



# 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.

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.  
DOI: 10.1111/1365-2656.12577

Made available through Montana State University's [ScholarWorks](#)  
[scholarworks.montana.edu](http://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. Paterson<sup>1\*</sup>, Jay J. Rotella<sup>1</sup>, Jennifer M. Mannas<sup>1,2</sup> and Robert A. Garrett<sup>1</sup>

<sup>1</sup>Ecology Department, Montana State University, Bozeman, MT 59717, USA; and <sup>2</sup>Progressive 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 (Skibieli, Dobson & Murie 2009; Baron *et al.* 2010; Skibieli, 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 (Schubert *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.

\*Correspondence author. E-mail: terrillpaterson@gmail.com

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, Heflin & 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 (Millar 1977; Oftedal 1985; Gittleman & Thompson 1988; Boyd & McCann 1989; Ochoa-Acuña, 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 (~1.0), 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 (Hirshfield & 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 state 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 post-parturition mass gain and weaning mass (Hill 1987). To more clearly partition the potential maternal effects associated with in utero maternal allocation from those associated with post-parturition maternal allocation through lactation, we included pup parturition mass (centred using the mean) as a covariate in analyses of early- and late-lactation daily mass gains. Finally, because Weddell seal pups gain mass rapidly throughout the lactation period (Wheatley *et al.* 2006) and weather and logistical delays sometimes forced us to weigh pups one to three days after parturition, we used deviation from the target age (DTA, or days since birth) to account for variation in pup weight due to the timing of weighing.

#### 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 interannual 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

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:  $\beta_{\text{Maternal Age}} = 6.02$ ,  $\text{SE} = 0.83$ ;  $\beta_{\text{Maternal Age}^2} = -0.54$ ,  $\text{SE} = 0.12$ ) and pups (quadratic form:  $\beta_{\text{Maternal Age}} = 0.22$ ,  $\text{SE} = 0.05$ ;  $\beta_{\text{Maternal Age}^2} = -0.024$ ,  $\text{SE} = 0.006$ ) (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,

**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

Model	Form	$\Delta$ WAIC	$R_m^2$	$R_c^2$
Post-parturition maternal mass	Null	46.54	0.13	0.18
	Linear	22.01	0.21	0.23
	Quadratic	0	0.24	0.30
	Logarithm	7.45	0.23	0.27
	1-threshold	7.11	0.24	0.28
Post-parturition pup mass	2-threshold	6.95	0.24	0.29
	Null	27.19	0.12	0.36
	Linear	18.58	0.13	0.37
Early-lactation gain	Quadratic	0	0.15	0.40
	Logarithm	7.46	0.14	0.39
	1-threshold	9.89	0.17	0.40
	2-threshold	3.67	0.15	0.39
	Null	49.68	0.24	0.54
Late-lactation gain	Linear	22.34	0.28	0.57
	Quadratic	14.81	0.29	0.57
	Logarithm	6.72	0.29	0.58
	1-threshold	0	0.30	0.58
	2-threshold	0.83	0.30	0.58
Late-lactation gain	Null	10.89	0.09	0.34
	Linear	4.20	0.11	0.35
	Quadratic	5.62	0.11	0.36
	Logarithm	0	0.11	0.36
	1-threshold	1.92	0.11	0.36
	2-threshold	1.73	0.11	0.36

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 youngest mothers up to the threshold of approximately 12 years (threshold = 11.9,  $\text{SE} = 0.84$ ) ( $\beta_{\text{Maternal Age}} = 0.09$ ,  $\text{SE} = 0.02$ ), then continued to increase with maternal age at a diminished rate ( $\beta_{\text{Maternal Age}} = 0.01$ ,  $\text{SE} = 0.006$ ). During the late lactation period, the most supported model used the logarithm of maternal age and suggests that daily gains increase with maternal age to a pseudothreshold ( $\beta_{\log(\text{Maternal Age})} = 0.16$ ,  $\text{SE} = 0.05$ ). Pups born to younger (and therefore lighter) mothers are predicted to have lower post-parturition masses than prime-aged mothers and the *lowest* daily gains throughout lactation, whereas pups born to older (and also lighter) mothers also have lower post-parturition masses but have

