Patterns of age-related change in reproductive effort differ in the pre-natal and post-natal periods in a long-lived mammal

Authors: John T. Paterson, Jay J. Rotella, Jennifer M. Mannas, and Robert A. Garrott

This is the peer reviewed version of the following article: [Paterson, John T, Jay J Rotella, Jennifer M Mannas, and Robert A Garrott. "Patterns of age-related change in reproductive effort differ in the pre-natal and post-natal periods in a long-lived mammal." Journal of Animal Ecology 85, no. 6 (September 2016): 1540-1551.], which has been published in final form at https://dx.doi.org/10.1111/1365-2656.12577. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.


Made available through Montana State University’s ScholarWorks scholarworks.montana.edu
Patterns of age-related change in reproductive effort differ in the pre-natal and post-natal periods in a long-lived mammal

John T. Paterson1*, Jay J. Rotella1, Jennifer M. Mannas1,2 and Robert A. Garrott1

1Ecology Department, Montana State University, Bozeman, MT 59717, USA; and 2Progressive Animal Welfare Society, Lynnwood, WA 98046, USA

Summary

1. Age-related changes in maternal reproductive allocation for long-lived species are a key prediction from life-history theory.
2. Theoretical and empirical work suggests that allocation may increase with age due to constraint (increases with experience) or restraint (increases with age in the face of declining residual reproductive value), and may decrease among the oldest aged animals due to senescence in reproductive function.
3. Here, we use a hierarchical modelling approach to investigate the age-related patterns of change in maternal reproductive effort in the Weddell seal, a long-lived marine mammal with a protracted period of maternal care during which mothers allocate a large proportion of body mass while feeding little.
4. We find that maternal allocation increases with age for young mothers during both the pre-natal and post-natal periods. In contrast, older mothers demonstrate a senescent decline in pre-natal allocation but allocate more of their declining resources to their offspring during the post-natal period. We also find strong evidence for the importance of individual effects in reproductive allocation among mothers: some mothers consistently produce heavier (or lighter) pups than expected.
5. Our results indicate that maternal allocation changes over a mother’s reproductive life span and that age-specific differences differ in notable ways in pre-natal and post-natal periods.

Key-words: Antarctica, reproductive allocation, Ross Sea, senescence, terminal allocation, Weddell seal

Introduction

The allocation of energy to reproduction is a central component of an organism’s life history and has consequences for the fitness of both offspring and parent (Smith & Fretwell 1974; Stearns 1992; Roff 2002). Maternal allocation is linked to the growth and development of offspring and strongly associated with early survival (Skibiel, Dobson & Murie 2009; Baron et al. 2010; Skibiel, Speakman & Hood 2013). Moreover, the effects of early maternal allocation may be long-lasting. Empirical work suggests an association between the level of allocation and an offspring’s future survival, recruitment and reproduction (Hackman et al. 1983; Kruuk et al. 1999; Lindström 1999; Lummaa & Clutton-Brock 2002; Lummaa 2003; Bateson et al. 2004), a connection likely mediated through the permanent response of critical body systems, for example the immune system, to the level of provisioning early in life (Lucas 1991; Hales & Barker 2001; Gluckman et al. 2005; McMullen et al. 2012). The amount of energy allocated to offspring is ultimately limited by the finite resources of the mother, and her ability to acquire and allocate those resources to reproduction (King, Roff & Fairbairn 2011). Therefore, environmental conditions may directly affect allocation strategies by varying resource availability (Schuett et al. 2009). However, there is ample evidence to suggest that maternal allocation further varies according to maternal characteristics, such that the amount of energy allocated to offspring varies over the reproductive life span of the mother independently of the environment.
There is evidence for both within-individual increases (Gadgil & Bossert 1970; Curio 1983; Forslund & Pärt 1995) and decreases (Kirkwood & Austad 2000; Mysterud et al. 2001) in allocation over an individual’s reproductive life span, and a series of non-mutually exclusive hypotheses relate the potential mechanisms at work. As individuals age, they commonly improve in reproductive performance as they acquire experience and skills, consistent with the constraint hypothesis (Curio 1983; Bowen et al. 2006). The reproductive restraint hypothesis (Gadgil & Bossert 1970; Pianka & Parker 1975) predicts that the degree of allocation is driven by the residual reproductive value (expected future fecundity) of an individual. Therefore, as individuals age, they should allocate more resources to current offspring in the face of fewer expected future reproductive events, that is, the terminal investment hypothesis. When increases in reproductive allocation are not necessarily associated with fitness costs, the pattern of increasing allocation with age is ‘terminal allocation’ (Weladji et al. 2010). In contrast, declines in reproductive performance for older animals may be driven by senescence (Medawar 1946; Williams 1957; Kirkwood 1981). These patterns are not mutually exclusive. Individuals undergoing senescent declines in some measures of reproduction or survival can demonstrate simultaneous increases in other measures of reproductive performance, for example, in female moose (Alces alces) (Ericsson et al. 2001) and reindeer (Rangifer tarandus) (Weladji et al. 2010). Moreover, senescent declines in reproductive effort can be followed by increases in the same component of effort for the terminal breeding attempt (Froy et al. 2013) or when the immune system of individuals is compromised (Velando, Drummond & Torres 2006). In addition to broad changes in the patterns of allocation over the life of individuals, allocation may also vary over the shorter term. In the face of finite resources, parental allocation is constrained by the canonical life-history trade-off between allocation to current offspring and potential consequences to survival and future reproduction (Stearns 1989, 1992; Roff 2002), leading to costs of reproduction. Thus, individuals’ previous reproductive experience (either in terms of the number of reproductive events or in terms of relative allocation of energy to those events (Creighton, Helfin & Belk 2009; Martin & Festa-Bianchet 2011) may affect current and future allocation independently from age-related patterns.

