

ASSESSING WEDDELL SEAL MATERNAL INVESTMENT IN OFFSPRING

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERISTY
Bozeman, Montana

May 2011

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ACKNOWLEDGMENTS

I would like to thank my graduate advisor, Robert Garrott, and committee members Jay Rotella and Kathi Irvine for their advice and assistance with all aspects of this research. I would also like to thank Kelly Proffitt for all of her guidance before and during my graduate career. I would also like to thank my fellow graduate students in the Ecology Department for their encouragement, friendships, and support. A huge thank you to my family for supporting me throughout my graduate career.

For providing assistance in the field I would like to thank Glenn Stauffer, Shawn Farry, Megan O'Reilly, Jessica Farrer, Trent Roussin, Adia Sovie, Subash Lele, Kirstie Yeager, and all of the previous field technicians who have collected data throughout the life of the project. I would also like to thank all of the employees from Raytheon Polar Services for all of their help with logistics on and off the ice. Funding for this project was provided by the National Science Foundation, OPP-0225110.

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ABSTRACT

Reproduction is costly and involves a number of sequential physiological processes that require different levels of energetic investment. In mammalian species gestation and lactation require the most energy and the amount of energy invested in reproduction is reflected in litter size at birth and by offspring growth through weaning. The object of this study was to describe variation in Weddell seal (*Leptonychotes weddellii*) pup mass at birth and during several ages of the lactation/nursing period, and to evaluate the ability of several maternal traits to explain this variation. Mass measurements were collected from 887 pups at parturition and throughout lactation in Erebus Bay, Antarctica during the 2004 through 2010 field seasons and maternal traits were taken from a long term database. Analysis demonstrated high individual variation in pup mass within a season and modest variation among seasons which suggests that pup mass may be correlated with individual animal attributes rather than annual variation in environmental conditions. Maternal age, a female's reproductive status the previous season and their interaction were found to be the most influential maternal traits. Pup body mass at parturition and during lactation showed maternal age-related variation with evidence of senescence during pre-partum investment and terminal investment during post-partum investment. A female's reproductive status in one season affected her reproductive investment during lactation in consecutive seasons but that effect was correlated with age. Younger females who pupped in consecutive seasons weaned larger pups than those females who were of the same age and did not give birth in consecutive seasons. The opposite was found to be true for older females. The variation in the affect of maternal traits on maternal investment may be due to the increased energy requirement of lactation, age specific changes in reproductive costs, and a senescent decline in physiological function.

INTRODUCTION

Life history theory predicts that individuals face physiological tradeoffs between current and future reproduction (Williams 1966, Stearns 1992, Gustafsson 1994, Festa-Bianchet and Jorgenson 1998, Crocker et al. 2001). These tradeoffs ultimately lead to reproductive costs which can influence survival, fecundity, condition of the female (Gadgil and Bossert 1970, Stearns 1976, Bryant 1979, Clutton-Brock et al. 1983), and offspring survival (Gustafsson et al. 1994). Reproduction itself is costly and involves a number of sequential physiological processes that require different levels of energetic investment (Gittleman and Thompson 1988). In mammalian species gestation and lactation require the most energy (Ofstedal 1985, Gittleman and Thompson 1988, Boyd and McCann 1989, Robbins 1993, Bowen et al. 2001) with reproducing females having from 17 to 32% greater energy requirements during gestation and 65 to 215% greater energy expenditure during lactation compared to non-reproducing females (Robbins 1993). The amount of energy invested in reproduction is reflected in litter size at birth (Millar 1977, Ofstedal 1985, Gittleman and Thompson 1988, Boyd and McCann 1989, Ochoa-Acuña et al. 1998) and by offspring growth through weaning (Gittleman and Thompson 1988, Pomeroy et al. 1999). Thus mass measurements of offspring taken at parturition and during lactation can be used to quantify individual maternal investment in reproduction and evaluate hypotheses related to individual variation in energetic investment (Robbins and Robbins 1979, Kovaks and Lavigne 1986, Derocher and Stirling 1998, Georges and Guinet 2000, Bowen et al. 2001).

Research on maternal investment in large-bodied long-lived mammals is of interest because of their prolonged period of maternal care during gestation and lactation (Maestriperi and Mateo 2009). Many such species rely on acquired body reserves to fulfill the energy requirements of reproduction and lactation (Festa-Bianchet et al. 1998), which in turn influences offspring size (Maestriperi and Mateo 2009). Phocid seals are a group of large marine mammals that have delayed sexual maturity, are long lived and slow growing, and generally rely on acquired body reserves to meet the energy requirements of lactation (Bowen 2009, Boness and Bowen 1996). The Weddell seal (*Leptonychotes weddellii*) is one of the largest phocid species and inhabits the fast ice around the coast of Antarctica. These seals are highly philopatric and give birth to one pup in predictable colonies, on the shore-fast ice during the pupping season (Stirling 1969). The 5- to 6-week lactation period of Weddell seals, during which they stay in close proximity to their pup (Stirling 1969), is one of the longest of the phocid seals (Schulz et al. 2005). Females fast during the lactation period, so post-partum investment in their pup is derived almost exclusively from stored body reserves (Wheatley et al. 2006), making them an excellent species for studies of variability in maternal energetic investment. Energy transfer from mom to pup is dramatic and variable in Weddell seals with females losing, on average approximately 40% of their post-partum mass and pups more than tripling their birth weight during lactation (Wheatley et al. 2006).

This study was conducted on the Erebus Bay population of Weddell seals which is located in McMurdo Sound, the most southern portion of the Ross Sea. A long term demographic study based on individually tagged seals has been conducted on this

population providing detailed information on female reproductive histories (Hill 1987, Cameron et al. 2004, Hadley et al. 2006) that may give us insights into what maternal traits are associated with individual variation in energetic investment in reproduction. The objectives for this study were to (1) describe variation in pup mass at birth and during several ages of the lactation/nursing period, and (2) to evaluate the ability of several maternal traits to explain this variation.

Predictions

I evaluated possible sources of variation in pup mass during the period of maternal dependency that are associated with both dynamic maternal attributes that change over the life of an individual, as well as static attributes that are constant throughout an individual's life (Bergeron et al. 2011). Three dynamic maternal attributes were evaluated. I expected pup mass to vary with maternal age, to vary depending on when the pup was born within the birthing period, and to vary depending on whether or not the female produced a pup during the previous reproductive cycle. I also expected pup mass to vary depending on 2 static maternal attributes- the age the female began to reproduce and maternal identity.

Maternal body size of adult female Weddell seals varies throughout life in a predictable pattern, increasing in early life, peaking during mid-life, and declining in late life (Proffitt et al. 2007a). Maternal body size represents potential resources available to be invested in pup production (Wheatley et al. 2006); however, there is a tradeoff between investing body resources in reproduction and a mother's future survival likely resulting in changes in an individual's reproductive investment with age (Clutton-Brock

1983; Weimerskirch 1992, Bowen et al. 1994, Festa-Bianchet et al. 1995). Reproductive investment increases with maternal age until senescence; this may be due to selection, breeding experience, or younger females investing less into reproduction because of an increased mortality risk (Bowen 2006). There are 2 competing hypotheses of how maternal investment should change when a female reaches senescence. The senescence hypothesis predicts a decline in reproductive investment paralleling the decline in maternal body size in the oldest age classes and has support from a number of studies across diverse taxa (Weimerskirch et al. 1992, Packer 1998, Weladji et al. 2002, Bowen et al. 2006). Alternatively, there is also support for the terminal investment hypothesis which predicts females will increase investment, relative to the female's body size, late in life when the probability of future reproduction is low (Gagil and Bossert 1970, Isaac and Johnson 2005, McNamara et al. 2009). Thus there are two possible predicted age-specific patterns of pup mass related to maternal age, a quadratic pattern similar to that documented for the senescent decline in Weddell seal maternal body mass (Proffitt et al. 2007a) or an asymptotic pattern as predicted by the terminal investment hypothesis.

Timing of birth is variable for species with synchronous birthing periods (Bowyer 1991, Rachlow and Bowyer 1991, Boyd 1996, Adams and Dale 1998) and may be correlated with offspring mass. Timing of birth is determined by the female; with mothers in better condition (higher nutritional status) giving birth earlier in the season to larger offspring (Boyd and McCann 1989, Soto et al. 2004) and offspring born later in the season have been shown to have lower birth mass (Bowen 2009) and reduced survival (Festa-Bianchet 1988, Lunn and Boyd 1993, Proffitt et al. 2010). Thus, I predicted that

pup mass would be correlated with timing of parturition with parturition and lactation masses decreasing with birth date.

A female's reproductive status in one season may affect her offspring's phenotype and survival in subsequent seasons. There are reproductive costs associated with each bout of reproduction, and females who reproduce often may decrease their survival quicker (McNamara et al. 2009) and negatively affect future reproduction (Hirshfield and Tinkle 1969, Guinness et al. 1978, Festa-Bianchet 1988, Hadley 2007). Females who have not invested energy in gestation and lactation the previous season do not have to acquire as many resources as females who gave birth and invested in offspring (Neuhaus 2000). Alternatively, females that are able to reproduce in consecutive years may be of higher quality (Clutton-Brock 1984) and able to recover resources more quickly, thus consistently producing larger offspring. I predicted that the effect of a female's previous reproductive status would be correlated with offspring mass at birth and throughout lactation. The effect of whether a female reproduced in one season on her ability to invest in reproduction the next, however, may depend on the female's age. Recovering mass loss due to reproduction might be more difficult for the younger and older females because of their relatively smaller size and hence, body reserves, compared to prime age females. In addition, continuing body growth of young females reduces availability of acquired energy for reproduction and physiological changes associated with senescence may reduce foraging efficiency of old females thus contributing to the hypothesized age-specific effects. Thus I predicted that there would be an interaction between maternal age and her reproductive status the previous season.

Age at primiparity was considered a static maternal attribute and the relationship between it and pup mass was evaluated. Variability in age at primiparity within and among species has been documented (Reiter and LeBoeuf 1991, Harvey and Zammuto 1985, Hadley et al. 2006) and this variation can affect individual fitness and lifetime reproductive output (Stearns 1976, 1992, Festa-Bianchet et al. 1995, Hadley et al. 2006). For many long-lived species reproduction begins before individuals have finished growing, so females who start reproducing at a younger age may endure more reproductive costs associated with the tradeoff between growth and reproduction (Gadgil and Bossert 1970, Roff 1992, Ellis et al. 2000). However, Weddell seal females that reach primiparity at a younger age may increase their individual fitness and are thought to be of higher quality (Hadley et al. 2006). Therefore I predicted that females younger at primiparity would produce larger pups. In addition, I also evaluated maternal identity, an attribute that can be considered a generalized index of fixed individual phenotypic variation and expected strong support in the data for this effect (Cam et al. 2002, van de Pol and Verhulst 2006, Aubry et al. 2010).

MATERIALS AND METHODS

Study System

This study was conducted on the population of Weddell seals that inhabit Erebus Bay, located on the west coast of Ross Island, Antarctica ($77^{\circ}37'12''$ to $77^{\circ}52'12''$ S, $166^{\circ}18'$ to 167° E; see Cameron and Siniff [2004] for description and map of study area). Sea ice accumulation in Erebus Bay during the austral winter covers the Bay with thick fast ice. Tidal cracks form in the sea ice along the coast of Ross Island and adjacent islands. During the austral spring, Weddell seals use these cracks to haul out onto the sea ice to give birth, forming 8-14 pupping colonies (Stirling 1969). Each year 300-600 pups are born at the colonies during the pupping season from mid October through November (Cameron and Siniff 2004). Mothers remain in close association with their pups throughout the 30-45 day lactation period. Since 1969 newborn Weddell seal pups have been marked with individually numbered, livestock tags in the inter-digital webbing of each hind flipper (Siniff et. al 1977). Broken and missing tags of adult seals have been replaced throughout the years to maintain a database of known-age animals. Beginning in early November of each season, six to eight mark-resight surveys were conducted throughout the study area. At the time of tagging and during each survey, the date, location, tag numbers, and relative's tag numbers (mother-pup pairs) were recorded and added to the long-term database. At the end of the 2009 season approximately 92% of the Erebus Bay seals were marked and approximately 75% of these marked individuals were of known age.

Body Mass Measurements and Development of Response Variables

Pup mass measurements were obtained during the 2004 through 2010 field seasons (Oct. 10 thru Dec. 10). Pupping colonies were surveyed every 24 to 48 hours to identify newborn pups. Pups were opportunistically selected for mass measurements with an attempt to distribute the sample throughout the pupping season and among as broad a distribution of mom ages as possible in the later years when field computers provided access to information on mom's age. Pups judged to be 24 to 72 hours old, based on the presence of a frozen placenta and condition of the umbilicus, were selected for sampling and weighed. There was an attempt to locate these individuals again at approximately 20 and 35 days old to obtain additional mass measurements. Weddell seals typically nurse their pups for approximately 30-45 days (Stirling 1969, Wheatley et. al 2006); thus the 20- and 35-day measurements were considered mid- and late-lactation masses, respectively. Colonies were visited at two to three day intervals, but pups targeted for mass measurements were not always located on initial searches as they begin periodic swimming bouts at approximately 10 to 12 days old (Stirling 1969, Wheatley et. al 2006). Thus, I began searching to reweigh pups approximately one week prior to their target date and, if they could not be located, continued searching until approximately one week past the target date. Pups were weighed by rolling them into a restraining bag and lifting them off the ground using a spring scale or by placing them on a digital weighing platform. Both of these methods were accurate to within 0.5 kg.

Model Covariates

Maternal attributes derived from the long-term database included maternal age, age at primiparity, and whether the female gave birth to a pup the previous year.

Maternal age (Age) was defined as years since the animal was tagged as a pup. Age at primiparity (AgeFirst) was defined as the age of the female when she gave birth to her first pup. . Popped previous (PupPrev) was defined as whether the female gave birth during the previous season. Timing of birth during the pupping season was also used as a covariate and was represented as days since October 1st (BTime); for example, a pup born on October 21 would be assigned a BTime of 20. Due to inclement weather and pups spending time in the water, pups were often not weighed exactly on the mid- and late-lactation target dates. Weddell seal pups gain weight rapidly throughout the nursing period, (Hill 1987 and Wheatley et. al 2006), thus, I used deviation from target age (DTA) as a covariate to account for the variation in pup age at time of weighing. For example, a pup that was weighed at 22 days old instead of the mid-lactation target age of 20 days old had a DTA of 2 and a pup weighed at 18 days old had a DTA of -2.

