

SOURCES OF VARIATION IN MATERNAL ALLOCATION TO OFFSPRING
DURING LACTATION IN THE WEDDELL SEAL

by

Kaitlin Rose Macdonald

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ABSTRACT

Variation in the allocation of energy to reproduction by mothers can have fitness consequences for mothers and offspring. Diverse features of a mother, and annual environmental fluctuations may affect the amount of energy a mother allocates to offspring and may obscure age-specific patterns that are of interest when evaluating predictions made from existing life history theory. To properly evaluate possible sources of variation, especially age-specific variation in maternal allocation, analyses of data for known-age mothers with a wide range of ages, diverse reproductive histories, and multiple measures of allocation to reproduction are needed. We used data from a long-term study of Weddell seals that were individually marked as pups and monitored annually and a Bayesian hierarchical modeling framework to characterize age-specific variation in maternal allocation and test predictions about age-specific variation while considering additional maternal features that might influence maternal allocation. Based on masses for 311 mothers and associated pups from 2002 to 2016, we found that maternal allocation was moderately associated with maternal age and strongly associated with maternal body mass at birth of her pup. We found that heavier mothers lost a greater proportion of mass during the entire lactation period but that the efficiency with which mothers transferred this mass to their pups was lower than that of lighter individuals. The proportion of mass lost by a mother during the entire lactation period was greater for mothers that had reproduced the previous year and for those who started reproducing young, which suggests that individual quality and perhaps experience are determinants of maternal allocation in this species. Our study did not find support for our predictions that older mothers would allocate more body reserves, be more efficient at transferring mass during early lactation, or alter their behavior in ways that would improve mass transfer efficiency during late lactation, relative to prime-age mothers. The large variation we found in energy allocation to pups translates to large variation in pup weaning mass. Our results highlight that maternal multiple features should be considered when evaluating patterns of age-specific variation in maternal allocation.

SOURCES OF VARIATION IN MATERNAL ALLOCATION TO OFFSPRING DURING LACTATION IN THE WEDDELL SEAL

Introduction

Maternal allocation, or the energy mothers allocate to reproduction, can have implications for survival and fitness of both mothers and offspring (Mousseau & Fox, 1998; Lindström, 1999). For offspring, reduced growth or limited resources early in life can have consequences for later development, reproduction and survival (Lummaa & Clutton-Brock, 2002; Oosthuizen et al. 2015), even if compensation for poor early growth occurs (Metcalf & Monaghan, 2001). Variation in energetic allocation to reproduction can therefore influence population vital rates and is important to our understanding of life history theory and population ecology (Benton, St Clair, & Plaistow, 2008; Clutton-Brock & Sheldon, 2010). Sources of variation in maternal allocation may include environmental conditions as well as features of a mother that are static through life (e.g., age at first reproduction) or that may vary each year (e.g., age). Studies are needed that simultaneously assess diverse sources of variation in maternal energy allocation to reproduction and how allocation might vary over an individual's lifetime.

Life history theory predicts that reproductive effort should vary with age as the result of a trade-off among an individual's reproductive output, physiological maintenance, and survival given that a finite amount of energy is available for life functions (Stearns, 1992). Because of such trade-offs, allocation of resources to

reproduction is expected to depend on an individual's residual reproductive value and to vary with age so as to optimize an individual's lifetime fitness (Williams, 1966; Pianka & Parker, 1975). Late in life, when residual reproductive value is low, the terminal-investment hypothesis predicts that an individual should increase the proportion of energy that is allocated to reproduction at a cost to future survival or reproduction (Gadgil & Bossert, 1970). Support for the terminal-investment hypothesis requires evidence of fitness costs associated with an increase in energy allocated to reproduction in the face of declining reproductive value (Clutton-Brock, 1984). When fitness costs associated with increases in energetic allocation to reproduction cannot be assessed or are not detected, increases in energetic allocation are termed terminal allocation rather than terminal investment (Weladji et al. 2009). Although evidence for terminal investment has been established in a few experimental studies (Velando, Drummond, & Torres, 2006; Creighton et al. 2009), more studies of natural populations are needed as previous work on wild animals have either found no support for increases in energetic allocation to reproduction with age (Bowen, Iverson, Mcmillan, & Boness, 2006) or have only been able to identify terminal allocation (Weladji et al., 2009; Froy et al. 2013). When assessing predictions from life history theory regarding age-specific variation in maternal allocation, it is important to consider possible additional sources of variation that can occur within and among individuals and affect maternal investment in reproduction.

Heterogeneity in individual quality can result in patterns of reproductive effort across ages that differ at the individual level versus the population level (Cam et al., 2002). Such a difference can occur if individuals within a cohort vary in quality (i.e.,

latent fitness characteristics), and poor quality individuals tend to selectively disappear from the population earlier in life such that the average quality of an individual remaining alive in the population gradually increases as the cohort ages (Vaupel, Manton, & Stallard, 1979; Forslund & Pärt, 1995). If present, selective disappearance can mask underlying age-specific patterns at the individual level if not considered specifically when evaluating measures of reproductive effort (Beauplet et al. 2006; Bouwhuis et al. 2009; Hamel, Craine, & Towne, 2012; Paterson, 2017).

Other maternal features can also influence allocation of energy by an individual mother to reproduction. Age at first reproduction can be an important static predictor of an individual's reproductive success (Forslund & Pärt, 1995). Long-lived species that first recruit at an earlier age may suffer costs from reproduction to survival and future reproduction (Gadgil & Bossert, 1970; Krüger, 2005; Reiter & Boeuf, 1991). Regardless, more robust individuals might be able to better withstand costs of recruiting to the breeding population at an earlier age (Cam et al., 2002), and evidence suggests earlier age at first reproduction is associated with higher reproductive success in some species (Bérubé, Festa-Bianchet, & Jorgenson, 1999; Aubry et al. 2009; Hayward et al. 2014). Other maternal attributes vary through a mother's life and can influence current reproduction or have carry-over effects on future reproduction. Because reproduction is costly, an individual's reproductive status in the previous year might influence reproductive expenditures in the current year (Pomeroy et al. 1999; Hamel et al., 2012). Compared to females that reproduced in the previous year, individuals that did not reproduce might be able to accumulate greater body stores and allocate more to the

current reproductive attempt (Green, 1990; Lunn, Boyd, & Croxall, 1994). The cost of previous reproduction might also vary with individual quality such that low-quality mothers must skip reproduction to recover body reserves, whereas high-quality mothers can recover more quickly and sustain back-to-back reproductive attempts (Hamel et al. 2009). Maternal parturition mass, which can vary among individuals and across an individual's life, is an indicator of the body reserves or resources available to a mother for lactation and maintenance (Gittleman & Thompson, 1988), in species that rely heavily on stored reserves during lactation. Relationships have been drawn between maternal parturition mass and milk yield, relative maternal mass loss (Wheatley et al. 2006; Wheatley et al. 2008) and rate of mass loss (Mellish, Iverson, & Bowen, 1999) during lactation. Maternal parturition mass exhibits a negative relationship with apparent mass conversion efficiency in some species such that larger female mammals may provide more absolute energy to offspring but do so less efficiently (Testa, Hill, & Siniff, 1989; Festa-Bianchet & Jorgenson, 1998; Carlini et al. 2004). Reproductive experience has also been reported to be positively related to reproductive allocation because an individual becomes more skilled at reproduction and self-maintenance with experience (Curio, 1983). Additionally, old individuals might increase their reproductive success by using acquired experience to better target maternal allocation during critical growth periods (Cameron et al. 2000).

Variables external to a mother can also influence how she allocates her energy to reproduction. Sex-bias in reproductive effort is predicted for polygynous species by Trivers and Willard (1973). When high variance in male reproductive success exists, it is

predicted that high-quality mothers will increase their fitness by allocating more energy during maternal care to male offspring than female offspring (Trivers & Willard, 1973). This sex bias has been observed in several mammal species (Hewison & Gaillard, 1999; Proffitt, Garrott, & Rotella, 2008a; Hinde, 2009). Additionally, maternal milk composition (Wheatley et al. 2006) and milk yield (Hinde, 2009) can vary with offspring sex, and energy requirements can differ for male and female offspring (Wheatley et al. 2006). Environmental variations can influence prey availability and abundance, which can, in turn, influence the resources available for reproduction and the body condition of females entering lactation (Crocker et al. 2001). Weaning mass of offspring, which reflects resource acquisition and allocation of mothers, has been linked to environmental conditions (Proffitt et al. 2007a). In long-lived species, years of low resource availability are expected to decrease the allocation of resources to reproduction as a means of improving survival rates during challenging conditions (Clutton-Brock, 1991; Festa-Bianchet & Jorgenson, 1998).

Studies evaluating variation in maternal allocation, especially age-specific patterns of variation, must account for diverse factors that can influence an individual's ability to reproduce (Forslund & Pärt, 1995), including static and dynamic attributes of a mother and possible annual variation in environmental conditions. Thus, data on maternal allocation are needed from large numbers of individuals that span a wide variety of ages and that have known reproductive histories. Ideally, measurements of both the energy available for reproduction as well as the energy allocated to reproduction should be available and different metrics of maternal allocation should be considered to avoid

biased estimates of allocation (Clutton-Brock, 1984; Descamps et al. 2007). Additional studies of how maternal allocation varies with maternal characteristics, offspring sex, and year in long-lived polygynous species are needed to disentangle the influence of these variables of interest from maternal age (Clutton-Brock & Sheldon, 2010). Here we assessed diverse sources of variation in maternal allocation of the Weddell seal using mass measurements from 311 mother-pup pairs and 255 known-age mothers collected over 12 years.

Characteristics of the Weddell seal make this marine mammal a model organism for investigating potential sources of variation in maternal allocation. A mother typically gives birth to a single pup in any given year and is the sole provider of parental care, which permits measurement of energetic allocation that is not complicated by multiple offspring or shared parental care. Lactation is considered to be the costliest period of reproduction for female mammals (Gittleman & Thompson, 1988). Therefore, variation in reproductive allocation during lactation should reflect the trade-off between current and future reproduction (Gittleman & Thompson, 1988). The ability of an individual to feed and acquire mass each year prior to the reproductive season determines the reserves available to be allocated to offspring, this is reflected in maternal parturition mass. Females give birth on fast ice, relying primarily on stored body reserves to support the energetic requirements of lactation. Therefore, measurement of maternal mass loss during lactation indicates energy allocated to the pup and somatic maintenance (Wheatley et al. 2006) and can be used as a proxy for maternal allocation of energy to reproduction. Although some supplemental feeding by females is thought to occur at the end of

lactation, the gains for mothers are likely nominal (Wheatley et al. 2008). Weddell seals are easily approached and do not respond aggressively to humans, which allows for efficient, non-invasive data collection. Surveys of the Erebus Bay study area have been conducted regularly during each year's pup-producing period for several decades. During surveys, crews tag newborns and record mother-pup associations. Due to the strong site fidelity of Weddell seals (Stirling, 1969), accurate reproductive histories are available for a large sample of known-age females and include information on age at first reproduction, age-specific parity, and reproductive skipping events.