**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

	Post-parturition maternal mass (kg)	Post-parturition pup mass (kg)	Early-lactation gain (kg day <sup>-1</sup> )	Late-lactation gain (kg day <sup>-1</sup> )
Intercept	<b>463.61 (6.27)</b>	<b>30.96 (0.41)</b>	<b>2.31 (0.05)</b>	<b>1.50 (0.13)</b>
Maternal age <sup>a</sup>	<b>6.02 (0.83)</b>	<b>0.22 (0.05)</b>		
(Maternal age) <sup>2</sup>	<b>-0.54 (0.12)</b>	<b>-0.024 (0.006)</b>		
log(Maternal age) <sup>a</sup>				<b>0.16 (0.05)</b>
<i>Threshold model</i>				
Maternal age <sup>a</sup> , age < threshold			<b>0.09 (0.02)</b>	
Maternal age <sup>a</sup> , age ≥ threshold			<b>0.01 (0.006)</b>	
threshold <sup>b</sup>			<b>11.91 (0.84)</b>	
First-time breeder last year <sup>c</sup>	6.57 (14.14)	-0.09 (0.65)	-0.06 (0.08)	<b>-0.27 (0.10)</b>
Pre-breeder last year	-2.18 (12.19)	-0.80 (0.57)	<b>-0.17 (0.07)</b>	<b>-0.30 (0.09)</b>
Experienced, skipped last year	-3.87 (6.59)	<b>0.66 (0.32)</b>	0.07 (0.04)	-0.03 (0.05)
The number of previous pups	3.44 (2.07)	<b>0.28 (0.098)</b>	-0.02 (0.01)	-0.006 (0.02)
DTA		<b>1.81 (0.48)</b>		
Birthdate <sup>a</sup>		<b>0.11 (0.030)</b>	0.002 (0.003)	-0.004 (0.005)
(Birthdate) <sup>2</sup>		<b>-0.012 (0.004)</b>	0.00 (0.00)	0.00 (0.001)
Post-parturition pup mass			<b>0.031 (0.004)</b>	0.001 (0.005)
Sex – female		0.12 (0.26)	0.02 (0.03)	0.00 (0.04)
σ <sub>mother</sub>		<b>1.89 (0.21)</b>	<b>0.28 (0.02)</b>	<b>0.28 (0.03)</b>
σ <sub>year</sub>	<b>11.51 (6.10)</b>	<b>0.83 (0.35)</b>	<b>0.06 (0.03)</b>	<b>0.13 (0.05)</b>
σ	<b>46.89 (1.93)</b>	<b>3.26 (0.12)</b>	<b>0.35 (0.01)</b>	<b>0.50 (0.02)</b>

<sup>a</sup>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.

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

<sup>c</sup>The reference level for reproductive experience is a mother who was experienced and had a pup last year.

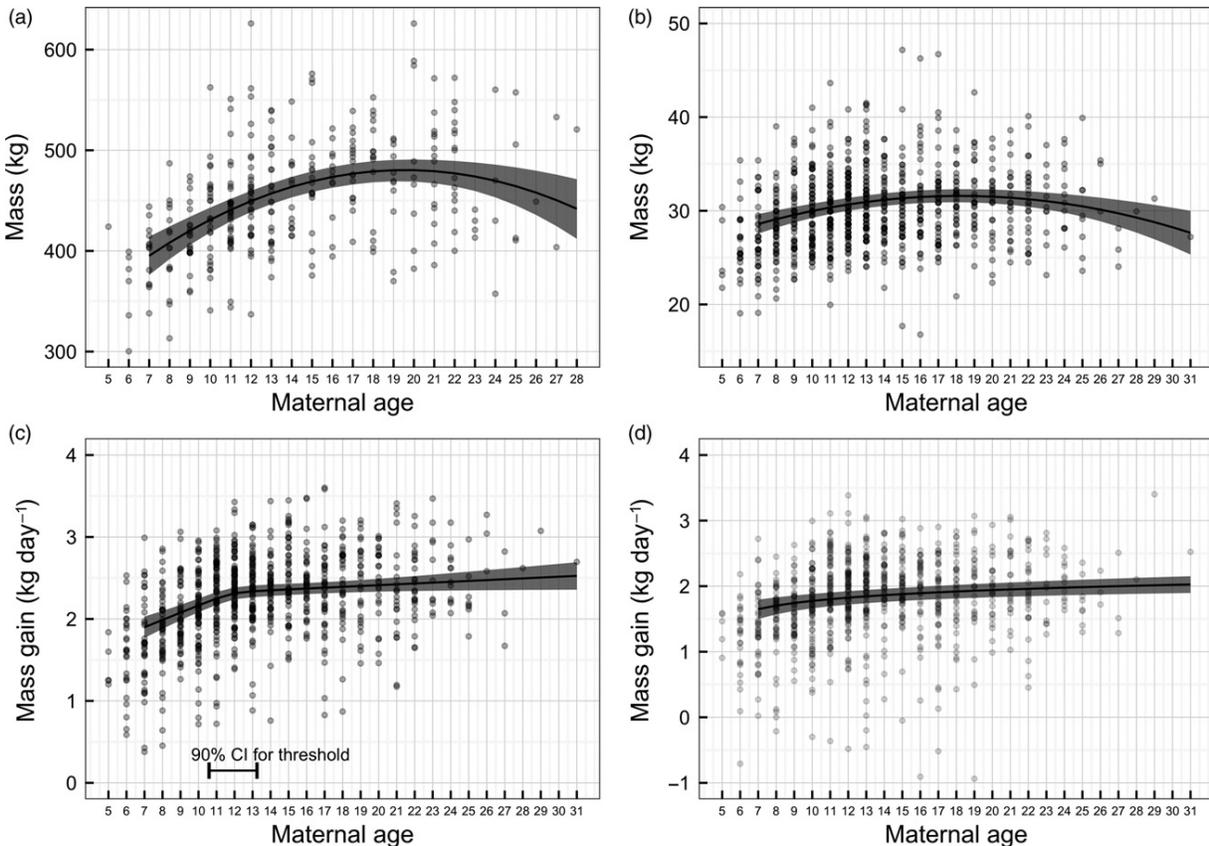
the *highest* daily gains throughout lactation (Fig. 1). It is the combination of post-parturition mass and daily mass gain through late lactation that determines weaning mass. Thus, based on predictions from the fixed-effects portion of models for parturition through late lactation, we find evidence 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 ( $\beta_{N \text{ Previous Pups}} = 0.28$ , 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 post-natal 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 ( $\beta_{\text{Parturition Mass}} = 0.03$ , 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 ( $\sigma_{\text{mom}} = 1.89$  kg) as well as for daily gains made during early lactation ( $\sigma_{\text{mom}} = 0.28$  kg day<sup>-1</sup>)