Variation in reproductive allocation at the population level is likely the result of within-individual changes in maternal allocation due to senescence, restraint or constraint as well as between-individual differences due to selection, reproductive experience and individual quality. When frail individuals die at higher rates with increasing age such that higher-quality individuals dominate at older ages, the average reproductive performance of survivors increases with age (Vaupel, Manton & Stallard 1979). The possibility that apparent increases with age might be due to selection underscores the importance of accounting for individual heterogeneity in the population. There is also compelling evidence for individual variation in reproductive traits, with females of similar life histories differing in key traits (van de Pol & Verhulst 2006; Stopher et al. 2008). Moreover, given that reproductive allocation might incur a cost, allocation patterns can also be mediated by the degree to which an individual can meet, and recover from, the energetic demands of current reproduction (Van Noordwijk & de Jong 1986; Stearns 1989). Hence, latent variation in individual reproductive ability, and viability selection that preserves high-quality individuals, can influence the patterns of observed reproductive allocation, which highlights the need to account for individual effects when assessing reproductive allocation (Clutton-Brock 1984; Hamel et al. 2009).

In long-lived polygynous organisms, reproductive allocation can vary depending on offspring sex (Hewison & Gaillard 1999), maternal attributes such as age and experience (Derocher & Stirling 1998; Bowen et al. 2006) and environmental conditions (Garroway & Broders 2007). Moreover, prior work suggests that the patterns of reproductive allocation within individuals may differ in the prenatal and post-natal periods (Lock et al. 2007; Weladji et al. 2010). In mammals, these two periods reflect the different physiological processes of gestation and lactation (Oftedal 1985). Pre-natal allocation during gestation is reflected in litter size and offspring mass at birth (Miller 1977; Oftedal 1985; Gittleman & Thompson 1988; Boyd & McCann 1989; Ochoa-Acua, Francis & Boness 1998), whereas offspring mass gains from birth through weaning should reflect post-natal maternal allocation during lactation (Gittleman & Thompson 1988; Pomeroy et al. 1999). Consequently, analyses of variation in offspring mass from parturition through weaning should be useful for evaluating hypotheses related to individual variation in allocation during two different periods (Robbins & Robbins 1979; Kovacs & Lavigne 1986; Derocher & Stirling 1998; Georges & Guinet 2000; Bowen et al. 2001).

The Weddell seal (Leptonychotes weddelli), which inhabits the fast ice around the coast of Antarctica, is a model organism with which to investigate the variation in maternal allocation. Females are large bodied, long lived, have flexible reproductive schedules, produce a single offspring and raise their young without assistance from males. They are highly philopatric to natal sites where they raise young in predictable colonies on the shore-fast ice during the austral spring (Stirling 1969). During the inferred 5- to 6-week lactation period, which is one of the longest among phocid seals (Schulz & Bowen 2005), females stay in close proximity to their pups and are readily approached by humans, which provides an excellent opportunity to assess maternal masses for a large sample of mothers. Females largely fast through the lactation period, implying that post-natal allocation of energy to offspring is predominately derived from body reserves acquired prior to parturition (Wheatley et al. 2006). Moreover, energy transfer from mom to pup is both
dramatic and variable with females losing, on average, 40% of their post-partum mass, and pups more than tripling their birth weight during the lactation period (Wheatley et al. 2006).

Here, we used the mass of mothers and pups soon after parturition, and the rate of mass gain during early lactation (parturition to ~20 days) and late lactation (~20 to ~35 days) to assess the patterns of reproductive energy allocation during both the pre-natal and post-natal periods. In doing so, we evaluated the relative support for a variety of evolutionary hypotheses regarding allocation of energy to offspring. Reproductive constraint will be supported if reproductive allocation increases with reproductive experience and/or age for the younger mothers. Senescence will be supported if reproductive allocation decreases with age for older mothers. In contrast, an increase in reproductive allocation with age would support terminal allocation. We used a large sample of pups from known-age mothers, and a separate, smaller sample of known-age mothers from approximately the same period. We evaluated the functional relationship between maternal post-parturition mass and maternal age (updating previous work (Proffitt et al. 2007) with a larger data set). We then compared the pattern of maternal masses with age to the pattern of pup parturition masses and mass gains during early and late lactation with maternal age. Furthermore, while controlling for key offspring characteristics, we assessed the influence of maternal breeding experience and reproductive experience the previous year on post-parturition pup masses and daily gains during early and late lactation to test for more complicated patterns of pre-natal and post-natal allocation separate from maternal age.