In addition to the favorable characteristics of Weddell seals and the breadth of data available from this study, a great deal is known regarding attributes of maternal allocation in this species. There is evidence of senescence in maternal parturition mass (Proffitt et al. 2007b). Recent work on the Erebus Bay population of Weddell seals found that, when compared with prime-age females, older mothers tend to weigh less and give birth to lighter pups. However, pups born to old females have higher rates of mass gain during lactation and so achieve weaning masses that are similar to values for pups born to prime-age females (Paterson et al. 2016). The pattern of maternal allocation found in the study population can be reasonably explained by three competing hypotheses: 1) increasing energetic allocation with age (terminal-allocation hypothesis), 2) apparent increases in efficiency of mass transfer between mother and pup with maternal age due to selective disappearance of frail individuals (physiology hypothesis), and 3) greater levels of feeding by older mothers during late lactation, which would provide them with additional energy beyond body reserves accrued pre-partum (behavioral hypothesis).

Additionally, a combination of these three hypotheses might also explain the apparent increased growth rates during lactation of pups born to older mothers. Although the sample of mothers in our study did not demonstrate declines in maternal parturition mass, pups born to old mothers still had lower parturition masses and achieved higher growth rates than did pups produced by prime and young age mothers.

This study used mass measurements of mothers and pups directly following parturition (parturition mass), approximately 20 days post-parturition (mid-mass), and 35 days post-parturition (late-mass) to assess our three hypotheses while also considering other static and dynamic features of mothers and accounting for annual variation due to external factors in maternal allocation. Given previous findings, we predicted that older females would allocate a greater proportion of their body reserves (maternal parturition mass) during lactation. The terminal-allocation hypothesis would be supported by evidence of a positive relationship between maternal age and proportion of maternal parturition mass lost during the entire lactation period (~1-35 days post-parturition).

If the increased rate of growth in pups of older females cannot be explained by increases in maternal allocation, it is also possible that the mass transfer efficiency of mothers (amount of pup mass gained per unit of mass lost by a mother) improves at the population level through selective disappearance of lower-quality individuals. Specifically, if variation in physiological efficiency is consistent within individuals and positively correlated with survival, a higher proportion of high-quality individuals would be found in the females at the oldest ages than what is found in prime-age individuals (physiology hypothesis). Although links between physiological efficiency and an

individual's survival rate are unknown in Weddell seals, previous work did report individual variation in mass transfer efficiency for the species (Testa et al. 1989; Wheatley et al. 2006). The extent to which such individual variation is due to differences in physiology, the length of the lactation period, or the ability to obtain food and supplement stored body reserves is unknown. However, research in the livestock industry has found evidence for consistent, heritable differences in measures of lactation efficiency among individuals (Bergsma et al. 2008; VandeHaar et al. 2016), which likely lead to differences in fitness (Gilbert et al. 2012; Spurlock et al. 2012). To further assess the physiological hypothesis, mass transfer efficiency measures are needed across the lactation period. Further, to eliminate confounding effects, such as potential foraging of females and differences in weaning dates that would alter calculated mass transfer efficiency, efficiency should be evaluated in the early-lactation period (~1-20 days post-parturition) when all mothers can reasonably be expected to be nursing. The physiology hypothesis would be supported by evidence of increased mass transfer efficiency during early lactation with increasing age.

Females primarily fast throughout lactation but several studies of this population suggest that some feeding does occur (Tedman & Bryden, 1979; Testa et al. 1989; Wheatley et al. 2008). The extent to which females feed to supplement body reserves during late lactation is unknown, but it is a potential behavioral mechanism by which older females could increase allocation of energy to pups without allocating proportionally more body reserves than do younger females. The behavioral hypothesis would be supported by evidence for no variation in mass transfer efficiency with

maternal age during early lactation accompanied by evidence for increases in mass transfer efficiency with maternal age during late lactation (20-35 days post-parturition).

We used mass measurements of mothers and pups throughout lactation for a sample of known-age mothers with known reproductive histories to 1) characterize age-specific variation in maternal allocation and 2) test three hypotheses that explain age-specific variation in maternal allocation while considering age-independent factors that might also influence maternal allocation.

Methods

Study System

Erebus Bay is an embayment along the western coast of Ross Island, Antarctica (-77.62° to -77.87°S, 166.3° to 167.0°E) and forms the boundaries of the study area. Sea ice cracks are created and persist from the tidal action where sea ice meets Ross Island and smaller islands within the bay. During the austral spring, female Weddell seals use the sea ice cracks to haul out on the sea ice, forming 8-14 pupping colonies (Stirling, 1969). The study population consists of seals found within the Erebus Bay study area. Pupping in the area occurs on the sea ice from late October through November, with the peak of pupping occurring around the last week of October (Stirling, 1969; Rotella, Paterson, & Garrott, 2016). Mothers typically remain close to pups during the approximately 30-45 day lactation period, during which females primarily fast (Tedman & Bryden, 1979; Wheatley et al. 2008). Weddell seal females typically first produce a pup at 7 or 8 years of age and give birth to a single pup per reproductive event (Hadley et

al. 2006). Each year, all pups born in the study population are marked in the interdigital webbing of the rear flipper with individually identifiable livestock tags, and, since 1973, four to eight mark-recapture surveys of the population have been carried out annually (Cameron & Siniff, 2004). Weddell seals are philopatric to natal areas and adult females return to the study area to give birth (Cameron & Siniff, 2004). Due to the philopatric nature of Weddell seals and the project's long-term mark-resight efforts, age and reproductive histories are known for many females.

Sampling Design

Data on body mass of mothers and pups throughout lactation were obtained on a sample of animals. Efforts were made to obtain a representative sample of mothers and pups in the population by sampling across major pupping colonies. Because of our interest in age-related patterns of maternal allocation, we attempted to obtain adequate samples for mothers in three different age classes: young (4-10 years), prime (11-17 years) and old (18+ years). Because most Weddell seal females begin producing pups before age 11 (Hadley et al. 2006), we used 11 years-of-age as our cut-off between young and prime age classes. Because senescent declines in the form of decreasing maternal post-parturition mass after 18 years-of-age have been found in Weddell seals (Proffitt et al. 2007b), we used 17 years-of-age as the cut-off between prime and old age classes.

Colonies were visited every 24-48 hours throughout each pupping season to identify newborn pups and to associate each mother with her pup. Each year since 2002, a sample of pups that were judged to have been born within 24-72 hours to known-age mothers were weighed using a spring scale or digital weighing platform and attempts

were made to locate and weigh these pups again at approximately 20 and 35 days of age to obtain mid- and late-lactation mass measurements (Paterson et al. 2016). We obtained mass data for mothers associated with pups in the mass study at three different times after parturition: 1-4 days later, 15-25 days later, and 30-40 days later using either a digital weighing platform, photogrammetric methods, or both (Ireland et al. 2006; Paterson et al. 2016). Due to the difficulty in obtaining maternal mass measurements with the weighing platform throughout lactation, photogrammetry has been used to estimate the mass of Weddell seal mothers since 2002. Photogrammetric mass estimates are based on regression models that relate photogrammetric measurements to mass values from the weighing platform that were obtained from a subset of mothers that were weighed on the platform and for which we also obtained photogrammetric measures on the same or a proximal day.

Photographs of mothers from 2002-2010 were taken using a two-dimensional photogrammetry technique outlined by Ireland et al. (2006). Photographs were collected from two perspectives, overhead and ground-level side, while the seal lay in a standard position. Photographs were taken using specially designed, remotely-operated cameras attached to overhead and side-view booms. A scale bar marked with 20-cm increments was included in all photographs in a standardized position relative to the seal and used to calibrate measurements during image analysis. Two-dimensional photographs were processed using image analysis software ImageJ (Schneider, Rasband, & Eliceiri, 2012) to obtain morphometric measurements of mothers. The outline of seals on both overhead and side-view photographs were drawn excluding fore- and rear-flippers, to determine the

area of the seal. Overhead width was measured as the widest distance across the chest of the seal and side-view height was measured as the longest distance from the bottom to the top edge of the seal. Due to the logistical issues associated with the two-dimensional photogrammetry technique in the field a new technique was adopted after 2010.

For photogrammetry data collected during 2012-2016, photographs of mothers were taken and analyzed using a three-dimensional photogrammetry technique outlined by de Bruyn et al. (2009). In the field, six 1-m long bars, marked at 20-cm lengths were laid around the female seal and used in image processing to position the image within the three-dimensional space and define a measurement scale. We took photographs from eight angles (0° , 45° , 90° , 135° , 180° , 225° , 270° , 315°) around the female at varying heights, starting at the head. We took photographs of females lying in a natural resting position and retained photograph sets for which a minimal amount of head or body movement existed among photographs in the set. Photographs were taken with Panasonic Lumix DMC-TS5 and Panasonic Lumix DMC-TS30 cameras calibrated using either a single large calibration grid or multiple small calibration grids. Photographs were processed using PhotoModeler software (Version 2016.0.8.1825, EOS Systems) to obtain three-dimensional models and volume estimates for each seal. Sets of photographs were manually oriented in three-dimensional space by marking defined color segments of scale bars and referencing points between photographs. Once a scale was defined, silhouettes of the seal were drawn and digitally combined to obtain a three-dimensional model and subsequent volume. Morphometric measurements from photogrammetry were related to

mass measurements using linear regression to obtain mass estimates (see statistical procedures below).

Model Covariates

We included several combinations of variables intrinsic and extrinsic to mothers that we predicted would be associated with variation in maternal allocation of energy to reproduction in a set of competing models. Because our primary goal was to explore the relationship between maternal energetic allocation and maternal age, maternal age was the key variable of interest in our competing models. Different trends of maternal energetic allocation with age were evaluated using different functional forms of maternal age in candidate models. A model with a linear functional form of age was evaluated to assess whether maternal energetic allocation increases or decreases with age in a consistent fashion. We evaluated a model with a quadratic functional form of maternal age to assess whether reproductive allocation attributes either declined or improved with age (the two possibilities could be accommodated by either negative or positive signs, respectively, for the coefficient associated with the age-squared term in the model). We evaluated a model with a logarithmic functional form of age to investigate the possibility that increases (or decreases) in reproductive allocation might slow or reach a pseudo-threshold at older ages.