Offspring parturition mass is considered an indicator of pre-natal maternal investment (Oftedal 1985, Kovacs and Lavigne 1986, Ochoa-Acuña et al. 1998) and is positively correlated with post-parturition mass gain and weaning mass (Hill 1987). Thus to more clearly partition potential maternal effects associated with in utero maternal investment from those associated with post-parturition maternal investment through lactation, pup parturition mass was used as a covariate in analyses of mid- and late-lactation mass response variables.

Statistical Analysis

I focused on maternal attributes and their affect on pre- and post-partum investment and developed a priori hypotheses, expressed as competing models, regarding the relationship between maternal traits and pup masses. These models were divided into three suites, one for each response variable (parturition, mid-lactation, and late-lactation mass), representing progressively increasing maternal energetic investment. Models in each suite were evaluated using linear mixed effects models fit in program R version 2.12.1 (R Development Core Team 2010) and the extension package for linear and nonlinear mixed effects models (nlme, Pinheiro et al. 2010).

I followed the strategy for mixed-effects modeling described by Zuur et al. (2009) to evaluate models in each suite. Specifically, I first evaluated whether there was support for including a random effect. A recent study of lactation performance in grey seals (*Halichoerus grypus*) provides evidence of inherent differences among individuals in their ability to effectively transfer milk resources to their offspring (Lang et al. 2009); this may be true for pre-natal investment as well. Thus, maternal identity was treated as a random effect to account for potential genetic differences among individuals because some mothers were associated with multiple pups that were used in this study. To evaluate the need to include maternal id as a random effect, I compared the most complex fixed-effects-only model in each suite, which included all covariates and interactions, to a model with the same fixed effects and the random effect of maternal id using Akaike's information criterion corrected for small sample size (AICc) based on restricted maximum likelihood (REML). I then evaluated competing combinations of fixed effects

(Age, AgeFirst, BTime, and PupPrev) to determine which structure is most supported by the data based on maximum likelihood (ML). Lastly, I obtained the best parameter estimates from the top models in each suite based on REML.

Top models were considered those with a ΔAICc score < 4 ; covariate weights, coefficient estimates and variance estimates were also calculated for each covariate in top models as well as Akaike model weights (w_i) to address model selection uncertainty (Burnham and Anderson 2002). I assessed collinearity among covariates by calculating pairwise correlations, excluding any combination of covariates from models with a coefficient of determination >0.4 . Model averaging using the R extension `AICcmoavg` was used to generate model-averaged predictions to visualize the biological effect size of covariates (Mazerolle 2010). If the data supported the inclusion of maternal identity, the random intercept values were predicted for each female who had multiple pups in the dataset using the top model from the parturition, mid- and late-lactation suites to assess the biological importance of the random effect. These values were calculated with the linear mixed effects models using the R extension `lme4` (Bates and Maechler 2010).

Each model suite contained 25 models including all possible combinations of the maternal covariates Age, AgeFirst, PupPrev, BTime, as well as an interaction between Age and PupPrev (Appendix A). Maternal age was evaluated in two forms; quadratic and asymptotic, which represent competing biological relationships between maternal age and pup mass. The quadratic form predicts a maximum or minimum response will occur at intermediate values of the covariate with lesser or greater effects at the extremes and was expressed as $\beta_i x_i + \beta_{i+1} x_i^2$. The asymptotic form predicts the response variable

approaches, but never reaches, an asymptote as x_i increases or decreases and was expressed as $\beta_i \ln(x_i)$. Linear relationships were considered for all other covariates in the a priori model suites.

All models in all suites included either the quadratic or asymptotic form of Age and the deviation from target age (DTA) covariate. In addition all models in the mid- and late-lactation suites included pup parturition mass as a covariate; accounting for prenatal maternal effects, thus allowing a clear assessment of maternal effects during the energetically costly post-partum period when maternal investment is fueled almost exclusively by rapid depletion of body reserves (Hill 1987 and Wheatley et al. 2006). The small proportion (6%) of parturition masses that were not obtained at the target age of 1 day old were adjusted by the DTA coefficient estimate from the top model in the parturition mass suite to estimate the mass of each of these pups when 1 day old.

Based on the outcome of the a priori model-selection results, I conducted exploratory analysis to determine if non-maternal covariates were also correlated with maternal investment and to generate hypotheses for future work. Offspring mass has been shown to be correlated with offspring sex for several species, with males being heavier (Green and Rothstein 1991, Boyd 1996, Birgersson and Ekvall 1997). Thus, I investigated whether offspring mass was significantly different between male and female pups, predicting males would be heavier at birth and throughout lactation. Annual variation in the marine environment may also affect pup mass due to associated variation in food resources available to reproducing females (Wheatley et al. 2006). Numerous studies have demonstrated an association between the El-Nino Southern Oscillation

(ENSO) and various measures of body condition and demographic performance of marine birds and mammals (Anderson 1989, Cruz and Cruz 1990, Vergani et al. 2001); including Weddell seals (Proffitt et al. 2007a). Therefore, I considered an index of the strength of ENSO, the Southern Oscillation Index (Bureau of Meteorology 2010), as a covariate in exploratory analyses. I calculated the Southern Oscillation Index for 2004 through 2010 as a 3-month running average (Kwok and Comiso 2002, Proffitt et al. 2007b) for the summer (Sum_{SOI}) and winter (Win_{SOI}) periods. I predicted that negative phases of Southern Oscillation would have a negative effect resulting in lower pup masses at birth and throughout lactation. Offspring sex and environmental conditions were added to the most supported models in each model suite and all possible combinations of maternal and non-maternal covariates were evaluated. Exploratory models were compared using AIC_c and changes in ΔAIC_c scores were used to evaluate if models were improved with the covariate additions.

RESULTS

A total of 1056 pups were weighed at parturition from 2004 to 2010. Of those pups sampled, 887 had known age moms and were included in analyses. The number of pups weighed at parturition ranged from 89 to 195, with 35 to 162 mid-lactation mass measurements, and 27 to 150 late-lactation masses obtained annually (Table 1). Pooling samples across all years, mean pup parturition mass was 30.1 kg ($n = 887$, $SD = 4.4$, range 14.5 – 45.5, $CV = 0.15$), mean mid-lactation mass was 71.8 kg ($n = 544$, $SD = 12.6$, range 31.8 – 104.5, $CV = 0.18$), and mean late-lactation mass was 99.7 kg ($n = 478$, $SD = 18.7$, range 31.4 – 145.5, $CV = 0.19$). Age-specific pup masses were highly variable within years, whereas annual medians for age-specific masses varied little among years (Figure 1).

Pups from a total of 496 different adult females were sampled during the study. Forty-eight percent ($n = 240$) of the females were associated with multiple pup measurements at parturition, 24% ($n = 121$) were associated with multiple pup measurements at mid-lactation and 20% ($n = 98$) were associated with multiple pup measurements at late-lactation (Table 2). Mothers had an average age of 13 years ($SD = 4.6$, range 5-28) and mean age at first reproduction of 7.8 years ($SD = 1.7$, range 4-16). Average parturition date was 27.1 days after October 1st ($SD = 6.9$, range 11-51). Mean days since target age for measuring mass was 0.08 days ($SD = 0.34$, range 0-3) for parturition mass, -0.39 days ($SD = 2.16$, range -4-6) for mid-lactation mass, and 0.87 days ($SD = 2.98$, range -6-16) for late-lactation mass. Of the 887 pups weighed, 48% ($n = 422$) had mothers who produced a pup the previous year (Appendix A). Mean value for the

summer southern oscillation index was -0.64 (SD= 9.59, range -11.8 -16), winter southern oscillation index was 4.15 (SD=11.50, range -9.97- 21.43) and there were mass measurements taken at parturition from 453 females and 434 male pups.

A Priori Model Selection

The random effect of maternal ID was strongly supported with the mixed effects models receiving ≥ 0.99 of the model weight in each model suite (Table 3). The data indicated that individual females produced pups that were as much as approximately 6 kg, 21 kg, and 55 kg different than others with the same covariate conditions at parturition, mid- and late-lactation, respectively (Figure 2). Therefore, mixed models were subsequently used for evaluating a priori model structures for fixed effects. Each model suite contained 25 a priori models (Appendix B) that were used to evaluate correlations between maternal attributes and pup parturition, mid-lactation, and late-lactation response variables.

Pre-partum Investment

In the parturition mass suite, 3 models had a ΔAIC_c score < 4 (Table 4): All 3 models included $Age_{(quad)}$, BTime and AgeFirst. The 2nd ranked model also included PupPrev, and the 3rd ranked model included an interaction between $Age_{(quad)}$ and PupPrev. It appears that other top models in the parturition suite gained support because they included the most supported model with the addition of other covariates. These models were considered to include uninformative parameters due to confidence intervals of the

additional covariates spanning zero and AIC_c scores approximately 2 AIC_c units more than the top-ranked models (Arnold 2010, Table 4). Other models in the suite were not well supported by the data ($AIC_c \geq 5.0$) and $Age_{(asym)}$ did not appear in any of the models supported by the data ($AIC_c \geq 18.4$). Coefficient estimates from the top model indicated that the relationship between pup parturition mass and maternal age was best characterized by the quadratic form ($\hat{\beta}_{MomAge} = 1.5$, $SE=0.22$, $\hat{\beta}_{MomAgeSq} = -0.04$, $SE=0.01$), with predicted parturition mass increasing with maternal age until the female reached the age of 17 and then declining for pups of mothers >17 years old (Figure 3). Using model averaging and holding all covariates at their mean, except maternal age, predicted parturition mass for a pup of a young mother (age 5) was 25.3 kg (CI=24.1, 26.5), a prime-aged mother (age 17) was 31.5 kg (CI=31.0, 32.0), and a senescent mother (age 26) was 28.6 kg (CI=26.9, 30.3). Coefficient estimates for BTime and AgeFirst were stable for all well-supported models with confidence intervals that did not span zero. Results do not support our predictions that pup parturition mass would be negatively correlated with BTime ($\hat{\beta}_{BTime} = 0.10$, $SE=0.02$ for top-ranked model, Figure 4) but did support our prediction that pup mass would be negatively correlated with AgeFirst ($\hat{\beta}_{AgeFirst} = -0.29$, $SE=0.10$ for top-ranked model, Figure 5). Although PupPrev and the interaction between Age and PupPrev appeared in the 2nd and 3rd models respectively, all coefficient confidence intervals spanned zero (Table 5).

Post-partum Investment

Model selection results for the variation in pup mass during lactation supported 4 top models for mid-lactation and 7 for late-lactation (Table 4). The top ranked model in both suites included $\text{Age}_{(\text{asym})}$, BTime, PupPrev and the interaction between $\text{Age}_{(\text{asym})}$ and PupPrev, other well supported models included 1 or 2 additional covariates (Table 4). Similar to the pre-natal analysis other top models in the post-partum model suites gained support because they also included the most supported model with the addition of other covariates. These models were also considered to include uninformative parameters. The 4th ranked model in the mid-lactation analysis included the same covariates as the top ranked model, but with a different form of Age. The 2nd ranked models in the late-lactation suite included $\text{Age}_{(\text{quad})}$, and BTime, and the 3rd ranked model was a simple generalization of the 2nd model with 3 terms added for PupPrev and its interaction with $\text{Age}_{(\text{quad})}$, but coefficients of all 3 of the terms involving PupPrev had 95% confidence intervals that widely overlapped zero (Table 5).

Unlike parturition mass, the relationship between maternal age and mid-lactation pup mass was best characterized by the asymptotic form indicating that pup mass increases with maternal age throughout the entire range of mother's ages (Fig. 3), supporting the terminal investment hypothesis. Using model averaging and holding all covariates at their mean, except maternal age, predicted mid-lactation mass for a pup of a young mother during mid-lactation was 67.5 kg (CI=63.4,71.5), a prime-aged mother was 73.8 kg (CI=73.8, 77.7), and an old age class mother was 76.7 kg (CI=73.2, 80.1). Both forms of age were supported in the late-lactation analysis and model averaging revealed

that pup mass increases with maternal age up to the middle age class, but there is uncertainty in the form of the relationship in the oldest age classes (Figure 3). The model averaged predicted late-lactation body mass for a pup of a young mother was 83.9 kg (CI= 73.5, 94.3), a prime aged mother was 104.6 kg (CI=101.4, 107.8) and an old age class female was 103.8 kg (CI=92.4, 115.2).

Unlike parturition mass, estimates from the top models in the late-lactation suite indicated a negative relationship between late lactation mass and BTime ($\hat{\beta}_{lateBTime} = -0.41$, SE=0.13, Figure 4) supporting our prediction. Although BTime was included in the top ranking models in the mid-lactation analysis all confidence intervals spanned zero ($\hat{\beta}_{midBTime} = -0.13$, SE=0.07, Table 5). There was a positive relationship between lactation mass and PupPrev ($\hat{\beta}_{midPupPrev} = 19.48$, SE=5.31, $\hat{\beta}_{latePupPrev} = 27.14$, SE=9.43). There was support that a female's pupping status during the previous season was correlated with mass during mid-lactation the next, but the effect was dependent on the female's age supporting our prediction. The data suggests pups of young females who pupped the previous year were heavier than the mean while pups born to old females who pupped the previous year were lighter than the mean (Figure 6).

As expected, DTA was found to be well-supported in all model suites. Top model estimates showed a positive relationship between DTA and pup mass at parturition and throughout lactation (Table 5). The affect of DTA on pup mass was similar for partition ($\hat{\beta}_{partDTA} = 1.76$, SE=0.38), and mid-lactation models ($\hat{\beta}_{midDTA} = 1.62$, SE=0.24), and decreased substantially in the late-lactation model ($\hat{\beta}_{lateDTA} = 0.86$, SE=0.20). Birth mass had a positive relationship with mid- and late-lactation masses

(Table 5). Top model coefficient estimates for birth mass were similar for both suites ($\hat{\beta}_{midBirthMass} = 1.61$, SE=0.10, $\hat{\beta}_{lateBirthMass} = 1.76$, SE=0.17).

