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The effect of maternal traits on rearing success in pacific harbor seals (Phoca vitulina richardsii)

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By

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ABSTRACT

Reproductive success in species that care for their young is affected by the rearing strategy utilized. Otariids are known as income breeders because they continue to forage during a rearing time of about one year while leaving pups on land; their rearing success is related to attendance patterns. On the other end of the continuum, large phocids are described as capital breeders, fasting on shore during a rearing time from 4 to 50 days. Their rearing success is based on maternal body mass. Harbor seals (*Phoca vitulina*) don't appear to follow either of these two strategies fully and which maternal traits affect their rearing success is unknown. During two breeding seasons I observed 54 harbor seal females and their pups at Gertrude Island, USA, to describe their rearing strategy and determine how maternal traits affect rearing success. Using my data and a long-term database of individual females at the haul-out site, I modelled the effect of female age, size, experience, and attendance behavior on the health of the pup. Harbor seals reared their pups for 26.4 days ±14.3 (n= 77 pups) and took swimming trips during 35.6% of my observations, taking their pups with them on 98.6% of those trips. High pup health at weaning was best explained by increased maternal rearing time, decreased distance from other seals, previous success and increased time resting. The size of the female did not affect rearing success. My results indicate that harbor seals in south Puget Sound fell somewhere between capital and income breeding strategies on the continuum and that they required different traits than those employed by income and capital breeders to successfully rear their pups.

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INTRODUCTION

All reproductive strategies utilized by animals are based on a balance between the energy expended in reproduction and offspring success. Species that invest time in their young's success beyond their birth typically employ one of two distinct strategies: capital or income breeding. Capital breeders forego foraging during the rearing period and rely on previously gained energy stores to pass to their young, while income breeders continue foraging during the rearing period to gain energy (Boness and Bowen 1996; Stephens et al. 2009; Stephens et al. 2013). These two strategies have been well studied in migratory birds where different species rely on either reproductive strategy, depending on their migratory patterns (Guillemain et al. 2008). These strategies lead to different rearing behaviors and determine which maternal traits are crucial for the successful rearing of the young. In capital breeders, the amount of maternal energy stores before birth is the most important trait driving successful reproduction (Burns et al. 2004; Guillemain et al. 2008; Lang et al. 2009; Gustine et al. 2010). Income breeders, however, rely most heavily on maternal foraging and care behaviors to pass acquired energy from the mother to the young (Burns et al. 2004; Guillemain et al. 2008; Hobson and Jehl 2010; Andersen et al. 2012). While many species use one of these two strategies, others appear to utilize alternative strategies that rely both on maternal energy stores and foraging during the rearing time, yet we know very little about these alternative strategies.

Pinniped species (seals, sea lions and walruses) have been characterized as either income or capital breeders (Burns et al. 2004; Champagne et al. 2012). Pinniped income breeders nurse and rear their young for relatively long periods of time (typically one year) while continuing to forage to gain energy stores for nursing. They leave their pups on land while foraging, often for extended periods. Typically, otariids (fur seals and sea lions) are income breeders; for instance, female Steller sea lions (*Eumetopias jubatus*) nurse their pups for an average of one year before weaning (Higgins et al. 1988). Pinniped capital breeders gain large pre-natal energy stores to nurse and rear their young for relatively short periods of time anywhere from 4 to 50 days using the previously-attained fat stores (Boness and Bowen 1996; Champagne et al. 2012). Large phocid species such as northern elephant seals (*Mirounga angustirostris*) and grey seals (*Halichoerus grypus*) are described as capital breeders for their use of these fasting tactics (Kovacs and Lavigne, 1986; Crocker et al. 2001; Lang et al. 2009). The success of each reproductive strategy has been described for a variety of species. In pinnipeds, success appears to depend on different traits. In income breeders, it is the continuous energy transfer through lactation and attendance of the female throughout rearing. While in capital breeders it is the pre-parturition body mass (Kovacs and Lavigne 1986; Higgins et al. 1988; Iverson et al. 1993; Houston et al. 2007). Despite our knowledge of the maternal traits that increase rearing success in income and capital breeders, we know little about potential intermediate-breeding pinnipeds.

An intermediate-breeding pinniped would bridge the gap between otariids and large phocids. Small phocids such as the harbor (*Phoca vitulina*) and ringed (*Pusa hispida*) seals are not characterized as capital breeders because they do not achieve the prenatal mass necessary to support the female and pup during rearing and therefore may continue to forage, however minimally, to maintain energy stores during nursing (Kocavs and Lavigne, 1986; Burns et al. 2004). Yet, these species do not appear to forage to the same extent as income breeders. Thus, harbor seals may not solely rely on pre-natal energy stores or on continuous and long-term foraging (Boness et al. 1994). Rather, they nurse their young for 4-6 weeks, during which they often swim with their pups in what are assumed to be foraging trips (Stein 1989). It appears however that these are at most opportunistic trips that cannot produce the energy necessary to sustain nursing (Washington Department of Fish and Wildlife (WDFW) unpublished data). Because harbor seals use a rearing strategy that can be characterized as neither income nor capital, they could be classified as some kind of intermediate breeder or fit somewhere in between the two extremes. Though they have not been previously classified this way, we suspect it is an accurate description of their breeding strategy.

The harbor seal is an excellent study organism to characterize this potential intermediate breeding style and reveal the traits responsible for its success in rearing pups. Unlike other small phocids, harbor seals are commonly found near humans, such as in the Salish Sea, USA, making them accessible for observations, and their population dynamics and biology have been well studied (Boness et al. 1994; Jeffries et al. 2003; Huber et al. 2010). Based on what is currently known about harbor seals it seems reasonable to hypothesize that harbor seal females employ an intermediate breeding strategy, and that success would be related with a combination of maternal traits: age, body mass, rearing experience and care behaviors. Older and larger females should have an advantage when transferring energy through milk from energy stores (behaving more like a capital breeder). Younger, smaller and/or less experienced females could compensate for their disadvantages with increased active care behaviors (behaving more like an income breeder). I predicted that the weaning health of pups reared by females of comparable masses would be higher if the mother displayed more active care behaviors. High pup weaning mass and pup health at weaning give the pup a greater chance of survival due to high energy stores to live off of as it learns to forage on its own (Muelbert et al. 2003).

I examined the attendance patterns of females and the maternal traits that correlate with rearing success and pup development in a presumably intermediate-breeding species: the harbor seal. I characterized the attendance patterns of harbor seal females during the rearing time to determine if their breeding strategy fell between capital and income strategies, then tested for a relationship between female age, body mass, rearing experience and active pup care behaviors with the health of the pup at weaning.

METHODS AND MATERIALS

Study site

I studied the maternal traits affecting rearing success in a suspected intermediate-breeding pinniped at Gertrude Island in south Puget Sound, Washington, USA. Harbor seals at this haul-out site have been studied for over 40 years by researchers from WDFW and the National Marine Mammal Laboratory (NMML). There are long-term data on 331 females that have been captured, tagged, measured, identified and followed throughout their lifetime. Including 245 females captured before adulthood that are either of known age or were estimated accurately within two years. This includes data on females' rearing experience and pupping history that currently use Gertrude Island during pupping season (WDFW/NMML unpublished data).

The haul-out site on Gertrude Island covers approximately 0.25 acres on a small islet in Still Harbor off the north side of McNeil Island, a closed and secure island centered at 47.2156°N and 122.6614° W (Figure 1). The two islands and the surrounding waters make up a closed wildlife refuge maintained by WDFW, the Department of Corrections and the Department of Social Health Sciences (DSHS). McNeil Island is closed to the public and access is restricted, making the haul-out site at Gertrude Island relatively undisturbed by people and the behavior of seals as natural as possible. Throughout the year, harbor seals haul out on a long land spit to rest. At the height of pupping and rearing season —which occurs from end of June to the end of September— upwards of 700 seals have been recorded there (Lambourn et al. 2012). Over the last 20 years the annual peak pup count has ranged from 80-140 pups, making the site an ideal rookery to study young seals (Lambourn et al. 2012). Given the existence of prior data and the limited disturbance by humans, harbor seals at Gertrude Island are an ideal system to examine the influence of maternal traits on the rearing success of pups in a putative intermediate breeder.