**Materials and methods**

**STUDY SYSTEM**

This study was conducted on the population of Weddell seals that inhabits Erebus Bay, located on the west coast of Ross Island, Antarctica. Sea ice accumulation in Erebus Bay during the austral winter covers the bay with thick sea ice. During the austral spring, Weddell seals use tidal cracks to haul out onto the sea ice to give birth in 8–14 pupping colonies (Stirling 1969). These animals are highly philopatric, and the probability of a female who recruited to the breeding population subsequently breeding elsewhere is extremely low (Cameron et al. 2007; Hadley, Rotella & Garrott 2007). Moreover, the on-ice detection rate is extremely high (~10), ensuring that all mother–pup pairs are detected each year (Hadley et al. 2006). Each year ~400–500 pups are born during the pupping season from mid-October through November (Cameron & Siniff 2004). Since 1969 newborn Weddell seal pups have been marked with individually numbered tags in the interdigital 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 data base of known-age animals. Since 1973, six to eight mark–resight surveys have been conducted throughout the study area each year, beginning in early November. At the time of tagging and during each survey, the date, location, tag numbers and relative’s tag numbers were recorded into the long-term data base.

**PUP AND MATERNAL MASS MEASUREMENTS**

Pup mass measurements were obtained during the 2004 through 2014 field season (October 10 through December 10). Pupping colonies were surveyed every 24 to 48 h to identify newborn pups. Pups from known-age females were opportunistically selected for mass measurements with an attempt to distribute the sample throughout the pupping season and among as broad a distribution of maternal ages as possible, with priority given to known-age females with pups already in the mass study. Pups judged to be 24 to 72 h old, based on the presence of a frozen placenta and condition of the umbilicus, were selected for sampling and weighed. Considerable effort was made to locate these pups again at 20 and 35 days post-parturition for additional mass measurements, near the middle and end of the lactation period, respectively (Wheatley et al. 2006). However, due to weather and logistical constraints in the study area, not all pups were weighed at exactly 20 and 35 days. As a result, early-lactation mass measurements were obtained from 16 to 26 days; late-lactation masses were obtained from 29 to 41 days. Only pups with all three measurements are included in this study (n = 856 animals over 11 years). Pre-weaning survival in these pups is very high [0.79-0.98, depending on birth timing and maternal characteristics (Proffitt, Rotella & Garrott 2010)]; thus, pups that were missing measurements were most likely simply not observed during surveys, rather than dead. Daily mass gains from parturition to early lactation were calculated as the difference in mass measurements divided by the number of days between the measurements; daily mass gains from early lactation to late lactation were similarly calculated. This method explicitly linearizes the mass gains during the lactation period. Maternal mass measurements were made close to parturition (within two days) over the same period (2004 to 2014, excluding 2013) on a subset of mothers (n = 321 measurements on 214 animals) using a digital weighing platform and subject to the same survey protocols, that is, sampling frequency and age stratification.

**MATERNAL ATTRIBUTES**

We investigated a variety of dynamic and static features of mothers. Maternal age was a covariate of central interest, and we investigated its relationship to maternal and pup mass using a variety of functional forms. A female’s reproductive status in one season may affect reproductive allocation to future reproduction either negatively through reproductive costs (Hirschfield & Tinkle 1975; Guinness, Albon & Clutton-Brock 1978; Festa-Bianchet, Gaillard & Jorgenson 1998; Hadley, Rotella & Garrott 2007) or positively if females that reproduce often are also those that are better at acquiring resources for recovering from past reproduction and preparing for future reproduction (Clutton-Brock 1984).

We therefore developed two measures of breeding experience. The first covariate was a categorical measure of a female’s maternal status in the previous year using the categories: pre-breeder (never reproduced: individual ages ranging from 5 to 14), first-time breeder (reproduced for the first time last year, ages 6–13), an experienced breeder who pupped (ages 7–31) or an experienced breeder who skipped reproduction (ages 7–29). This
covariate was used to assess a potential relationship between allocation in the previous year and allocation in the current year. The second covariate, the number of previous pups, was a measure of the number of pups born to a mother in all previous years. Initial work on this data set suggests that parity is highly correlated with maternal age, making the results of regression difficult to interpret. Therefore, we developed this metric as an age-specific measure of reproductive experience (and therefore useful as an index of individual quality), constructed by centring a female’s number of previous pups using the mean number of previous pups for that maternal age.

PUP ATTRIBUTES (FOR USE IN MODELS OF PUP MASS)

The timing of parturition within a season has been shown to be associated with offspring mass in seals (Boltnev & York 2001; Bowen et al. 2001, 2004). In particular, unpublished work from this study suggests that the largest pups are born near the mean date of birth (October 28) with smaller pups born earlier and later. We thus used a quadratic form for the influence of the timing of birth on pup mass. Similar to the maternal age covariate, we centred parturition dates using the mean and then squared it to produce the quadratic term. We included a binary variable that indicated whether a pup was female or not. Offspring parturition mass is considered an indicator of pre-natal maternal allocation (Oftedal 1985; Kovacs & Lavigne 1986; Ochoa-Acuña, Francis & Boness 1998) and has been positively correlated with pup attributes (for use in models of pup mass) as independent.

Random Effects

Individual phenotypic variation can have profound effects on the degree of maternal allocation in seals (Lunn, Boyd & Croxall 1994; Mellish, Iverson & Bowen 1999), and for many mothers considered here, we had multiple measures of post-parturition maternal mass at different ages and mass data from multiple offspring. To account for phenotypic variation and the unbalanced repeated-measures data structure, we included a random effect for maternal identity in models of post-parturition pup mass and both early- and late-lactation daily mass gain (simple adjustment to the intercept). We also included a random effect of year (simple adjustment to the intercept) to model intrannual variation in maternal allocation that may reflect changing environmental conditions. We did not have a sufficient number of repeated maternal mass measurements across years to support a random effect for maternal identity in models of post-parturition maternal mass, and we treated each observation as independent.