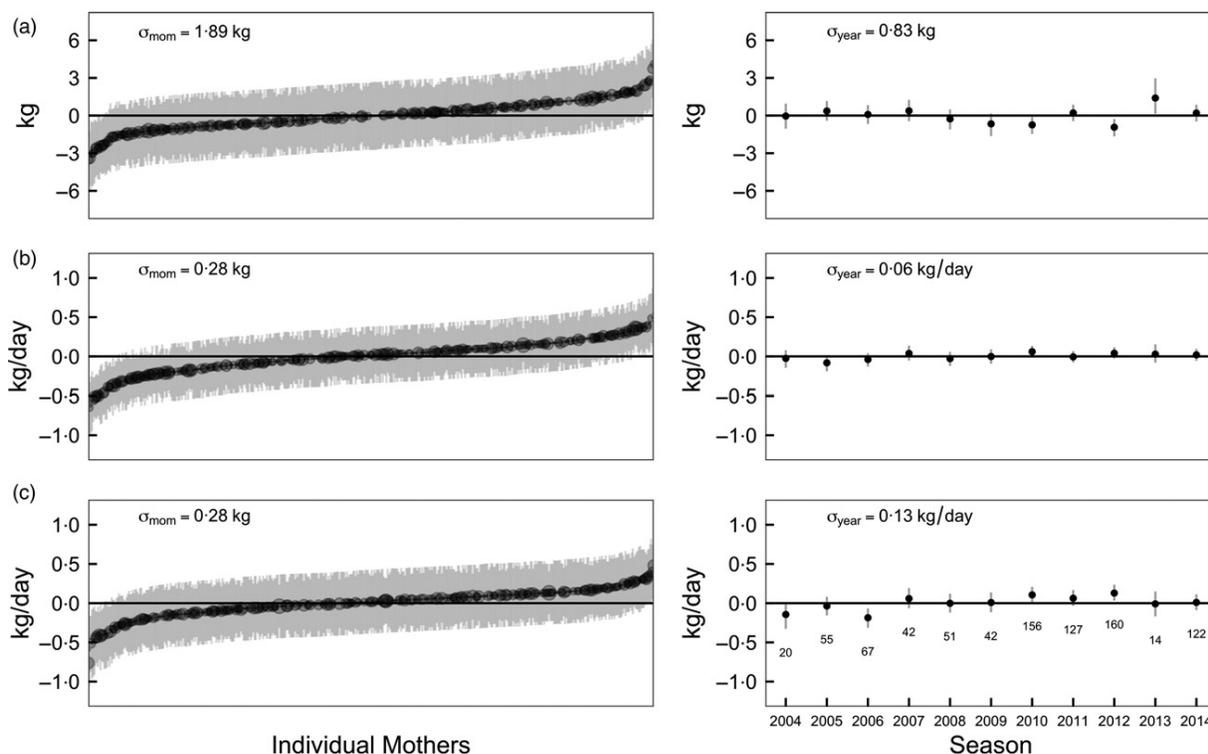
**Fig. 1.** Posterior credible intervals (90%) for the mean response (using approximate posterior distributions for fixed-effects regression parameters) for (a) post-parturition maternal mass, (b) post-parturition pup mass, (c) daily gains during early lactation and (d) daily gains during late lactation. 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).