Exploratory Models

Post hoc exploratory analyses revealed that adding environmental covariates (Appendix C) improved the most supported a priori models in all three model suites. Model selection results for the parturition mass suite resulted in 4 top models which all included Win_{SOI} and Sum_{SOI} (Table 6, Appendix D). The addition of Win_{SOI} and Sum_{SOI} improved the AIC_c score of the top a priori model, which included the same maternal covariates, by 6.99 units. Coefficient estimates from the top model were not in the predicted direction, estimates were small but confidence limits did not span zero ($\hat{\beta}_{WinSOI} = -0.03$, SE=0.01, $\hat{\beta}_{SumSOI} = -0.04$, SE=0.01).

Unlike parturition mass, the only environmental covariate that appeared in the top models in the mid- and late-lactation suites was Win_{SOI}. Model selection results for mid- and late-lactation suites resulted in 6 and 5 top exploratory models respectively (Table 6). The top ranked model in the mid-lactation suite also included Age_(asym), PupPrev and its interaction with Age_(asym). The addition of Win_{SOI} improved the AIC_c score of the top a priori model, which included the same maternal covariates, by 2.36 units. The top ranked model in the late-lactation suite contained similar covariates to the mid-lactation suite with the addition of BTime and PupSex. The addition of Win_{SOI} improved the AIC_c score of the top a priori model by 4.02 units. Unlike the results for the parturition mass model coefficient estimates from the top models in mid- and late-lactation suites were in the

predicted positive direction, coefficient estimates for the late-lactation suite were relatively large with confidence intervals that did not span zero (mid-lactation: $\hat{\beta}_{midWinsoi} = 0.09$, SE=0.03, late-lactation: $\hat{\beta}_{lateWinsoi} = 0.19$, SE=0.06). The addition of SOI covariates also strengthened support for the asymptotic form of maternal age which is consistent with the mid-lactation suite results in that all top models included the asymptotic form of maternal age.

Adding PupSex to the most supported a priori models in all three model suites did not improve AIC_c scores in any model suite and 95% confidence intervals of coefficient estimates spanned zero ($\hat{\beta}_{PupSex} = -0.34$, SE= 0.26; $\hat{\beta}_{midPupSex} = 0.45$, SE= 0.70; $\hat{\beta}_{latePupSex} = 0.34$, SE= 1.24), thus there was no support for a correlation between pup mass and sex.

DISCUSSION

I found that maternal effects were correlated with variation in pup mass at parturition, mid-lactation, and late lactation. My study thus provided insights about the correlation between maternal traits and pre-natal and post-partum maternal investment. I found evidence suggesting that there are differences between individual females and their ability to invest in pre- and post-partum maternal care. Maternal age was found to be associated with all three stages of maternal investment, birth date and age at first reproduction were found to be correlated with pre-natal investment, and birth date and reproductive status the previous season were found to be correlated with post-natal investment. Further, I found that the relationship between maternal age and investment varied throughout the pre-natal and post-partum periods.

Random Effect

There was a strong maternal identity effect on pup mass at parturition and throughout lactation. Individual variation in survival and reproductive performance is an important component of natural selection (Cam et al. 2002) and variations may link to genetic or phenotypic traits of the female (Mellish et al. 1999). Individual variation in different aspects of reproduction is documented in domestic (Montano-Burmudez et al. 1990, Meyer et al. 1994, Analla et al. 1996, Sanna et al. 1997, Van Tassel et al. 1999) and wild ungulates (Gjostein et al. 2004), several pinniped species (Mellish et al 1999, Crocker et al. 2001 Lang et al. 2005, 2009), bats (Stern et al. 1997), and marmosets

(Power et al. 2008). I found that offspring size at parturition, mid- and late-lactation differed as much as approximately 6 kg, 20 kg, and 40 kg respectively, for individual females with the same covariate conditions. Our results regarding effects of maternal identity are similar to the effects of maternal identity on grey seal lactation performance (Lang et al. 2009). Lang et al. (2009) demonstrated consistent differences among individual females monitored over multiple pupping cycles with respect to variability in milk composition, daily milk output, and offspring lactation length. Individual variation has primarily been studied during the lactation period, but variation in pup parturition masses attributable to maternal identity suggests that individual variations may also be correlated with in-utero investment in offspring.

Age Effect and Investment

Maternal age was the most supported covariate in models explaining variations in parturition, mid- and late-lactation pup masses, which indicates that maternal age is correlated with pre- and post-natal investment, similar to other pinniped species (Ellis et al. 2000, Bowen et al. 2009). As I predicted, the relationship between pup parturition mass and maternal age was quadratic indicating evidence of senescence during pre-natal investment. Birth mass increased with maternal age over the younger age classes, reached a maximum in the middle age class, and declined amongst the oldest ages. This relationship mirrors the quadratic relationship between maternal age and maternal post partum mass found in Weddell seals (Proffitt et al. 2007a) and other pinniped species (Bowen et al. 2006, 2009), and suggests that pup parturition mass is strongly correlated

with maternal post-partum mass. Additionally, this relationship suggests that pre-natal investment in offspring is a direct reflection of maternal body mass. The senescent decline in pre-natal investment observed in Weddell seals may be the result of increased maternal maintenance costs (Innes et al. 1987, Testa et al. 1989, Pomeroy et al. 1999), a senescent decline in uterine and placental function (Wilsher & Allen 2003, Dwyer et al. 2005), a reduction in foraging efficiency and hence resource acquisition due to muscle senescence (Hindle et al. 2009), a senescent reduction of nutrients transferred to the fetus (Bowen et al. 2006), or some combination of these mechanisms.

In contrast to pre-natal investment in offspring, I found that the relationship between post-partum investment in offspring and maternal age was asymptotic, indicating support for the terminal investment hypothesis. Mid- and late-lactation pup masses increased with maternal age, but the magnitude of increase declined as females reach the oldest age classes. There was some ambiguity in the relationship between late-lactation pup masses and maternal age. Model averaged predictions indicated a dramatic flattening of the predicted late-lactation pup mass for the oldest age classes, as compared to the pronounced decline in predicted pup parturition mass for the oldest age classes. Female Weddell seal body mass has been shown to decrease in the oldest age class (Proffitt et al. 2007a); however evidence from this study suggests that older females are weaning larger pups and therefore investing a higher proportion of their body mass. Although few other mammalian studies have found evidence of increased investment in reproduction late in life, evidence of terminal investment in some aspects of reproductive

investment have been found in moose (Ericsson et al. 2001), red deer (Clutton-Brock 1984), Barbary macaques (Paul et al. 1993) and grey seals (Bowen et al. 2006).

The observed differences in age-specific relationships between pre-natal and post-partum investment may be due to offspring growth being limited by physiological constraints in-utero preventing selection to favor an increase in maternal investment at that time (Clutton-Brock 1984). On the other hand, selection may favor an increase in maternal investment during a time when offspring survival is higher (Clutton-Brock 1984) resulting in increased maternal investment during lactation. This may be the case for Weddell seals due to their high pre-weaning survival (Proffitt et al. 2010).

Timing of Birth

Pup birth mass was positively correlated with birth date, which contradicted our prediction. I found pups born later in the season were heavier than pups born earlier in the season. Weddell seals in Erebus Bay give birth from mid-October through November (Cameron and Siniff 2004), a time that environmental conditions may change and favor offspring of females that give birth at one time over another (Bowen 2009). Therefore, it may be beneficial for females to prolong the gestation period and give birth later in the season when conditions are more likely favorable to offspring survival. This strategy may also result in larger pups. However, females who give birth too late in the pupping season may have a shorter lactation period due to sea ice breakup, and this may negatively affect a pup's weight at weaning and subsequent survival (Proffitt et al. 2008).

Age at Primiparity

As predicted, maternal age at first reproduction was inversely related to pre-natal investment. Females that recruited at a younger age gave birth to heavier pups than females that delayed reproduction to later in life, even though they are a smaller size at parturition (Proffitt et al. 2007a). In Erebus Bay, Weddell seals average age at primiparity is approximately 7 years old, however this attribute is highly variable and individuals may begin reproducing as early as age 4 or as late as age 14 (Hadley et al. 2006). Females who recruit at a younger age are hypothesized to be of higher quality (Hadley et al. 2006) and may possess characteristics that allow them to start reproducing sooner than their counterparts. Females who reach primiparity at a younger age may be of superior body condition (Reiter and LeBoeuf 1991). Females that are younger at primiparity may have inherently higher reproduction capabilities (Cam et al. 2002, Hadley et al. 2006) and selection may favor genotypes that successfully breed earlier in life (Reiter and LeBoeuf 1991). In northern elephant seals, females that produced the most offspring throughout their lifetime were those who started reproducing at a young age (LeBoeuf and Reiter 1988).

Female's Reproductive Status

I found no evidence that pup parturition mass was correlated with maternal pupping status the previous year, but we did find strong support in the data that pup mid and late lactation mass was correlated with maternal pupping status the previous year. However, as predicted, the effect of maternal reproductive status on pup mass was age

dependent. Reproduction is energetically costly and successful reproduction in one year may negatively affect female survival and fecundity in consecutive years (Clutton-Brock et al. 1983). Hadley et al. (2007) found a modest reduction in female Weddell seal survival probability following a reproductive event. In most capital breeding species, reproduction begins before females have attained maximum body size. Thus, females may face higher reproductive costs if they reproduce at a younger age and this investment would be expected to negatively affect a female's ability to invest in reproduction the following year. Hadley et al. (2007) found evidence of such costs of reproduction in young age class animals. Our results demonstrated that young female Weddell seals weaned heavier pups if they gave birth the previous season than females of the same age that had not produced a pup the previous year. This result suggests that young females who are able to successfully reproduce in consecutive years may be of higher quality.

In contrast, older Weddell seal females who pupped in consecutive years weaned smaller pups which suggests that older females may have fewer resources available to invest in pups during the lactation period. This may be due to a senescent decline in physiological function associated with milk production and transfer (Bowen et al. 2006), the reduction of adult female body mass as they age into senescence (Proffitt et al. 2007a), or increased reproductive costs (Ericsson et al. 2001). There are negative effects associated with reproductive costs on adult survival and future reproductive success (Nilsson et al. 1996), this is particularly evident in the old age class and occurs as a reduction in reproductive effort (measured here as maternal investment) in consecutive breeding seasons (Gustaffson et al. 1988). Additionally, there is an increased effect of

reproductive costs in older females as they spend more resources on reproduction than their younger counterparts (Ericsson et al. 2001). This may also be true of Weddell seal females as I hypothesize that older females invest a higher proportion of their body mass into their pup at weaning.

Environmental Effects

Environmental variations can have profound effects on the biotic components of marine ecosystems (Walther et al. 2002, Weimerskirch et al. 2003). Recent studies on this Weddell seal population have demonstrated correlations between measures of environmental variation and maternal post-parturition mass, as well as a number of vital rates (Hadley et al. 2006, 2007, Proffitt et al. 2007a,b, 2008, Garrott et al. in review, Rotella et al. in review). Summer sea ice extent has been shown to have a negative relationship with pup weaning mass and adult parturition mass, while summer SOI was shown to have the opposite relationship (Proffitt et al. 2007a, Proffitt et al. 2008). The addition of SOI covariates to the top a priori model for each pup mass model suite substantially strengthened AIC_c scores, suggesting that environmental conditions are also important in explaining variation in maternal investment in pups. Such environmental effects represent another dynamic maternal effect, but one that would likely affect the entire population of reproducing females (i.e., a cohort effect), as opposed to the other dynamic and static maternal attributes considered in this study that are specific to the individual.

El-Nino southern oscillation (ENSO), measured by SOI is a large scale oceanic process that is correlated with sea surface temperatures and currents; in turn affecting the formation and retreat of sea ice (Kwok and Comiso 2002). Low southern oscillation index is associated with high sea ice extent which is correlated with the abundance and distribution of primary producers (Hadley et al. 2007, Ross and Quetin 1991, Loeb et al. 1997, Ainley et al. 1998). Summer and winter SOI were shown to have a negative relationship with pre-natal investment suggesting investment was greater following years with high sea ice extent, while winter southern oscillation was shown to have a positive relationship with post-partum investment. Shifts in sea ice formation and retreat are suspected to influence the abundance and distribution of fish species consumed by Weddell seals during the pregnancy period (Proffitt et al 2007a) that would ultimately affect a female's ability to invest in her pup during gestation and lactation.

Although winter and summer oscillation index were shown to be statistically significant the biological significance of their affects are minor (Appendix E). The data suggests that pup mass changes by approximately 1kg, 3kg, and 6kg, as you move from the lowest to the highest values of SOI, for parturition, mid- and late-lactation respectively. Additional research will be needed to understand the possible correlation between maternal investment and environmental variations, possibly using more regional environmental indices, such as sea-ice extent (Cavalieri et al. 1991) and the Antarctic Dipole (Yuan and Li 2008), which have recently been correlated with cohort recruitment probability in the study population (Garrott et al. in review). Currently these

environmental indices are only available through 2007 due to difficulties with the satellite-based passive microwave sensors used to calculate these metrics.

My research demonstrates that some maternal characteristics are correlated with maternal investment including maternal age, a female's reproductive status in consecutive seasons and their interaction. I found an asymptotic relationship between maternal age and pup mass during lactation which supports the terminal investment hypothesis, although there was some ambiguity during the late-lactation period. This age-specific relationship may be due to older females investing a higher proportion of their body mass into lactation than younger individuals. Future research should focus on maternal investment during the lactation period by measuring female mass loss and the amount of mass gained by her pup and then comparing among age classes. This will also help resolve the ambiguity found during late-lactation. There is also evidence that environmental conditions may be correlated with investment as well. As more environmental covariates are being developed for the Ross Sea region of Antarctica, future research should focus on environmental conditions and which specific ones will help explain the variation in pup mass. Doing this will link environmental conditions to mass dynamics of Weddell seals and more specifically the environment's affect on maternal investment, bettering our understanding of Weddell seal life history.

Table 1. Distribution of the number of Weddell seal pups sampled annually for each mass measurement from the 2004 through 2010 field seasons. Pups weighed at parturition were 1-3 days old, mid-lactation weights were obtain when pups were 16 - 26 days old (mean = 20 days old), and late-lactation weights were obtained when pups were 29 - 51 days old (mean = 37 days old).

Year	Mass measurement		
	Parturition	Mid-Lactation	Late-Lactation
2004	89	35	27
2005	114	74	61
2006	98	78	66
2007	106	50	45
2008	137	73	58
2009	149	69	67
2010	195	162	150
Total	887	541	474

Table 2. Distribution of the total number of adult female Weddell seals who's pups were sampled in multiple pupping seasons for each mass measurement from the 2004 through 2010 field seasons.