Data collection

I observed and photographed harbor seals from 3 blinds located on Gertrude and McNeil Islands during the 2013 and 2014 breeding seasons under NMFS Permit No. 13430-01. The blind on Gertrude Island was accessible by boat or by walking across the land bridge from McNeil Island exposed during low tide (Figure 1). The other blind locations were accessible by car and foot. Observation location was opportunistically chosen based on where the hauled out seals were most visible. I focused on marked females, focal females, that were choosing to haul out and rear pups at this site. The observations began in mid-June to avoid missing any births by focal females and were continued through September or until the last focal female's pup was weaned. Throughout the study seasons, 4-5 days per week were spent observing the haul-out to maximize the number of observations for all mother-and-pup pairs. Focal females were chosen to include the age range of breeding females (4 years to ~25 years). These females were identified by brands on their sides; these brands have been present since their initial captures, which occurred as early as 1993 until 2011 (WDFW/NMML, unpublished data). High-definition photos documented all sightings for later re-identification and confirmation of behavioral observations. Once birthing occurred, behavioral observations were conducted and pup health was assessed using a rating system developed in conjunction with WDFW biologists.

Age and size of females

For each branded female observed with a pup throughout the season, the age and pupping history data were accessed from the capture and re-sight databases of WDFW/NMML. The female's current age was calculated from her actual or estimated cohort, which was determined by WDFW/NMML at initial capture depending on age at capture: adult females at capture were given an estimated age of 4 years (as the earliest breeding age possible), sub-adults were given an age estimate of 2 or 3 years based on size, while yearlings were given an age of 1 year, and pups were given an age of zero years. Pups and yearlings are distinguishable by their very small size and the time of year they were captured. I calculated the pupping history from the number of years the female was re-sighted with a pup, which was obtained from the re-sight database. From previous capture-recapture data of Gertrude Island females, I developed a regression comparing individual mass to age using accurate previous data. The data used for the regression came from known age females captured multiple times and reweighed each time since 1985 (WDFW/NMML unpublished data). Only weight and age data used were from females that had been accurately verified (n=46). While assigning individuals to size classes is somewhat subjective, other studies on phocids have successfully employed similar methods (Baker et al. 2011). I identified six size classes (Table 1), which were later compared to the weights in the regression. The regression was created as an additional means to validate my size classes by comparing recently weighed adult focal females that had been assigned a size class.

To limit the subjectivity of assigning size classes to each female, I implemented a procedure whereby I and another experienced harbor seal researcher independently assigned harbor seals to a size class (Table 1) and justified our choice using photographs from the season and a comparison to the adult seals and pups around them. When our size assignments differed, we averaged the two values. To avoid perception bias from knowing the age of the females, the observers assigned size classes without looking at the history data of the female. I then compared the most recent capture weight of known individuals' weights to the mean of the regression model to validate the estimated weights for each described size class based on the standard deviations from the average values in the regression. A similar approach has been used to estimate sizes of monk seals in Hawaii (Baker et al. 2011).

Attendance patterns

I described the attendance patterns of the harbor seals to determine if they were characteristic of an intermediate breeding strategy. I monitored female and pup care behavior during two breeding seasons, determining the occurrence of females at the haul-out and whether they left pups on shore while on swimming/foraging trips or the pup followed. I also determined whether female behavior changed as the pup aged. Finally, previous data from WDFW/NMML's long-term data set were used to determine historic pupping date and rearing duration for each individual female by accounting for known birthing times from previous years. For each female pupping dates from previous years were used to determine when pupping occurred, dates were converted into day of year, averaged, and the standard deviations around an average pupping date per female was determined.

Pup care behavior observations

Following Martin and Bateson (2007), I recorded several mother and pup care behavioral states and events using focal sampling methodology on each focal female and pup pair (Table 2). I conducted two types of behavioral observations (Table 2). First, I opportunistically selected a focal female and pup pair and observed them for 30 min after which I switched to another pair. In this manner I observed all pairs present at the haul-out site. Behavioral state durations were recorded using a stop watch noting changes at the time they occurred; for behavioral events I used yes/no tally of occurrences to record the total number of each type of event occurring in the pair over the observation period.

Secondly, I monitored all present focal female-pup pairs simultaneously by scanning the haul-out continuously to record location, proximity, and the pairs' departures from the haul-out site throughout the day. Up to three observers focused on different portions of the haul-out to accurately account for each of the pairs in all the sections of the haul-out. The seals did not move fast on land so, through continuous scanning of the respective sections, the observers were able to account for movements in and out of the water for all the present pairs. The location of the pairs on the haul-out site was determined according to a previously-developed grid that relied on fixed objects placed on the haul-out site months prior to the first breeding season of the study (Figure 3). Given that harbor seals also hauled-out away from the site at Gertrude Island, periodic sweeps were conducted by driving and/or boating around McNeil and Gertrude Islands using a spotting scope to detect any individuals and/or pairs of interest and noting the status of the female and the pup. Proximity of female and pup to each other and to other seals was determined in harbor seal body lengths by opportunistically selecting one mother-pup pair and continuously observing for 30 min, then moving to another pair, and repeating this process throughout the day for the pairs that were present. If proximity changed over the observation period the values assigned for adult body-length measurements were averaged per minute of observation to reduce the observational time into single independent measurements for each variable measured.

Pup health measurements

The health of the pup was assessed qualitatively using a rating score develop in conjunction with WDFW biologists (Tables 3,4). For each pup I noted: overall body condition based on the presence of bony protrusions, lanugo (premature pup, evident by a white coat) vs. mature pup at birth, umbilicus, umbilical discharge, any visible injury, and discharge from nose/mouth/eyes. These signs were recorded during field observations and then reviewed at the end of the season in conjunction with another skilled researcher based on high-definition photographs taken during the observations. This health assessment was conducted once at the beginning of each day throughout the rearing period. For analyses, I only used the initial rating and the rating at weaning. High-definition photos of the focal females and their pups were also taken during the rearing period to verify the health of the pup and to validate the rating scores.

Data analyses

To describe the attendance pattern of harbor seal females it was important to account for changes in maternal behavior over the rearing time so a repeated measures analysis was used. Correlation analysis was used to reduce the behavior variables and reduce any collinearity before modelling the age of a pup to change in behavioral variables over the entire rearing time. Variables were selected through correlation analysis by finding highly significant correlations ($p<0.025$) and then using the variables with the least collinear relationships and the highest significance. A repeated-measures generalized linear model (GLM) was used to model these behavioral changes over the rearing period. Pup age was assigned as the dependent variable with the behavioral variables being used as fixed factors that would be related to pup age. For analysis of behavioral trend pattern changes over rearing time only behavioral data from 22 focal females that had at least three days of observation and for which the age of the pup was known were used in this analysis, making this data set have a total of 129 observations. The results from the GLM were used to describe any behavioral changes that can be attributed to the pup aging rather than to female traits.

To determine the female traits related to rearing success I used generalized linear mixed effect models (GLMMs), this time utilizing all the female/pup pairs (n=77 pairs). Two pup-related measures of rearing success were used as dependent variables: health rating at weaning and health rating change during the rearing period. I averaged the reported observational data for each female/pup pair to meet independence assumptions for GLMM analysis so each pair had only one set of observations, demographic data, and timing data (n=77 pairs). Health rating at weaning (Tables 3,4) was the score given the last time the pup was seen with the mother. Health rating change was determined by calculating the percent change from the first health rating to the health rating at weaning, the change value could be zero, positive or negative. The fixed factors used were individual female mass, female age, pupping history/experience and the indices of pup-care behavior. I ran pairwise Kendall ranking correlations between all the female traits to reduce collinear variables and get a better understanding of the dependence between variables. These were reduced by selecting significantly correlated behaviors ($p < 0.025$) and eliminating the most frequently correlated variables, to avoid problems of collinearity. It is possible that rearing success was also related to stochastic factors such as human interactions while away from the haul-out, disturbance/predation at time of birth, the genetics of the pup, the behavior of the pup or other external events not observed. To account for these random affects, I included the identity of the individual female as a random factor in the model. For modeling in GLMMs I was able to use data from females who were observed with pups in both seasons. For the health rating at weaning, the response variables did not fall under a normal distribution. For the end pup health rating data I transformed the health rating scores by multiplying all of them by 2 and generating another set of values by subtracting the transformed values from 10; I then combined both sets to use in the model with a binomial distribution. The response variable of health rating change also did not fit a normal distribution. To utilize the non-normal Gamma distribution, which accounts for a positive range, I transformed health rating proportional values by adding 1.5 to all values in order to eliminate any negative values and zeros. The models of best fit were determined using the lowest AIC value. All statistical analyses were run with R v. i386 2.15.2 and SigmaPlot v. 11.

Previous literature reports that for a pup to be successful post weaning a rearing time of 4-6 weeks but no less than three weeks of attendance by a female in necessary (Jeffries et al 2000, Zier and Gaydos, 2014). Because many of the females were observed only once or twice, the survival or mortality of their pups could not be determined, of the 77 pups only 52 had known mortality. As a result, mortality was not analyzed statistically; however the trends are described. Mortality/survival was measured by photo ID of pups post-mortem. Pups were also presumed deceased even when the carcass was not recovered if a female was seen without her pup numerous times before rearing time should have been completed. However, a total mortality percent for the haul-out was found as in previous years at this haul-out by finding the peak pup count before the end of pupping season, adding the number of dead pups found on the haul-out and dividing the number of dead pups by that total pup value.