and late lactation ( $\sigma_{\text{mom}} = 0.28 \text{ kg day}^{-1}$ ). 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 ( $-1.62 \text{ kg}$ ) 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  $0.64 \text{ kg day}^{-1}$  and  $0.55 \text{ kg day}^{-1}$ , 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 –  $\sigma_{\text{year}} = 11.59 \text{ kg}$ ; post-parturition pup mass –  $\sigma_{\text{year}} = 0.83 \text{ kg}$ ; daily gains in early lactation –  $\sigma_{\text{year}} = 0.06 \text{ kg day}^{-1}$ ; daily gains during late lactation –  $\sigma_{\text{year}} = 0.13 \text{ kg day}^{-1}$ ). 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; Arnborn, 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. 2.** Approximate distributions (mean and 90% credible interval) of random effects for maternal identity and year from models for post-parturition pup mass (a), daily gains during early lactation (b) and daily gains during late lactation (c). For random effects from maternal identity, the point size represents the number of repeated measures from an individual mom with the largest point representing  $n = 6$  and the smallest representing  $n = 1$ . For yearly random effects, the number below the 90% credible interval is the sample size within each year.

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, Arnborn & Boyd 1996; Pomeroy *et al.* 1999; Keech *et al.* 2000; Parker & Loisel 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, Bijmens & Dhondt 1993; McMahon, Burton & Bester 2000; Ailsa, Bernie & Barker 2001; Côté & Festa-Bianchet 2001; Proffitt, Garrott & Rotella 2008) and future reproductive success (Festa-Bianchet, Jorgenson & 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

has implications for maternal survival; the increased allocation could cause mortality to increase in addition to the actuarial senescence arising from declining physiological function.

## Acknowledgements

We thank the many graduate students and field technicians who have collected data on this project. This project was supported by the National Science Foundation, Division of Polar Programs (Grant No. ANT-1141326 to J.J.R., R.A.G. and Donald B. Siniff) and prior NSF Grants to R.A.G., J.J.R., D.B.S. and J. Ward Testa. Logistical support for fieldwork in Antarctica was provided by Lockheed Martin, Raytheon Polar Services Company, Antarctic Support Associates, the United States Navy and Air Force and Petroleum Helicopters Incorporated.

## Data accessibility

Data are available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.tk5ph> (Paterson *et al.* 2016).