Times Sampled	Mass measurement		
	Parturition	Mid-Lactation	Late-Lactation
2	138	81	64
3	64	26	25
4	29	11	6
5	3	2	3
6	5	1	0
7	1	0	0
Total	240	121	98

Table 3. Model selection results for comparing the fixed- and mixed-effects models within each model suite. Fixed Age(quad) and Fixed Age(asym) represent the most complex model for the quadratic form (DTA + Age + AgeSq + Btime + PupPrev + AgeFirst + (Age * PupPrev) + (AgeSq * PupPrev)) and asymptotic form of age (DTA + lnAge + BTime + PupPrev + AgeFirst + (lnAge * PupPrev)) respectively. Mixed Age(quad) and Mixed Age(asym) represent the most complex model for the quadratic and asymptotic form of age and include the random effect of maternal identity. The number of parameters (K), the ΔAIC_c value, and the Akaike weight (w_i) for each model are presented.

Model	K	ΔAIC_c	w_i
Parturition Mass Suite			
Mixed Age(quad)	11	0.00	0.99
Fixed Age(quad)	10	8.84	0.01
Mixed Age(asym)	9	0.00	0.99
Fixed Age (asym)	8	9.95	0.01
Mid-Lactation Suite			
Mixed Age(quad)	12	0.00	1.00
Fixed Age(quad)	11	19.99	0.00
Mixed Age(asym)	10	0.00	1.00
Fixed Age (asym)	9	22.68	0.00
Late Lactation Suite			
Mixed Age(quad)	12	0.00	1.00
Fixed Age(quad)	11	32.83	0.00
Mixed Age(asym)	10	0.00	1.00
Fixed Age (asym)	9	43.21	0.00

Table 4. Model selection results for a priori models examining effects of covariates on variation in Weddell seal pup parturition, mid-lactation, and late-lactation masses. Covariates included the quadratic ($Age_{(quad)}$) and asymptotic form ($Age_{(asym)}$) of maternal age, age at primiparity ($AgeFirst$), timing of birth ($BTime$), and pupped the previous season ($PupPrev$). Deviation from target age was included in all models in each suite and adjusted pup parturition mass was included in all models in the mid- and late-lactation suites. The a priori models with weight are presented along with the number of parameters (K), AIC_c , the ΔAIC_c value, and the Akaike weight (w_i) for each model suite.

ID	Model	K	AIC_c	ΔAIC_c	w_i
Parturition Mass Suite					
1	$Age_{(quad)} + BTime + AgeFirst$	8	4929.1	0.00	0.63
2	$Age_{(quad)} + BTime + AgeFirst + PupPrev$	9	4930.1	1.97	0.23
3	$Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev)$	11	4932.5	3.42	0.10
Mid-Lactation Suite					
1	$Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev)$	9	3817.9	0.00	0.43
2	$Age_{(asym)} + BTime + PupPrev + AgeFirst + (Age_{(asym)} * PupPrev)$	10	3819.9	1.95	0.16
3	$Age_{(asym)} + PupPrev + (Age_{(asym)} * PupPrev)$	8	3820.0	2.07	0.15
4	$Age_{(quad)} + BTime + PupPrev + (Age_{(quad)} * PupPrev)$	11	3821.3	3.36	0.08
Late Lactation Suite					
1	$Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev)$	9	3839.9	0.00	0.27
2	$Age_{(quad)} + BTime$	8	3840.4	0.57	0.20
3	$Age_{(quad)} + BTime + PupPrev + (Age_{(quad)} * PupPrev)$	11	3841.6	1.74	0.11
4	$Age_{(asym)} + BTime + PupPrev + AgeFirst + (Age_{(asym)} * PupPrev)$	10	3841.9	2.08	0.10
5	$Age_{(quad)} + BTime + AgeFirst$	9	3842.2	2.38	0.08
6	$Age_{(quad)} + BTime + PupPrev$	9	3842.5	2.62	0.07
7	$Age_{(quad)} + BTime + PupPrev + AgeFirst + (Age_{(quad)} * PupPrev)$	12	3843.5	3.69	0.04

Table 5. Coefficient values (β_i) and 95% confidence intervals (in parentheses)¹ for covariates from the most supported models for each of the three model suites indentified through AIC model comparisons examining variation in pup mass.

Covariate	Model ID			
	1	2	3	4
Parturition Model Suite				
DTA	1.76 (1.01,2.51)	1.77 (1.03,2.51)	1.79 (1.05,2.54)	
Age	1.41 (1.05,1.78)	1.45 (1.08,1.82)	1.51 (1.05,1.98)	
Age _(quad)	-0.04 (-0.05,-0.02)	-0.04 (-0.05,-0.03)	-0.04 (-0.06,-0.03)	
BTime	0.11 (0.06,0.15)	0.11 (0.07,0.15)	0.11 (0.07,0.15)	
PupPrev		-0.28 (-0.81,0.25)	2.13 (-2.65,6.93)	
AgeFirst	-0.24 (-0.42,-0.06)	-0.26 (-0.44,-0.08)	-0.26 (-0.44,-0.08)	
Age*PupPrev			-0.30 (-0.99,0.39)	
Age _(quad) *PupPrev			0.01 (-0.02,0.03)	
Mid-Lactation Model Suite				
DTA	1.62 (1.16,2.08)	1.62 (1.15,2.08)	1.60 (1.14,2.06)	1.59 (1.13,2.05)
BirthMass	1.60 (1.42,1.80)	1.60 (1.41,1.79)	1.56 (1.38,1.75)	1.59 (1.40,1.78)
Age _(asym)	13.10 (10.24,13.10)	13.17 (10.24,16.09)	13.30 (10.40,16.20)	
Age				3.00 (1.79,4.22)
Age _(quad)				-0.07 (-0.11,-0.03)
BTime	-0.13 (-0.26,0.00)	-0.13 (-0.26,0.00)		-0.12 (-0.25,0.01)
PupPrev	19.48 (9.06,29.90)	19.47 (9.04,29.89)	19.21 (8.77,29.65)	16.51 (3.76,29.27)
AgeFirst		-0.09 (-0.56,0.39)		
Age _(asym) *PupPrev	-7.48 (-11.52,-3.43)	-7.49 (-11.53,-3.45)	-7.44 (-11.48,-3.39)	
Age*PupPrev				-1.92 (-3.71,-0.12)

Age _(quad) *PupPrev				0.05 (-0.01,0.11)
Late-Lactation Model Suite				
DTA	0.86 (0.46,1.27)	0.85 (0.45,1.24)	0.84 (0.44,1.24)	0.87 (0.46,1.27)
BirthMass	1.76 (1.42,2.09)	1.71 (1.37,2.06)	1.71 (1.37,2.06)	1.76 (1.42,2.09)
Age _(asym)	22.39 (17.13,27.65)			22.36 (17.07,27.66)
Age		5.17 (3.42,6.91)	5.22 (3.04,7.39)	
Age _(quad)		-0.14 (-0.19,-0.08)	-0.13 (-0.20,-0.05)	
PupPrev	27.14 (8.63,45.65)		13.41 (-9.35,36.17)	27.15 (8.63,45.66)
BTime	-0.41 (-0.67,-0.15)	-0.40 (-0.66,-0.14)	-0.40 (-0.66,-0.13)	-0.41 (-0.67,-0.14)
AgeFirst				0.36 (-0.83,0.91)
Age _(asym) *PupPrev	-10.46 (-17.60,-3.33)			-10.46 (-17.60,-3.32)
Age*PupPrev			-1.33 (-4.50,1.83)	
Age _(quad) *PupPrev			0.02 (-0.08,0.12)	

¹ Bold notation denotes coefficient estimates with 95% confidence intervals that do not span zero. Abbreviations and model ID are explained in Table 4.

Table 6. Model selection results for exploratory models examining effects of covariates on variation in Weddell seal pup parturition, mid- and late-lactation masses. Covariates included the quadratic ($Age_{(quad)}$) and asymptotic form ($Age_{(asym)}$) of maternal age, age at primiparity (Age_{First}), timing of birth ($BTime$), pupped the previous season ($PupPrev$), winter southern oscillation index (Win_{SOI}), summer southern oscillation index (Sum_{SOI}), and pup sex ($PupSex$). Deviation from target age was included in all models in all model suites and adjusted pup parturition mass was included in all models in the mid- and late-lactation suites. The exploratory models with significant weight are presented along with the number of parameters (K), AIC_c , ΔAIC_c , and the Akaike weight (w_i) for each model suite.

ID	Model	K	AIC_c	ΔAIC_c	w_i
Parturition Mass Suite					
1	$Age_{(quad)} + BTime + Age_{First} + Win_{SOI} + Sum_{SOI}$	10	4922.1	0.00	0.30
2	$Age_{(quad)} + BTime + Age_{First} + Win_{SOI} + Sum_{SOI} + PupSex$	11	4922.5	0.38	0.25
3	$Age_{(quad)} + BTime + Age_{First} + PupPrev + Win_{SOI} + Sum_{SOI}$	11	4924.0	1.91	0.11
4	$Age_{(quad)} + BTime + Age_{First} + PupPrev + Win_{SOI} + Sum_{SOI} + PupSex$	12	4924.5	2.35	0.09
Mid-Lactation Suite					
1	$Age_{(asym)} + PupPrev + (Age_{(asym)} * PupPrev) + Win_{SOI}$	9	3815.7	0.00	0.29
2	$Age_{(asym)} + PupPrev + (Age_{(asym)} * PupPrev) + Win_{SOI} + PupSex$	10	3816.2	0.54	0.22
3	$Age_{(asym)} + PupPrev + (Age_{(asym)} * PupPrev)$	8	3817.3	1.64	0.13
4	$Age_{(asym)} + PupPrev + (Age_{(asym)} * PupPrev) + PupSex$	9	3817.7	2.02	0.10
5	$Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev)$	9	3818.9	3.24	0.06
6	$Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + PupSex$	10	3819.5	3.84	0.04
Late Lactation Suite					
1	$Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + Win_{SOI} + PupSex$	11	3829.9	0.00	0.30
2	$Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + Win_{SOI}$	10	3830.1	0.24	0.27
3	$Age_{(asym)} + BTime + PupPrev + Age_{First} + (Age_{(asym)} * PupPrev) + Win_{SOI} + PupSex$	12	3831.7	1.86	0.12
4	$Age_{(asym)} + BTime + PupPrev + Age_{First} + (Age_{(asym)} * PupPrev) + Win_{SOI}$	11	3832.0	2.09	0.11

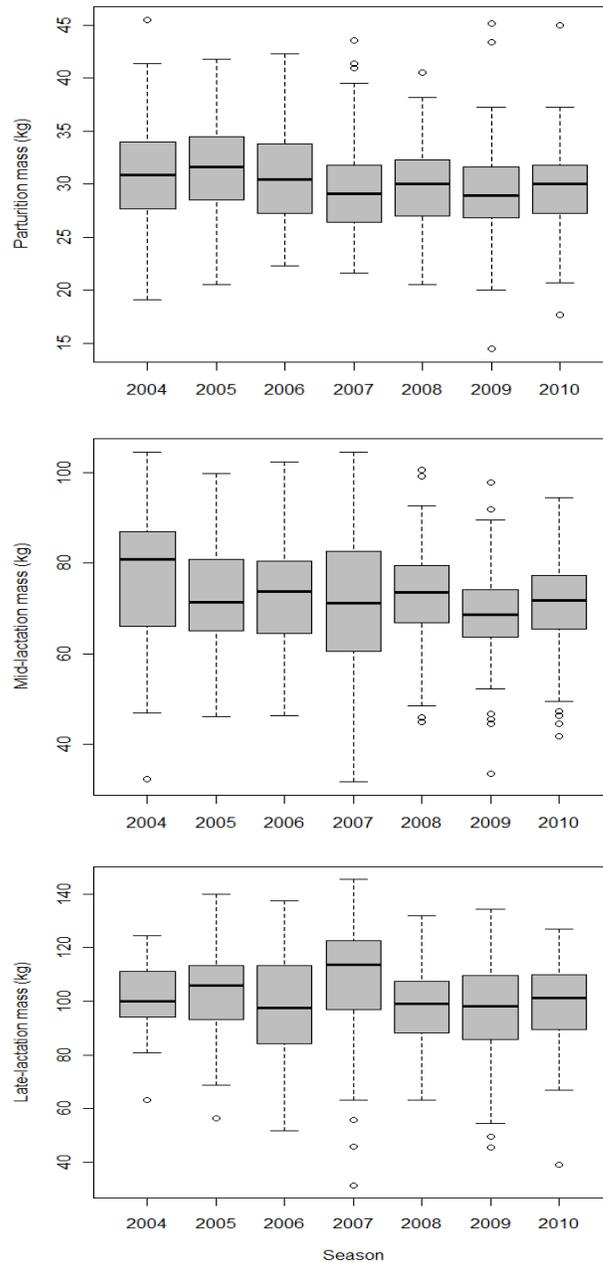


Figure 1. Annual variation in parturition, mid- and late-lactation masses of Weddell seal pups born in Erebus Bay, Antarctica 2004 through 2010. Annually, 80-195 pups were weighed at parturition, 35-162 pups were weighed during mid-lactation and 27-150 pups were weighed during late-lactation, resulting in a total sample size of 887 used in analysis. Median pup mass is represented by the thick line in the middle of the boxes. The 25th and 75th percentiles are represented by thin lines at the bottom and top of each box, respectively. The whiskers represent 2 standard deviations and open circles represent outliers.