RESULTS

During the 2013 and 2014 field seasons, a total of 54 adult females were observed with pups, 23 of these females were observed in 2013 and 2014 with different pups. All observed females ranged from 5 to 24 years of age. In both 2013 and 2014, the first full-term pups were born on June 27th. The last nursing pups seen with a female were recorded on September 12th and September 16th in 2013 and 2014, respectively. In 2013 a total of 50 pups were found dead on Gertrude Island, in 2014 only 23 dead pups were found on the same haul-out site. The highest pup count for the entire population on Gertrude Island was 118 in 2013 (August 27th) and 122 in 2014 (August 16th). Therefore mortality percent for the haul-out site was 30% and 16% in 2013 and 2014, respectively.

Age and size of females

Female size was strongly related with female age until 9 or 10 years of age (Figure 2; adjusted r^2=0.75 , $p<0.0001$, n=46). The nonlinear regression of exponential rise to a maximum equation with 2-parameters for the data set was: Weight=70.8*(1-exp(-

0.39*Age)), Constraints: b>0. Based on these results, the estimated weights for each female size class validated through this regression are described in Table 5.

Attendance patterns

A total of 202 30-min observations were conducted over two seasons for the 54 individual focal females and their pups used in this analysis, 23 females were observed in both season with different pups, giving a total of 77 pups or female/pup pairs. In general, harbor seal females spent about 4 weeks with their pup and did not leave them behind, even when departing the haul-out site. Of the females whose pups were not determined deceased, the length of time with the pup was 26.4 days ±14.3 SD (n=38 female/pup pairs). Females were regularly observed coming and going from the harbor with pups following. The vast majority of pairs were observed together the entire observation time including while swimming. During 72 of the 202 observations (35.6% of the total), time was spent swimming and for 71 of those, one member of the pair was following the other into the water (98.6% of trips). The one observation where a female left the haul-out without the pup following involved a pair that was never seen together again. In fact, they were only seen together for nine days during the season leading to a mortality determination.

Of the 54 females, 9 were seen once without their pups. Of these, 6 occurred when weaning was imminent and the breeding season had started. The remaining three females who left pups on shore were observed leaving their pup on the haul-out for a few minutes; in all these cases the pups were asleep and/or had a poor health rating. The females who did this returned within minutes to the pup to nose and rest again. Three pups were seen leaving the haul out without their females at the end of their rearing time. One observation of female 123 occurred when the pup was one month old. The pup left the haul out after being spooked by seals and female 123 didn't follow, this was the second to last time the pair was observed together. An observation of female 488 and her pup in 2014 occurred in which the pup left and swam to another portion of the haul out while female 488 was sleeping. When she woke up she very actively started searching for her pup all over the haul out until it was found. The last pup leaving on its own was female 689's pup. This pup left the haul out without the mother, but within a minute of pup leaving she followed. The only nursing pups observed alone during the peak pupping season were starving, were usually in a group high up on the spit near the blind, and were never observed being attended by any females. They were usually later found dead in the same location.

Female behaviors that were correlated for reduction purposes are seen in Table 6 and many were interestingly correlated with pup age. From repeated measures GLM I found that as pup age increased, number of bonding events, time moving, and proximity of female to pup decreased, while nursing and amount of time resting increased (Tables 7-8). This was also indicated by the large difference in the averages between the first and last week of the study (Table 9).

Based on WDFW's capture data, the pupping date of each individual female occurred within a week from the prior year (see Appendix II for average pup date and standard deviations for each individual female). The pupping date was strongly positively correlated with the age of the female in the correlation analysis of the two seasons of focal observations with older females pupping later in the season (Kendall's Tau rank correlation: Kendall- RT = 0.26, $p<0.001$, $n=77$).

Traits related to rearing success

Many behavioral variables were strongly correlated with each other and to previous maternal success (Table 10). No behaviors were significantly correlated with maternal age. Size was positively related with number of protective events, age and previous years of success. Protective events were correlated with amount of time alert and the number of bonding events. Amount of time moving was also significantly correlated with proximity to other seals. Bonding events were correlated with amount of time alert, moving and side of haul out they chose to haul out on. Amount of time moving was correlated with proximity to others and distance from tip chosen. However, percent of previous successful experience was related to many behaviors (Table 10). Six females were affecting some of the correlations given that their behaviors were outliers to the behaviors of the majority of the females. However, the significance of the correlations were not driven by these outlying females after a strict measure of significance was used (see Appendix I). Life history data for all females observed are found in Appendix II.

I did not use the following behavior variables for the GLMM analysis: time alert, time swimming, bonding events, and side of haul out. These variables were all significantly correlated with many other variables. The behavioral variables used in the GLMMs were female age (fA), female size (fS), years of previous pups (Yp), previous success percentage (%S), first day with pup (fdP), days spent with pup (Dw/P), time moving (tM), time resting (tR), distance from tip (DfrT), distance to other seals (dTO), distance of pup to female (MP), protective events (PtE), time nursing (tN), and the individual random factor (Indv).

Health rating change of the pup was best predicted by female age, female size, percent previous success, the days spent with the pup, time spent moving, haul-out location’s distance from the tip, distance to other seals, and the random individual affect (Tables 11-12). The health rating of the pup at the end of the season was related to female age, percent previous experience, number of days spent with the pup, and distance from the tip of the haul-out site, distance to other seals and the random individual affect (Tables 13-14). While location selections were related to many other behavioral variable it is interesting to note that a few locations on the haul out were found to be frequented by females with pups more than others (Figure 3).

Regarding pup mortality for individual female/pup pairs, 11 pups were confirmed as lost or deceased before weaning. There were eight females over the age of 20 years and one of those lost her pup, while there were 22 females at or below the age of 10 years and two lost their pup. There were 25 females between the age of 11 and 19 years and of those, seven lost their pup. Six of the females that had confirmed lost pups were large females, two were medium, one was medium/large, and one was small/medium. Two females had 10 or more years of previous pups and both had 50% success rate over those previous years.

DISCUSSION

Attendance patterns and an intermediate –breeding strategy

Harbor seal females apparently employed a breeding strategy that falls somewhere between capital and income breeding strategies. They did not remain on shore and offload nutrients throughout the entire rearing time, hence they did not resemble capital-breeding pinnipeds entirely. However, they did not leave their pups on shore while on foraging trips as reported by Boness et al. (1994), but rather pups followed the females on swimming trips. This finding indicates that harbor seals did not adhere to an income-breeding strategy either.

If these findings are observed in other regions, it seems that perhaps a term such as intermediate breeding is appropriate for the species.

In my study, females in South Puget Sound left daily on swimming bouts and the pups remained with them 98.6% of the time. This finding differs from observations in different populations of harbor seals; in the Sable Islands, Nova Scotia, females swam 55.4% of the time and pups swam with them 39.8% of that time (Bowen et al. 1999). At Gertrude Island the few minutes of observations during which females that successfully reared their pup left it on shore, the females were observed swimming near the haul-out. This observation suggests that females likely left land momentarily, perhaps to meet thermoregulation needs during the hot summer months. Six of the nine females observed without their pups once were seen alone the day before the last observations with their pup, which could be merely a part of the weaning process. The breeding season for harbor seals is at the end of pupping season, so it is possible that the female is out breeding with males as her pup starts to wean (Scheffer, 1944; Boness et al. 2006). The harbor seal pup's ability to swim at birth allows it to follow its mother on swimming trips and potentially learn foraging techniques from her early on and throughout the entire rearing time unlike the income breeding otariids (Boness 2009; Burns 2009). Since harbor seals' rearing time is much shorter than typical income breeders, which aren't as capable of diving as soon after birth (Rehberg and Burns 2008), pups would seem to benefit from learning as much as possible from the female before weaning. However, due to incomplete muscle development pups are not able to dive as deep as their mother even post-weaning so they rely on the mass gained through rearing until they can forage effectively (Prewitt et al. 2010). Given that pups did not appear to forego swimming trips during rearing, like true capital breeders do, my finding suggests that harbor seals mediate the divide between these two strategies.