In addition to maternal age, we also included a variety of other covariates. We included maternal mass at the start of the specific period of lactation being evaluated in a given analysis. Specifically, we included maternal parturition mass in the terminal-allocation (data from ~1 and 35 d post-parturition) and physiology models (data from ~1

and 20 d post-parturition) and mid-lactation mass in the behavioral model (data from ~20 and 35 d post-parturition) to control for absolute reserves available to a mother at the start of lactation or the second-half of lactation, respectively. We included age of first reproduction in all models as it has been shown to be associated with individual quality of Weddell seals (Hadley et al. 2006). To account for prior maternal experience, we also included a measure of each female's relative parity, which measured how a female's age-specific parity value compared to the average value for other females her age. A recent assessment of costs of reproduction in our study population found that there was evidence of reproductive costs to the probability of reproducing in the next year (Chambert et al. 2013), suggesting reproduction the previous year may be important to maternal allocation. Therefore, we included a binary variable that indicated whether a female was recorded with a pup the previous season in all models to evaluate possible changes in maternal allocation as a function of a female's breeding status in the previous year. We included pup sex as a covariate in all models to account for possible differential maternal energetic allocation to male versus female pups. Environmental variation over the course of this study was large and included the presence of the B-15 iceberg fragments in the Ross Sea (Arrigo & van Dijken, 2004; Thrush & Cummings, 2011). These fragments had a negative effect on reproductive rates of this population (Chambert, Rotella, & Garrott, 2012), and it is possible that this and other sources of environmental variation led to differences in reproductive effort and efficiency for females breeding in different years. Accordingly, we included a random effect of year in all models to account for environmental variability. Some mothers were sampled in multiple years, and thus, a

random effect of individual was also included in all models to account for possible lack of independence among repeated measures of individual mothers.

Statistical Procedures

Mass estimation equations for photogrammetry were fit using linear regression in the R statistical computing environment (R Core Team, 2018). To identify a predictive mass-estimation equation for the two-dimensional photogrammetry, we performed all-possible-subset regression using the MuMIn package in R (Bartoń, 2018). Best supported models were chosen using the Akaike Information Criterion for small sample sizes (AIC_C) (Burnham & Anderson, 2002). The full model included the following variables: overhead area, overhead width, side-view height, and side-view area. To assess models with even moderate support, all models within five AIC_C units of the top model were considered as a potential predictive model (Burnham & Anderson, 2002). The subset of potential predictive models were evaluated using the predicted sum of squares (PRESS) criterion following the methodology of Ireland et al. (2006). The PRESS criterion selects for small prediction errors and identifies models with higher predictive ability (Neter, Wasserman, & Kutner, 1990). The top mass-estimation model for two-dimensional photogrammetry was selected as the model with the lowest PRESS value. Model diagnostics suggested an influential observation. Subsequent model selection was performed with and without the observation resulting in the same top model, and the observation was removed before choosing the top predictive model. The top mass-estimation model for two-dimensional photogrammetry included overhead area, overhead width, and side-view area measurements. The mass estimation model for the two-

dimensional photogrammetry had an adjusted R^2 value of 0.797. When the mass estimation regression was evaluated at the mean of the dependent variables (overhead area, overhead width and side-view area), the prediction error was 9.0% of the mean measured mass.

A predictive mass-estimation equation for the three-dimensional photogrammetry was identified by performing a simple linear regression of volume versus mass. Although mass estimates from three-dimensional photogrammetry have been calculated by multiplying volume measurements and known mammal densities (de Bruyn et al. 2009, Beltran et al. 2018), such estimates typically require use of correction factors. For the mass-estimation work presented here, we performed a simple linear regression of known female masses against their respective volume estimates, which yielded a mass estimation equation specific to this population that did not require any correction factor. An influential observation was identified while assessing model diagnostics and the analysis was performed with and without the observation. Removal of the influential observation did not change the coefficient estimates of the mass-estimation model in a meaningful way, and the point was left out of the final mass-estimation model. The mass-estimation regression for three-dimensional photogrammetry resulted in an adjusted R^2 value of 0.903. When the mass-estimation regression was evaluated at the mean volume estimate, the prediction error was 4.92% of the mean measured mass. Although prediction errors were modest and were less than 10% of the mean measured mass, it was important we account for them when making inferences from the mass estimates. Measurement error can bias coefficient estimates as well as diminish explanatory power if not accounted for

(Proffitt et al. 2007c). Therefore, we used a modeling framework that allowed us to account for measurement error related to photogrammetric mass estimation when evaluating sources of variation in maternal allocation.

We employed a Bayesian modeling framework to assess sources of variation in maternal energy allocation while accounting for 1) measurement errors associated with maternal masses and 2) the hierarchical nature of our data that included multiple mother-pup pairs per year and repeated measures of some mothers in multiple years. Models were fit in JAGS 4.3.0 (Plummer, 2003) through the R interface using package R2jags (Su & Yajima, 2015). All continuous predictor variables were centered and scaled by 2 standard deviations so that numeric variables could be interpreted on the same scale as binary variables (Gelman, 2008). Three chains were run in parallel for each model with each chain creating 40,000 Markov Chain Monte Carlo (MCMC) samples for the terminal-allocation models and 80,000 MCMC samples for the physiology models after discarding 10,000 burn-in samples. The sample size available for assessing the behavior hypothesis was smaller, and convergence took longer, therefore three parallel chains were run with each chain creating 200,000 MCMC samples after discarding 70,000 burn-in samples for the behavior models. We assessed model convergence using the potential scale-reduction factor known as the Gelman-Rubin statistic (Gelman & Rubin, 1992), the Geweke diagnostic which compares whether the beginning and end of each MCMC are equal, and visual inspection of trace plots to confirm model convergence based on functions and outputs from the R package ggcmc (Fernández-i-Marín, 2016). Random effects for year and individual were assumed to be normally distributed around a mean of

zero with variance σ_{year} and $\sigma_{\text{individual}}$, respectively. We used weakly informative priors for fixed and random effects in the model. For fixed effects, we used uniform priors $U(-10,10)$. For variance parameters, we used uniform priors set to be non-negative $U(0,50)$.

Three different types of mass measurements and their associated prediction errors were included in the analyses. We considered the mass of a mother that was weighed on the weigh platform to be an accurate measure of the true mass of a female and to have a prediction error of zero. For each mass estimated from two-dimensional and three-dimensional photogrammetry, we used the relevant mass-prediction regression model to obtain the mass estimate and its associated prediction error. In the subsequent Bayesian modeling of sources of variation in maternal allocation, each of our mass estimates were modeled as being normally distributed about a female's true maternal mass and dispersed according to the associated prediction error (0.01 was added to each prediction error to avoid computational issues associated with values of 0 for prediction error). True maternal masses were included in the models as latent variables. Covariate relationships with mass estimates were evaluated by relating covariates to true maternal mass as described below for each model type (example code is provided in Appendix A).

In the terminal-allocation model (data from ~1 and 35 d post-parturition), latent values of true maternal parturition mass and true maternal late-lactation mass were used to provide information on true proportion mass loss, which was then modeled as a function of covariates of interest. For the physiology model (data from ~1 and 20 d post-parturition), latent values of true maternal parturition mass and true maternal mid-lactation mass were used to measure mass loss by mothers, pup mass measurements at

parturition and mid-lactation mass provided information on daily mass gain by pups, and mass transfer efficiency (daily pup mass gain divided by latent daily maternal mass loss) was subsequently modeled as a function of covariates of interest. The behavior model was identical to the physiology model except that it focused on mass transfer efficiency during late-lactation (data from ~20 and 35 d post-parturition). Thus, in the physiology model, mid-lactation mass took the place of parturition mass in the behavior model, and late-lactation mass took the place of mid-lactation mass in the behavior model. When modeling proportion mass loss and mass transfer efficiency, we used a logit-link between the response variable and linear functions of the covariates and regression coefficients to constrain estimated mean response values to be between zero and one.

For each model type (terminal-allocation, physiology, and behavior), we evaluated 4 functional forms of maternal age (null, linear, quadratic, and pseudo-threshold [logarithmic]). Each model contained the following covariates as described above: age at first reproduction, maternal parturition mass (maternal mid-mass for the behavior models), reproductive status the previous year, and pup sex. Each model also contained random effects of individual and year (code for the linear functional form of each model type is provided in Appendix A).

Posterior predictive checks were used to assess goodness of fit for each of our top models. Visual inspection of replicated data generated under the model plotted against the observed data can be an informative model checking exercise and ensures that the model adequately predicts the observed data (Chambert, Rotella, & Higgs, 2014; Gelman, Meng, & Stern, 1996). For the top model of each hypothesis assessed, we

visually inspected plots of mass measurements from photogrammetry and the weigh-platform against posterior predictions of the mean mass for each individual (replicated data). In particular, we ensured our observed data were contained within the 95% credible intervals of our replicated data, and that there was no systematic bias in the difference between observed and replicated data.

The Bayesian predictive information criterion (BPIC) is a true Bayesian leave-one-out cross-validation method that evaluates the predictive ability of models and is appropriate for use with hierarchical models (Gelman, Hwang, & Vehtari, 2014). The properties of BPIC fit our needs for model selection and allowed us to evaluate the predictive ability for each type of mass measurement. We calculated BPIC values using the procedures set out by Link & Sauer (2016), which involves performing leave one out cross-validation (LOOCV) and summing the log conditional predictive ordinates for all observations. The conditional predictive ordinate (CPO) is the probability density of a given observation conditional on the posterior predictive distribution when the observation is omitted (Hooten & Hobbs, 2015). In the model structures that we used, each of our response variables was constructed using multiple maternal mass observations. Thus, BPIC values were calculated by simultaneously omitting each maternal mass measurement used to calculate the response variable in the model. For example, for the terminal-allocation and physiology models, maternal parturition and mid-lactation mass were simultaneously omitted during the LOOCV runs. Each cross-validation analysis was run with a single chain of 10,000 samples that began at a point where convergence had already been achieved; leave-one-out sampling for different

observations was done in parallel on multiple cores to improve efficiency using the R package snowfall (Knaus, 2015). We performed z-tests on pairs of BPIC values from each model suite to obtain a measure of the magnitude of difference in predictive ability between different models (Link & Sauer, 2016). We used logistic regression to assess all hypotheses, therefore all coefficient estimates are reported on the log-odds scale. We also present predicted values for a reference mother with specific characteristics on the real parameter scale to convey results in a biologically meaningful way. Reference values for a reference mother were set at the mean for age, age at first reproduction, and mass at parturition or mid-lactation, reproductive status was for a mother that did not reproduce the previous season and pup sex was set to be female. For reference mothers all random effects were set to zero. When reporting results for coefficient estimates, we present 90% highest density intervals (HDIs). We consider estimates with 90% HDI values that do not overlap zero to be of interest. We use changes in predicted values along with the associated uncertainty to assess biological significance of results.