## References

- Adams, L.G. (2005) Effects of maternal characteristics and climatic variation on birth masses of Alaskan caribou. *Journal of Mammalogy*, **86**, 506–513.
- Ailsa, J.H., Bernie, J.M. & Barker, J.R. (2001) Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Animal Ecology*, **70**, 138–149.
- Anderson, S.S. & Fedak, M.A. (1987) Grey seal, *Halichoerus grypus*, energetics: females invest more in male offspring. *Journal of Zoology*, **211**, 667–679.
- Arnomb, T., Fedak, M.A. & Boyd, I.L. (1997) Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology*, **78**, 471–483.
- Arnomb, T., Fedak, M.A. & Rothery, P. (1994) Offspring sex ratio in relation to female size in southern elephant seals, *Mirounga leonina*. *Behavioral Ecology and Sociobiology*, **35**, 373–378.
- Baron, J.-P., Galliard, L., Tully, T., & Ferrière, R. (2010) Cohort variation in offspring growth and survival: prenatal and postnatal factors in a late-maturing viviparous snake. *Journal of Animal Ecology*, **79**, 640–649.
- Bateson, P., Barker, D., Clutton-Brock, T., Deb, D., D'Udine, B., Foley, R.A. *et al.* (2004) Developmental plasticity and human health. *Nature*, **430**, 419–421.
- Boltnev, A.I. & York, A.E. (2001) Maternal investment in northern fur seals (*Callorhinus ursinus*): interrelationships among mothers' age, size, parturition date, offspring size and sex ratios. *Journal of Zoology*, **254**, 219–228.
- Bowen, W.D., Ellis, S.L., Iverson, S.J. & Boness, D.J. (2001) Maternal effects on offspring growth rate and weaning mass in harbour seals. *Canadian Journal of Zoology*, **79**, 1088–1101.
- Bowen, W., Ellis, S.L., Iverson, S.J. & Boness, D.J. (2004) Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. *Journal of Zoology*, **261**, 155–163.
- Bowen, W.D., Iverson, S.J., Mcmillan, J.I. & Boness, D.J. (2006) Reproductive performance in grey seals: age-related improvement and senescence in a capital breeder. *Journal of Animal Ecology*, **75**, 1340–1351.
- Bowen, W., Heyer, C.E., Mcmillan, J.I., & Iverson, S.J. (2015) Offspring size at weaning affects survival to recruitment and reproductive performance of primiparous gray seals. *Ecology and Evolution*, **5**, 1412–1424.
- Boyd, I.L. & McCann, T.S. (1989) Pre-natal investment in reproduction by female Antarctic fur seals. *Behavioral Ecology and Sociobiology*, **24**, 377–385.
- Cam, E. & Monnat, J.Y. (2000) Stratification based on reproductive state reveals contrasting patterns of age-related variation in demographic parameters in the kittiwake. *Oikos*, **90**, 560–574.
- Cam, E., Hines, J.E., Monnat, J.-Y., Nichols, J.D. & Danchin, E. (1998) Are adult nonbreeders prudent parents? The kittiwake model. *Ecology*, **79**, 2917–2930.
- Cameron, M.F. & Siniff, D.B. (2004) Age-specific survival, abundance, and immigration rates of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. *Canadian Journal of Zoology*, **82**, 601–615.
- Cameron, M.F., Siniff, D.B., Proffitt, K.M. & Garrott, R.A. (2007) Site fidelity of Weddell seals: the effects of sex and age. *Antarctic Science*, **19**, 149–155.
- Carvalho, C.M., Polson, N.G. & Scott, J.G. (2010) The horseshoe estimator for sparse signals. *Biometrika*, **97**, 465–480.
- Chambert, T., Rotella, J.J., Higgs, M.D. & Garrott, R.A. (2013) Individual heterogeneity in reproductive rates and cost of reproduction in a long-lived vertebrate. *Ecology and Evolution*, **3**, 2047–2060.
- Clutton-Brock, T.H. (1984) Reproductive effort and terminal investment in iteroparous animals. *American Naturalist*, **123**, 212–229.
- Côté, S.D. & Festa-Bianchet, M. (2001) Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia*, **127**, 230–238.
- Creighton, J.C., Heflin, N.D. & Belk, M.C. (2009) Cost of reproduction, resource quality, and terminal investment in a burying beetle. *The American Naturalist*, **174**, 673–684.
- Cubaynes, S., Doherty, P.F., Schreiber, E.A. & Gimenez, O. (2011) To breed or not to breed: a seabird's response to extreme climatic events. *Biology Letters*, **7**, 303–306.
- Curio, E. (1983) Why do young birds reproduce less well? *Ibis*, **125**, 400–404.
- Denwood, M. (2016) *Runjags: Interface Utilities, Model Templates, Parallel Computing Methods and Additional Distributions for MCMC Models in JAGS*. <https://cran.r-project.org/web/packages/runjags/vignettes/User-Guide.pdf>
- Derocher, A.E. & Stirling, I. (1998) Maternal investment and factors affecting offspring size in polar bears (*Ursus maritimus*). *Journal of Zoology*, **245**, 253–260.
- Ericsson, G., Wallin, K., Ball, J.P. & Broberg, M. (2001) Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. *Ecology*, **82**, 1613–1620.
- Fedak, M.A., Arnomb, T. & Boyd, I.L. (1996) The relation between the size of southern elephant seal mothers, the growth of their pups, and the use of maternal energy, fat, and protein during lactation. *Physiological Zoology*, **69**, 887–911.
- Festa-Bianchet, M., Gaillard, J.-M. & Jorgenson, J.T. (1998) Mass-and density-dependent reproductive success and reproductive costs in a capital breeder. *The American Naturalist*, **152**, 367–379.
- Festa-Bianchet, M., Jorgenson, J.T. & Réale, D. (2000) Early development, adult mass, and reproductive success in bighorn sheep. *Behavioral Ecology*, **11**, 633–639.
- Festa-Bianchet, M., King, W.J., Jorgenson, J.T., Smith, K.G. & Wishart, W.D. (1996) The development of sexual dimorphism: seasonal and lifetime mass changes in bighorn sheep. *Canadian Journal of Zoology*, **74**, 330–342.
- Forslund, P. & Pärt, T. (1995) Age and reproduction in birds—hypotheses and tests. *Trends in Ecology & Evolution*, **10**, 374–378.
- Froy, H., Phillips, R.A., Wood, A.G., Nussey, D.H. & Lewis, S. (2013) Age-related variation in reproductive traits in the wandering albatross: evidence for terminal improvement following senescence. *Ecology Letters*, **16**, 642–649.
- Gadgil, M. & Bossert, W.H. (1970) Life historical consequences of natural selection. *The American Naturalist*, **104**, 1–24.
- Garroway, C.J. & Broders, H.G. (2007) Adjustment of reproductive investment and offspring sex ratio in white-tailed deer (*Odocoileus virginianus*) in relation to winter severity. *Journal of Mammalogy*, **88**, 1305–1311.
- Gelman, A., Hwang, J. & Vehtari, A. (2014) Understanding predictive information criteria for Bayesian models. *Statistics and Computing*, **24**, 997–1016.
- Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences. *Statistical Science*, **7**, 457–472.
- Georges, J.-Y. & Guinet, C. (2000) Maternal care in the subantarctic fur seals on Amsterdam Island. *Ecology*, **81**, 295–308.
- Gittleman, J.L. & Thompson, S.D. (1988) Energy allocation in mammalian reproduction. *American Zoologist*, **28**, 863–875.
- Gluckman, P.D., Hanson, M.A., Morton, S.M. & Pinal, C.S. (2005) Life-long echoes—a critical analysis of the developmental origins of adult disease model. *Neonatology*, **87**, 127–139.
- Guinness, F.E., Albon, S.D. & Clutton-Brock, T.H. (1978) Factors affecting reproduction in red deer (*Cervus elaphus*) hinds on Rhum. *Journal of Reproduction and Fertility*, **54**, 325–334.