Stephens et al. (2009) suggest that the categorization of breeding strategy follows a continuum between the extremes of capital and income breeding strategies. My results support the idea that harbor seals used a strategy between these two extremes. They also indicate that harbor seals did not leave their pups on shore as previously believed. Pinniped biologists have consistently adhered to utilizing these two terms when attributing strategy labels to species without allowing for mediating strategies like the one I propose. If conception of this continuum is adopted in the field it would eliminate many misconceptions about these extremely variable pinnipeds. There is little evidence that harbor seals in Washington are able to maintain an income while passing it on to the pup for development (WDFW, unpublished data), in this regard they may be more similar to the capital breeding pinnipeds. However, their behaviors were not consistent with a capital breeding strategy, perhaps due to the precocial nature of pups and the locations on which this species chooses to haul out. Pup precociousness in harbor seals might be related to the presence of terrestrial predators and at Gertrude Island, along with many other haul outs in the area, to the loss of available land on which to haul-out at high tide.

Pupping season timing and the placement of a species on the continuum of breeding strategies may be driven by food availability and seasonality (Stephens et al. 2009; 2013). Harbor seals are viewed as generalist feeders able to exploit prey populations throughout the year; however, in the Salish Sea this generalist behavior appears to be also comprised of individual specialists (Lance et al. 2012; Bromaghin et al. 2013). As well, there appear to be differences in the prey consumed by female and male harbor seals in the Salish Sea. During the pupping season, female harbor seals are eating small estuarine fishes (Bjorland et al. 2015). At Gertrude Island then, females could be opportunistically feeding on small estuarine fishes in shallow areas while on swimming trips with pups; teaching them how to forage on small fish which the pup will be able to forage for and handle on its own after weaning. During the pupping season, female harbor seals with pups do not dive as deep as they do during the rest of the season but nonetheless still undergo diving trips (Boness et al 1994). It is unclear if females swimming with pups foraged and taught their pups how to forage at Gertrude Island. Although the idea is plausible and would explain the ability of females to maintain some mass during the breeding season, a study placing tags to follow the movements and dives of females and pups, and collecting scat to determine their diet is needed to confirm this assertion. My findings support the argument that harbor seals behaved neither like income nor like capital breeders, but rather followed a strategy in between both extremes. Work in other regions can establish how pervasive this type of strategy is in the species.

Female traits related to rearing success

Several female traits were related to rearing success of pups for both measures of rearing success (ending pup health rating and pup health rating change over rearing): days spent with pup, age of female, female size, percent success of previous reproduction experience, proximity to other seals, distance from tip, and time spent moving. The behavioral trait that factored most significantly into success in both rearing success models was the amount of time the female spent with the pup before weaning. This finding is similar to results found in the Sable Island harbor seals where seals that increased amount of time with pup were able to nurse their pups to higher masses (Bowen et al. 2001). In my study, decreased distance to other seals was related with a higher health rating of the pup. Unlike previously predicted, age seems to be negatively related to pup survival. Life history of previously successful individual females appeared to have an effect on success and behavioral choices. A smaller size was implicated and related to a greater health rating change over rearing.

A positive change in pup health rating over the rearing time was driven by maternal behavioral factors and demographic female traits. There was a significant negative relationship between female age and size with successfully changing the health rating of the pup. I believe this finding is related to the fact that younger, smaller females had initially smaller pups with lower health rating and therefore had the most possibility for greatly altering their pups' health rating over rearing. If this idea is correct, a female would need to actively adjust her behavior to greatly alter her pup's starting health rating. Days spent with pup over rearing was significantly related to a higher positive pup health rating change, where a decreased distance from other seals proved to lead to a higher health rating change over the rearing time. The trend relating isolation to decreased pup health was apparent in the relationship between decreased proximity to other seals and improving health rating. It may be that females were choosing to isolate themselves from the other seals in response to the decreased viability of their pup. Isolating her pup could be driven by the pup's immediate health rather than a preventative behavioral measure. An increase in moving indicates that females were more actively monitoring their pups and their surroundings to increase the pup's health rating. However, in the model amount of time moving was not significantly related to the increase in health change but was kept in the model regardless, perhaps due to a collinearity issue with distance from tip and distance to other seals, which were both kept in the model.

While percent success was kept in the model, it again was not significantly related to health rating change. However, it was positively related to an increased health rating change. I suspect that its importance in the best fit model was related to this factor's collinearity with many behavioral variables. However, its positive relationship with higher increase in health rating change over rearing indicates that maternal behaviors were important factors affecting health rating change. While percent previous success was not significant in effecting the model, it was negatively related with ending pup health rating. The same collinear effects were most likely driving its place in this model, but its smaller negative relationship may be related to the negative effect of the behavioral variables kept in the model that percent previous success were correlated with. Many behaviors were strongly correlated with percent of previous witnessed pupping success, implying that previous experience may be driving current behavioral trends in a female, and once a female found a behavioral pattern that worked for her, she utilizes it more in the future. Of the three demographic characteristics (age, size and experience), successful experience was the most correlated with pup care behaviors. This is understandable considering these animals are relatively intelligent and able to reproduce for many years; they are bound to learn from previous success and failure. Maternal age has previously been positively related to pupping success and trends in behavior (Boness 1996; Ellis et al. 2000). However, this population is unique in also having life history data on many females so I was able to utilize experience as an individual trait independent of age.

Increased age had a significant negative effect on the ending pup health rating, which contradicts research which reported that pup mass increases with maternal age (Ellis et al. 2000; Bowen et al. 2001). My findings indicate that the older a female becomes, the more difficult it may be for her to have successful pups; there were fewer older females pupping than there were females 10-20 years of age. This indicated that as females age past 20 years of age they produce pups less often than younger females. This trend is typical for many species of animals, including humans, where an age range of highest productivity is observed (Blums and Clark 2004). The discrepancy between my results and previous findings can be explained by the extent of the data set, my data included known age females beyond 20 years of age, whereas previous studies termed the oldest females as 11+ years of age (Bowen et al 2001). As such, the 10 –20 year-old females I observed had the highest relative number of pups of the three different age groups, which then agrees with the findings of Bowen et al. (2001) and Ellis et al. (2000). My findings also suggest that females beyond 20 years of age were reaching the end of their fecundity life span. A comprehensive study of these behaviors hasn't been conducted before in conjunction with life history traits, therefore there is little alternative explanations for these trends in other populations.

Some female behaviors changed as the pup became older, regardless of female age, size and experience. The decrease in bonding events over the course of the season suggests that bonding through nose touches is crucial earlier in the pup's life to solidify maternal and pup bonding, which then carries through the rest of pupping season. This finding is in agreement with previous research characterizing nose-touching as important to mother-pup recognition (Boness 1996; Ellis et al 2000). It is crucial that early in life pups are allowed to bond significantly with their mother to ensure recognition and maternal bond. Time spent nursing increased over the pupping season significantly, suggesting that as the pup increased in size, its need to nurse increased as well given that bigger animals require more calories to subsist (Iverson et al 1993; Muelbert et al 2003; Burns et al 2004; Lang et al 2009). The amount of time spent resting also increased over the course of the season, which may indicate that as the pup ages it requires additional time to digest and transfer the additional milk into fat for increased growth.

Not all females that weaned healthy pups showed all the traits that correlated with rearing success, showing that a combination of traits and perhaps other variables unaccounted for in my study affect success. For instance, three old females weaned healthy pups despite their age; however, they were seen to keep their pups for longer than four weeks which was one of the traits driving success for this population in general. Female 488 was extra-large and has a 100% success rate over 5 years of pupping while being of medium age, otherwise size did not have a relationship with success in the rest of the seal population. Unlike the main trait driving success in the northern elephant seal (*Mirounga angustirostris*), a capital-breeding pinniped (Iverson et al. 1993; Crocker et al 2001), body mass did not have a significant positive effect on rearing success. Body mass of harbor seals at Sable Island, Nova Scotia did not have a great effect on success either (Ellis et al 2000). In the case of the females at Gertrude Island only one female was seen driving any correlation with success, an extra-large female 488, however her inclusion did not affect the model. There were females such as 745 which had premature pups that were not thriving, but through increased attendance and prolonged rearing time were able to rear successfully. The effect of increased days spent with pup and rearing success can be explained easily; attending the pup longer allows the female to transfer more fat and nutrients to the pup, thus ensuring its survival to a weaning age. The larger a pup is at weaning, the higher chance it has of surviving on its own (Burns et al 2004).

As the weaning mass of the pup is extremely influential on its post-rearing survival (Cottrell et al. 2002; Muelbert et al 2003) one would expect the larger females to be able to increase this success and get their pups larger. This was only seen with the extra-large female 488 whose pups both years were given a health rating score of 5 and her pup in 2014 was seen a week after rearing on the haul out by itself continuing to thrive. Since she was the largest female and the only one labeled as an extra-large female with a pup we can't assume this significant correlation is attributed completely to her size. It requires further study of extra-large females compared to others to determine whether at an extra-large sized female is set up for higher success.