Results

We collected 745 mass measurements for mothers during three different time periods (Table 1). Data from mother-pup pairs for which either the pup died or the mother and pup were not sighted together during the lactation period of interest were omitted. The final dataset contained information from 311 individual mothers, and some mothers provided data in multiple seasons (Table 2). Mass measurements were collected across a wide range of maternal ages and masses (Fig. 1). Most maternal mass

observations were obtained within three days of target sampling dates; 13.8% (n=103) were obtained outside of that time window and actual departures from target dates were accounted for in modeling (see code in Appendix A). The data included a wide range of maternal ages, with a mean age of 13.7 years (SD = 5.14, range: 5-26). Observations were obtained in 12 different years between 2002 and 2016, with annual sample sizes ranging from three mothers in 2012 to 63 mothers in 2016. Observations were obtained from 12 different years for the full lactation period, nine different years for the early lactation period, and eight years for the late lactation period. Mean age of first reproduction for mothers in the sample was 7.33 years (SD = 5.14, range: 4-13). The sex ratio of pups was nearly equal with 49.8% (n = 155) of the pups being male. A nearly equal number of mothers did and did not produce a pup in the year prior to when we sampled them with a pup; 47.6% (n = 148) did not reproduce in the previous year.

Table 1. The number of observations for each mass measurement method by mass-measurement period. Maternal and pup mean mass with associated standard deviations and ranges in kilograms based on naïve mass measurements are listed for each mass-measurement period.

	Parturition	Mid-lactation	End-lactation
Weigh-platform	142	18	23
Two-dimensional	75	88	118
Three-dimensional	81	99	101
Total observations	298	205	242
Maternal mean mass (SD)	441.78 (53.00)	352.69 (41.23)	293.10 (37.86)
Maternal mass range	278.19 – 609.20	239.84 – 472.84	193.59 – 401.81

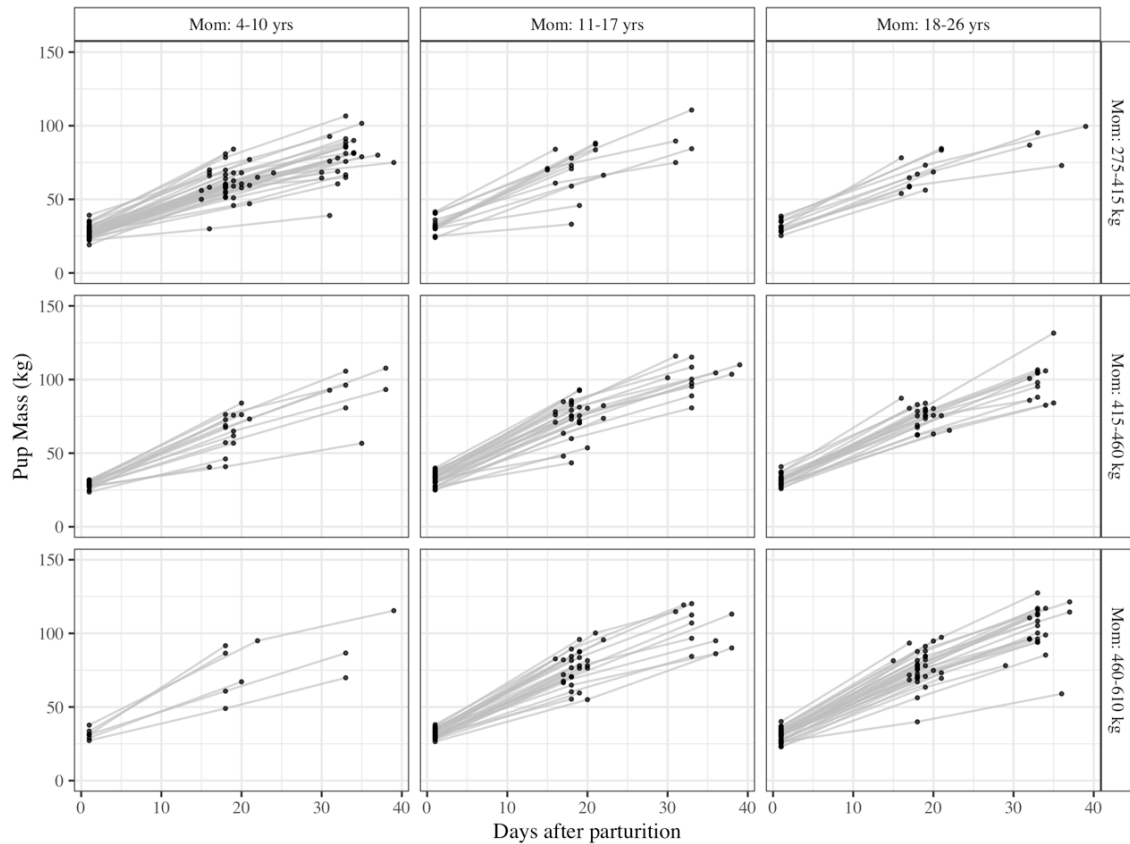
Table 1 Continued

Pup mean mass (SD)	30.84 (4.26)	70.95 (12.92)	94.43 (16.84)
Pup mass range	19.1 – 41.50	29.98 – 100.24	39.01 – 131.54

Table 2. The number of observations per individual mother for each mass-measurement period. The total number of individual mothers for each mass-measurement period and the number of total observations are listed at the bottom of the table.

No. repeated observations per individual mother	Number of individual mothers		
	Full lactation	Early lactation	Late lactation
1	155	156	99
2	34	14	8
3	2	2	0
Total Individuals	191	172	107
Total observations	229	190	115

Figure 1. Pup masses at parturition, mid- and end of lactation by maternal age class (young, old, prime) and naïve maternal parturition mass (light, average, heavy).



Model Assessment

Models for each hypothesis suite were initially fit with a covariate for relative parity. Due to the lack of support for inclusion of relative parity and given that relative parity was quite correlated with age of first reproduction and with reproductive status in the previous year, relative parity was dropped from consideration. Posterior predictive checks for the top model for each mass-estimation period indicated that each model was able to generate data that were distributed similarly to the observed data. Specifically, for each of the top models, all observed mass values were contained centrally within the 95% credible intervals for mass values generated from the model, and we found no strong

pattern in differences between observed and replicated data among maternal ages or maternal masses.

Terminal-Allocation Hypothesis

The mean proportion mass loss of mothers during lactation was 0.333 (range: 0.07-0.48) based on our naïve mass measurements and before accounting for measurement error. After we modeled the data and accounted for measurement error, estimates of proportion mass loss were shrunk towards the mean. Model convergence was achieved for each of the competing functional forms of maternal age. The results did not support our prediction of terminal allocation (Table 3). Specifically, we did not find support for our prediction that proportion of mass lost by mothers over the entire lactation period would increase with maternal age. The best supported model of proportion mass loss included the logarithmic functional form of maternal age model (Table 4). In that model, the coefficient relating proportion mass loss to age was negative ($\hat{\beta}_{\ln(\text{MaternalAge})} = -0.085$, SE = 0.051) and provides some evidence that the proportion of mass lost during lactation declined slightly with age (Fig. 1). The top model predicts that an 8 year-old mother with the reference covariate values would have a proportion mass loss of 0.342 (90% HDI: 0.323, 0.362), which would be 151.0 kg (142.5, 159.6) in a typical year. In contrast, a 14 year-old mother is predicted to have a proportion mass loss of 0.329 (0.310, 0.348) and to lose 145.1 kg (90% HDI: 136.7, 153.4). A 26 year-old mother is predicted to have a proportion mass loss of 0.315 (0.286, 0.341) and to lose 138.8 kg (126.5, 150.2). Although the model with the logarithmic functional form of maternal age was the top model in the suite, the model with a quadratic functional form of age was the second-

most supported and did not differ in its predictive ability ($P = 0.19$). Highest density intervals associated with estimates at each age from the two models overlapped almost completely (Appendix B). Therefore, predictions from all well-supported models were similar and none provided evidence of age-related increases in energy allocation.

Table 3. Coefficient estimates (mean of the posterior distribution) for the top model of each of the three hypotheses evaluated, reported on the log-odds scale. Continuous variables were centered using the mean and scaled by two standard deviations. Coefficients for which the 90% highest density interval did not include zero are in bold.

Variable	Terminal Allocation Hypothesis		Physiology Hypothesis		Behavioral Hypothesis	
	Log Maternal Age Model		Quadratic Maternal Age Model		Linear Maternal Age Model	
	Estimate (SE)	90 % HDI	Estimate (SE)	90% HDI	Estimate (SE)	90% HDI
Intercept	-0.703 (0.052)	-0.787, -0.622	-0.102 (0.156)	-0.359, 0.143	-0.091 (0.298)	-0.655, 0.527
ln(Maternal Age)	-0.085 (0.051)	-0.169, -0.002				
Maternal Age			0.257 (0.144)	0.020, 0.490	0.315 (0.261)	-0.191, 0.840
Maternal Age ²			-0.224 (0.257)	-0.645, 0.197		
Age Primiparity	-0.075 (0.043)	-0.145, -0.004	0.011 (0.125)	-0.194, 0.215	0.235 (0.217)	-0.199, 0.671
Maternal Parturition Mass	0.229 (0.050)	0.148, 0.311	-0.252 (0.132)	-0.464, -0.029		
Maternal Mid-Lactation Mass					-0.210 (0.291)	-0.779, 0.364
Reproductive Status (t-1)	0.086 (0.043)	0.016, 0.158	0.088 (0.113)	-0.097, 0.272	-0.019 (0.199)	-0.419, 0.368
Pup Sex	-0.0004 (0.045)	-0.075, 0.073	-0.021 (0.106)	-0.192, 0.152	0.048 (0.197)	-0.350, 0.428
Measurement Days	0.104 (0.042)	0.035, 0.173				

Table 4. Model selection results for the terminal-allocation, physiology and behavior hypothesis model suites. BPIC values are calculated using leave-one-out cross validation, and higher values reflect greater predictive ability of the model. The top model for each hypothesis model suite is shown in bold. Shown is the p-value from the two-sided z-test of the difference in predictive ability between the top model (in bold) and the model of that row.