- Hackman, E., Emanuel, I., Van Belle, G. & Daling, J. (1983) Maternal birth weight and subsequent pregnancy outcome. *JAMA*, **250**, 2016–2019.
- Hadley, G.L., Rotella, J.J. & Garrott, R.A. (2007) Evaluation of reproductive costs for Weddell seals in Erebus Bay, Antarctica. *Journal of Animal Ecology*, **76**, 448–458.
- Hadley, G.L., Rotella, J.J., Garrott, R.A. & Nichols, J.D. (2006) Variation in probability of first reproduction of Weddell seals. *Journal of Animal Ecology*, **75**, 1058–1070.
- Hales, C.N. & Barker, D.J. (2001) The thrifty phenotype hypothesis. *British Medical Bulletin*, **60**, 5–20.
- Hamel, S., Craine, J.M. & Towne, E.G. (2012) Maternal allocation in bison: co-occurrence of senescence, cost of reproduction, and individual quality. *Ecological Applications*, **22**, 1628–1639.
- Hamel, S., Côté, S.D., Gaillard, J.-M. & Festa-Bianchet, M. (2009) Individual variation in reproductive costs of reproduction: high-quality females always do better. *Journal of Animal Ecology*, **78**, 143–151.
- Hewison, A.M. & Gaillard, J.-M. (1999) Successful sons or advantaged daughters? The Trivers-Willard model and sex-biased maternal investment in ungulates. *Trends in Ecology & Evolution*, **14**, 229–234.
- Hill, S.E.B. (1987) *Reproductive ecology of Weddell Seals (Leptonychotes Weddellii) in McMurdo Sound, Antarctica*. PhD Dissertation, University of Minnesota, Minneapolis, MN, USA.
- Hindle, A.G., Horning, M., Mellish, J.-A.E. & Lawler, J.M. (2009a) Diving into old age: muscular senescence in a large-bodied, long-lived mammal, the Weddell seal (*Leptonychotes weddellii*). *Journal of Experimental Biology*, **212**, 790–796.
- Hindle, A.G., Lawler, J.M., Campbell, K.L. & Horning, M. (2009b) Muscle senescence in short-lived wild mammals, the soricine shrews *Blarina brevicauda* and *Sorex palustris*. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, **311**, 358–367.
- Hirshfield, M.F. & Tinkle, D.W. (1975) Natural selection and the evolution of reproductive effort. *Proceedings of the National Academy of Sciences of the United States of America*, **72**, 2227–2231.
- Hoerl, A.E. & Kennard, R.W. (1970) Ridge regression: biased estimation for nonorthogonal problems. *Technometrics*, **12**, 55–67.
- Hooten, M.B. & Hobbs, N.T. (2015) A guide to Bayesian model selection for ecologists. *Ecological Monographs*, **85**, 3–28.
- Innes, S., Lavigne, D.M., Earle, W.M. & Kovacs, K.M. (1987) Feeding rates of seals and whales. *The Journal of Animal Ecology*, **56**, 115–130.
- Keech, M.A., Bowyer, R.T., Jay, M., Hoef, V., Boertje, R.D., Dale, B.W. et al. (2000) Life-history consequences of maternal condition in Alaskan moose. *The Journal of Wildlife Management*, **64**, 450–462.
- King, E.G., Roff, D.A. & Fairbairn, D.J. (2011) Trade-off acquisition and allocation in *Gryllus firmus*: a test of the Y model. *Journal of Evolutionary Biology*, **24**, 256–264.
- Kirkwood, T.B.L. (1981) Repair and its evolution: survival versus reproduction. *Physiological Ecology: An Evolutionary Approach To Resource Use*, (eds C.R. Townsend & P. Calow), pp. 165–189. Blackwell Scientific Publications, Oxford, UK.
- Kirkwood, T.B. & Austad, S.N. (2000) Why do we age? *Nature*, **408**, 233–238.
- Kovacs, K.M. & Lavigne, D.M. (1986) Maternal investment and neonatal growth in phocid seals. *The Journal of Animal Ecology*, **55**, 1035–1051.
- Kruuk, L.E.B., Clutton-Brock, T.H., Rose, K.E. & Guinness, F.E. (1999) Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proceedings of the Royal Society of London B: Biological Sciences*, **266**, 1655–1661.
- Lang, S.L.C., Iverson, S.J. & Bowen, W.D. (2009) Repeatability in lactation performance and the consequences for maternal reproductive success in gray seals. *Ecology*, **90**, 2513–2523.
- Lindström, J. (1999) Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, **14**, 343–348.
- Lock, J.E., Smiseth, P.T., Moore, P.J. & Moore, A.J. (2007) Coadaptation of prenatal and postnatal maternal effects. *The American Naturalist*, **170**, 709–718.