From the observations of the same females in both years I saw multiple females behaving differently with different pups. Some were seen keeping pups for different lengths of time and/or being more protective of one pup compared to the other. This is interesting and another example of these females being highly variable and intelligent enough to alter behavioral strategies based on their pup's individual needs. This system is complicated as there are extraneous factors that are impacting the success of the pup regardless of their mother's ability to care for them. Even prime aged, attentive females could lose their pup due to environmental factors like being spooked and separated before bonding, disturbed and separated by human interaction, boating traffic or any other myriad of unlucky occurrences.

Based on counts of the total number of pups and dead pups, there was a much higher mortality in 2013 than in 2014. The two seasons were similar in timing of first pup and last nursing pup, with the same high pup count for the season. However, the timing of the high count was much earlier in 2014 than in 2013. The two seasons differed in that the majority of pups were born earlier in the 2014 season and therefore weaned earlier. At the same time, the fact that pupping date was fixed for individual females over the years and that there was a correlation between female age and her pupping date indicate that several factors influence pupping date, which has been gradually becoming earlier in the year for this population. NMML/WDFW's database indicate that pupping season previously peaked in middle to late August, whereas the peak in my study occurred in the middle of July. Other populations of harbor seals have also experienced a shift in pupping date to an earlier time of year and has been attributed to environmental factors and food availability (Reijnders et al. 2010). Further work on external environmental factors, female and pup genetics, hormones and tandem activities is needed at Gertrude Island to determine the cause(s) for the shift in pupping season.

My study is the first to adequately document swimming trips by females and their pups during rearing time and present evidence which supports the argument that harbor seals employ a potential intermediate breeding strategy. Unlike capital breeders, in which body mass is crucial to rearing success, and income breeders, in which foraging and attendance patterns are related to success (Higgins et al. 1988; Iverson et al. 1993), the traits indicative of a successful rearing strategy in my study were an increased amount of time with the pup, pupping date, decreased age, previous successful experience and level of isolation from other seals. Thus, the strategy used by harbor seals is not only different from an income or capital strategy but also requires a combination of traits not necessarily correlated with success in either of the other two strategies. At the same time, the individual variability observed in my results indicates that successful rearing can be accomplished by any number or combination of traits. Although this study provided evidence to answer the question what makes a successful harbor seal mother, further research is needed to examine the influence of individual behavior in such success.

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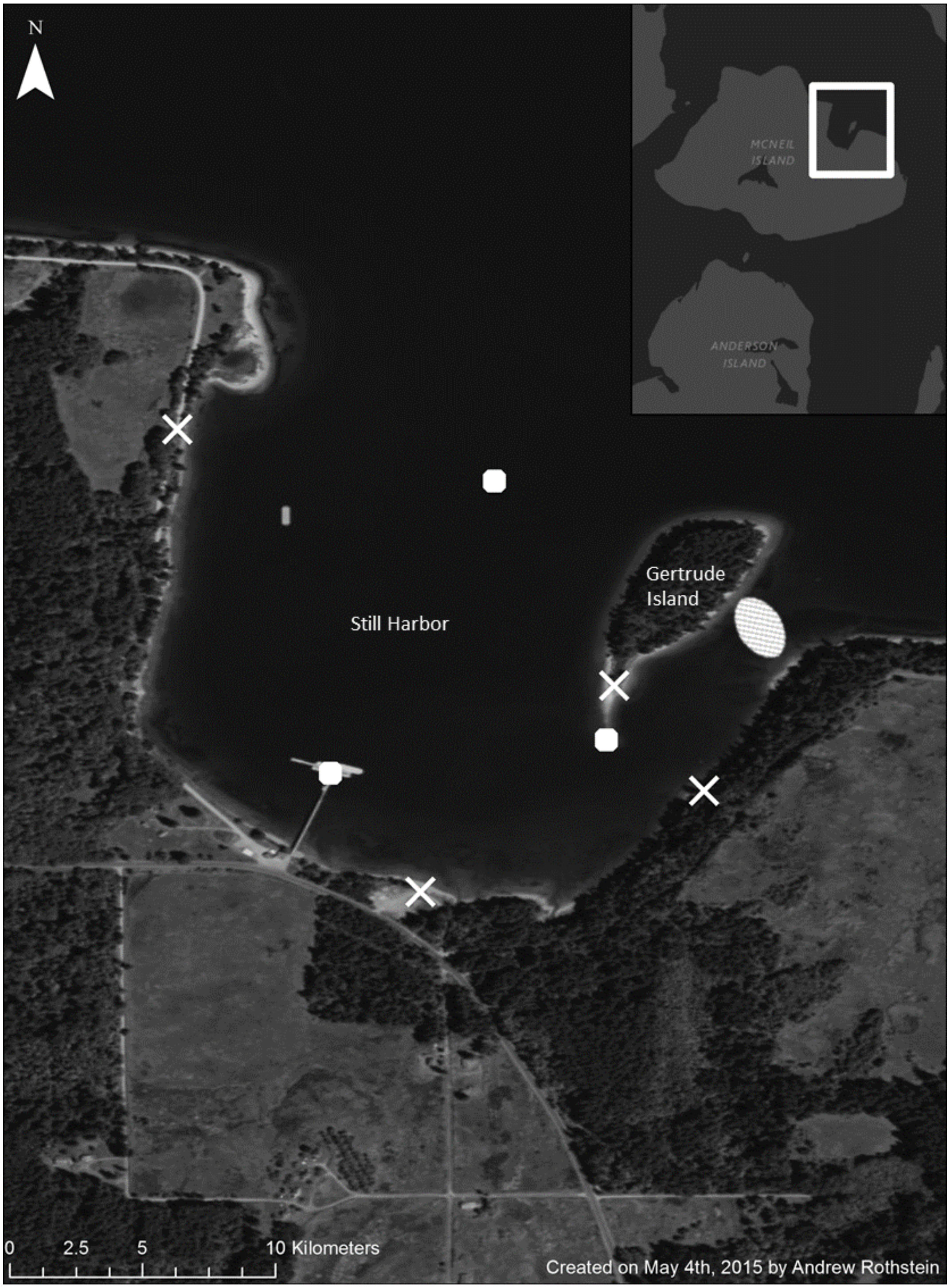

Figure 1. A map of study sight in Still Harbor indicating the locations of observation locations with “X”, haul out sites with spots and the land bridge (shaded oval) used at low tide to cross from McNeil Island to Gertrude Island to access the observation blinds on it. Inlay of McNeil island indicating Still harbor in relation to the surrounding island.

Table 1. Female size classes. Descriptions are based on recapture data of Gertrude Island females during, post-pupping season.

Size Class	Description
1	Small female, about twice the size of a typical pup and less than half the size of large adult males.
1.5	Small/medium female, over twice the size of a typical pup, about half the size of large adult males.
2	Medium female, about three times the size of a typical pup and over half the size large adult males.
2.5	Medium/large female, over three times the size of a typical pup and about two-thirds the size of large adult males.
3	Large female, about four time the size of a typical pup and about three-fourths the size of large adult males.
3.5	Extra-large female, about four times the size of a typical pup but very robust and very near the size of large adult males.

Table 2. Behavioral events and states used in the 30-minute focal observations of harbor seal females at Gertrude Island. Location and proximity choices used in both the 30-minute focal observations and the scanning throughout entire day's observation. Traits represent behavioral traits that were based on the entire rearing time.

Events	Description
Nose touch	Touches the nose of the pup.
Nudging	Touches the body of the pup (but not the nose) to nudge it to either move or nurse.
Scanning	Holds head up in the air, moving it around.
Lunge	Thrusts head at other seals but does not attempt to bite.
Biting	Bites at other seals.
Nursing	Allows pup to nurse
State	**Description**
Resting	On land or in shallow water, eyes open and/or closed head lying flat on land.
Alert	On land or in shallow water, eyes open and head up in the air.
Moving	Any movement on land.
Swimming	In water, including shallow water, fully submerged and actively moving.
Location	**Description**
Selection	Where the pair was hauled out during observation
Proximity of pair	Estimating distance between female and pup in seal body lengths
Proximity to others	Estimating distance between the pair and the nearest neighboring seal.
Time on haul out	Amount of time the pair were on the haul-out throughout the entire observation.
Trait	**Description**
First day with pup	The day of pupping season that the female either gave birth or was seen with a pup that appeared to be less than a week old.
Days spent with pup	The number of days the female tended to the pup before weaning.

Table 3. Pup health visual assessment rating system for pups 0-2 days old.

Rating	Description
1 = poor	> 50% lanugo coat, skinny seen by protruding bones at shoulder and hip, any obvious deformities, hunched back.
2 = fair	≤ 50% lanugo coat, can see slightly protruding bones at shoulders or hips, no external injuries or noticeable deformities.
3 = good	Full term pup seen by no lanugo coat; average size seen by lack of protruding bones but has a distinct thin neck, no external injuries or discharges
4 = very good	Robust, no protruding bones observed, no external injuries
5 = excellent	Very robust, neck is very thick, no external injuries present

Table 4. Pup health visual assessment rating system for pups >2 days old.