Model	Terminal Allocation Hypothesis Suite		Physiology Hypothesis Suite		Behavior Hypothesis Suite	
	BPIC Value	Z-test	BPIC Value	Z-test	BPIC Value	Z-test
Null	-2330.528	0.015	-1939.017	<0.0001	-1135.318	0.536
Linear Age	-2328.245	0.029	-1935.306	0.004	-1132.657	-----
Log Age	-2327.158	-----	-1934.438	0.018	-1135.011	0.295
Quadratic Age	-2327.967	0.190	-1931.324	-----	-1139.093	0.023

Several covariates other than age were associated with proportion mass loss and results that follow are based on the most-supported model. The strongest finding was a positive relationship between proportion mass loss and maternal mass (Fig. 1). Proportion mass losses for reference mothers weighing 375, 450, and 525 kg are predicted to be 0.302 (90% HDI: 0.280, 0.323), 0.335 (0.317, 0.353), and 0.371 (0.349, 0.393), respectively (Fig 1). Heavier mothers lose a greater proportion of a larger mass, which yields substantial differences in the predicted amounts of mass being allocated to the pup by the 375-, 450-, and 525-kg reference mothers: predicted mass loss values are 113.1 kg (90% HDI:104.9, 121.0), 150.9 kg (142.5, 159.0), and 194.8 kg (183.0, 206.5), respectively.

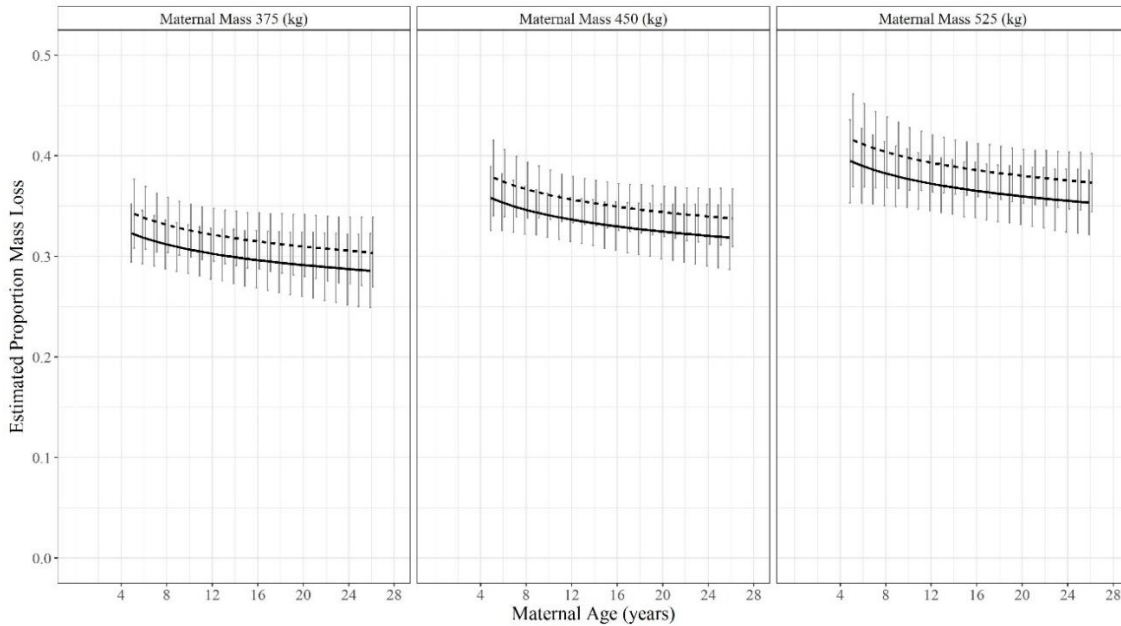
The relationship between a female's proportion mass loss and her reproductive status in the previous year was positive (Fig. 1), which was the opposite of our expectation. Predicted differences are modest but non-zero: a reference mother that

reproduced the previous year is predicted to lose 0.019 more of her mass (90% HDI: 0.003, 0.035) than a mother that did not reproduce the previous year, which translates to a difference of 8.5 kg (1.5, 15.6) of mass loss. Mothers who first started reproducing at an earlier age are also predicted to lose a greater proportion of their mass during lactation. For example, a reference mother that reached primiparity at 5 years of age is expected to have a proportion mass loss of 0.345 (90% HDI: 0.321, 0.367), which is higher than the value for a mother that reached primiparity at 10 years of age (0.316; HDI: 0.294, 0.339). These changes result in an estimated mass loss of 152.0 kg (90% HDI: 141.8, 161.7) for a mother that reached primiparity at 5 years of age versus 139.5 kg (129.5, 149.4) for a mother that didn't start reproducing until 10 years of age. There was little support for a relationship between the proportion of mass a mother lost during lactation and the sex of her pup ($\hat{\beta}_{PupSex} = -0.0004$; SE = 0.045). Estimated variance components associated with random year effects ($\hat{\sigma}_{year} = 0.106$) and individual effects ($\hat{\sigma}_{individual} = 0.039$) were modest in size (Appendix C).

Overall, our results indicate that heavy mothers that started reproducing early in life and reproduced the previous year lose the greatest proportion and amount of mass. For example, a heavy mother that reproduced last year and started reproducing early in life (parturition mass = 525 kg, age of 1st reproduction = 5 yrs old) is estimated to have a proportion mass loss of 0.406 (90% HDI: 0.379, 0.432) and to lose 212.98 kg (199.10, 226.61). In contrast, a light mother that did not reproduce the previous year and started reproducing later in life (parturition mass = 375 kg, age of 1st reproduction = 10 yrs old)

is estimated to have a proportion mass loss of 0.287 (90% HDI: 0.262, 0.312) and to lose 107.79 kg (98.14, 116.90).

Figure 2. The predicted relationship between proportion of mass lost by a mother during the entire lactation period and maternal age binned by light, average and heavy masses, with 95% HDIs of estimates. Solid lines indicate a mother that reproduced the previous year and dashed lines indicate a mother that did not reproduce the previous season.



Physiology Hypothesis

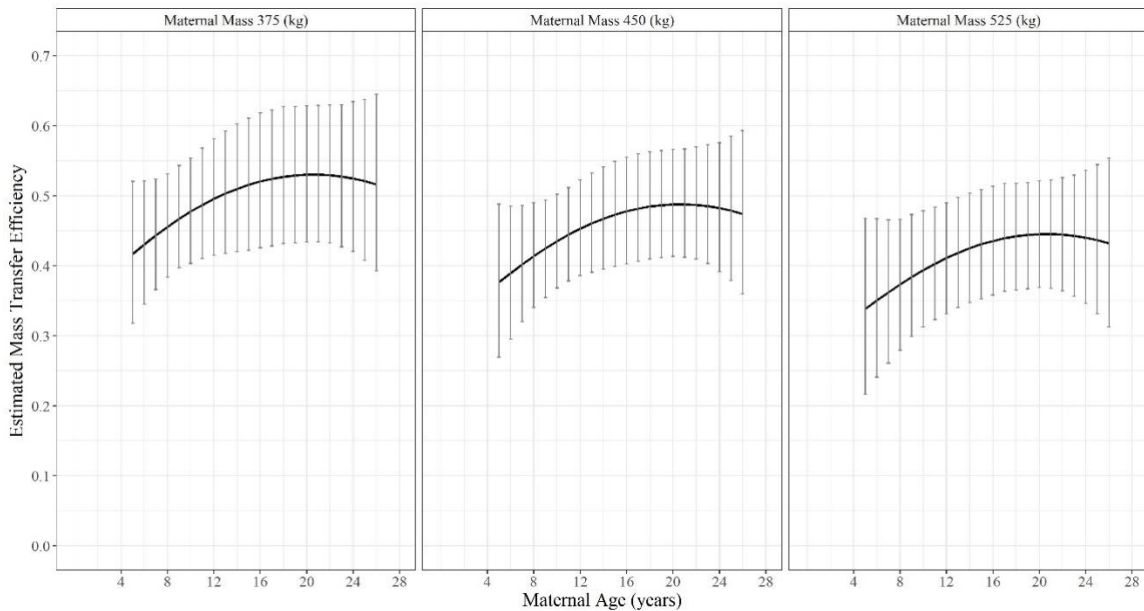
The mean mass transfer efficiency (kg pup gained/kg mother lost) for the early lactation period (data from day 1 and 20 of lactation) was 0.497 (range: 0.120-2.624) based on the naïve mass measurements. Once we modeled these data and accounted for measurement error, mass estimates shrunk toward the mean, which reduced variation in estimated true mass transfer efficiency. Model convergence was achieved for each of the competing functional forms of age. The model with a quadratic functional form for age was the best-supported for the physiology hypothesis ($\hat{\beta}_{MaternalAge} = 0.258$, SE = 0.1436;

$\hat{\beta}_{MaternalAge^2} = -0.224$, SE = 0.257), although the quadratic-age coefficient estimate did contain zero at the 90% HDI (Table 3). Mass transfer efficiency during early lactation is predicted to increase early in maternal life, peak at 21 years of age, and decline slightly at the oldest ages (Fig. 3). Mothers that are 8-, 14- and 26-years old and have reference values for other covariates are predicted to have mass transfer efficiencies of 0.419 (90% HDI: 0.350, 0.480), 0.473 (0.410, 0.533), and 0.479 (0.380, 0.577), respectively. Over the 20-day early-lactation period, a pup born to a mother with reference values that lost 100 kg would gain 0.7 kg (90% HDI: -0.1, 0.1) more to a 26-year-old mother than a pup born to a 14 year-old mother and 5.4 kg (-0.5, 11.1) more than the pup of an 8 year-old mother.

Maternal parturition mass was the only covariate that had an estimated coefficient with a 90% HDI (Table 3) that did not overlap zero. Maternal parturition mass was negatively related to mass transfer efficiency early in lactation, and heavier females were estimated to be less efficient at transferring the mass they lost to their pups (Fig. 3). Mothers weighing 375, 450, and 525 kg and having reference values for other covariates are predicted to transfer the following proportions of each kg of mass they lose to their pups: 0.512 (90% HDI: 0.434-0.588), 0.470 (0.406-0.529), and 0.427 (0.362-0.493), respectively. Given a mass loss of 100 kg during early lactation, those estimates translate to transfers of 51.2 kg (90% HDI: 43.4, 58.8), 47.0 kg (40.6, 52.9) and 42.7 kg (36.2, 49.3) to pups, for mothers weighing 375, 450, and 525 kg, respectively. The estimated coefficient associated with a female's reproductive status in the previous year was positive but had a 90% HDI that slightly spanned zero ($\hat{\beta}_{Repro\ Status} = 0.088$, SE =

0.112). We found no evidence for relationships between mass transfer efficiency early in lactation and either age at first reproduction or pup sex. Older, lighter mothers are predicted to have the highest rates of mass transfer efficiency, but the precision of the estimates makes such inferences weak (Fig. 3). Estimated values for random effects of year and individuals were both low ($\hat{\sigma}_{year} = 0.151$, $\hat{\sigma}_{individual} = 0.079$) (Appendix C).