- Loison, A. & Strand, O. (2005) Allometry and variability of resource allocation to reproduction in a wild reindeer population. *Behavioral Ecology*, **16**, 624–633.
- Lucas, A. (1991) Programming by early nutrition in man. *The Childhood Environment and Adult Disease*, **1991**, 38–55.
- Lummaa, V. (2003) Early developmental conditions and reproductive success in humans: downstream effects of prenatal famine, birth-weight, and timing of birth. *American Journal of Human Biology*, **15**, 370–379.
- Lummaa, V. & Clutton-Brock, T. (2002) Early development, survival and reproduction in humans. *Trends in Ecology & Evolution*, **17**, 141–147.
- Lunn, N.J., Boyd, I.L. & Croxall, J.P. (1994) Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *Journal of Animal Ecology*, **63**, 827–840.
- Martin, J.G. & Festa-Bianchet, M. (2011) Sex ratio bias and reproductive strategies: What sex to produce when? *Ecology*, **92**, 441–449.
- McLaren, I. (1993) Growth in pinnipeds. *Biological Reviews*, **68**, 1–79.
- McMahon, C.R., Burton, H.R. & Bester, M.N. (2000) Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science*, **12**, 149–153.
- McMullen, S., Langley-Evans, S.C., Gambling, L., Lang, C., Swali, A. & McArdle, H.J. (2012) A common cause for a common phenotype: the gatekeeper hypothesis in fetal programming. *Medical Hypotheses*, **78**, 88–94.
- Medawar, P.B. (1946) Old age and natural death. *Modern Quarterly*, **1**, 30–56.
- Mellish, J.-A.E., Iverson, S.J. & Bowen, W.D. (1999) Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. *Physiological and Biochemical Zoology*, **72**, 677–690.
- Millar, J.S. (1977) Adaptive features of mammalian reproduction. *Evolution*, **31**, 370–386.
- Mysterud, A., Yoccoz, N.G., Stenseth, N.C. & Langvatn, R. (2001) Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. *Proceedings of the Royal Society of London B: Biological Sciences*, **268**, 911–919.
- Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142.
- Nussey, D.H., Coulson, T., Delorme, D., Clutton-Brock, T.H., Pemberton, J.M., Festa-Bianchet, M. et al. (2011) Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. *Ecology*, **92**, 1936–1947.
- Ochoa-Acuña, H., Francis, J.M. & Boness, D.J. (1998) Interannual variation in birth mass and postnatal growth rate of Juan Fernandez fur seals. *Canadian Journal of Zoology*, **76**, 978–983.
- Oftedal, O.T. (1985) Pregnancy and lactation. *Bioenergetics of Wild Herbivores*, **10**, 215–238.
- Park, T. & Casella, G. (2008) The bayesian lasso. *Journal of the American Statistical Association*, **103**, 681–686.
- Parker, T.H. & Loiselle, B. (2002) Maternal condition, reproductive investment, and offspring sex ratio in captive red junglefowl (*Gallus gallus*). *The Auk*, **119**, 840–845.
- Paterson, J.T., Rotella, J.J., Mannas, J.M. & Garrott, R.A. (2016) Data from: Patterns of age-related change in reproductive allocation differ in the prenatal and postnatal periods in a long-lived mammal. *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.tk5ph>.
- Pianka, E.R. & Parker, W.S. (1975) Age-specific reproductive tactics. *American Naturalist*, **109**, 453–464.
- Plummer, M. (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, p. 125. Technische Universität Wien, Wien, Austria.
- van de Pol, M. & Verhulst, S. (2006) Age-dependent traits: a new statistical model to separate within- and between-individual effects. *The American Naturalist*, **167**, 766–773.
- Pomeroy, P.P., Fedak, M.A., Rothery, P. & Anderson, S. (1999) Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *Journal of Animal Ecology*, **68**, 235–253.
- Proffitt, K.M., Garrott, R.A. & Rotella, J.J. (2008) Long-term evaluation of body mass at weaning and postweaning survival rates of Weddell seals in Erebus Bay, Antarctica. *Marine Mammal Science*, **24**, 677–689.
