with ***eyes closed***

LOW ACTIVE (LA) = small head movement, low level vocalization, sitting up with eyes open, scratching/grooming, female copulation, nursing.

SUCKLING = (S) suckling or searching for nipple

FOCAL SCANS

FOCAL SCAN BEHAVIOUR (1)

R = resting	-lying down or head up with eyes closed
LA = low active	-sitting up with eyes open, small head movements, low vocalizations, scratching/grooming
PL = play	-playing with objects (i.e. kelp) or with others
S = suckle	-searching for nipple, suckling
Wa = water	-swimming, playing in water on rock shelves, jumping in and out
M = Movement	-moving around haulout, (walking)
A = aggressive	-biting, hostile interactions, mock fighting, displays
V = Vocalization	-loud vocalizations
O = other	
99 = obscured	-hard to make out individual, uncertain

FOCAL ANIMAL ASSOCIATION (2) (nearest neighbour)

1 alone
2 with juvenile
3 with mother
4 with mature female
5 with bull
6 with SAM
7 with other

The measure of association will be one adult female body length. If the animal is more than one adult female body length from anyone else, it will be considered alone. If there are several animals within on adult body length to the focal, the animal nearest to the focal will be considered its associate. If several animals are equidistant to the focal, then it will be marked as ‘other’.

Appendix 3. Disturbance data sheet

MISC. DISTURBANCE AND EVENTS Michelle Marcotte
SW BROTHERS 2004-2005 **STELLER WATCH**

DATE (DD/MM/YY)	TIME	EVENT	REACTION	# HEADS UP	% HEADS UP	# INTO WATER	VOCAL ↑/ ↓ /=	COMMENTS/ INITIALS

EVENT- Aircraft, Vessel, Bird, Whale(s), Unknown, Other

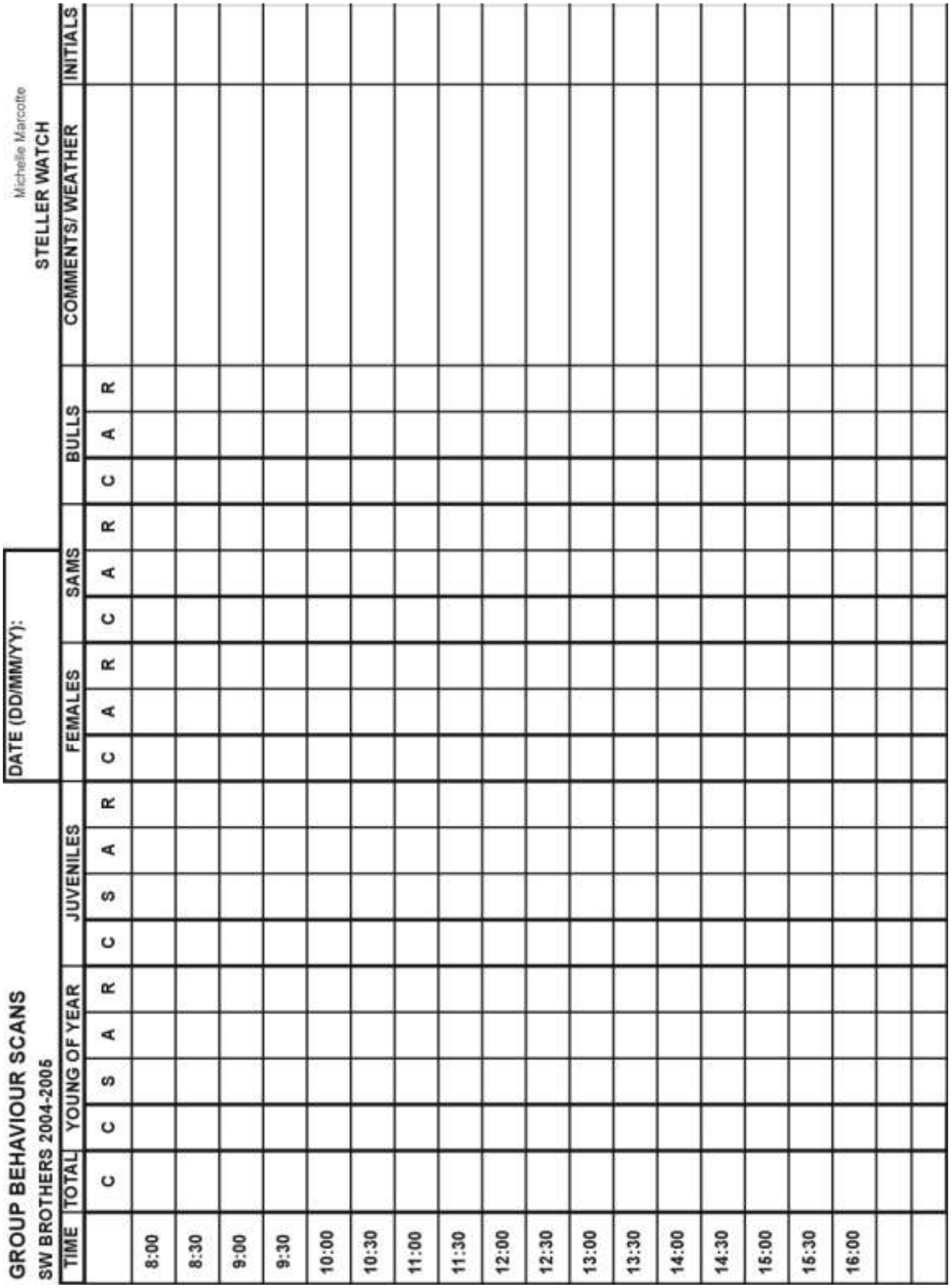
REACTION:

