MATERNAL ENERGY ALLOCATION IN A CAPITAL BREEDER: THE GREY SEAL (*HALICHOERUS GRYPUS*)

by

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Para los Sanchez y los Arias, que me dan fuerza con su apoyo y su amor.
Los quiero.

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Abstract

Parental allocation animals is largely in the form of maternal allocation. In mammals, lactation accounts for the largest proportion of maternal allocation. Lactation is the most energetically costly aspect of reproduction in female mammals. To support the energetic costs of lactation, mammals have developed different strategies related to feeding during the breeding period. Among those strategies, capital breeding mammals exploit the ability to store nutrients and resources to fuel milk production and fast or reduce feeding during most or all the lactation period. As such, the degree of maternal energy allocation can be measured through maternal mass loss. Phocids include some of the most extreme capital breeding mammals. This study examined the predictors and consequences of multiple elements of maternal energy allocation in a capital breeding phocid: the grey seal (*Halichoerus grypus*). I analyzed maternal and pup characteristics from 222 females as possible predictors of total maternal mass loss, relative maternal mass loss, duration of the lactation period, mass transfer efficiency, initial pup mass, relative pup mass gain and pup weaning mass. Some females were studied in multiple years providing 325 observations between 1992 and 2011. My study showed that postpartum mass and female age had significant effects on multiple aspects of maternal energy allocation, including total maternal mass loss, lactation duration, pup birth mass and weaning mass. Heavier females at parturition allocated more body mass and therefore energy to offspring than lighter females. In most aspects of maternal allocation investigated in this study, female age followed the pattern of increased allocation early in life, a plateau in non-growing prime females followed by a decline in older females. Female breeding experience (i.e., parity) also affected maternal allocation, albeit less strongly, to increased pup birth mass, proportional pup mass gain and weaning mass. Females that lactated longer produced pups with greater proportional pup mass gain and pup weaning mass. Finally, females that gave birth to male pups lost greater total mass and weaned heavier pups than those that gave birth to female pups.

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Chapter 1: Introduction

Energy storage and energy expenditure are one of the most important drivers of animal life history strategies (Iverson et al. 2010). Among the key uses of energy is parental investment, defined as investment by the parents that increases an offspring's chances of survival at the cost of the parent (Hamel et al. 2012**)** and the ability to invest in future offspring (Trivers 1972). The allocation provided to offspring influences development and growth; juvenile development can have long-lasting consequences on fitness and survival in adult life (e.g., Lindstrom 1999, Ylönen et al. 2004, Skibiel et al. 2009, Coté et al. 2001*b,* Ellis et al. 2000). Therefore, understanding the factors affecting parental allocation of nutrients to offspring can provide greater insight into life history strategies and the dynamics of populations (Hamel et al. 2012). As most of parental allocation in animals is maternal; the study of maternal energy allocation to offspring can provide a better understanding of the evolution of maternal strategies in mammals.

Among vertebrate taxa, investment strategies include differences in litter size, nest and offspring protection, and methods of feeding dependent young (Trivers 1972). Each strategy is often associated with a trade-off; for example, having a larger litter increases the probability of having more offspring wean successfully, whereas having a smaller litter increases the energy that parents can invest in each individual offspring, thereby increasing that offspring's chances of survival (Trivers 1972). A large component of this investment is the energy expended to provide nutrients to rapidly growing offspring. This allocation has direct impact on the fitness of offspring and parents alike (Trivers 1972, Festa-Bianchet et al. 1998). There is a continuum of feeding strategies during reproduction between income breeders and capital breeders. Among mammals, income breeding strategies are fueled by regular feeding from the female during the lactation period to fuel milk production. Capital breeding females, on the other hand, fast or greatly reduce feeding during the lactation period and rely solely or mostly on the energy stored prior to parturition to provision offspring (Jonsson 1997; Festa-Bianchet et al. 1998). Thus, maternal mass is more important to capital breeders than income breeders (Boyd 2000). In pinnipeds, income breeders, like Antarctic fur seals (*Arctocephalus gazella*), have foraging trips that depend on proximity to breeding grounds, the fasting ability of their offspring and the reproductive physiology of the adults (Costa 1993). Allocation in capital breeders, on the other hand, relies on accumulated body reserves (Stearns 1992, Jonsson 1997), and therefore capital breeding allocation strategies are highly dependent on body condition (Festa-Bianchet et al. 1998, Dobson et al. 1999). Bison (*Bison bison*), and many phocid species and baleen whales are examples of extreme capital breeding mammals (Bowen et al. 1985, Costa et al. 1986, Iverson et al. 1993).