- Proffitt, K.M., Rotella, J.J. & Garrott, R.A. (2010) Effects of pup age, maternal age, and birth date on pre-weaning survival rates of Weddell seals in Erebus Bay, Antarctica. *Oikos*, **119**, 1255–1264.
- Proffitt, K.M., Garrott, R.A., Rotella, J.J. & Wheatley, K.E. (2007) Environmental and senescent related variations in Weddell seal body mass: implications for age-specific reproductive performance. *Oikos*, **116**, 1683–1690.
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Robbins, C.T. & Robbins, B.L. (1979) Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. *American Naturalist*, **114**, 101–116.
- Roff, D.A. (2002) *Life History Evolution*. Sinauer Associates, Inc., Sunderland, MA, USA.
- Schubert, K.A., de Vries, G., Vaanholt, L.M., Meijer, H.A., Daan, S. & Verhulst, S. (2009) Maternal energy allocation to offspring increases with environmental quality in house mice. *The American Naturalist*, **173**, 831–840.
- Schulz, T.M. & Bowen, W.D. (2005) The evolution of lactation strategies in pinnipeds: a phylogenetic analysis. *Ecological Monographs*, **75**, 159–177.
- Siniff, D.B., DeMaster, D.P., Hofman, R.J. & Eberhardt, L.L. (1977) An analysis of the dynamics of a Weddell seal population. *Ecological Monographs*, **47**, 319–335.
- Skibieli, A.L., Dobson, F.S. & Murie, J.O. (2009) Maternal influences on reproduction in two populations of Columbian ground squirrels. *Ecological Monographs*, **79**, 325–341.
- Skibieli, A.L., Speakman, J.R. & Hood, W.R. (2013) Testing the predictions of energy allocation decisions in the evolution of life-history trade-offs. *Functional Ecology*, **27**, 1382–1391.
- Smith, C.C. & Fretwell, S.D. (1974) The optimal balance between size and number of offspring. *American Naturalist*, **108**, 499–506.
- Stearns, S.C. (1989) Trade-offs in life-history evolution. *Functional Ecology*, **3**, 259–268.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, UK.
- Stirling, I. (1969) Ecology of the Weddell seal in McMurdo Sound, Antarctica. *Ecology*, **50**, 573–586.
- Stopher, K.V., Pemberton, J.M., Clutton-Brock, T.H. & Coulson, T. (2008) Individual differences, density dependence and offspring birth traits in a population of red deer. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2137–2145.
- Vaida, F. & Blanchard, S. (2005) Conditional Akaike information for mixed-effects models. *Biometrika*, **92**, 351–370.
- Van Noordwijk, A.J. & de Jong, G. (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. *American Naturalist*, **128**, 137–142.
- Vaupel, J.W., Manton, K.G. & Stallard, E. (1979) The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography*, **16**, 439–454.
- Velando, A., Drummond, H. & Torres, R. (2006) Senescent birds redouble reproductive effort when ill: confirmation of the terminal investment hypothesis. *Proceedings of the Royal Society of London B: Biological Sciences*, **273**, 1443–1448.
- Watanabe, S. (2010) Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *The Journal of Machine Learning Research*, **11**, 3571–3594.
- Wauters, L., Bijnens, L. & Dhondt, A.A. (1993) Body mass at weaning and juvenile recruitment in the red squirrel. *Journal of Animal Ecology*, **62**, 280–286.
- Weladji, R.B., Holand, Ø., Gaillard, J.-M., Yoccoz, N.G., Mysterud, A., Nieminen, M. *et al.* (2010) Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence? *Oecologia*, **162**, 261–271.
- Wheatley, K.E., Bradshaw, C.J.A., Davis, L.S., Harcourt, R.G. & Hindell, M.A. (2006) Influence of maternal mass and condition on energy transfer in Weddell seals. *Journal of Animal Ecology*, **75**, 724–733.
- Williams, G.C. (1957) Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, **11**, 398–411.
- Wolcott, D.M., Reitz, R.L. & Weckerly, F.W. (2015) Biological and environmental influences on parturition date and birth mass of a seasonal breeder. *PLoS ONE*, **10**, e0124431.

Received 4 February 2016; accepted 13 July 2016

Handling Editor: Jean-Michel Gaillard

## Supporting Information

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.