STATISTICAL ANALYSIS

We utilized a Bayesian hierarchical modelling approach to investigate the patterns of maternal and pup masses in relation to static and dynamic attributes of both the mother and pup. We were primarily interested in evaluating the relative support for each of five functional forms for maternal age in each of the four model suites, conditional on the inclusion of a modest number of maternal and pup characteristics as covariates in each model. For comparison, we included a null model that included all covariates except maternal age. We evaluated the relative support for linear, quadratic, logarithmic, single threshold and double threshold models. Linear models allow for a constant positive, negative or no relationship between the response and maternal age. In contrast, quadratic and logarithmic models allow for changes in the response with age such that the magnitude of the change (slope of the curve) itself varies, with the former allowing for an initial improvement with age followed by a subsequent decline and the latter allowing for an increase with maternal age for the youngest animals followed by more modest increases with age. In contrast to the smooth curves implied by the quadratic and logarithmic models, threshold models (also known as piecewise, or segmented models) allow for different relationships on either side of the threshold (or breakpoint) (e.g. Weladji et al. (2010)). Here, we used single threshold and double threshold models with linear relationships on either side of each threshold. The former allows for a linear increase/decrease in the response variable with maternal age up to the threshold, followed by a separate linear increase/decrease. Double threshold models allow for similar relationships between two thresholds and could, for example, be used to model a steady increase in a trait, to a plateau, and subsequent decline. A priori, we restricted the different linear relationships to be continuous at the thresholds such that the slope of the lines changed on either side of a threshold, but not the intercept; that is, we did not allow for disjointed line segments in our models. A strength of our Bayesian approach is that the thresholds are themselves treated as model parameters to be estimated from the data, yielding a straightforward measure of uncertainty that is easy to incorporate into model selection and prediction.

We used a similar approach for the four distinct suites of mass measurements: post-parturition maternal mass, post-parturition pup mass and daily mass gains during early and late lactation were each separately modelled using a Gaussian error structure (with variance $\sigma^2$) with the mean function of maternal and pup characteristics (Appendix S1, Supporting Information). We investigated the use of shrinkage priors on all model coefficients and their effect on our inference, specifically Bayesian interpretations of ridge (Hoerl & Kennard 1970), lasso (Park & Casella 2008) and horseshoe (Carvalho, Polson & Scott 2010) regularization methods. The results were nearly identical, and we present here the results using comparatively diffuse priors. For each of the regression coefficients for the fixed effects (maternal and pup characteristics), we used independent, vague normal priors. We assumed that the random effects were drawn from independent normal distributions with means equal to 0 and standard deviations ($\sigma_{\text{mother}}$, $\sigma_{\text{year}}$). We used independent inverse-gamma priors for each variance parameter within each model ($\sigma_{\text{mother}}^2$, $\sigma_{\text{year}}^2$ and $\sigma^2$). For the single threshold models, we assigned uniform priors for the threshold, defined from maternal age 6 to 29. For double threshold model, it is necessary to specify two ranges for potential thresholds, and we used uniform priors defined from 1543. © 2016 The Authors. Journal of Animal Ecology © 2016 British Ecological Society, Journal of Animal Ecology, 85, 1540–1551
ages 6 to 17 for the first threshold and from ages 17 to 29 for the second threshold.

We fit all models using the `runjags` package (Denwood 2016), which serves as an interface to the JAGS software (Plummer 2003), to implement MCMC sampling in the R programming environment (R Core Team 2015). Four chains were run for each model with 60,000 samples per chain, and 10,000 samples discarded as burn-in, resulting in 50,000 samples per chain used for posterior inference. Posterior convergence was assessed both graphically and with the Gelman–Rubin statistic (Gelman & Rubin 1992), $\hat{R}$ (convergence assumed for values $\hat{R} < 1.01$). Model fit was assessed using (i) a posterior predictive check comparing the sum of squared residuals for the observed data to that for replicated data generated under the model and (ii) a graph of the residuals plotted against maternal age to check whether model fit was driven by the comparatively larger number of young animals or whether model fit was reasonable across maternal ages.

We used the fully Bayesian Watanabe–Akaike Information Criterion (WAIC) to estimate the relative predictive ability of each model in the four model suites (Watanabe 2010; Hooten & Hobbs 2015). There is some question as to what constitutes predictive ability (as assessed by various information criteria) in the presence of within- and between-individual variation and imbalanced data (Vaida & Blanchard 2005; Gelman, Hwang & Vehtari 2014), and we acknowledge we are using WAIC to compare models across all levels of variation. We assessed the relative support for each model using $\Delta$WAIC values, similar in interpretation to $\Delta$AIC values. We also assessed the model fit using a hierarchical implementation of the classical $R^2$ (Nakagawa & Schielzeth 2013).