Mammals have a life history trait that distinguishes them from other groups of animals: lactation (Iverson 2003, Oftedal 2012). Some non-mammalian taxa exhibit “lactation-like” behaviour (e.g., doves, pigeons, emperor penguins, fulmars), using strategies that allow them to store energy (e.g., in food pouches or oil sacs) that can be transferred to offspring later (Horseman & Buntin 1995, Iverson 2003, Oftedal 2012**)**. Nonetheless, in no other group is the process as physiologically demanding as lactation, nor is the fluid as complex as the milk produced by the mammary gland (Iverson 2003, Oftedal 2012). Lactation is thought to have originally evolved in the synapsids, during the Carboniferous period (Sidor & Hopson 1998, Oftedal 2002, Kemp 2005), primarily as a mechanism to store nutrient rich food for offspring (Oftedal 2012). The capacity to provide offspring with digestible, nutritious, and concentrated food as milk allowed mammals to develop different reproductive strategies (Oftedal 2012). These differences include milk composition, yield, lactation duration and suckling frequency (Iverson 2003). For example, fat content in milk of the Rhinocerontidae family is less than 1% but can be up to 60% in some phocid species (Iverson et al. 1993, Oftedal & Iverson 1995*b*). In general, those groups which nurse frequently tend to have the most dilute milks with high sugar composition, whereas groups that nurse infrequently have more concentrated milk (Iverson 2003). Marine mammals tend to have the most concentrated milk, because of the need to conserve water and energy during fasting (Iverson 2003); in particular the pinnipeds have concentrated milk that is very high in fat (otariids 32-50%; phocids 47-61%) (Iverson 1993, Iverson et al. 1993, Oftedal & Iverson 1995*a*, Iverson 2003).

Lactation has been described as the most important, and most energetically costly aspect of a female mammal's lifecycle and certainly represents the greatest cost of reproduction (Hanwell & Peaker 1977, Millar 1977, Randolph et al. 1977, Oftedal 1985). Females typically adjust to the increased metabolic costs of lactation by increasing their daily energy intake (Gittleman & Thompson 1988), however the rate of ingestion differs greatly among groups (Fleming et al. 1981). To alleviate the overall cost of lactation, many larger mammals build up large energy stores in preparation (Lindstedt & Boyce 1985). Furthermore, during lactation, some species will reduce the energy allocated to processes not associated with milk production; this is known as metabolic compensation (Racey & Speakman 1987, Mellish et al. 2000).

Female capital breeders (many mysticete cetaceans, ursids, some ungulates and some phocids) fast during lactation, relying completely on the stored energy (Stearns 1992, Reilly et al. 1996, Jonsson 1997, Mellish et al. 1999*a*, Hamel et al. 2012). In these species, reproductive success (including lactation), is largely a function of maternal body size, which relates to energy storage capacity (Millar 1977, Eisenberg 1981, Calder 1984, Millar 1984, Schmidt-Nielson 1984, Gittleman 1986, Martin & Festa-Bianchet 2010). Although mothers with greater body mass may not necessarily wean heavier young, a greater mass should allow them to sustain a lower overhead cost of reproduction; and while heavier mothers can produce heavier offspring, they typically allocate relatively fewer resources than lighter mothers (Hamel et al. 2012). Capital provisioning permits animals to have shorter lactation durations, to conserve body water and protein, with the concomitant result of thereby reducing the overhead costs of lactation to the mother (Anderson & Fedak 1987*a*, Iverson 2003, Schulz & Bowen 2005). For example, phocid seal species are known to have short and intense lactation period and wean their pups rapidly compared to other mammalian species (Fedak & Anderson 1982, Bonner 1984, Ortiz et al. 1984, Costa et al. 1986).

Variation in the magnitude of body mass loss reflect some of the key differences in energy allocation strategies among pinnipeds. Pinnipeds are large marine mammals that produce a single offspring at each reproductive event (Boyd 2000). Within the pinnipeds, there are examples of both income breeders (otariids: sea lions and fur seals) and capital breeders (most phocid seals) (Boyd 2000). There is significant variation in lactation duration between the two groups; otariids can have lactation periods between 4-12 months, whereas phocid lactation periods can be between 4-45 days (Schulz and Bowen 2004). Hooded seals (*Crystophora cristata*) are one the most extreme examples of capital breeders, with lactation periods lasting less than four days (Bowen et al. 1985). Lactation usually ends abruptly, and pups then undergo a month-long post-weaning fast (Bowen et al. 1987).