Figure 3. The predicted relationship between mass transfer efficiency during early lactation and maternal age, binned by light, average and heavy mothers, with 95% HDIs of estimates.



Behavioral Hypothesis

For the late-lactation period, mean mass transfer efficiency based on naïve mass measurements was 0.505 (range: 0.079-2.078). Mass estimates were shrunk toward the mean after accounting for measurement error, resulting in mass transfer estimates

contained between zero and one. The best-supported model assessing mass transfer efficiency during late lactation included a linear functional form of maternal age. However, 90% HDIs for all coefficients associated with covariates of interest spanned zero. Z-tests comparing predictive abilities of competing models indicated that a model without maternal age and a logarithmic functional form of maternal age had similar predictive abilities to that of the top model (Table 4). Further, coefficient estimates from the top model were all quite imprecise such that there is only weak evidence of any meaningful differences across covariate values. For example, the coefficient associated with maternal age was positive but had a 90% HDI that overlapped zero quite broadly ($\hat{\beta}_{Maternal\ age} = 0.315$, SE = 0.261). Based on predictions from the linear age model, 8-, 14-, and 26-year-old mothers with reference values are estimated to have a mass transfer efficiency of 0.437 (90% HDI: 0.315, 0.562), 0.476 (0.363, 0.590) and 0.554 (0.401, 0.707), respectively. The estimates presented above are contained within wide HDIs and estimated relationships between mass transfer efficiency and maternal age based on models containing either logarithmic and linear functional forms of maternal age are similarly weak and imprecise (Appendix B).

Evaluation Across Three Allocation Analyses

The covariate that had the largest influence on proportion mass lost during the entire lactation period and mass transfer efficiency during the early lactation period was maternal parturition mass. Compared to a light (375 kg) mother, a heavy (525 kg) mother is predicted to lose nearly twice as much mass (194.8 kg vs. 113.1 kg) during lactation.

The light mom is predicted to transfer 51.2% of mass lost during early lactation to her pup, while the heavy mom is predicted to transfer 42.7%. Although the relationship between maternal mid-lactation mass and mass transfer efficiency during late lactation was imprecisely estimated, there was not a large difference in the mean modeled mass transfer efficiency between the early and late lactation periods (early: 0.480 (90% HDI: 0.419, 0.536) vs. late: 0.498 (0.412, 0.602)). Regardless of the negative relationship found between mass transfer efficiency and maternal parturition mass during early lactation, differences in proportion mass lost between heavy and light mothers clearly lead to differences in weaning mass of pups (Fig. 1). Maternal age, age at first reproduction, and reproduction status in the previous season, although influential, had small to moderate associations with maternal allocation.

Discussion

Our results provided evidence that both static and dynamic features of a mother influenced the proportion of mass she lost during lactation. The most important feature was the amount of body reserves that a mother had at the beginning of lactation. Mothers that were heavier at parturition lost a greater proportion of their larger mass during lactation than did lighter mothers but were less efficient at transferring this greater mass to pups during the early lactation period. Regardless of their reduced mass transfer efficiency, the heaviest mothers still allocated the most mass to their pups during lactation based on posterior predictions. Other maternal features had more modest influences on the energetic allocation of mothers during lactation. Specifically, mothers

that started reproducing earlier in life and that reproduced the previous season lost a greater proportion of mass during lactation. Despite predictions to the contrary, we found only modest evidence of relationships between a mother's age and the proportion of mass lost and the efficiency with which she transferred her mass to her pup.

We demonstrated only a weak negative relationship between the proportion of mass lost by mothers over the course of lactation and maternal age after accounting for other variables thought to influence maternal allocation. Results from the log maternal age model are counter to our prediction that old mothers would increase the proportion of mass they allocated to pups during lactation and provides no support for the terminal allocation hypothesis. In contrast with our results, two studies of other mammals have reported that the proportion of maternal mass loss during lactation either increased or did not change with increasing maternal age (Isaac & Johnson, 2005; Descamps et al. 2007). It is notable that the species in the studies with contrasting results are considered income breeders and feed throughout lactation, whereas Weddell seals rely heavily on stored capital. Perhaps older mothers that rely on feeding for energy during lactation may increase activity in an attempt to supplement reserves while older capital breeders may decrease activity as a way to spare energy for lactation. In the future, as studies of capital- versus income-breeding strategies continue, it will be useful to evaluate whether evidence for terminal allocation tends to be more pervasive in income breeders. The decline in the proportion of mass lost by mothers also contradicts results from another Phocid species, the northern elephant seal *Mirounga angustirostris*, where no relationship was found between either proportion of mass lost or proportion energy loss (Crocker et al. 2001;

McDonald & Crocker, 2006). It is important to note that the elephant seal studies did not control for maternal parturition mass, which hampers our ability to fully evaluate why our results might differ from theirs. Our mean estimate for the proportion of mass lost by mothers during the 35-day lactation period we monitored 0.335 (90% HDI: 0.286, 0.387) is slightly lower than rates for the entire lactation period reported by earlier work on our study population: 0.37 (Braun Hill, 1987) and 0.385 (SE = 0.002) in 2003 and 0.415 in 2002 (SE = 0.001) (Wheatley et al. 2006). The differences between our results and earlier work may be attributed to that fact that we had a larger range of maternal ages, and our measurement period was less than 35 days whereas the previous studies included measurement periods greater than 40 days.

Although we did not obtain data from a large sample of mothers in multiple years, females that were monitored repeatedly did allow us to estimate the random effect of individual. The estimated variance associated with individuals was low, which suggests that individual heterogeneity in energy allocation that was not explained by our covariates is modest and that unexplained heterogeneity does not explain why we found evidence for declines in proportion mass loss with maternal age.

We found that maternal parturition mass had a strong, positive relationship with the proportion of mass lost by mothers during lactation and was the more important determinant than other covariates. Our finding that heavier mothers lost a greater proportion of mass during lactation, is consistent with results from a previous study of Weddell seals, although this previous study was unable to account for maternal age and other maternal features (Wheatley et al. 2006). A study of southern elephant seals

Mirounga leonina detected a weak negative relationship between maternal parturition mass and proportion mass lost (Fedak, Arnborn, & Boyd, 1996), although this study did not have data to consider age or other maternal reproductive features in the analysis. Few studies have explicitly modeled the relationship between the proportion of mass lost during lactation and maternal parturition mass, instead assessing absolute mass loss, and demonstrating a positive relationship between mass loss during lactation and maternal parturition mass (Pomeroy et al., 1999; Crocker et al. 2001; Carlini et al. 2004). Our results add to previous knowledge by explicitly modeling proportion of mass lost during lactation while accounting for other maternal features, and this allowed us to assess the relative allocation of mothers. We agree with suggestions by previous authors (Carlini et al. 1997; Gittleman & Thompson, 1988) that the increase in proportion of mass lost by heavier mothers is at least in part because heavier mothers have greater reserves to draw from during lactation and can therefore lose a greater proportion of their reserves before hitting a threshold at which they can no longer support the energetic demands of lactation. As mentioned earlier, in the future, it would be useful to have more work conducted on datasets that include a broad suite of covariates including age, mass, and reproductive history as well as environmental conditions.

We found evidence that females that produced a pup in the previous year tended to lose a greater proportion of mass in the current year when compared to females who had not reproduced in the previous year. Our findings contrast with results of several studies of other mammal species that have reported that the effort of reproducing in the previous year reduces an individual's ability to allocate resources to current reproduction

(Green, 1990; Lunn et al. 1994; Martin et al. 2010). A modest number of first time mothers were included in our analysis which could lower estimates of proportion mass lost by mothers that did not reproduce the previous year, if these mothers differ from first time mothers in maternal allocation. Being a first time mother has been found to have a weak negative association with pup mass gain during both early and late lactation in this population (Paterson et al. 2016) and future analyses should account for the presence of first time mothers when evaluating the effect of reproduction in the previous year. If a female's probability of reproducing in repeated years is positively linked to her underlying fitness, this could also serve to explain the positive relationship we found between reproduction in the previous year and energy allocation to reproduction in the current year's reproduction (Cam et al. 1998; Beauplet et al. 2006). We believe that a female Weddell seal's ability to reproduce regularly likely is an important metric for individual quality, as has been suggested in recent work on our study population (Chambert et al. 2013; Paterson, 2017). However, an additional or alternative possibility exists that mothers that reproduced the previous year lose a greater proportion of mass due to additional reproductive experience. Specifically, reproductive status was highly correlated with relative parity, a measure of reproductive experience, in our data. It is possible that because we were unable to include reproductive parity in our models, reproductive status may simply be an index of reproductive experience. A more complete understanding of the role of individual heterogeneity versus the benefits of gaining reproductive experience will require additional years of data that provide more repeated

measures of individuals to compare the importance of the relevant static (individual) and dynamic (experience) traits.

Mothers that started reproducing earlier in life lost a greater proportion of their mass during lactation. Life history theory predicts a female should wait to recruit until the benefits of mounting the energy required for current reproduction outweigh the costs to a female's survival and future reproduction (Stearns, 1992). Female Weddell seals that begin reproducing earlier in life may be of superior quality and better able to withstand the energetic cost of reproduction at a younger age than are females that are primiparous later in life (Hadley et al. 2006; Paterson, 2017). This same pattern has also been reported for other species (Martin & Festa-Bianchet, 2012; Fay et al. 2016).

Our results regarding the relationship between mass transfer efficiency and maternal age during the early lactation period indicate that efficiency increased most rapidly early in a mother's life and continued to gradually increase up to 21 years of age (efficiency was similar from 16 through 21 years of age) after which slight declines might have occurred (precision was poor at the oldest ages). In contrast with our a priori thinking, our estimated relationship between mass transfer efficiency and maternal age provided no support for our physiology hypothesis which predicted that the oldest mothers would be more efficient than prime-age mothers. An earlier evaluation of this question for our study population failed to find evidence of a relationship between maternal age and mass transfer efficiency (Wheatley et al. 2006). However, that study, which did much more detailed physiology work than was done in our study, had a much smaller sample of animals and maternal ages to work with, and the relationship which

was evident in our work may not have been clear because it was estimated across a narrower range of maternal ages, than in our study.