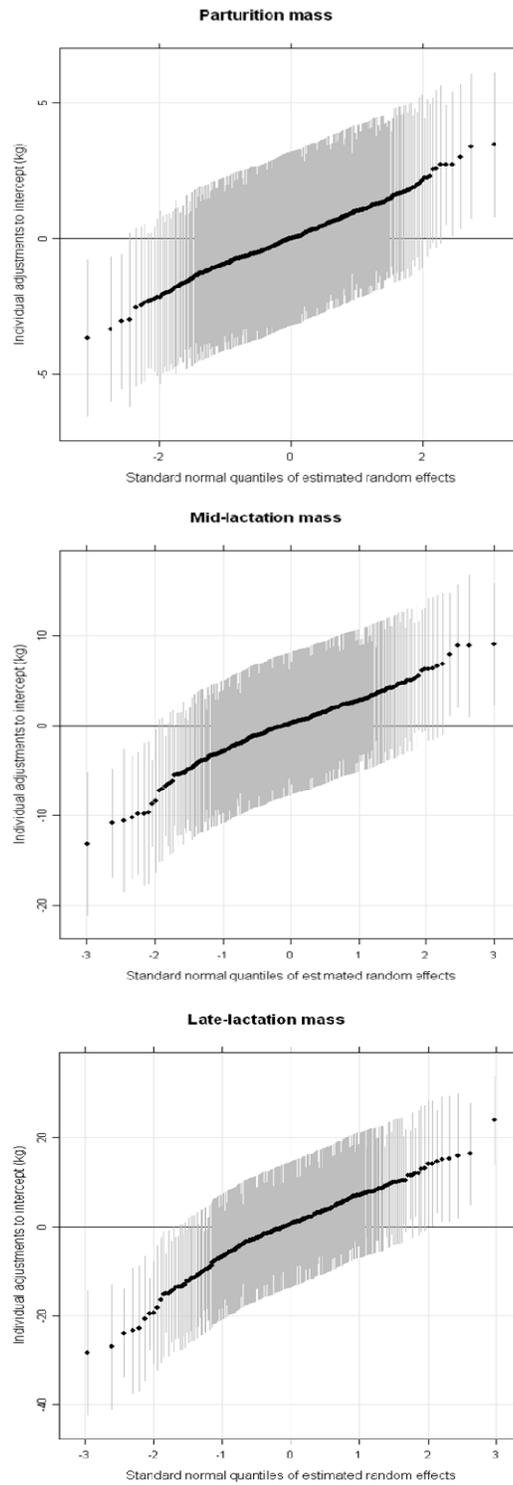


Figure 2. Predicted intercept adjustments for each adult female Weddell seals who's pups were sampled for parturition, mid-, and late-lactation mass from 2004 through 2010 (see Table 2).

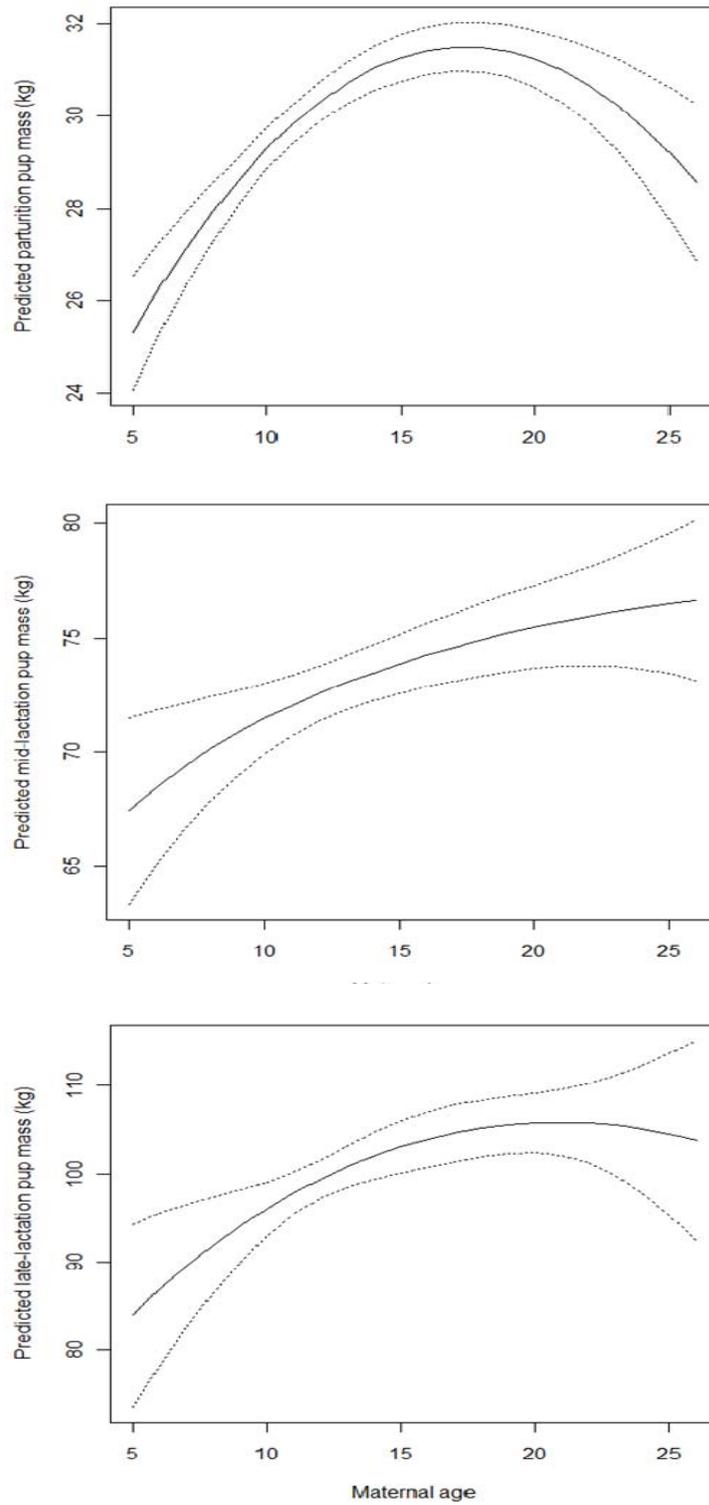


Figure 3. Model-averaged predicted mean pup mass (solid line) and 95% confident intervals (dashed line) for Weddell seal pups with mothers of varying ages.

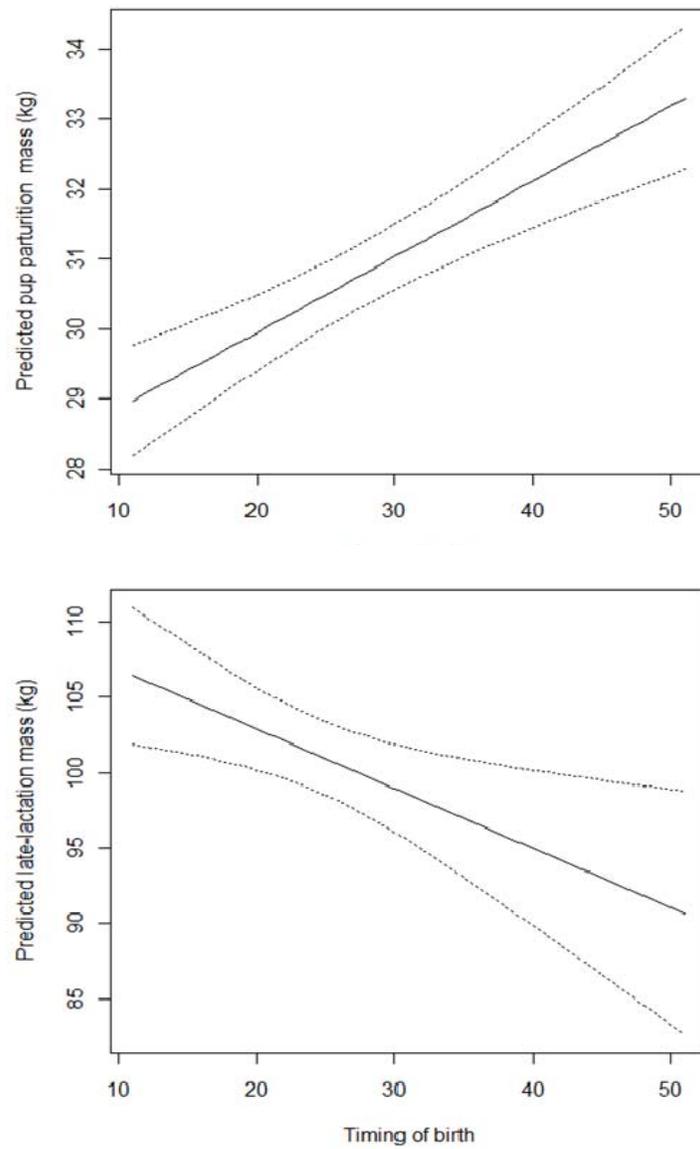


Figure 4. Model-averaged predicted mean pup mass (solid line) and 95% confident intervals (dashed lines) for Weddell seal pups with varying birth dates.

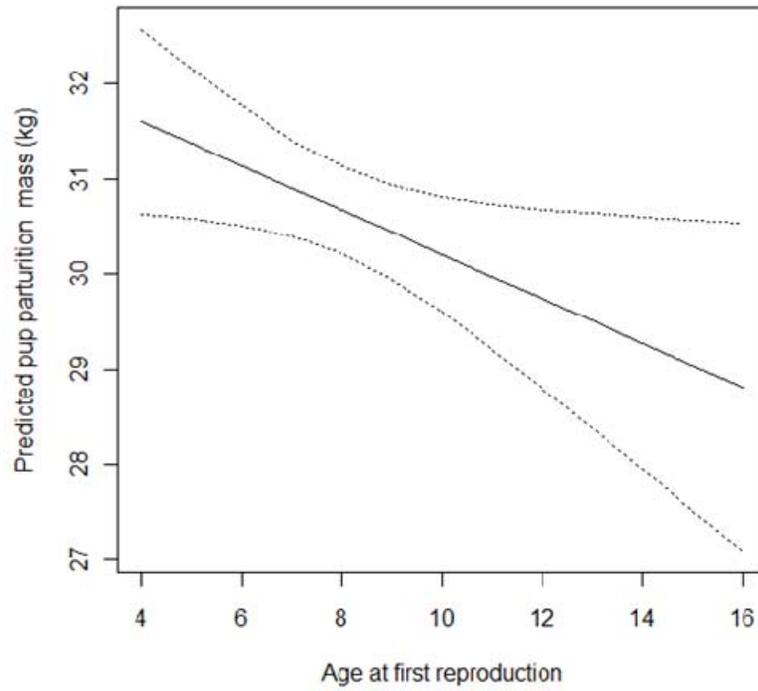


Figure 5. Model-averaged predicted mean pup mass at parturition (solid lines) and 95% confidence intervals (dashed lines) from mothers with varying ages at first reproduction.

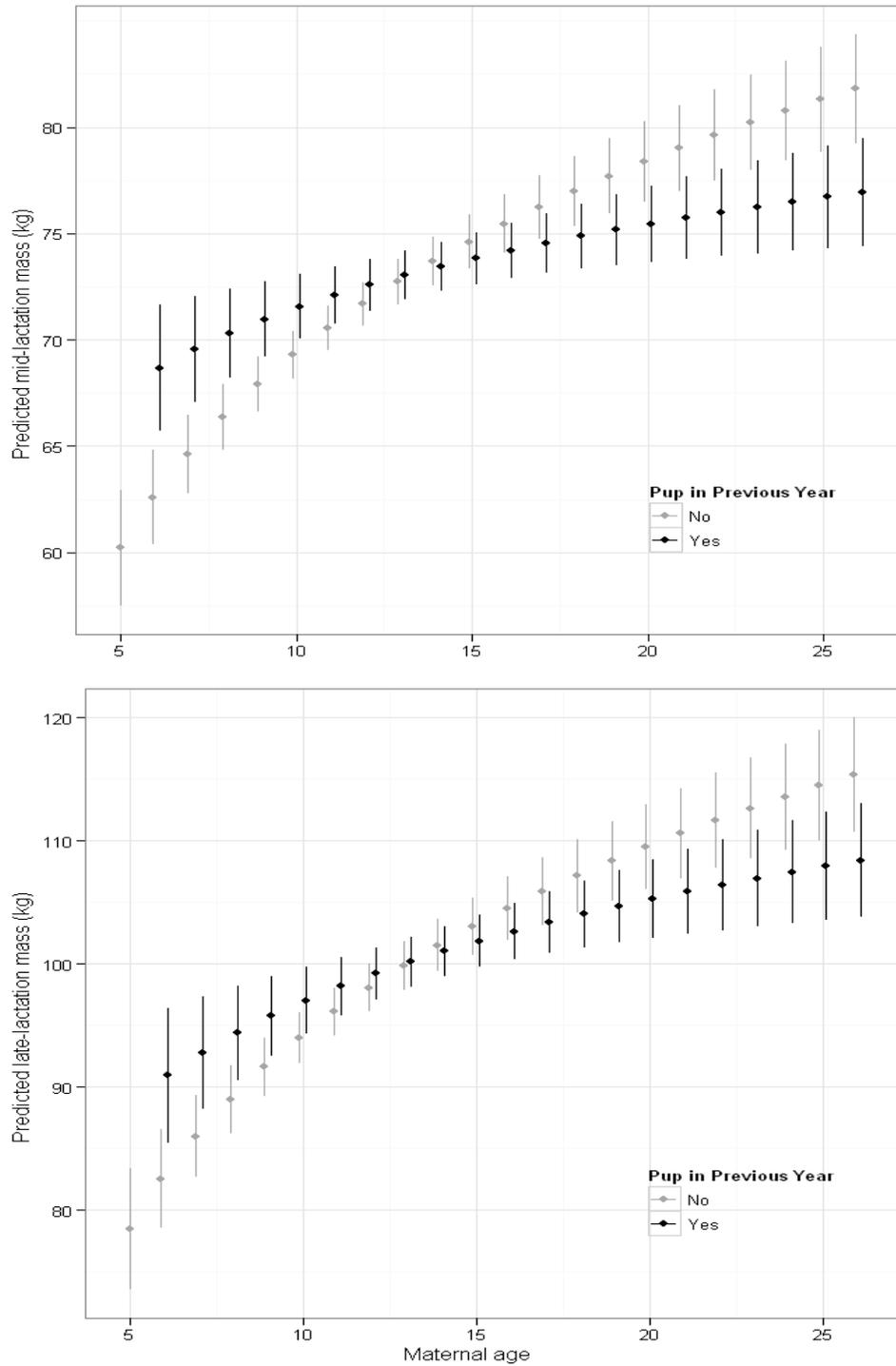


Figure 6. The predicted mid- and late-lactation masses (points) with standard error bars for Weddell seal pups born to mothers of varying ages who gave birth the previous season (black) and who did not give birth the previous season (gray).