### Results

We found strong evidence that both maternal and pup masses near parturition initially increased with maternal age and then declined for older mothers (Table 1). Specifically, we found that as maternal age increased, post-parturition masses initially increased and then eventually decreased for both mothers (quadratic form: $\beta_{\text{Maternal Age}} = 6.02$, SE = 0.83; $\beta_{\text{Maternal Age}}^2 = -0.54$, SE = 0.12) and pups (quadratic form: $\beta_{\text{Maternal Age}} = 0.22$, SE = 0.05; $\beta_{\text{Maternal Age}}^2 = -0.024$, SE = 0.006) (Table 2). Based on the results from the fixed effects, post-parturition maternal mass for an experienced mother who had a pup last year and had an average amount of breeding experience is expected to average 395 kg (90% credible interval, CI: 376, 414) at age 7, peak at 480 kg (469, 490) at age 20 and decline to a minimum of 442 kg (412, 471) at age 28. Similarly, predicted post-parturition masses for pups increased from 29 kg (28, 30) for 7-year-old mothers [with a predicted mass of 395 kg (376, 414)], peak at 32 kg (31, 33) for 18-year-old mothers [with a predicted mass of 479 kg (468, 489)] and decline to 28 kg (25, 30) by the maternal age of 31 [with a predicted mass of 410 kg (365, 454)]. Furthermore, we found that pups born to experienced mothers who skipped reproduction last year had slightly higher parturition masses compared to pups born to experienced mothers who had a pup last year, suggesting a potential cost of reproduction. The close correspondence in the patterns of change (increase, peak and decline with increasing maternal age) for post-parturition masses of mothers and pups strongly suggests early-life improvements in maternal allocation, which is consistent with the constraint hypothesis, and senescent declines in energy allocation late in life.

In striking contrast, results for the post-natal period indicate that old mothers allocate proportionally more of their body reserves than younger, heavier mothers. The most heavily supported functional form of maternal age in models of daily gains during early lactation was the single threshold model. Daily mass gains during early lactation increased with maternal age rapidly among the prime-aged mothers and the second threshold.

<table>
<thead>
<tr>
<th>Model</th>
<th>Form</th>
<th>$\Delta$WAIC</th>
<th>$R^2_{\text{in}}$</th>
<th>$R^2_{\text{c}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Post-parturition</td>
<td>Null</td>
<td>46.54</td>
<td>0.13</td>
<td>0.18</td>
</tr>
<tr>
<td>maternal mass</td>
<td>Linear</td>
<td>22.01</td>
<td>0.21</td>
<td>0.23</td>
</tr>
<tr>
<td></td>
<td>Quadratic</td>
<td>0.97</td>
<td>0.24</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td>Logarithm</td>
<td>7.45</td>
<td>0.23</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>1-threshold</td>
<td>7.11</td>
<td>0.24</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td>2-threshold</td>
<td>6.95</td>
<td>0.24</td>
<td>0.29</td>
</tr>
<tr>
<td>Post-parturition</td>
<td>Null</td>
<td>27.19</td>
<td>0.12</td>
<td>0.36</td>
</tr>
<tr>
<td>pup mass</td>
<td>Linear</td>
<td>18.58</td>
<td>0.13</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>Quadratic</td>
<td>0.15</td>
<td>0.40</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Logarithm</td>
<td>7.46</td>
<td>0.14</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>1-threshold</td>
<td>9.89</td>
<td>0.17</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td>2-threshold</td>
<td>3.67</td>
<td>0.15</td>
<td>0.39</td>
</tr>
<tr>
<td>Early-lactation gain</td>
<td>Null</td>
<td>49.68</td>
<td>0.24</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td>Linear</td>
<td>22.34</td>
<td>0.28</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>Quadratic</td>
<td>14.81</td>
<td>0.29</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>Logarithm</td>
<td>6.72</td>
<td>0.29</td>
<td>0.58</td>
</tr>
<tr>
<td></td>
<td>1-threshold</td>
<td>0.30</td>
<td>0.58</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2-threshold</td>
<td>0.83</td>
<td>0.30</td>
<td>0.58</td>
</tr>
<tr>
<td>Late-lactation gain</td>
<td>Null</td>
<td>10.89</td>
<td>0.09</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>Linear</td>
<td>4.20</td>
<td>0.11</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>Quadratic</td>
<td>5.62</td>
<td>0.11</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>Logarithm</td>
<td>0.11</td>
<td>0.36</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1-threshold</td>
<td>1.92</td>
<td>0.11</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>2-threshold</td>
<td>1.73</td>
<td>0.11</td>
<td>0.36</td>
</tr>
</tbody>
</table>

Table 1. Model comparison results using $\Delta$WAIC (Widely Applicable Information Criterion, which has a similar interpretation to $\Delta$AIC scores) and both marginal $R^2$ (fixed effects) and conditional $R^2$ (fixed and random effects) values. Lower $\Delta$WAIC scores suggest more parsimonious and better-predicting models.
Table 2. Regression coefficient estimates (mean of the approximate posterior distribution, standard error in parentheses) for the factors influencing post-parturition maternal mass, post-parturition pup mass, daily gain through early lactation and daily gain from early through late lactation. Coefficients in boldface are those for which the 95% credible interval does not include zero.