1. DETECTION- one or more animals with head raised and oriented toward potential disturbance

2. ALARMED- one or more animal move from its resting area, but did not enter the water

3. DISTURBED- more than one animal entered the water

Appendix 4. Group behaviour scans data sheet (main haulout and other sites)



GROUP BEHAVIOUR SCANS

SW BROTHERS 2004-2005

DATE (DD/MM/YY):

Michelle Marcotte

STELLER WATCH

TIME	TOTAL	YOUNG OF YEAR				JUVENILES				FEMALES			SAMS			BULLS			COMMENTS/ WEATHER	INITIALS
	C	C	S	A	R	C	S	A	R	C	A	R	C	A	R	C	A	R		
8:00																				
8:30																				
9:00																				
9:30																				
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13:00																				
13:30																				
14:00																				
14:30																				
15:00																				
15:30																				
16:00																				

GROUP BEHAVIOUR SCANS- OTHER SITES

SW BROTHERS 2004-2005

DATE (DD/MM/YY):

Michelle Marcotte

STELLER WATCH

TIME	YOUNG OF YEAR		JUVENILES		FEMALES	SAMS	BULLS	FOCALS	BEHAVIOUR/ ASSOCIATION	SITE LOCATION	COMMENTS/ WEATHER	INITIALS
	C	S	C	S	C	C	C					

Appendix 5. Davis Weatherlink Apparent Temperature

The Davis Weatherlink collects a range of environmental data including temperature, UV index, wind direction, wind speed, humidity, and calculates a number of indices of apparent temperature. These include:

Wind chill- takes into account how the speed of the wind affects perception of air temperature.

Heat index- uses temperature and relative humidity to determine how hot the air actually 'feels'. When humidity is low, the apparent temperature will be lower than the air temperature, since perspiration evaporates rapidly to cool the body. However, when humidity is high, the apparent temperature is perceived to be higher than the actual air temperature, because perspiration evaporates more slowly. Heat index is insignificant below 14°C.

Temperature/Humidity/Sun/Wind (THSW) Index- uses humidity and temperature like the Heat Index, but also includes the heating effects of sunshine and cooling effects of wind to calculate an apparent temperature of what it 'feels' like out in the sun.

Humidity- the amount of water vapour in the air, which varies with air temperature and pressure. *Relative humidity* takes into account these factors and offers a humidity reading which reflects the amount of water vapour in the air as a percentage of the amount the air is capable of holding. Relative humidity is an important factor in determining the amount of evaporation from plants and wet surfaces since warm air with low humidity has a large capacity to absorb extra water vapour.

Appendix 6. Modified Beaufort scale weather codes

SKY (1)

0 clear - no clouds, sunny, a few high wisps of white
1 scattered clouds - a few clouds scattered throughout the sky
2 partly cloudy - very cloudy but you can still make out the sky in some areas
3 overcast - no distinguishable cloud shapes, more of a homogenous grey
4 light fog - not too much, haulout visible
5 heavy fog - view of haulout and land features is severely limited
6 drizzle - misty, spitting rain
7 rain - full blown raining
8 snow - flakes
9 hail - solid rain

WIND (2)

0 calm - no wind, smoke would rise vertical
1 light breeze - wind can be felt on face, leaves are rustling
2 moderate breeze - raises paper, small branches are moving
3 strong breeze - large branches moving, would be hard to use an umbrella
4 gale - breaks twigs off trees, generally impedes movement

WAVE (3)

0 flat calm - sea is like a mirror
1 peaks, no caps - ripples, waves with no white on top
2 white caps - waves with white foam on crests
3 white caps greater 2ft
4 white caps greater 6ft

SWELL (4)

0 less 4 ft
1 greater 4 ft
2 greater 10ft

(e.g., Sky = partly cloudy, windy = strong breeze, wave = peaks, no caps, swell = less 4 ft would be written as, 2210)