Some phocids produce large young capable of consuming high-fat milk during short lactation periods (Bonner 1984, Oftedal et al. 1987, 1988, 1993). During the lactation period, phocid females will very rapidly deplete energy stores as they nurse their pups (Mellish et al. 1999*b*). For example, in a ~27 day lactation period, adult elephant seal (*Mirounga spp.*) females can lose ~42% of their body mass (Costa et al. 1986). On the other hand, hooded seals will lose ~9-17% of initial mass over 4 days (Mellish et al. 1999*b*), incurring a much lower cost of lactation than other phocid species (Mellish et al. 1999*b*). To accommodate this energy output, females are known to spend most of lactation sleeping and will stay relatively close to their site of parturition (Costa et al. 1986).

Maternal allocation can vary through-out the lifetime of a female depending on her physiological state (McNamara & Houston 1996), parity (Broussard et al. 2003), and age (Derocher & Stirling 1998, Packer et al. 1998). Previous studies on capital breeders have highlighted maternal and offspring characteristics that affect maternal energy allocation in several terrestrial and aquatic species (e.g. Hamel et al. 2012, Iverson et al. 1993, Arnbom et al. 1997, Fessler et al. 2005). For pups, pup growth rate, birth mass and pup sex have been investigated and found to be important (Bowen et al. 2001, Ellis et al. 2000, Hogg et al. 1992, Ylönen et al. 2004). In Chapter 2, I investigate the effects of different maternal and offspring characteristics on maternal energy allocation of a capital breeding phocid.

Maternal energy allocation during a given breeding period can have immediate and long-term consequences for both female and offspring (Linström 1999). In mammals, female reproductive costs vary with feeding strategies during the breeding season. Income breeding females must undergo longer lactation periods and allocate additional energy to body metabolism; capital breeding females undergo short and intense lactation periods associated with intense mass loss. Previous studies on maternal energy allocation in capital breeding animals have illustrated important maternal and pup characteristics that influence the degree of allocation from a female. Among those characteristics, maternal mass, age, and breeding experience have been highlighted in addition to pup sex and birth mass (e.g., Festa-Bianchet et al 2019, Mellish et al. 1999*b*). Despite the interest in maternal allocation, few studies have simultaneously investigated multiple sources of variation in maternal energy allocation to offspring and how allocation might vary over a broad range of ages in long-lived species (Patterson et al. 2016, Badger et al. 2020, MacDonald et al.

2020, Hamel et al. 2012). Such studies will be needed to gain a deeper understanding of the evolution of maternal allocation strategies in vertebrates, especially in capital breeding mammals. My study will contribute to further understanding of the sources of variation in maternal allocation in a large mammal. Furthermore, the findings of my research will contribute to a more comprehensive understanding of allocation in vertebrates.

Chapter 2: Influence of maternal and offspring traits on maternal energy allocation during lactation in a capital breeder

Introduction

Maternal energy allocation to offspring is likely to depend on the amount of food energy available to the mother (King et al. 2011). Mothers might adjust their allocation based on environmental conditions they experience in each reproductive period, as the availability of food may vary from one period to the next. We expect this to be particularly true in capital breeding species (many mysticete cetaceans, ursids, some ungulates and some phocids), where females finance the delivery of nutrients to offspring from stored body energy (Stearns 1992, Reilly et al. 1996, Jonsson 1997, Mellish et al. 1999a, Hamel et al. 2012). In these cases, reproductive success is largely a function of maternal body size, as larger females can storage more energy and may be in better body condition (Millar 1977, Eisenberg 1981, Calder 1984, Millar 1984, Schmidt-Nielson 1984, Gittleman 1986, Martin & Festa-Bianchet 2010). Thus, allocation strategies of capital breeders may be more dependent on maternal body condition than income breeders as females in better condition will have more resources to allocate to offspring. Not only will females in better condition have more energy and nutrients to allocate to offspring, but females also differ in the amount of energy available for allocation. Body mass is a good indicator of available fat stores in capital breeders, however there can be differences in body composition not accounted for by mass (Mellish et al. 1999*b*, Beck et al. 2003). While mothers with greater body mass may not necessarily wean heavier young, the greater mass should allow females to realize lower overhead costs of reproduction; and while heavier mothers can produce heavier offspring, they typically allocate relatively fewer resources than lighter mothers (Hamel et al. 2012).