<table>
<thead>
<tr>
<th></th>
<th>Post-parturition maternal mass (kg)</th>
<th>Post-parturition pup mass (kg)</th>
<th>Early-lactation gain (kg day$^{-1}$)</th>
<th>Late-lactation gain (kg day$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>463.61 (6.27)</td>
<td>30.96 (0.41)</td>
<td>2.31 (0.05)</td>
<td>1.50 (0.13)</td>
</tr>
<tr>
<td>Maternal age$^a$</td>
<td>6.02 (0.83)</td>
<td>0.22 (0.05)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Maternal age)$^2$</td>
<td>-0.54 (0.12)</td>
<td>-0.024 (0.006)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>log(Maternal age)$^b$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Threshold model</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maternal age$^a$, age &lt; threshold</td>
<td></td>
<td></td>
<td>0.09 (0.02)</td>
<td></td>
</tr>
<tr>
<td>Maternal age$^a$, age ≥ threshold</td>
<td></td>
<td></td>
<td>0.01 (0.006)</td>
<td>11.91 (0.84)</td>
</tr>
<tr>
<td>First-time breeder last year$^c$</td>
<td>6.57 (14.14)</td>
<td>-0.09 (0.65)</td>
<td>-0.06 (0.08)</td>
<td>-0.27 (0.10)</td>
</tr>
<tr>
<td>Pre-breeder last year</td>
<td>-2.18 (12.19)</td>
<td>-0.80 (0.57)</td>
<td>-0.17 (0.07)</td>
<td>-0.30 (0.09)</td>
</tr>
<tr>
<td>Experienced, skipped last year</td>
<td>-3.87 (6.59)</td>
<td>0.66 (0.32)</td>
<td>0.07 (0.04)</td>
<td>-0.03 (0.05)</td>
</tr>
<tr>
<td>The number of previous pups DTA</td>
<td>3.44 (2.07)</td>
<td>0.28 (0.098)</td>
<td>-0.02 (0.01)</td>
<td>-0.06 (0.02)</td>
</tr>
<tr>
<td>Birthdate$^a$</td>
<td>1.81 (0.48)</td>
<td>0.11 (0.030)</td>
<td>0.00 (0.00)</td>
<td>-0.004 (0.005)</td>
</tr>
<tr>
<td>(Birthdate)$^2$</td>
<td>-0.012 (0.004)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Post-parturition pup mass</td>
<td></td>
<td>0.031 (0.004)</td>
<td>0.001 (0.005)</td>
<td></td>
</tr>
<tr>
<td>Sex – female</td>
<td>0.12 (0.26)</td>
<td>0.02 (0.03)</td>
<td>0.00 (0.04)</td>
<td></td>
</tr>
<tr>
<td>$\sigma_{\text{mother}}$</td>
<td>1.89 (0.21)</td>
<td>0.28 (0.02)</td>
<td>0.28 (0.03)</td>
<td></td>
</tr>
<tr>
<td>$\sigma_{\text{year}}$</td>
<td>11.51 (6.10)</td>
<td>0.83 (0.35)</td>
<td>0.06 (0.03)</td>
<td>0.13 (0.05)</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>46.89 (1.93)</td>
<td>3.26 (0.12)</td>
<td>0.35 (0.01)</td>
<td>0.50 (0.02)</td>
</tr>
</tbody>
</table>

$^a$The linear predictor was first centred and then squared to produce quadratic covariates; maternal ages were transformed by subtracting the minimum age and adding a small constant for the logarithmic form.

$^b$All models were fit using centred maternal ages; this threshold has been back-transformed to the original scale to aid interpretation.

$^c$The reference level for reproductive experience is a mother who was experienced and had a pup last year.

The highest daily gains throughout lactation (Fig. 1). It is the combination of post-parturition mass and daily mass gain through late lactation that determines weaning mass. Thus, based on predictions from the fixed-effects portion of models for parturition through late lactation, we find evidence that pups born to older mothers experience increased gains throughout lactation such that the gap in birth masses is diminished by late lactation.

A mother’s age-specific breeding experience had a strong, positive relationship with her pup’s post-parturition mass ($\beta_{\text{Age}} \text{Previous Pups} = 0.28$, SE = 0.10) but not to subsequent daily gains during early or late lactation. Thus, mothers with greater-than-average reproductive experience for their age give birth to heavier pups, but do not allocate more resources to their offspring in the postnatal period. In contrast, a mother’s reproductive status in the previous year was strongly associated with the daily gain during both early and late lactation. Notably, pups born to mothers who were pre-breeders last year had daily mass gains during early lactation that were lower than those for mothers of any other reproductive class. During late lactation, both mothers who were pre-breeders or first-time breeders last year had lower mass gains than experienced mothers who either pupped or skipped last year (Table 2). The estimated differences in gains have a marked impact on pup mass late in lactation. For example, a pup born to an inexperienced mother who was a pre-breeder last year is predicted to weigh 3.3 kg and 7.9 kg less than a pup born to an experienced mother who pupped last year by 20 and 35 days post-parturition, respectively.

Pup characteristics were also related to parturition mass and mass gain. There was a quadratic effect of deviation from the mean birthdate of October 28 in this data set ($\beta_{\text{Birth date}} = 0.11$, SE = 0.03; $\beta_{\text{Birth date}}^2 = -0.012$, SE = 0.004), suggesting that pups born earlier in October and later in November were born smaller than those near the mean birthdate. However, birthdate was not associated with subsequent mass gains. Pups that were heavier than the mean at birth also had slightly higher daily gains through the early lactation period ($\beta_{\text{Birthdate \text{Mass}}} = 0.03$, SE = 0.004) such that the mass discrepancy at birth widened during early lactation. For a pup with a particularly heavy post-parturition mass (5 kg above the mean), this would translate into a gain of an extra 3 kg during early lactation. We did not find evidence that parturition mass or mass gains differed between male and female pups.