Rating	Description
1 = poor	Very skinny, protruding bones seen at shoulders and hips, skin loose on figure, may have external injuries or eye/nose/mouth discharge
2 = fair	Skinny, can see slight protruding bones at shoulders or hips, minimal if any external injuries or discharges
3 = good	Average size seen by lack of protruding bones but has a distinct thin neck, no external injuries or discharges
4 = very good	Robust , no protruding bones present, no external injuries
5 = excellent	Very robust, neck is very thick, no external injuries present

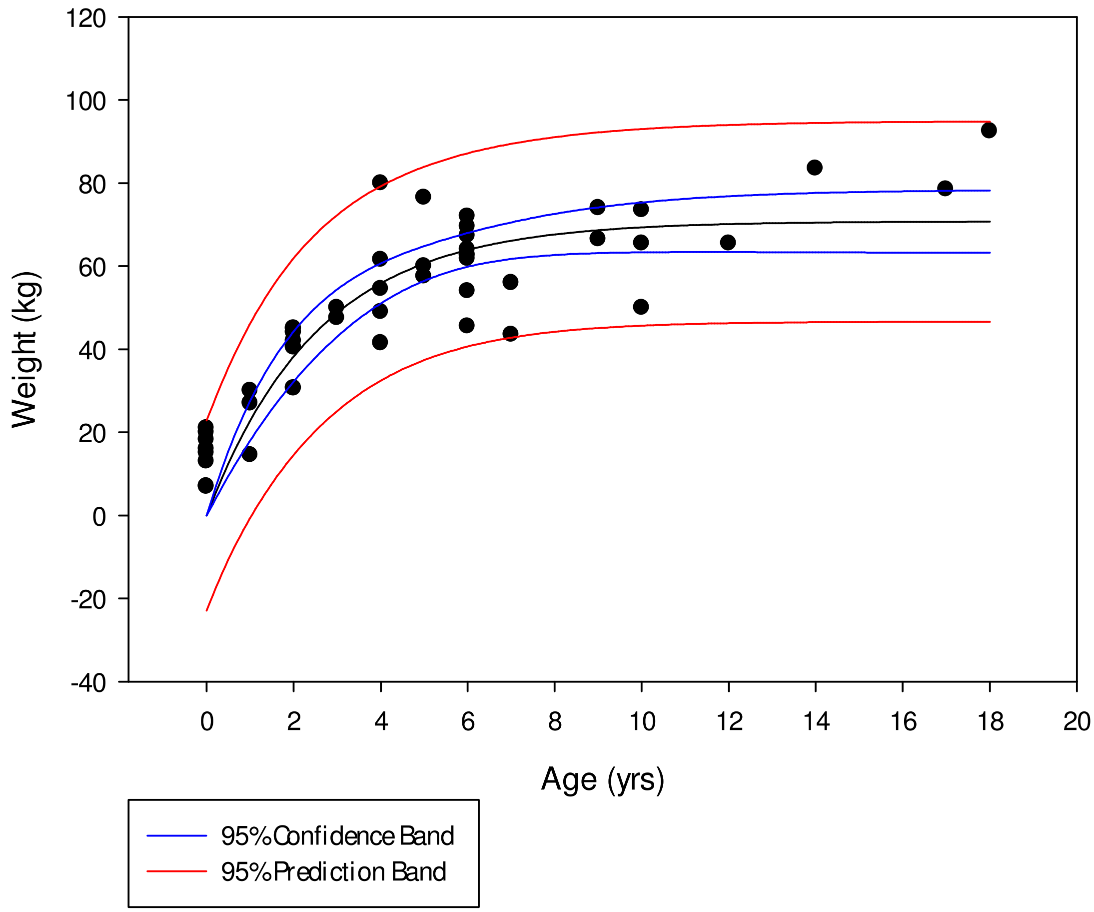

Figure 2. Regression of age and weight of females from Gertrude Island. Capture-recapture data since 1984 (WDFW unpublished data). Adjusted r^2=0.75 , p<0.0001, n=46. Equation: Weight=a*(1-exp(-b*Age)), Parameters: a= 70.8002 (SE= 3.788), b= 0.3889 (SE= 6.756e-2)

Table 5. Weight approximations for each size class based on the regression and comparing to recently weighed adult females in the data set.

Size Class	Approximate mass (kg)
1	≤ 40
1.5	40 - 50
2	50 - 60
2.5	60 – 70
3	70 – 80
3.5	Over 80

Table 6. Correlated behaviors over pup age in the repeated measures data set (n=22 females) with a total of n=129 observations. Used to reduce variables in model for change in behavior over pup age. (*variables kept in model)

Correlated behaviors	**Correlation statistic (T-value)**	**p-value**
Time resting* vs. Time alert	-0.44	< 0.01
Time resting* vs. Time moving*	-0.35	< 0.01
Time resting* vs. Time swimming	-0.51	< 0.01
Time resting* vs. Protective events	-0.33	< 0.01
Time resting* vs. Bonding events	-0.12	< 0.01
Time alert vs. Time moving*	0.24	< 0.01
Time alert vs. Proximity to others*	-0.19	< 0.01
Time alert vs. Bonding events*	0.44	< 0.01
Time alert vs. Protective events	0.42	< 0.01
Time moving* vs. Distance from tip	-0.17	< 0.025
Time moving* vs. Bonding events*	0.37	< 0.01
Time moving* vs. Protective events	0.21	< 0.01
Distance from tip vs. Side of haul out	0.48	< 0.01
Distance from tip vs. Proximity to others*	0.22	< 0.01
Side of haul out vs. Proximity to others*	0.23	< 0.01
Protective events vs. Proximity to others*	0.041	< 0.025
Protective events vs. Bonding events*	0.43	< 0.01

Table 7. Generalized Linear Model (GLM) results for behavioral changes over the pup's aging to weaning. Variables chosen by correlation analysis of data set from females with multiple observations over rearing time to completion at weaning (see Table 6). The model of best fit is represented by the lowest AIC value.

Model	**Df**	**AIC**	**ΔAIC**
Pup age ~ Time resting + Bonding events + Time nursing	122	965.15	□
Pup age ~ Time resting + Bonding events + Time nursing + proximity of pair	121	965.96	0.81
Pup age ~ Time resting + Bonding events + Time nursing + proximity of pair + Time moving	120	966.62	1.47
Pup age ~ Time resting + Bonding events + Time nursing + proximity of pair + proximity to others + Time moving	117	969.3	4.15

Table 8. Coefficients and statistical significance of factors for the best fit model for harbor seals female behavioral patterns as the pup aged.

Factor	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	9.124	2.87	3.174	0.0019 **
Time resting	0.0045	0.0020	2.26	0.0258 *
Bonding events	-0.305	0.132	-2.31	0.0223 *
Time nursing	0.0076	0.0032	2.37	0.0193 *

AIC: 965.15

Table 9. Values of attendance factors during first week of birth and last week of weaning (n= 41). Data from focal 30-min observations or simultaneous all-day observations (see Methods).

Attendance factor	**First week birth Avg.±SD**	**Last week weaning Avg.±SD**
Time swimming with pup (sec)	291.6±503.8	187.0±381.6
Time nursing (sec)	99.5±245.6	200.0±347.7
Bonding events	6.0±12.4	1.3±1.9
Proximity of female to pup (Body Lengths)	1.2±0.4	1.4±0.7
Proximity of pair to others (Body Lengths)	2.6±1.3	2.3±1.3
Time moving with pup (sec)	126.2±155.2	57.3±86.0
Time resting with pup (sec)	1098.2±559.6	1411.2±422.5