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APPENDICES

APPENDIX A

DISTRIBUTION OF DATA FOR MATERNAL
CHARACTERISTICS AND PUP MASSES

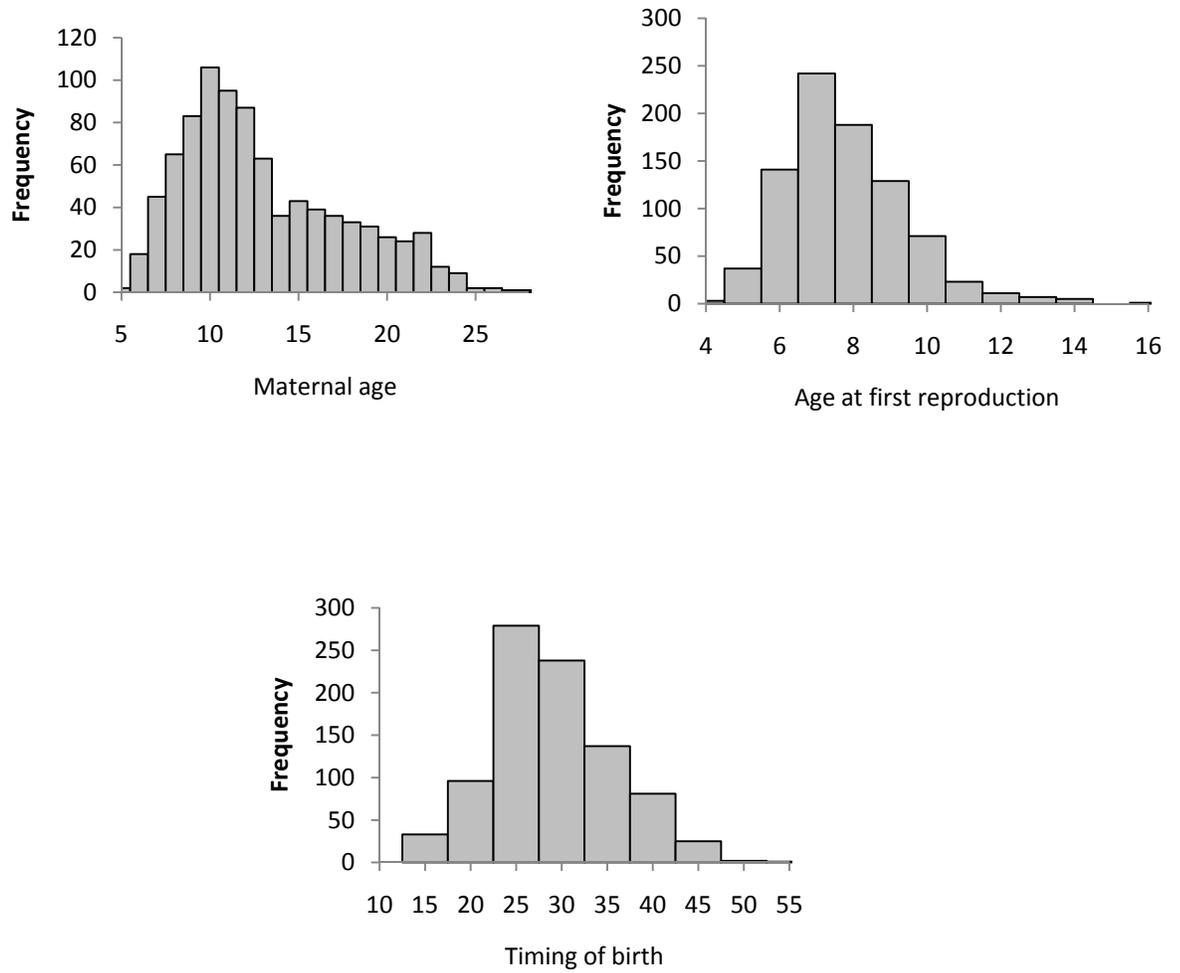


Figure 1. Distribution of data for maternal characteristics, age (Age), age at first reproduction (AgeFirst), and timing of birth (BTime) represented as days since October 1, for pup mass measurements collected during seven consecutive reproductive seasons (2004-2010 n=887).

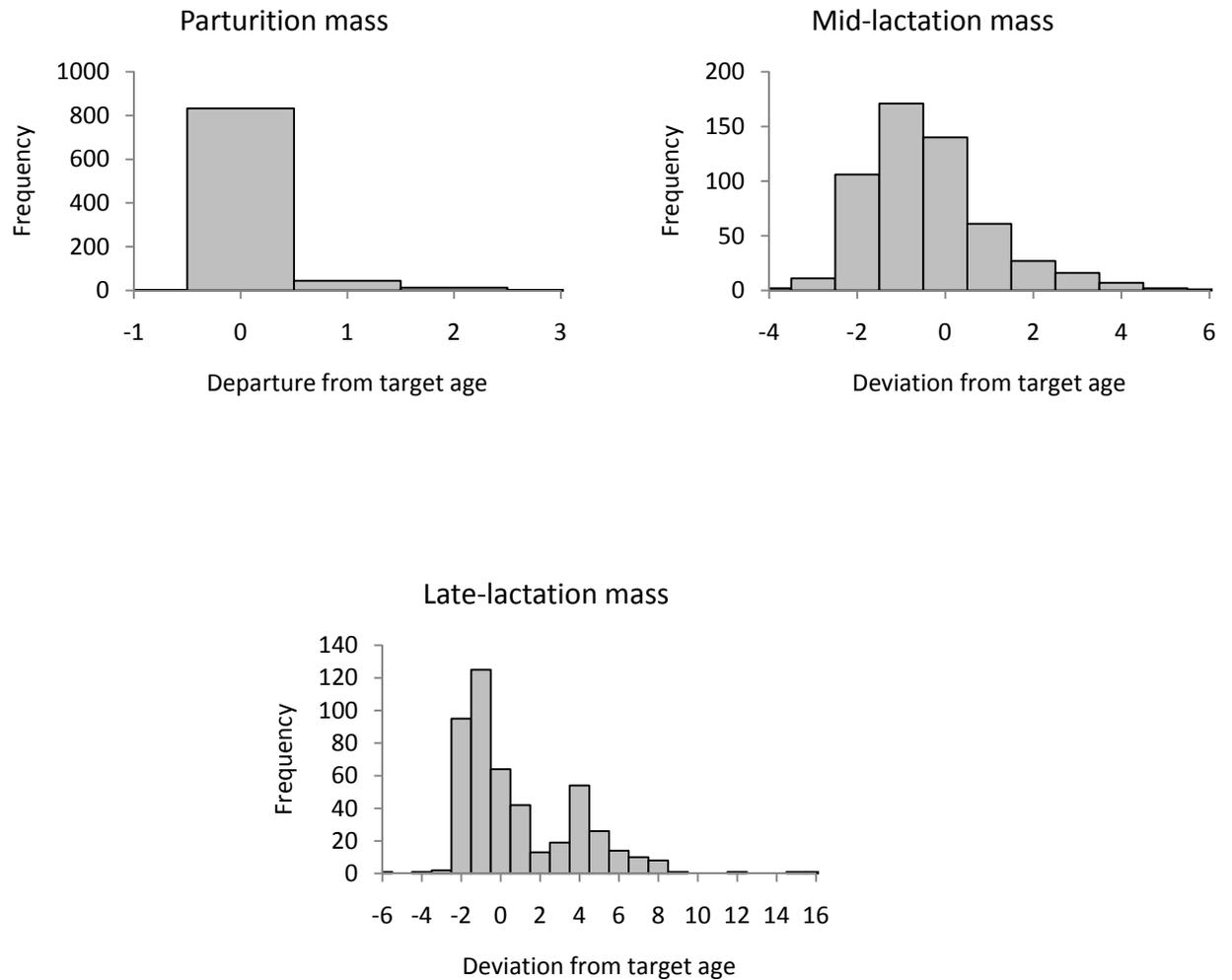


Figure 2. Distribution of data for deviation from target age for parturition, mid- and late-lactation mass measurements (DTA), for Weddell seal pups sampled during the 2004 through 2010 field seasons. DTA range for parturition was 0-2 (n=887), mid-lactation was -4-6 (n=541), and late-lactation was -6-16 (n=474).

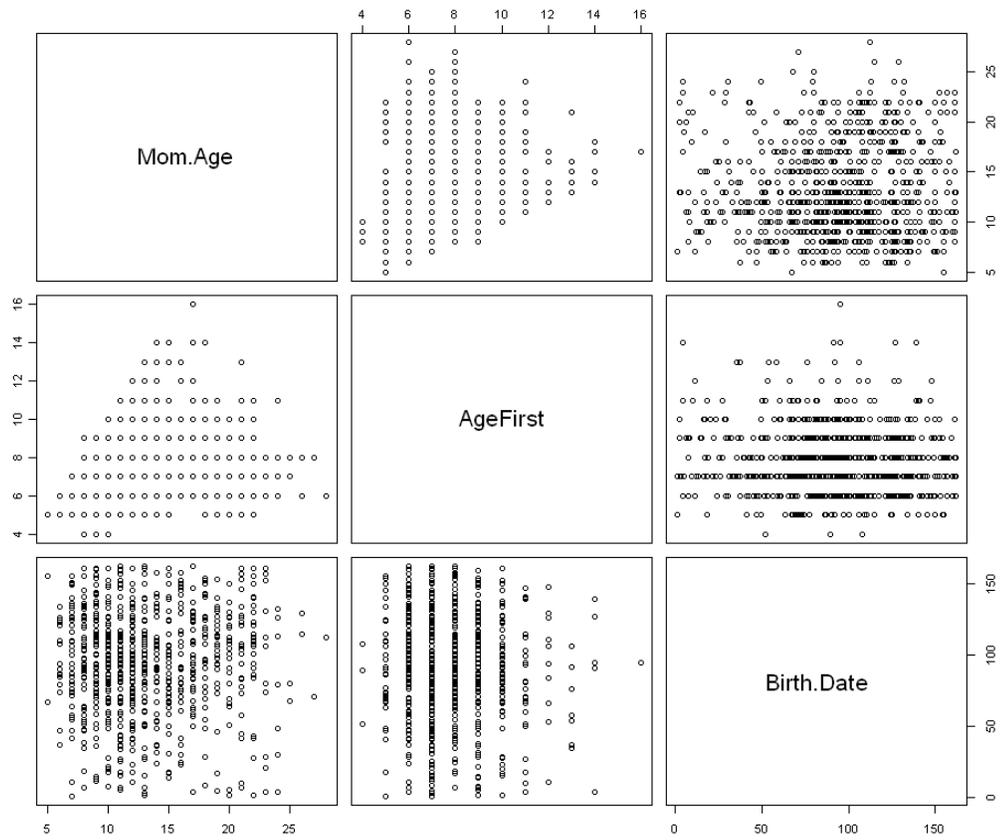
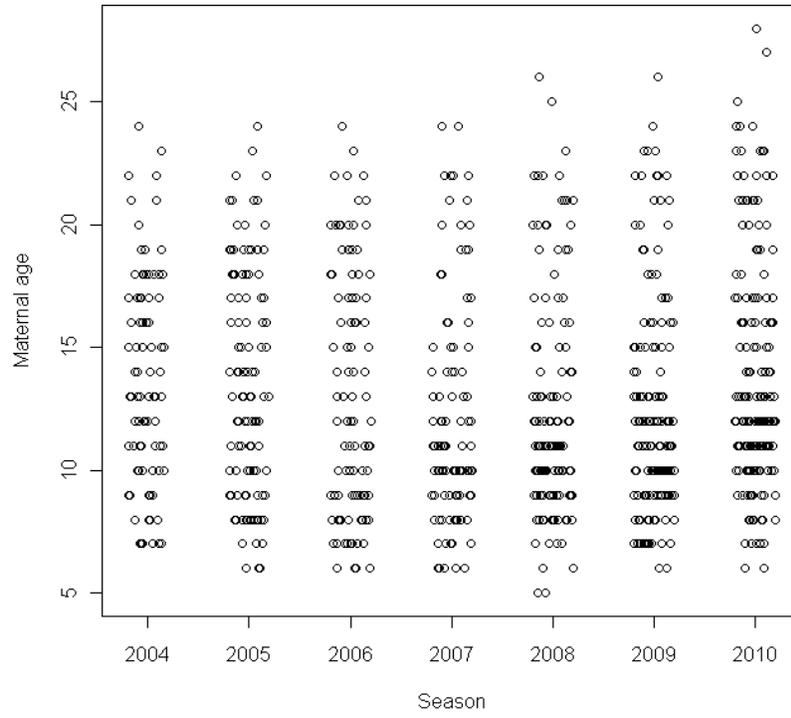
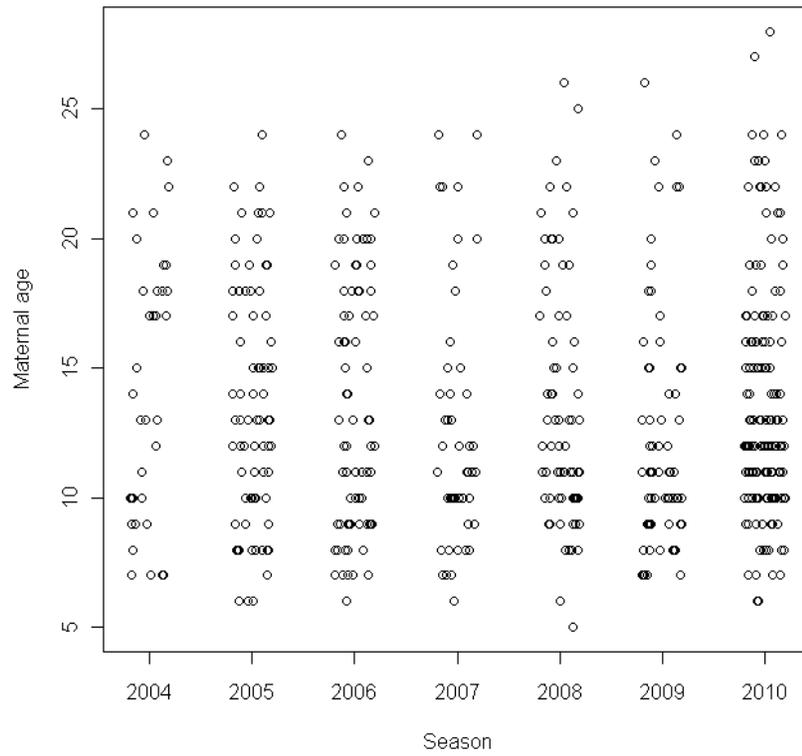


Figure 3. Matrix of scatter plots showing correlations between maternal attributes including maternal age (Mom.Age), age at primiparity (AgeFirst), and timing of birth (Birth.Date).