The quantity of parental resources delivered to offspring will depend, among other things, mainly on the rate, magnitude and duration of delivery. In mammals, milk delivered during lactation represents the main source of nutrients to rapidly developing offspring (Oftedal 1985). In capital breeding species, females must fuel their own metabolic requirements and the energy requirements of offspring from their stored body energy (Costa et al. 1986, Iverson et al. 1993). In pinnipeds, to accommodate these energy requirements, females are known to spend most of lactation sleeping, and will stay relatively close to their site of parturition (Kovacs 1987, Costa et al. 1986). Additionally, capital provisioning permits mammals to have shorter lactation durations, to conserve water and protein, thereby also reducing the overhead costs of lactation to the mother (Anderson & Fedak 1987*a*, Iverson 2003, Schulz & Bowen 2005). For example, most phocid seals are known to have short and intense lactation periods and wean pups abruptly (Fedak & Anderson 1982, Bonner 1984, Ortiz et al. 1984, Costa et al. 1986, Schulz ad Bowen 2005). Therefore, maternal mass loss over lactation integrates both rate and duration of delivery.

Although total maternal mass loss is a useful measure of allocation, decomposing mass loss into the component parts such as duration can provide additional insight. Furthermore, as females differ in body size and condition, expressing maternal allocation relative to maternal size ought to be a better measure of allocation than absolute mass loss alone (Hamel et al. 2012). Offspring body mass at weaning is often used as a measure of maternal allocation. This seems reasonable particularly in capital breeding species as offspring weaning mass is positively correlated with the mass lost by mothers. However, as females differ in size and condition, expressing allocation as a ratio of offspring mass to maternal mass should provide a better indication of the fitness consequences of allocation to both mother and offspring. In addition to size and condition, other maternal traits may influence allocation. In mammals, reproduction often varies with maternal age and reproductive experience (Fessler et al. 2005, Miller at al. 2006, Bowen et al. 2006, Lang et al. 2012). Additionally, allocation may also depend on the sex, size, and number of offspring (Hogg et al. 1992, Trivers 1972, Yang et al. 1989).

Grey seals (*Halichoerus grypus*) are medium sized capital-breeding phocids that inhabit both sides of the North Atlantic Ocean (Mansfield 1977, Iverson et al. 1993). The largest populations occur in Eastern Canada, with Sable Island comprising ~85% of pup production in that region (den Heyer et al. 2017). Grey seals are long-lived, iteroparous, capital breeders. Females give birth for the first time as early as age 4 years and continue to reproduce for several decades (Bowen et al. 2006). Although reproductively mature as early as 4 years, females continue to grow into their mid-teens (Bowen et al. 2006), thus providing an opportunity for trade-offs between maternal growth and energy allocation to offspring. As capital breeders, grey seal females accumulate body energy stores mainly in the form of blubber in the months prior to arriving at the breeding colony where they fast during the entire 16-18 days of lactation. Previous research has shown that heavier females produce larger offspring (Bowen et al. 2006), but the combined effects of maternal and offspring traits have not been simultaneously examined for a large sample. During the lactation period, mothers secrete large volumes of high-fat milk per day (Iverson et al. 1993). Grey seal females will lose ~68% of their initial fat stores to support milk production and maternal metabolism while pups gain ~ 35 kg of body mass on average (Bowen et al. 1992, Mellish et al. 1999a), however there is wide variation among individuals (Fedak & Anderson 1982, Reilly et al. 1996, Mellish et al. 1999a, Lang et al. 2009). Weaning is abrupt and signaled when the female leaves the colony and returns to forage at sea (Bowen 1991, Bowen et al. 2006). Following weaning, the pup will remain on land during a post-weaning fast of several weeks before going to sea on its first foraging trip (Noren et al. 2008).