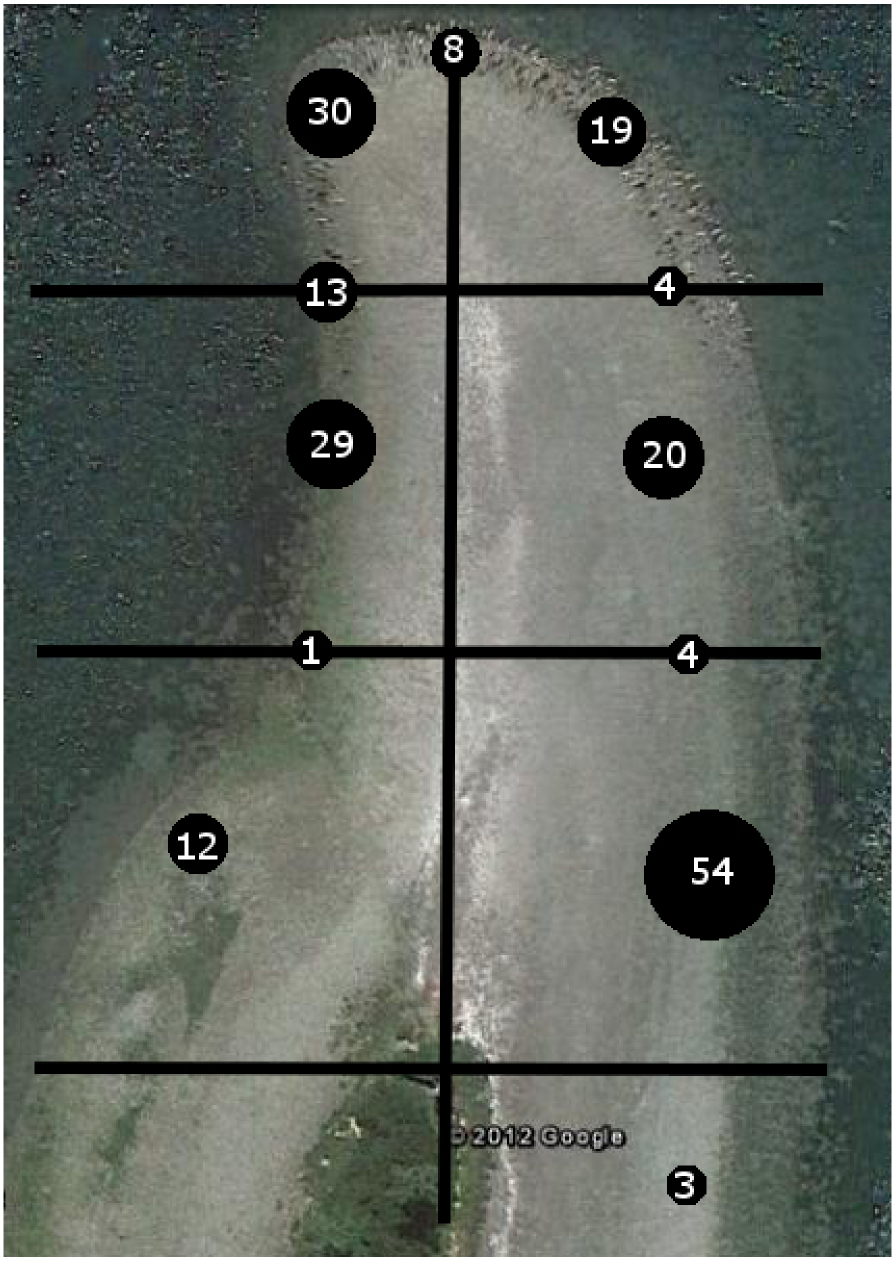

Figure 3. Locations selected by nursing female harbor seals. The circles represent the number of observed times in that section.

Table 10. Significantly correlated behavioral variables from observational data. The line indicates the separation of behavioral correlations and the included behaviors correlated with the life history variables. (* indicates variables kept for model)

Correlated behaviors	**Correlation statistic (T-value)**	**p-value**
Time resting* vs. Time alert	-0.23	< 0.01
Time resting *vs. Time swimming	-0.56	< 0.01
Time alert vs. Bonding events	0.39	< 0.01
Time alert vs. Protective events*	0.42	< 0.01
Time alert vs. Time moving*	0.19	< 0.02
Time moving* vs. Bonding events	0.27	< 0.01
Time moving* vs. Proximity to others*	0.22	< 0.01
Time moving* vs. Distance from tip*	0.12	< 0.02
Side of haul-out vs. Distance from tip*	0.35	< 0.01
Side of haul-out vs. Proximity to others*	0.21	< 0.025
Side of haul-out vs. bonding events	-0.22	< 0.02
Protective events* vs. Bonding events	0.38	< 0.01
Previous success (%)* vs. Days with pup*	0.29	< 0.01
Previous success (%)* vs. Time moving*	0.27	< 0.01
Previous success (%)* vs. Bonding events	0.21	< 0.02
Previous success (%)* vs. Protective Events*	0.31	< 0.01

Table 11. Evaluation of model selection of best fit model for change in health rating score (ΔHR) over the rearing time. The model of best fit is represented by the lowest AIC value. Variable acronyms: Female age (fA), female size (fS), years of previous pups (Yp), previous success percentage (%S), first day with pup (fdP), days spent with pup (Dw/P), time moving (tM), time resting (tR), distance from tip (DfrT), distance to other seals (dTO), distance of pup to female (MP), protective events (PtE), time nursing (tN), and the individual random factor (Indv)

Model	**Df**	**AIC**	**ΔAIC**
ΔHR ~ fA + fS + %S + Dw/P + tM + DfrT + dTO + Indv	41	-31.494	-
ΔHR ~ fA + fS + %S + Dw/P + DfrT + dTO + Indv	42	-31.083	0.41
ΔHR ~ fA + fS + %S + Dw/P + tM + tR + DfrT + dTO + Indv	40	-30.761	0.73
ΔHR ~ fA + fS + fdP + Dw/P + tM + tR + DfrT + dTO + Indv	47	-23.972	7.52
ΔHR ~ fA + fS + %S + fdP + Dw/P + tM +tR + DfrT + dTO + Indv	39	-29.756	1.74
ΔHR ~ fA + fS + %S + fdP + Dw/P + tM + tR + DfrT + dTO + tN + Indv	38	-28.834	2.66
ΔHR ~ fA + fS + Yp + %S + fdP + Dw/P + tM + tR + DfrT + dTO + tN + Indv	37	-27.042	4.45
ΔHR ~ fA + fS + Yp + %S + fdP + Dw/P + tM + tR + DfrT + dTO + MP + tN + Indv	36	-25.468	6.03
ΔHR ~ fA + fS + Yp + %S + fdP + Dw/P + tM + tR + DfrT + dTO + MP + PtE + tN + Indv	35	-23.55	7.94

Table 12. Coefficients statistical significance of factors for the best-fit model of change in health rating over rearing.

Factor	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	3.668	0.2620	14.00	<2e-16***
Age of female	-0.0546	0.01055	-5.178	6.32e-06 ***
Size of female	-0.1341	0.04883	-2.747	0.008899 **
Percent successful experience	0.0372	0.09602	0.388	0.700
Days spent with pup	0.00763	0.00215	3.546	0.000995 ***
Time spent moving	0.000378	0.00027	1.402	0.168
Distance from tip	-0.0596	0.01493	-3.991	0.000266 ***
Distance from other seals	-0.0769	0.02504	-3.072	0.003765 **
Individual – Random factor	-0.00157	0.00027	-5.938	5.30e-07 ***

AIC: -31.494

Table 13. Evaluation of model selection of best fit model for ending health rating score (EHR). The model of best fit is represented by the lowest AIC value. Variable acronyms: Female age (fA), female size (fS), years of previous pups (Yp), previous success percentage (%S), first day with pup (fdP), days spent with pup (Dw/P), time moving (tM), time resting (tR), distance from tip (DfrT), distance to other seals (dTO), distance of pup to female (MP), protective events (PtE), time nursing (tN), and the individual random factor (Indv)

Model	**df**	**AIC**	**ΔAIC**
EHR ~ fA + %S + Dw/P + DfrT + dTO + Indv	47	165.01	-
EHR ~ fA + %S + Dw/P + DfrT + Indv	50	178.45	13.44
EHR ~ fA + %S + fdP + Dw/P + DfrT + dTO + Indv	46	165.57	0.56
EHR ~ fA + Yp + %S + fdP + Dw/P + DfrT + dTO + Indv	45	166.09	1.08
EHR ~ fA + Yp + %S + fdP + Dw/P + DfrT + dTO + PtE +Indv	44	166.27	1.26
EHR ~ fA + Yp + %S + fdP + Dw/P + DfrT + dTO + MP + PtE + Indv	43	167.45	2.44
EHR ~ fA + Yp + %S + fdP + Dw/P + tM + DfrT + dTO + MP + PtE + Indv	42	169.2	4.19
EHR ~ fA + fS + Yp + %S + fdP + Dw/P + tM + DfrT + dTO + MP + PtE + Indv	41	170.92	5.91
EHR ~ fA + fS + Yp + fdP + Dw/P + tM + tR + DfrT + dTO + MP + PtE + Indv	48	200.71	35.7
EHR ~ fA + fS + Yp + %S + fdP + Dw/P + tM + tR + DfrT + dTO + MP + PtE + Indv	40	172.68	7.67
EHR ~ fA + fS + Yp + %S + fdP + Dw/P + tM + tR + DfrT + dTO + MP + PtE + tN + Indv	39	174.62	9.61

Table 14. Coefficients and statistical significance for the best-fit model of health rating at the end of the season.