Parturition mass



Mid-lactation mass



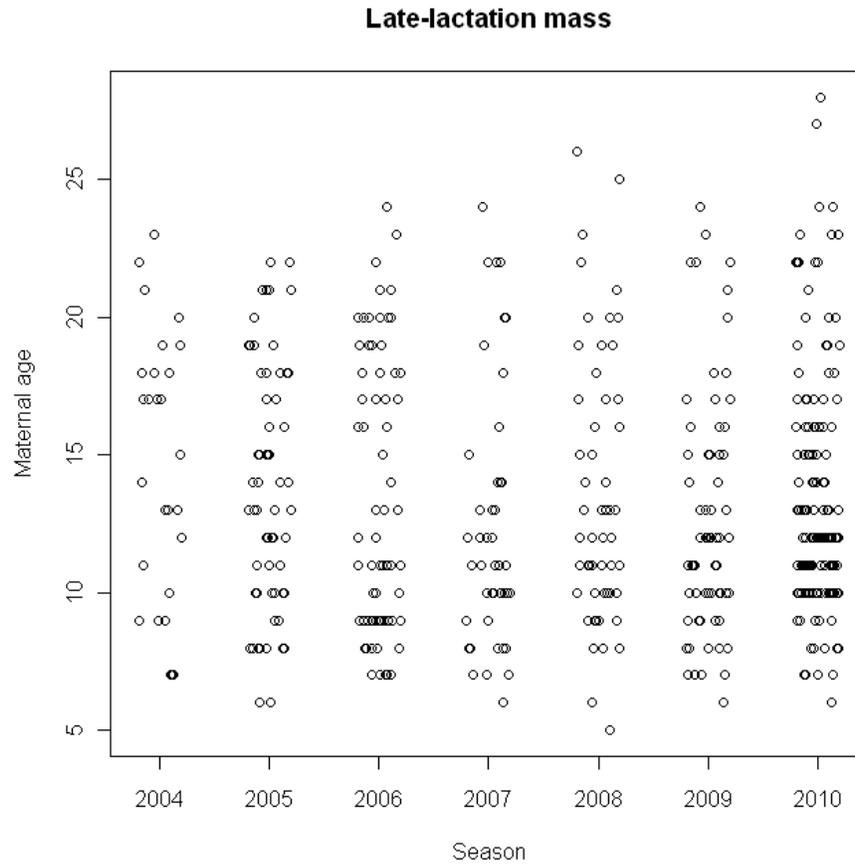


Figure 4. Jitter-plots of sample sizes of females for each maternal age for pup mass measurements collected at parturition ($n=887$), mid- ($n=541$) and late-lactation ($n=474$) during seven consecutive reproductive seasons (2004-2010). Each circle represents one female.

Table 1. Distribution of the total number of adult female Weddell seals who's pups were sampled at parturition for the young (<9 years old), middle (9 to 16 years old), and old (greater than 16 years old) age classes from the 2004 through 2010 field seasons.

Pup Mass Measurement	Age Class		
	<9	9 to 16	>16
Parturition	130	552	205
Mid-Lactation	72	330	138
Late-Lactation	59	298	118
Total	261	1180	446

APPENDIX B

A PRIORI MODELS USED FOR ANALYSIS

Table 1. List of 25 models used in each suite for a priori analysis. All models included DTA and models in the mid- and late-lactation analysis also included BirthMass.

NULL
$\text{Age}_{(\text{quad})}$
$\text{Age}_{(\text{quad})} + \text{BTime}$
$\text{Age}_{(\text{quad})} + \text{PupPrev}$
$\text{Age}_{(\text{quad})} + \text{AgeFirst}$
$\text{Age}_{(\text{quad})} + \text{BTime} + \text{PupPrev}$
$\text{Age}_{(\text{quad})} + \text{BTime} + \text{AgeFirst}$
$\text{Age}_{(\text{quad})} + \text{PupPrev} + \text{AgeFirst}$
$\text{Age}_{(\text{quad})} + \text{PupPrev} + (\text{Age}_{(\text{quad})} * \text{PupPrev})$
$\text{Age}_{(\text{quad})} + \text{BTime} + \text{PupPrev} + \text{AgeFirst}$
$\text{Age}_{(\text{quad})} + \text{PupPrev} + \text{AgeFirst} + (\text{Age}_{(\text{quad})} * \text{PupPrev})$
$\text{Age}_{(\text{quad})} + \text{BTime} + \text{PupPrev} + (\text{Age}_{(\text{quad})} * \text{PupPrev})$
$\text{Age}_{(\text{quad})} + \text{BTime} + \text{PupPrev} + \text{AgeFirst} + (\text{Age}_{(\text{quad})} * \text{PupPrev})$
$\text{Age}_{(\text{asym})}$
$\text{Age}_{(\text{asym})} + \text{BTime}$
$\text{Age}_{(\text{asym})} + \text{PupPrev}$
$\text{Age}_{(\text{asym})} + \text{AgeFirst}$
$\text{Age}_{(\text{asym})} + \text{BTime} + \text{PupPrev}$
$\text{Age}_{(\text{asym})} + \text{BTime} + \text{AgeFirst}$
$\text{Age}_{(\text{asym})} + \text{PupPrev} + \text{AgeFirst}$
$\text{Age}_{(\text{asym})} + \text{PupPrev} + (\text{Age}_{(\text{asym})} * \text{PupPrev})$
$\text{Age}_{(\text{asym})} + \text{BTime} + \text{PupPrev} + \text{AgeFirst}$
$\text{Age}_{(\text{asym})} + \text{PupPrev} + \text{AgeFirst} + (\text{Age}_{(\text{asym})} * \text{PupPrev})$
$\text{Age}_{(\text{asym})} + \text{BTime} + \text{PupPrev} + (\text{Age}_{(\text{asym})} * \text{PupPrev})$
$\text{Age}_{(\text{asym})} + \text{BTime} + \text{PupPrev} + \text{AgeFirst} + (\text{Age}_{(\text{asym})} * \text{PupPrev})$

APPENDIX C

EXPLANATORY MODELS USED FOR ANALYSIS

Table 1. List of models used for exploratory analysis. All models included DTA and models in the mid- and late-lactation suites also included BirthMass.

Parturition Mass Suite

$Age_{(quad)} + BTime + AgeFirst + PupSex$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + PupSex$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + PupSex$
 $Age_{(quad)} + BTime + AgeFirst + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + Win_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + Win_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + Win_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + Win_{SOI} + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + Win_{SOI} + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + Win_{SOI} + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupSex + Win_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + PupSex + Win_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + PupSex + Win_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupSex + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + PupSex + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + PupSex + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupSex + Win_{SOI} + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + PupSex + Win_{SOI} + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + PupSex + Win_{SOI} + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev)$

Mid-Lactation Suite

$Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + PupSex$
 $Age_{(asym)} + BTime + AgeFirst + PupPrev + (Age_{(asym)} * PupPrev) + PupSex$
 $Age_{(asym)} + PupPrev + (Age_{(asym)} * PupPrev) + PupSex$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + PupSex$
 $Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + Sum_{SOI}$
 $Age_{(asym)} + BTime + AgeFirst + PupPrev + (Age_{(asym)} * PupPrev) + Sum_{SOI}$
 $Age_{(asym)} + PupPrev + (Age_{(asym)} * PupPrev) + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + Sum_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + Win_{SOI}$
 $Age_{(asym)} + BTime + AgeFirst + PupPrev + (Age_{(asym)} * PupPrev) + Win_{SOI}$
 $Age_{(asym)} + PupPrev + (Age_{(asym)} * PupPrev) + Win_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + Win_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + Win_{SOI} + Sum_{SOI}$
 $Age_{(asym)} + BTime + AgeFirst + PupPrev + (Age_{(asym)} * PupPrev) + Win_{SOI} + Sum_{SOI}$

$Age_{(asym)} + PupPrev + (Age_{(asym)} * PupPrev) + Wins_{SOI} + Sums_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + Wins_{SOI} + Sums_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + PupSex + Wins_{SOI}$
 $Age_{(asym)} + BTime + AgeFirst + PupPrev + (Age_{(asym)} * PupPrev) + PupSex + Wins_{SOI}$
 $Age_{(asym)} + PupPrev + (Age_{(asym)} * PupPrev) + PupSex + Wins_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + PupSex + Wins_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + PupSex + Sums_{SOI}$
 $Age_{(asym)} + BTime + AgeFirst + PupPrev + (Age_{(asym)} * PupPrev) + PupSex + Sums_{SOI}$
 $Age_{(asym)} + PupPrev + (Age_{(asym)} * PupPrev) + PupSex + Sums_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + PupSex + Sums_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + PupSex + Wins_{SOI} + Sums_{SOI}$
 $Age_{(asym)} + BTime + AgeFirst + PupPrev + (Age_{(asym)} * PupPrev) + PupSex + Wins_{SOI}$
 $+ Sums_{SOI}$
 $Age_{(asym)} + PupPrev + (Age_{(asym)} * PupPrev) + PupSex + Wins_{SOI} + Sums_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev) + PupSex + Wins_{SOI} +$
 $Sums_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev)$
 $Age_{(asym)} + BTime + AgeFirst + PupPrev + (Age_{(asym)} * PupPrev)$
 $Age_{(asym)} + PupPrev + (Age_{(asym)} * PupPrev) + PupSex$
 $Age_{(quad)} + BTime + AgeFirst + PupPrev + (Age_{(quad)} * PupPrev)$

Late Lactation Suite

$Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + PupSex$
 $Age_{(quad)} + BTime + PupSex$
 $Age_{(quad)} + BTime + PupPrev + (Age_{(quad)} * PupPrev) + PupSex$
 $Age_{(asym)} + BTime + PupPrev + AgeFirst + (Age_{(asym)} * PupPrev) + PupSex$
 $Age_{(quad)} + BTime + AgeFirst + PupSex$
 $Age_{(quad)} + BTime + PupPrev + PupSex$
 $Age_{(quad)} + BTime + PupPrev + AgeFirst + (Age_{(quad)} * PupPrev) + PupSex$
 $Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + Sums_{SOI}$
 $Age_{(quad)} + BTime + Sums_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + (Age_{(quad)} * PupPrev) + Sums_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + AgeFirst + (Age_{(asym)} * PupPrev) + Sums_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + Sums_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + Sums_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + AgeFirst + (Age_{(quad)} * PupPrev) + Sums_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + Wins_{SOI}$
 $Age_{(quad)} + BTime + Wins_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + (Age_{(quad)} * PupPrev) + Wins_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + AgeFirst + (Age_{(asym)} * PupPrev) + Wins_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + Wins_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + Wins_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + AgeFirst + (Age_{(quad)} * PupPrev) + Wins_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + PupSex + Wins_{SOI}$
 $Age_{(quad)} + BTime + PupSex + Wins_{SOI}$

$Age_{(quad)} + BTime + PupPrev + (Age_{(quad)} * PupPrev) + PupSex + Win_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + AgeFirst + (Age_{(asym)} * PupPrev) + PupSex + Win_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupSex + Win_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + PupSex + Win_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + AgeFirst + (Age_{(quad)} * PupPrev) + PupSex + Win_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + PupSex + Sum_{SOI}$
 $Age_{(quad)} + BTime + PupSex + Sum_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + (Age_{(quad)} * PupPrev) + PupSex + Sum_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + AgeFirst + (Age_{(asym)} * PupPrev) + PupSex + Sum_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupSex + Sum_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + PupSex + Sum_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + AgeFirst + (Age_{(quad)} * PupPrev) + PupSex + Sum_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev) + PupSex + Sum_{SOI} + Win_{SOI}$
 $Age_{(quad)} + BTime + PupSex + Sum_{SOI} + Win_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + (Age_{(quad)} * PupPrev) + PupSex + Sum_{SOI} + Win_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + AgeFirst + (Age_{(asym)} * PupPrev) + PupSex + Sum_{SOI} + Win_{SOI}$
 $Age_{(quad)} + BTime + AgeFirst + PupSex + Sum_{SOI} + Win_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + PupSex + Sum_{SOI} + Win_{SOI}$
 $Age_{(quad)} + BTime + PupPrev + AgeFirst + (Age_{(quad)} * PupPrev) + PupSex + Sum_{SOI} + Win_{SOI}$
 $Age_{(asym)} + BTime + PupPrev + (Age_{(asym)} * PupPrev)$
 $Age_{(quad)} + BTime$
 $Age_{(quad)} + BTime + PupPrev + (Age_{(quad)} * PupPrev)$
 $Age_{(asym)} + BTime + PupPrev + AgeFirst + (Age_{(asym)} * PupPrev)$
 $Age_{(quad)} + BTime + AgeFirst$
 $Age_{(quad)} + BTime + PupPrev$
 $Age_{(quad)} + BTime + PupPrev + AgeFirst + (Age_{(quad)} * PupPrev)$

APPENDIX D

COEFFICIENT ESTIAMTES AND CONFIDENCE INTERVALS
FOR EXPLORATORY ANALYSIS

Table 1. Coefficient values (β_i) and 95% confidence intervals (in parentheses)¹ for covariates from the most supported models for each of the three model suites indentified through AIC model comparisons examining variation in pup mass.