Because the substantial improvements in mass transfer efficiency that we report here occurred primarily at the youngest maternal ages, when we know mothers are still recruiting for the first time (Hadley et al. 2006), and not in the older ages, when reproductive rates begin to decline and survival probabilities are lower (Paterson, 2017), it appears unlikely that patterns of mass transfer efficiency with maternal age are due to selective disappearance of more frail individuals. Mass transfer efficiency at the individual level is driven by many factors including metabolic overhead and hormones of the mother, milk composition, and milk yield (Castellini & Mellish, 2015). Additionally, pup attributes such as behavior and metabolism can also influence mass transfer efficiency (McDonald et al. 2012). Although there are many avenues through which improvements in mass transfer efficiency may be made, there is a small amount of evidence that mass transfer efficiency improves with reproductive experience. Mass transfer efficiency has been reported to be lower for primiparous mothers than for multiparous mothers in lab animals (Künkele & Kenagy, 1997; Künkele, 2000), whereas intensive work on wild grey seals *Halichoerus grypus* found no difference (Lang, Iverson, & Bowen, 2011). However, biopsies of grey seal mammary gland tissue do suggest that both the secretory capacity and storage capacity are reduced for primiparous individuals compared to multiparous individuals (Lang, Iverson, & Bowen, 2012). Our study was unable to determine the mechanism driving the relationship between maternal age and mass transfer efficiency and had limited data to estimate the influence of

individual identity on mass transfer efficiency. Future studies that analyze datasets containing many repeated observations of individuals throughout reproductive life will be important for improving understanding of the relative influences of maternal age and individual quality. Additionally, combining the knowledge from long-term population studies with targeted sampling for physiology studies will help identify physiological mechanisms driving variation in mass transfer efficiency of mothers.

Our results indicated that mothers that were heavier at parturition were less efficient at transferring mass to their pups. A reduction in mass transfer efficiency with increasing maternal parturition mass has been demonstrated in two previous Phocid studies (Carlini et al. 2004; Testa et al. 1989), but was not found in two others (Fedak et al. 1996; Wheatley et al. 2006). In northern elephant seals, a mother's body mass was negatively related to the lipid content of her milk, which was interpreted as evidence that heavier mothers have higher rates of metabolic water production and therefore produce milk with higher water content (Fowler et al. 2016). For Weddell seals, however, Wheatley et al. (2008) analyzed data for 25 mother-pup pairs and found no evidence for an effect of maternal parturition mass on milk composition within 6 days after parturition (Wheatley et al. 2008) although, the relationship was not evaluated during another period of lactation so maternal parturition mass may influence milk composition later in lactation. It has also been argued that mothers with more lean body mass have a higher metabolic overhead and therefore have lower rates of mass transfer efficiency (Fedak et al. 1996). For Weddell seals, however, body composition has been found to be similar across individuals and exhibit a weak relationship with maternal parturition mass

(Wheatley et al. 2006). It seems that the most likely explanation might be that suggested for southern elephant seals. Specifically, the ratio of protein to lipids used for maternal metabolism might be correlated with maternal parturition mass and not necessarily tied to a mother's body composition such that heavier mothers use more protein for body maintenance and have higher metabolic rates, which lowers their rates of mass transfer efficiency (Carlini et al. 2004). Continuing studies regarding the physiology of Phocid seals are needed and should be done across a wide range of maternal masses and ages to better understand the physiological mechanisms behind lactation variation.

We found no support for the behavioral hypothesis that older mothers change their behavior relative to other females during late lactation to supplement body reserves. There was no evidence for any relationship between maternal age and mass transfer efficiency during the late lactation period. Although a model with a linear functional form of maternal age was the best-supported model for the late-lactation period, its predictive ability was not meaningfully different from that of the null model or a model with a logarithmic functional form of maternal age. Evidence for (1) considerable variation in lactation lengths in Weddell seals (Wheatley et al. 2006) and (2) some feeding during the latter portion of lactation (Testa et al. 1989; Wheatley et al. 2008), suggest two possible ways in which mothers might alter their behavior to allow them to increase the growth of their pups. In our work, we did not find evidence of relationships between maternal features and mass transfer efficiency during late lactation. If individuals vary in the duration of lactation and/or rates of feeding despite having similar values for age, body mass, or other maternal features, this would help explain why we were unable to

associate mass transfer efficiency with maternal features. It is important to note that the dataset that we used to evaluate this hypothesis had a smaller sample size than what was available for our other analyses (Paterson et al. 2016). Future studies that monitor lactation duration and foraging behavior will be needed to assess such possibilities; such studies will be challenging but not impossible to do.

Conclusions

We found little support for the terminal allocation, physiology and behavioral hypotheses. We demonstrated that age effects are present in maternal allocation and mass transfer efficiency, but that maternal parturition mass was most strongly associated with the proportion of a mother's reserves that she allocated to her pup and the efficiency with which those reserves were transferred. We also found that age at first reproduction and reproductive status the previous year, which might be metrics associated with individual fitness, are moderately associated with variation in maternal allocation. There was considerable variation in maternal parturition mass in our data (e.g., based on naïve mass estimates, mean = 441.78 kg, SD = 53.00), modest variation in pup parturition mass (mean = 30.84 kg, SD = 4.26), and a considerable amount of variation in pup weaning masses (mean = 94.43 kg, SD = 16.84, Fig. 1).

Our results suggest that the considerable variation in maternal parturition mass most strongly associated with the large differences in the amount of energy allocated to different pups and therefore the weaning masses of pups. Variation in maternal ages is predicted to result in more modest differences in maternal allocation to pups. To illustrate, we can calculate expected differences in pup mass gain based on our results

regarding maternal parturition mass and maternal age. Light (375 kg), average (450 kg) and heavy (525 kg) mothers of average maternal age are predicted to lose 113.1, 150.9, and 194.8 kg of mass, respectively, during the first 35 days of lactation. In contrast, predicted mass loss values for mothers of different ages, but average weight, are much more similar. For example, young (8-year-old), prime (14-year-old), and old (26-year-old) mothers of mean parturition mass are predicted to lose 151.0, 145.1, and 138.8 kg, respectively. During early lactation, we found evidence that mass transfer efficiency decreased with maternal parturition mass. Using our estimated mass loss values, combining them with our estimated mass transfer efficiency values, and if two-thirds of the parturition mass a female loses during all 35 days of lactation is lost during early lactation, light, average, and heavy mothers of average maternal age are predicted to have pups that gain 38.6, 47.3, and 55.5 kg, respectively. In contrast, young, prime, and old mothers of average parturition mass are predicted to have pups that gain more similar amounts: 42.2, 45.8, and 44.3 kg, respectively. Assuming that one-third of the parturition mass a female loses during all 35 days of lactation is lost during late lactation and using our predictions for mass transfer efficiency during this period, light, average, and heavy mothers of average maternal age are predicted to have pups that gain 17.49, 21.3, and 25.5 kg, respectively, during late lactation. In contrast, young, prime and old mothers of average parturition mass are predicted to have pups that gain more similar amounts: 22.0, 23.0, and 25.6 kg, respectively. Combining results for the two lactation periods, light, average, and heavy mothers of average maternal age are predicted to have pups that gain 56.1, 68.6, and 80.7 kg over the 35-day lactation period, respectively. In contrast, young,

prime, and old mothers of average parturition mass are predicted to have pups that gain 64.2, 68.8, and 69.9 kg. These calculations of pup mass gain do not incorporate uncertainty but do serve to highlight the relative importance of maternal parturition mass versus maternal age to pup mass gains during lactation. Given previous evidence that weaning mass of pups in Weddell seals is positively related to pup survival during the juvenile period (Proffitt, Garrott, & Rotella, 2008b) and reports for diverse vertebrate species that it could affect survival and reproduction later in life (Lummaa & Clutton-Brock, 2002; Ronget et al. 2018), our results suggest avenues for future work.

Future work should focus on obtaining longitudinal data so that the relationship between age and maternal allocation can be more precisely estimated and the degree to which selective disappearance drives age-specific variation in mass transfer efficiency can be more extensively investigated. Although this study was able to determine patterns of maternal allocation during the approximate entire lactation period and early lactation period, our ability to determine whether mothers alter patterns during late lactation was limited by modest sample sizes, and patterns of energetic allocation to pups by mothers during late lactation should be further investigated. Our study was able to establish that maternal allocation varies with static and dynamic features of a mother and that these relationships vary with both the metric and time-period of measurement. Results from this study highlight the need to control for many factors when evaluating predictions of reproductive effort from life-history theory. Our finding that maternal parturition mass can have large consequences for a pup's weaning mass suggests that promising directions for study would be to investigate (1) the underlying sources of variation in maternal

parturition mass and (2) the relationship between maternal features that influence maternal allocation and offspring survival and reproductive success.

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APPENDICES

APPENDIX A

MODEL STRUCTURE FOR EACH MODEL TYPE

Model Structure for the Terminal Allocation Model

```

loss.lin.mod <- function() {
  for (i in 1:n.obs){
    M.B.true[i] ~ dnorm(mu, tau)
    M.B.pred[i] ~ dnorm(M.B.true[i], tau.M.B.pred[i])
    tau.M.B.pred[i] <- 1/pow(M.B.pred.err[i], 2)

    M.L.pred[i] ~ dnorm(M.L.true[i], tau.M.L.pred[i])
    tau.M.L.pred[i] <- 1/pow(M.L.pred.err[i], 2)

    M.L.true[i] ~ dnorm(E.M.L.true[i], tau.M.L.true)

    logit(ppn.loss[i]) <- logit.ppn.loss[i]
    logit.ppn.loss[i] <- b.int +
      b.mass * (M.B.true[i]-441)/(55*2) +
      b.age * momage.z[i] +
      b.days * days.z[i] +
      b.af * age.first.z[i] +
      b.rs * repro.stat[i] +
      b.sp * sexm[i] +
      ran.eff.yr[year[i]]+
      ran.eff.ind[id[i]]

    E.M.L.true[i] <- M.B.true[i] * (1 - ppn.loss[i])
  }

  for (i in 1:n.ind) {
    ran.eff.ind[i] <- z.ind[i] * sigma.ind
    z.ind[i] ~ dnorm(0, 1)
  }

  for (j in 1:n.yr) {
    ran.eff.yr[j] <- z.year[j] * sigma.yr
    z.year[j] ~ dnorm(0, 1)
  }

  # Priors
  mu ~ dnorm(0, 1.0E-8)
  sigma ~ dunif(0, 150)
  tau <- 1/pow(sigma, 2)
  sigma.M.L.true ~ dunif(0, 100)
  tau.M.L.true <- 1/pow(sigma.M.L.true, 2)
  b.int ~ dunif(-10, 10)
  b.mass ~ dunif(-10, 10)
  b.age ~ dunif(-10, 10)
  b.days ~ dunif(-10, 10)
  b.af ~ dunif(-10, 10)
  b.rs ~ dunif(-10, 10)
  b.sp ~ dunif(-10, 10)
  sigma.ind ~ dunif(0, 50)
  sigma.yr ~ dunif(0, 50)