We found compelling evidence for high variance of individual maternal effects (Fig. 2). Estimated standard deviations for the random effect of maternal identification (simple additive effect) were large for models of post-parturition pup mass ($\sigma_{\text{mother}} = 1.89$ kg) as well as for daily gains made during early lactation ($\sigma_{\text{mother}} = 0.28$ kg day$^{-1}$).
and late lactation ($\sigma_{\text{mum}} = 0.28$ kg day$^{-1}$). These effects translate into substantial differences in pups born to mothers with different identities but that were alike in other respects. For example, pups born to mothers with estimated random effects on post-parturition pup masses from the 95th percentile (1.86 kg) and 5th percentile (-1.62 kg) are estimated to have a birth mass difference of 3.48 kg, or approximately 12% of the mean parturition mass (30.06 kg). Similarly, the difference between the 95th percentile and 5th percentile point estimates for the effect of maternal identity on early- and late-lactation daily gains corresponds to the differences of 0.64 kg day$^{-1}$ and 0.55 kg day$^{-1}$, respectively, which results in differences in pup masses of approximately 12.8 kg over 20 days and 8.25 kg from 20 days to 35 days. In comparison, we found evidence that the expected values for pup mass and mass gain were quite consistent among years (post-parturition maternal mass – $\sigma_{\text{year}} = 11.59$ kg; post-parturition pup mass – $\sigma_{\text{year}} = 0.83$ kg; daily gains in early lactation – $\sigma_{\text{year}} = 0.06$ kg day$^{-1}$; daily gains during late lactation – $\sigma_{\text{year}} = 0.13$ kg day$^{-1}$). The inclusion of the two random effects explained as much or more of the variance compared to the fixed effects alone (Table 1).

The residuals plotted against maternal age (Fig. S1) indicate that the top models for each response variable were appropriate: no pattern in the residuals (particularly at older ages) suggests that the model fit across maternal ages. The more general posterior predictive check (Fig. S2) also indicates that the top models had an appropriate fit to the data.

**Discussion**

The pattern of energy allocation in the pre-natal period demonstrated here provides clear evidence for age-related increases in reproductive energy allocation for younger mothers and senescent declines for older mothers. We demonstrated that the masses of both mothers and pups soon after parturition increased early in a mother’s reproductive life, peaked in the late-teens and then decreased in old age. The increase in maternal mass early in a mother’s reproductive life span is consistent with previous work in pinnipeds and other species (McLaren 1993; Arnbom, Fedak & Rothery 1994; Festa-Bianchet et al. 1996; Bowen et al. 2006; Weladji et al. 2010; Hamel, Craine & Towne 2012) and likely reflects the continued somatic growth

---

**Fig. 1.** Posterior credible intervals (90%) for the mean response (using approximate posterior distributions for fixed-effects regression parameters) for (a) post-parturition maternal mass, (b) post-parturition pup mass, (c) daily gains during early lactation and (d) daily gains during late lactation. The predicted intervals are for an experienced mother who pupped last year (minimum age of 7 years in this data set) and a male pup (b through d), with all other variables held to the mean (0).
after first reproduction, as well as increased experience consistent with the constraint hypothesis. The senescent decline in maternal mass documented here is consistent with that demonstrated for some ungulates (Weladji et al. 2010; Nussey et al. 2011), but contrasts with previous results for grey seals (Bowen et al. 2006), which found senescent declines in several measures of reproductive energy allocation, but no evidence for a decrease in maternal mass close to parturition. The proximate causes of a senescent decline in maternal body mass could be due to diminished foraging efficiency connected to age-related declines in muscle function (Hindle et al. 2009a,b), and the resultant difficulty of meeting the higher maintenance costs associated with a larger mass (Innes et al. 1987; Pomeroy et al. 1999).

Regardless of the causes of age-related improvements and declines in maternal body mass, our results indicate that these changes transfer over to the birth mass of offspring; that is, pup mass close to birth in relation to maternal age follows the same pattern that maternal mass does close to birth. This finding is consistent with previous work on a diversity of species, indicating that maternal condition near parturition is a strong correlate of offspring size (Fedak, Arnbom & Boyd 1996; Pomeroy et al. 1999; Keech et al. 2000; Parker & Loiselle 2002; Adams 2005; Bowen et al. 2006). The amount of energy a mother can allocate to her offspring in the pre-natal period may be sharply limited by in utero physiological constraints (Clutton-Brock 1984), such as an allometric relationship between body weight and metabolic rate (Loison & Strand 2005), which limits the ability of an organism to increase allocation. However, we also found strong evidence for individual effects on pre-natal allocation, which suggests that individuals vary in terms of how they allocate resources. These individual effects are likely the combination of both static and dynamic traits sensu Cam & Monnat (2000), with the former (a measure of quality) potentially influencing the latter (time-varying, unmeasured covariates such as maternal mass or body length). The modest, positive relationship between post-parturition pup mass and age-specific breeding experience suggests that more experienced individuals allocate more energy than less experienced individuals of the same age (consistent with the constraint hypothesis), though we cannot rule out the changes in metabolic efficiency. Moreover, we found very strong evidence for strong individual maternal effects on pup masses near parturition. The heaviest pups therefore tend to be born to prime-aged mothers with above-average breeding experience and a large, positive individual effect.
The pattern of variation in reproductive energy allocation with maternal age is sharply different in the post-natal period than that found in the pre-natal period. The data strongly suggest that the amount of mass gained each day by pups during early lactation and late lactation increases with maternal age, increasing sharply among the youngest mothers and more modestly among older mothers. The increase in post-natal allocation early in maternal life likely reflects increases in maternal body mass and energy transfer to the pup (Wheatley et al. 2006). The fact that the single threshold model was most supported for daily gains during early lactation, whereas the logarithmic model was most supported for the late lactation period, most likely reflects a more dramatic increase in daily gains with maternal age during early lactation; that is, the improvement in reproductive performance is larger than can be well modelled using the more gradual logarithmic model. Biologically, we can speculate that the reproductive performance of younger, lighter females improves more dramatically during early lactation with age as their own mass increases. As the body reserves of mothers continue to decline through late lactation, the improvement in performance with age is more gradual and reflects the ability of mothers to nurse a pup through the long lactation period. In contrast to the results for younger mothers, the senescent decline in maternal body mass near parturition for older mothers demonstrated here, combined with the increased allocation for the oldest ages, indicates that older (and thereby lighter) mothers are allocating proportionally more energy to their offspring than prime-age or younger mothers, consistent with terminal allocation. This cross-sectional study could not directly assess the presence of a cost of reproduction associated with this increased allocation, which, if present, would support the terminal investment hypothesis (Weladji et al. 2010). In addition to the age-related pattern of post-natal energy allocation, we demonstrated strong evidence for individual effects on the allocation during the post-natal period. Together, these results indicate that older mothers with above-average individual effects are the females that allocate the most resources to their offspring.