Covariate	Model ID			
	1	2	3	4
Parturition Model Suite				
DTA	1.66 (0.91, 2.41)	1.67 (0.92, 2.42)	1.67 (0.92, 2.43)	1.68 (0.92, 2.43)
Age	1.38 (1.02, 2.41)	1.38 (1.02, 1.74)	1.40 (1.03, 1.76)	1.39 (1.03, 1.76)
Age(quad)	-0.04 (-0.05, -0.03)	-0.04 (-0.05, -0.03)	-0.04 (-0.05, -0.03)	-0.04 (-0.05, -0.03)
BTime	0.11 (0.07, 0.15)	0.11 (0.11, 0.15)	0.11 (0.07, 0.15)	0.11 (0.07, 0.15)
PupPrev			-0.11 (-0.65, 0.43)	-0.08 (-0.62, 0.46)
AgeFirst	-0.20 (-0.38, -0.03)	-0.21 (-0.39, -0.03)	-0.21 (-0.39, -0.03)	-0.21 (-0.39, -0.03)
Win _{SOI}	-0.03 (-0.06, -0.01)	-0.03 (-0.06, -0.01)	-0.03 (-0.06, -0.01)	-0.03 (-0.09, -0.01)
Sum _{SOI}	-0.04 (-0.67, -0.01)	-0.04 (-0.67, -0.01)	-0.04 (-0.39, -0.01)	-0.04 (-0.07, -0.01)
PupSex		-0.33 (-0.85, 0.18)		-0.33 (-0.85, 0.18)
Mid-Lactation Model Suite				
DTA	1.81 (1.33, 2.29)	1.81 (1.32, 2.28)	1.60 (1.13, 2.06)	1.59 (1.13, 2.06)
BirthMass	1.61 (1.42, 1.80)	1.61 (1.43, 1.80)	1.56 (1.38, 1.75)	1.57 (1.38, 1.76)
Age _(asym)	12.80 (9.88, 15.71)	12.80 (9.89, 15.72)	13.30 (10.38, 16.22)	13.31 (10.39, 16.23)
BTime				-0.13 (-0.26, 0.00)
PupPrev	19.13 (8.70, 29.55)	19.26 (8.82, 29.70)	19.21 (8.72, 29.71)	19.36 (8.86, 29.87)
Age _(asym) *PupPrev	-7.49 (-11.53, -3.44)	-7.54 (-11.59, -3.49)	-7.44 (-11.51, -3.36)	-7.50 (-11.57, -3.43)
Win _{SOI}	0.09 (0.03, 0.16)	0.09 (0.03, 0.16)		
PupSex		0.45 (-0.93, 1.83)		0.53 (-0.86, 1.91)
Late-Lactation Model Suite				

DTA	1.26 (0.79,1.74)	1.26 (0.79,1.74)	1.26 (0.79,1.74)	1.26 (0.79,1.73)
BirthMass	1.82 (1.48,2.16)	1.82 (1.48,2.16)	1.82 (1.48,2.16)	1.82 (1.48,2.16)
Age _(asym)	21.82 (16.55,27.09)	21.82 (16.55,27.07)	21.82 (16.58,27.19)	21.82 (16.58,27.18)
BTime	-0.33 (-0.61,-0.06)	-0.34 (-0.60,-0.07)	-0.33 (-0.60,-0.06)	-0.34 (-0.61,-0.07)
PupPrev	28.12 (9.58,46.63)	27.95 (9.49,46.42)	28.10 (9.56,46.64)	27.95 (9.47,46.43)
AgeFirst			-0.09 (-0.96,0.79)	-0.09 (-0.97,0.79)
Age _(asym) *PupPrev	-10.98 (-18.12,-3.83)	-10.91 (-18.03,-3.79)	-10.99 (-18.14,-3.84)	-10.92 (-18.05,-3.80)
Win _{SOI}	0.19 (0.07,0.32)	0.19 (0.07,0.32)	0.20 (0.07,0.32)	0.20 (0.07,0.32)
PupSex	0.34 (-2.10,2.78)		0.34 (-2.11,2.78)	

¹Bold notation denotes coefficient estimates with 95% confidence intervals that do not span zero. Abbreviations and model ID are explained in Table 6.

APPENDIX E

CORRELATION BETWEEN PUP MASSES AND
SOUTHERN OSCILLATION INDEX

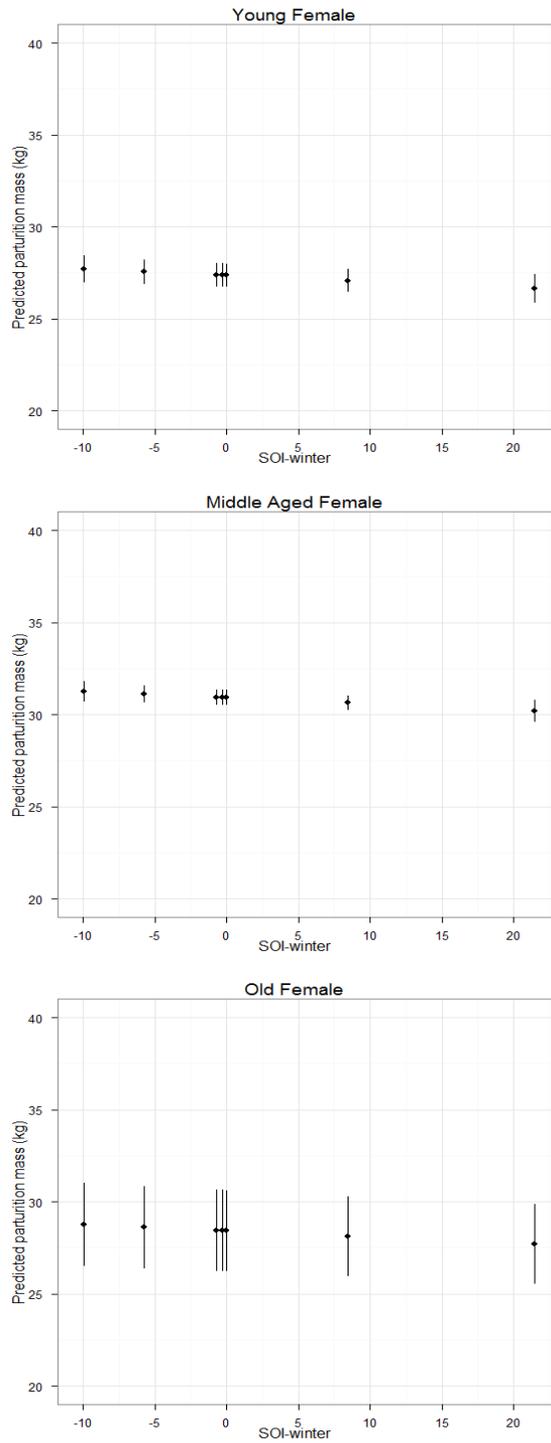


Figure 1. Predicted parturition masses (points) with standard error bars for Weddell seal pups born to young (age 7), middle (age 13), and old (age 20) at different values of the winter southern oscillation index.

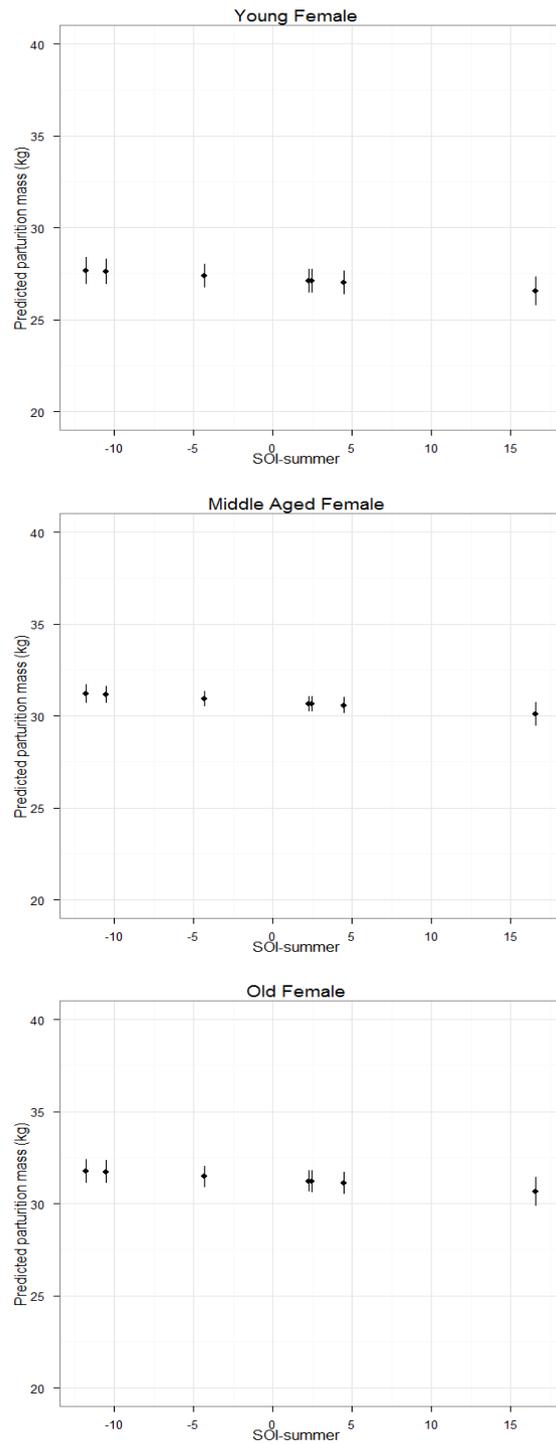


Figure 2. Predicted mid-lactation masses (points) with standard error bars for Weddell seal pups born to young (age 7), middle (age 13), and old (age 20) at different values of the summer southern oscillation index.

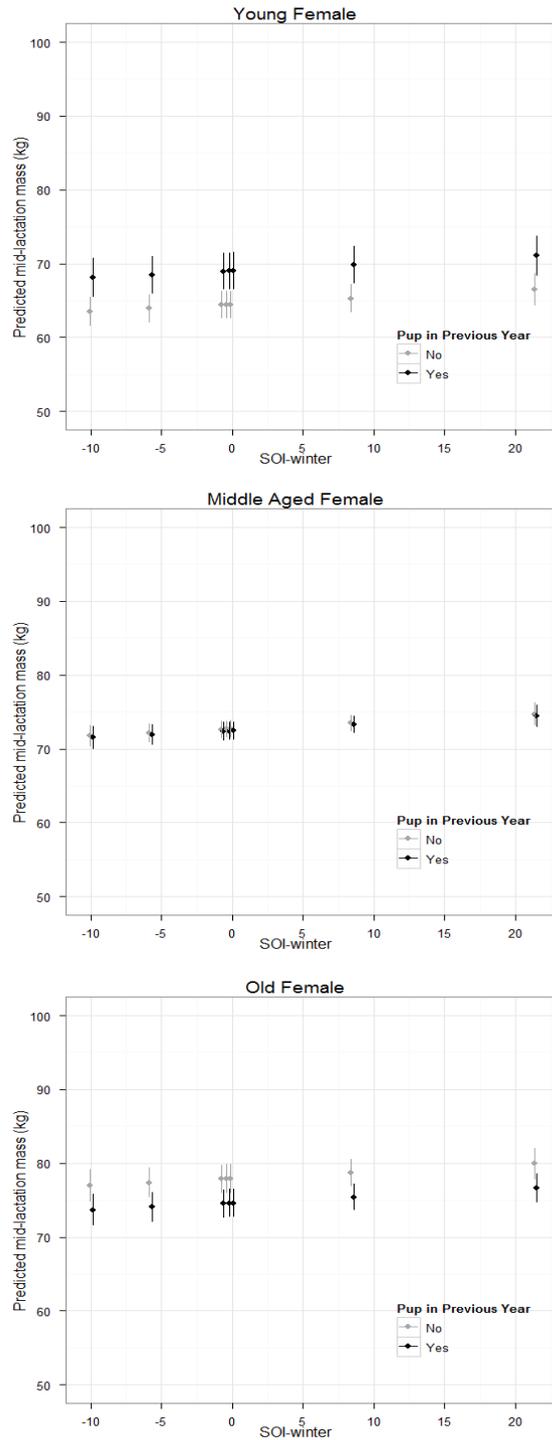


Figure 3. Predicted mid-lactation masses (points) with standard error bars for Weddell seal pups born to young (age 7), middle (age 13), and old (age 20) females who did (black) and did not give birth the previous season (gray) at different values of the winter southern oscillation index.

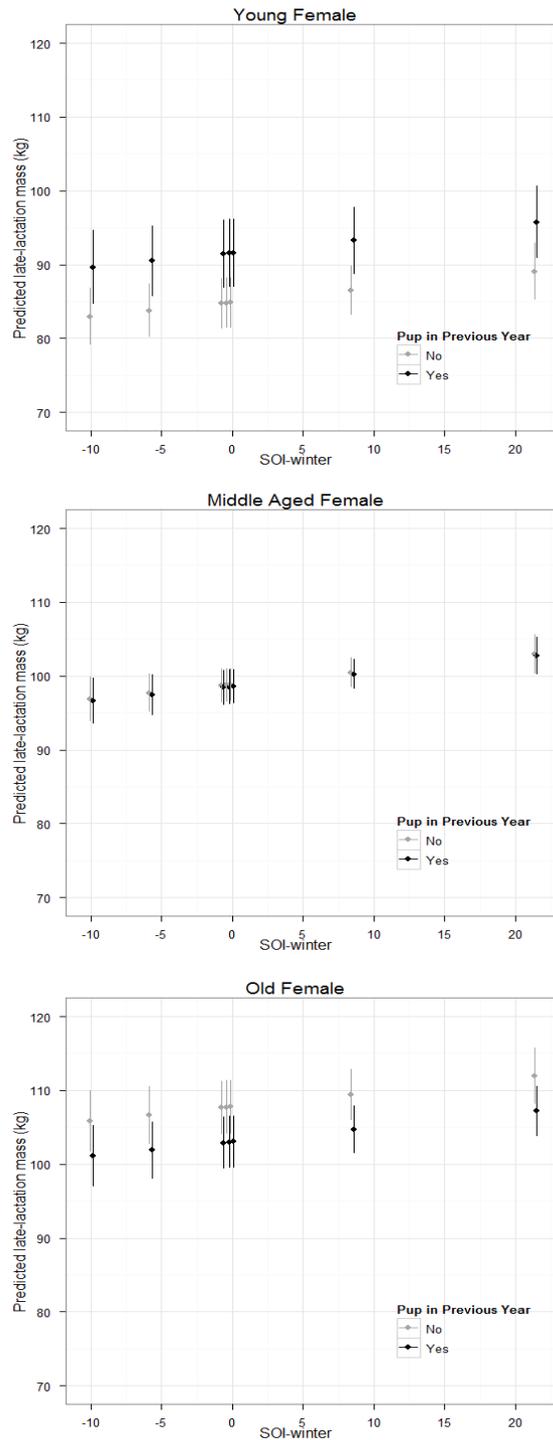


Figure 4. Predicted late-lactation masses (points) with standard error bars for Weddell seal pups born to young (age 7), middle (age 13), and old (age 20) females who did (black) and did not give birth the previous season (gray) at different values of the winter southern oscillation index.