```

```
}

```

Model Structure for the Physiology Model

```
early.mte.lin.mod <- function() {
  for (i in 1:n.obs){
    M.B.true[i] ~ dnorm(mu.B, tau.B)
    M.B.pred[i] ~ dnorm(M.B.true[i], tau.M.B.pred[i])
    tau.M.B.pred[i] <- 1/pow(M.B.pred.err[i], 2)

    M.M.pred[i] ~ dnorm(M.M.true[i], tau.M.M.pred[i])
    tau.M.M.pred[i] <- 1/pow(M.M.pred.err[i], 2)

    M.M.true[i] ~ dnorm(E.M.M.true[i], tau.M.M.true)

    E.M.M.true[i] <- M.B.true[i] - daily.pup.gain[i] * mom.days[i] / mass.tr.eff[i]

    logit(mass.tr.eff[i]) <- logit.mass.tr.eff[i]
    logit.mass.tr.eff[i] <- b.int +
      b.mass * (M.B.true[i]-441)/(53*2) +
      b.age.l * age.z[i] +
      b.af * age.first.z[i] +
      b.rs * repro.stat[i] +
      b.sp * sexm[i] +
      ran.eff.ind[id[i]] +
      ran.eff.yr[year[i]]

  }

  for (i in 1:n.ind) {
    ran.eff.ind[i] <- z.ind[i] * sigma.ind
    z.ind[i] ~ dnorm(0, 1)
  }

  for (j in 1:n.yr) {
    ran.eff.yr[j] <- z.year[j] * sigma.yr
    z.year[j] ~ dnorm(0, 1)
  }

  # Priors
  mu.B ~ dnorm(0, 1.0E-8)
  sigma.B ~ dunif(0, 150)
  tau.B <- 1/pow(sigma.B, 2)
  sigma.M.M.true ~ dunif(0, 100)
  tau.M.M.true <- 1/pow(sigma.M.M.true, 2)
  b.int ~ dunif(-10, 10)
  b.mass ~ dunif(-10, 10)
  b.age.l ~ dunif(-10, 10)
  b.af ~ dunif(-10, 10)
  b.rs ~ dunif(-10, 10)
}
```

```

b.sp ~ dunif(-10, 10)
sigma.ind ~ dunif(0, 50)
sigma.yr ~ dunif(0, 50)
}

```

Model Structure for the Behavioral Model

```

late.mte.lin.mod <- function() {
  for (i in 1:n.obs){

    M.M.pred[i] ~ dnorm(M.M.true[i], tau.M.M.pred[i])
    tau.M.M.pred[i] <- 1/pow(M.M.pred.err[i], 2)

    M.M.true[i] ~ dnorm(mu.M, tau.M)

    M.L.pred[i] ~ dnorm(M.L.true[i], tau.M.L.pred[i])
    tau.M.L.pred[i] <- 1/pow(M.L.pred.err[i], 2)

    M.L.true[i] ~ dnorm(E.M.L.true[i], tau.M.L.true)

    E.M.L.true[i] <- M.M.true[i] - daily.pup.gain[i] * mom.days[i] / mass.tr.eff[i]

    logit(mass.tr.eff[i]) <- logit.mass.tr.eff[i]
    logit.mass.tr.eff[i] <- b.int +
      b.mass * (M.M.true[i]-351)/(46*2) +
      b.age.l * age.z[i] +
      b.af * age.first.z[i] +
      b.rs * repro.stat[i] +
      b.sp * sexm[i] +
      ran.eff.ind[id[i]] +
      ran.eff.yr[year[i]]

  }

  for (i in 1:n.ind) {
    ran.eff.ind[i] <- z.ind[i] * sigma.ind
    z.ind[i] ~ dnorm(0, 1)
  }

  for (j in 1:n.yr) {
    ran.eff.yr[j] <- z.year[j] * sigma.yr
    z.year[j] ~ dnorm(0, 1)
  }

  # Priors
  mu.M ~ dnorm(0, 1.0E-8)
  sigma.M ~ dunif(0, 100)
  tau.M <- 1/pow(sigma.M, 2)
  sigma.M.L.true ~ dunif(0, 100)
  tau.M.L.true <- 1/pow(sigma.M.L.true, 2)
}

```

```
b.int ~ dunif(-10, 10)
b.mass ~ dunif(-10, 10)
b.age.l ~ dunif(-10, 10)
b.af ~ dunif(-10, 10)
b.rs ~ dunif(-10, 10)
b.sp ~ dunif(-10, 10)
sigma.ind ~ dunif(0, 50)
sigma.yr ~ dunif(0, 50)
}
```

APPENDIX B

COMPARISON OF MATERNAL AGE FUNCTIONAL FORMS

Comparison of maternal age functional forms estimated to have similar predictive ability

Figure 1. Comparison of proportion mass loss predictions for the log maternal age model and the quadratic age model for the entire lactation period with 95% HDIs.

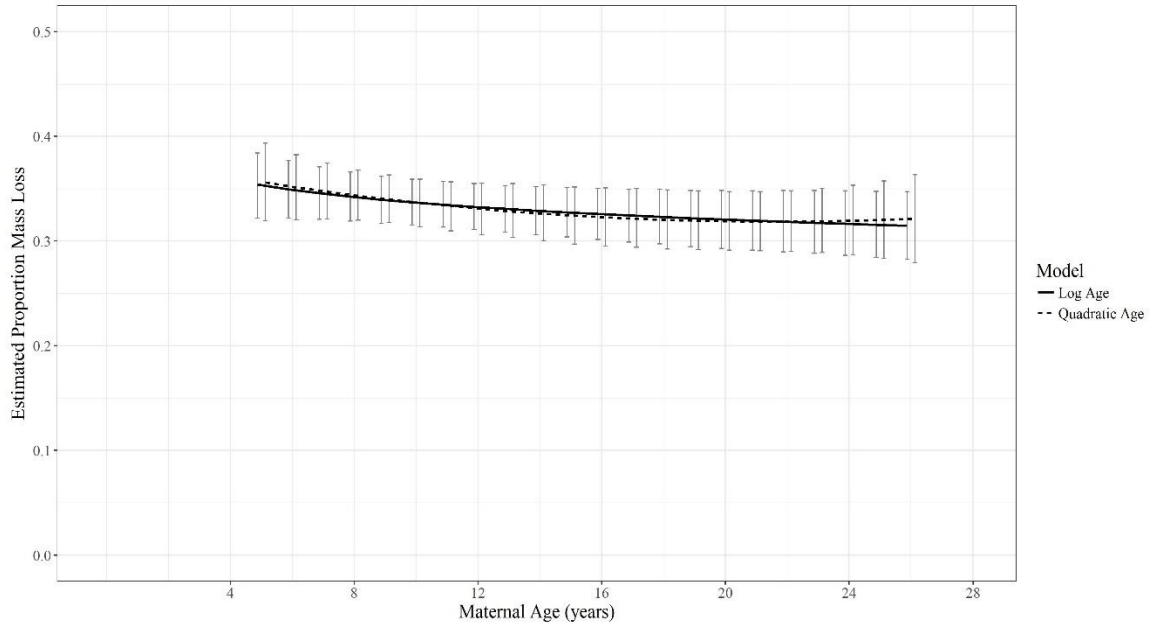
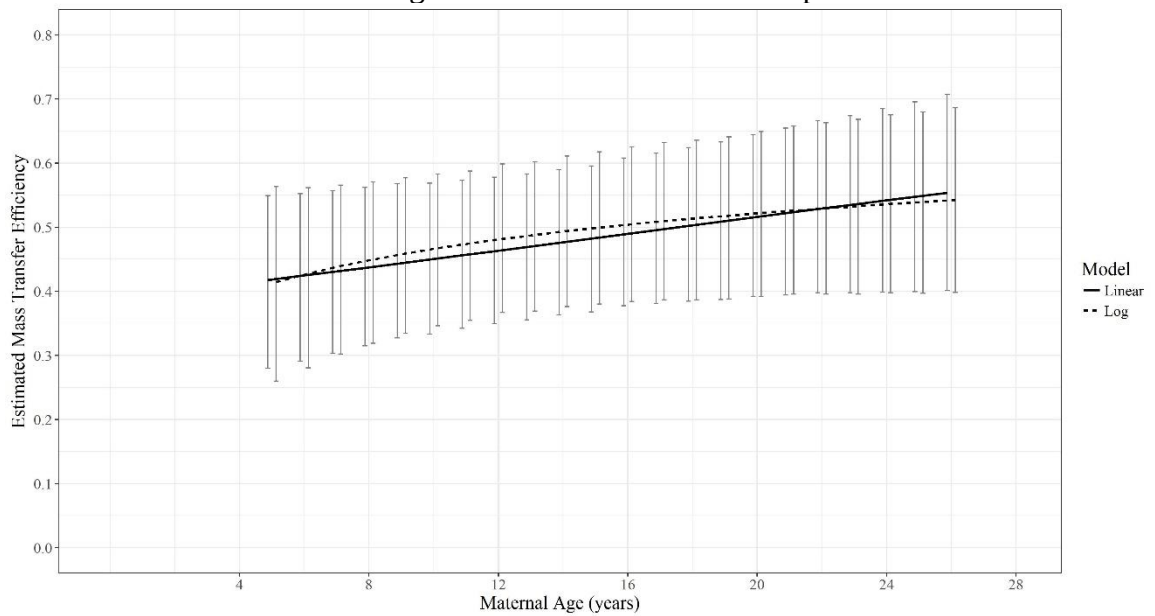


Figure 2. Comparison of mass transfer efficiency predictions for the log maternal age model and the linear maternal age model for the late-lactation period with 95% HDIs.



APPENDIX C

RANDOM EFFECTS FOR EACH MODEL TYPE

Figure 1. Random effects of year and individual mother for the top model of each model type 95% HDIs. (a) terminal allocation hypothesis, (b) physiology hypothesis and (c) behavioral hypothesis