The influence of the reproductive status of the mother in the previous year strongly suggests that post-natal energy allocation is higher for experienced mothers, but not appreciably different for experienced mothers that either skipped reproduction or had a pup last year. Reproductive skipping has been proposed as an adaptive tactic for low-quality individuals (Cam et al. 1998); that is, skipping allows a mother to acquire or conserve resources necessary to support offspring lactation, and found to help avoid the survival–reproduction trade-off (Cubaynes et al. 2011). In our study population, some individuals simply breed more often and yet still produce pups of typical quality (Chambert et al. 2013). Our work demonstrates that post-natal energy allocation to pups is roughly equal for experienced mothers who skipped reproduction in the previous year and those that had pups. Interestingly, we have some evidence that pups born to experienced mothers who skipped last year have a slightly higher post-parturition mass, compared to mothers who pupped last year. Together, these results suggest that skipping might be a means to ensure that a female has sufficient reserves to produce a pup; that is, some females require additional time to acquire resources to support lactation.

We have shown a stark contrast in reproductive energy allocation patterns during the pre-natal and post-natal periods. Though younger mothers increase allocation with age during both periods, we find that older mothers have senescent declines in allocation during the pre-natal period, followed by an increase in post-natal energy allocation, which is consistent with terminal allocation. In contrast to energy allocation in the pre-natal period (which may be tightly constrained), allocation in the post-natal period appears to be more flexible and a function of breeding experience and maternal age. This could reflect more opportunities for the differences due to variation in maternal care attributes, for example characteristics of lactation such as efficiency or milk quality (Anderson & Fedak 1987; Arnbom, Fedak & Boyd 1997; Mellish, Iverson & Bowen 1999), which this study cannot address. Moreover, the importance of individual maternal effects shown here suggests the individual-level variation in post-natal energy allocation performance, a result reported previously in other pinnipeds (Mellish, Iverson & Bowen 1999; Lang, Iverson & Bowen 2009) as well ungulates (Wolcott, Reitz & Weckerly 2015). This increase in post-natal allocation among the oldest mothers results in pup weaning masses commensurate with those from prime-aged mothers, implying that older mothers are compensating for diminished birth masses by increasing their energy allocation during lactation. This indicates that reproductive allocation changes over the length of a mother’s reproductive life span as well as within a single reproductive cycle as a function of age.

The age-related variation in energy allocation that we have shown in Weddell seal mothers has important consequences for population dynamics. Previous work across a variety of species has demonstrated that offspring weaning mass is positively associated with both juvenile survival (Wauters, Bijens & Dhondt 1993; McMahon, Burton & Bester 2000; Ailsa, Bernie & Barker 2001; Côté & Festa-Bianchet 2001; Proffitt, Garrott & Rotella 2008) and future reproductive success (Festa-Bianchet, Jørgenson & Réale 2000; Bowen et al. 2015). Our results imply that the pups with the highest weaning mass are born to experienced, prime-aged and older mothers with above-average individual effect on parturition masses and daily mass gains through the lactation period. Such pups would be expected to survive better than others given previous results that indicate that pup survival increases with maternal age in a pseudothreshold form in our study population (Hadley, Rotella & Garrott 2007). However, nursing and weaning a heavy pup during a senescent decline
Reproductive effort in a long-lived mammal


Reproductive effort in a long-lived mammal

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Residuals from each top model plotted against maternal age: (a) maternal masses near parturition with a quadratic form, (b) pup masses near parturition with a quadratic form, (c) daily mass gains during early lactation using a logarithmic form, and (d) daily mass gains during late lactation using a logarithmic form.

Fig. S2. Posterior predictive check that compares the sum of squared residuals for the observed data against that for replicated data generated from the posterior distribution for each of the top models: (a) maternal masses near parturition with a quadratic form, (b) pup masses near parturition with a quadratic form, (c) daily mass gains during early lactation using a logarithmic form, and (d) daily mass gains during late lactation using a logarithmic form.

Appendix S1. Our modeling approach was to investigate the relative amount of support for different functional forms for maternal age, conditional on the inclusion of a small number of covariates common to each model.