Factor	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	6.078990	1.9196	3.167	0.00154 **
Age of female	-0.177166	0.070773	-2.503	0.0123 *
Percent successful experience	-0.159345	0.430149	-0.370	0.711
Days spent with pup	0.049117	0.011050	4.445	8.79e-06 ***
Distance from tip	-0.167695	0.075373	-2.225	0.0261 *
Distance from other seals	-0.236385	0.109404	-2.161	0.0307 *
Individual Seal - Random	-0.003817	0.001763	-2.166	0.0304 *

AIC value: 165.01

APPENDIX I – Females behaving outside the parameters of the model successfully.

Females that behaved outside the normal parameters and were outliers in the correlations:

Female 614 was observed in both 2013 and 2014. In 2013 she reared her pup to completion with an ending health rating score of 4. Her behaviors were well within the normal values which created the model with her pup in 2013. However, her behaviors with her pup in 2014 were very different. There were two complete observations of this pair that were conducted two days apart in August. During these two observations she had increased protective events, on 8/10/2013 she had 20 protective events and on 8/12 she had 51 protective events which is 96.2% higher than the average of 1.9482 events/observations. She also was an outlier when it came to location selection, she chose to isolate herself and pup by hauling out behind the blind which is an outlier compared to the rest of behavioral location selection by the rest of the observations of the females.

Female 745 is a small female with high success and has a 95.06% higher bonding event amount than the average with 71 bonding events above the average of 3.5078 bonding events/observation. It should be noted that the observation which had 71 bonding events noted was recorded very recently after birth.

Female 739 was observed with higher than normal levels of bonding events and amount of time spent moving. Her bonding event number is 57 for one observation, it should be noted that the observation in which this occurred was taken very recently after birth. This value is 93.85% higher than average bonding events/observation. Her amount of time spent moving for an observation is 867 seconds which is 89.76% higher than the average of 88.7565 seconds/observation. However, the correlations between moving and the other factors were all still significant after removing 739's observations from the data set.

Female 627 is a small female that behaved outside the normal in three different variables. Her amount of movement per observation was 690 seconds/observation which is 87.14% higher than the average. The month in which she pupped was an outlier, she was the only focal female to pup in June. Her location selection was very different from the normal parameters, she chose to haul out on a floating sign the entire time she was rearing her pup in 2013, only about 6 seals can fit on this sign so she is extremely isolated from the majority of seals.

Female 395 was observed once in 2014 with her pup and was an outlier in both the correlation for years with pups vs. unique day of pupping season, and proximity of mom to pup vs. known successful experience. She has 12 years of previous pupping years. The first day of pupping season she was observed with a pup, the trend in the rest of the data indicates that there is a significant ($p < 3.33 \times 10^{-6}$) correlation between more experience and later days in the pupping season.

Female 488 is a very large female who behaved outside the normal in one variable; the amount of time spent alert during an observation was 1310 seconds which is 81.69% higher than the average of 239.9223 seconds of nursing/observation. Through the correlation analysis it was seen that 488 was driving the significant correlation ($p<0.0113$) between size and percent success from previous years of experience. 488 has a 100% success rate for her 5 years having pups. After removing her from the data it was seen that the correlation was no longer significant ($p < 0.948$). Therefore it does not appear that any significant relationship exists between size and percent of success for a female unless the female is extra-large like 488. However, as we only had one extra-large female in the form of 488 we can’t speculate that applies to all females of equal size.

APPENDIX II – Table of life history traits of focal females.

Table 15. Focal female life history data taken from the WDFW/NMML database.

Female ID	Known age	Cohort	Age	Year	Size class	Years with pups	Previous success	Average pupping day ± SD
5	yes	1993	20	2013	3	8	75.0%	224.7±3.8
25	no	1990	23	2013	3	15	86.7%	217.1±4.9
46	yes	1993	21	2014	2	6	33.3%	219±3
81	no	1990	23	2013	3	10	40.0%	219.8±2.9
89	no	1990	23	2013	3	12	41.7%	210.1±4.5
120	no	1992	21	2013	2	6	50.0%	
120	no	1992	22	2014	2	7	57.1%	217.5±6.7
123	yes	1993	20	2013	3	10	80.0%	
123	yes	1993	21	2014	3	11	81.8%	210.8±6.0
239	no	1994	19	2013	3	8	12.5%	214.1±9.5
331	yes	1998	15	2013	2	4	25.0%	210±9.6
374	no	1995	18	2013	2	8	50.0%	
374	no	1995	19	2014	2	9	44.4%	224.3±7.1
380	no	1989	24	2013	3	10	50.0%	211.4±6.1
388	yes	1999	14	2013	3	4	75.0%	206.4±4.1
394	no	1996	17	2013	2	8	75.0%	
394	no	1996	18	2014	2	9	66.7%	211.4±5.8
395	no	1996	18	2014	3	12	50.0%	208.1±8.3
401	no	1996	17	2013	3	1	0.0%	212.5±4.5
411	yes	2001	12	2013	1.5	4	50.0%	
411	yes	2001	13	2014	1.5	5	60.0%	208±2.9
421	no	1999	14	2013	2.5	7	85.7%	
421	no	1999	15	2014	2.5	8	87.5%	212±1
461	yes	2001	13	2014	2	3	66.7%	182±NA

462	no	1998	16	2014	2	5	60.0%	203±6.6
465	yes	2001	16	2014	3	8	37.5%	205±6
476	no	1998	12	2013	1.5	3	33.3%	212.8±20.4
482	no	2000	13	2013	2	3	33.3%	211±14.2
482	no	2000	14	2014	2	4	50.0%	
488	no	2002	11	2013	3.5	4	100.0%	
488	yes	2002	12	2014	3.5	5	100.0%	195.5±4.5
494	yes	2002	12	2014	2	5	0.0%	212.6±2.7
497	yes	2000	13	2013	2.5	4	75.0%	
497	no	2000	14	2014	2.5	5	80.0%	214.3±7.3
500	no	2000	14	2013	2	6	50.0%	201.4±6.4
507	no	1999	13	2014	1.5	6	33.3%	200.2±5.9
542	no	2002	11	2013	1.5	4	50.0%	206.5±3.5
545	no	2001	12	2013	2	4	50.0%	
545	no	2001	13	2014	2	5	40.0%	204±5.1
547	no	2001	12	2013	2	5	0.0%	199.6±9.1
562	no	2001	12	2013	2	4	25.0%	196.5±5.8
581	no	2002	11	2013	3	7	57.1%	
581	no	2002	12	2014	3	8	50.0%	202.8±7.9
606	no	2004	10	2014	2	1	0.0%	Unknown
614	no	2003	10	2013	1.5	2	50.0%	
614	no	2003	11	2014	2	3	66.7%	211±11.8
620	no	2004	10	2014	1.5	0	NA	220±NA
627	no	2004	9	2013	1	2	50.0%	182.3±5.4
632	no	2005	8	2013	2.5	3	33.3%	
632	no	2005	9	2014	2.5	4	25.0%	193.5±0.5
654	yes	2007	7	2014	1.5	0	NA	Unknown
672	no	2004	9	2013	1.5	2	50.0%	
672	no	2004	10	2014	2	3	33.3%	206±2.4

680	no	2007	6	2013	2	0	NA	
680	no	2007	7	2014	2.5	1	100.0%	197±NA
685	no	2005	8	2013	1	2	50.0%	
685	no	2005	9	2014	1.5	3	33.3%	223±5
689	yes	2008	5	2013	2	0	NA	
689	yes	2008	6	2014	2	1	100.0%	196.5±1.5
696	no	2007	6	2013	1	0	NA	182±NA
696	no	2007	7	2014	2	1	100.0%	
699	yes	2008	6	2014	2	0	NA	193±NA
703	no	2006	8	2014	1.5	1	0.0%	201±NA
717	no	2006	7	2013	2	1	0.0%	
717	no	2006	8	2014	2	2	50.0%	208.5±1.5
719	no	2008	5	2013	2	1	100.0%	
719	no	2008	6	2014	2	2	100.0%	189.7±2.6
720	no	2005	8	2013	1.5	2	50.0%	
720	no	2005	9	2014	1.5	3	33.3%	Unknown
734	yes	2008	6	2014	2	0	NA	
739	no	2006	7	2013	3	1	100.0%	188.5±2.5
745	no	2006	7	2013	1	1	100.0%	
745	no	2006	8	2014	2	2	100.0%	191.3±5.4
749	no	2006	7	2013	1.5	1	100.0%	
749	no	2006	8	2014	1.5	2	100.0%	213±8.5
758	no	2006	7	2013	1.5	1	0.0%	211±NA
781	no	2008	5	2013	1.5	0	NA	199±NA