Although the physiology and energetics of lactation in grey seals has been well studied (Fedak and Anderson 1982, Iverson et al. 1993, Mellish et al. 1999*a*, Mellish et al. 1999*c*, Lang et al. 2009, Lang et al. 2011*b*), less is known about the factors that influence energy allocation decisions of females to offspring (e.g., Pomeroy et al. 1999, Bowen et al. 2006). In this study I use both cross-sectional and longitudinal data on known-age individuals to test hypotheses about the factors influencing maternal energy allocation by grey seal females. Grey seals give birth to a single pup, simplifying the investigation of allocation by eliminating the variation in litter size and number and the effects of differing offspring sex ratio within and among litters. I examined allocation by first investigating the influence of maternal traits and then the consequences of this allocation for offspring. To do this, I examined the factors that influence total allocation, expressed as total maternal mass lost over the entire lactation period. Second, I examined lactation duration, one of the main components of allocation. I then examined maternal allocation relative to maternal body mass, expressed as the ratio of total mass loss to mass at parturition. Data on near birth mass allowed me to investigate prenatal allocation of maternal resources, whereas data on offspring weaning mass provide an opportunity to examine to consequence of postpartum allocation. I also examined the ratio of mass gain by offspring relative to mass loss by mothers to examine how the efficiency of nutrient transfer might vary with maternal and offspring traits. Finally, I examined the extent to which offspring body mass at weaning can be used as a measure of maternal energy allocation. Pup weaning mass has been used to infer maternal energy allocation (e.g. Fedak et al. 1996**,** Arnbom et al. 1997, Lang et al. 2009), however few studies have had a large sample to determine how representative weaning mass is of maternal allocation.

Methods

Field Methods

This study was conducted on Sable Island, Nova Scotia, Canada (43.9337° N, 59.9149° W) during the December- January breeding seasons from 1992 to 2011. Located along the outer edge of the Scotian Shelf (Figure 1), Sable Island is a crescent shaped, partially vegetated sand bar ~42.5 km in length. Over the course of this study, the number of pups born annually increased some 8-fold to 83,600 in 2016 (den Heyer et al. 2017). Females arrive on the island ~5 days prior to parturition and during this period they may move multiple times before selecting a birth site location (Weitzman et al. 2016). However, during the lactation period of approximately 16 days, females occupy the same general location (Boness and James 1979, Ambs et al. 1999).

The known-age females in this study were a subset of 3,387 females branded with a unique three or four letter/number combination shortly after they were weaned in 1969, 1970, 1973, 1974, 1985-1987, 1989 and 1998-2002. The presence of branded females in the breeding colony was determined by daily observations throughout the colony during other studies and weekly, whole island censuses that were conducted by 3-10 researchers on all-terrain vehicles. During each breeding period, approximately four to six weekly censuses were conducted. Due to the number of censuses, if a study female was on the island, there was an 85-90% chance that she was sighted (Bowen et al. 2020). The first time a female was sighted in the colony, her brand, GPS location, and lactation stage (based on pup pelage colour and morphology, Bowen et al. 2003*b*) were recorded. Pups born within ~ 24 hours were identified by the presence of fresh blood at the birth site, the presence of the expelled placenta, and the yellowish hue of their white birth pelage. Only pups with known or estimated birthdates within 24hr of birth were used in this study.

Once sighted, branded females and their offspring were sprayed with a small amount of alcohol soluble red dye to facilitate relocation in the colony of thousands of females. Study females were subsequently visited daily (without disturbance) to determine the date her offspring was weaned. Prior to weaning, pups were sexed and marked with semi-permanent, uniquely numbered tags so that a female's pup could be properly identified once the female had left. Adult females terminate lactation abruptly by leaving the colony and returning to sea, often overnight. Therefore, weaning was defined as the day a pup was sighted alone. On the day of weaning, pup sex was confirmed, and the pup was weighed.

Females were captured with a hand-held pole net and weighed from a tripod with a 300 ± 1 kg Salter spring balance (through 2012) or a 500 ± 1 kg Tractel load cell (2013 onward). Pups were captured with a smaller net and weighed using a 100 ± 0.5 kg Salter spring balance. We attempted to capture and weigh females and pups at day 3 and day 10 (prior to 1996) or day 12 (1996 onwards) after parturition to standardize initial body masses, and the change in masses of both mother and pup during lactation. Prior to 1996, most known-age females were young and had shorter lactation durations (12 – 13 days, e.g., Bowen et al. 2006), so the target measurement day was initially day 10. Females were not captured and weighed near weaning as previous experience indicated that weaning could be prematurely induced during female capture near the end of lactation. Initial maternal and pup masses were recorded on day 3 to allow the bond between mother and pup to develop thus avoiding the risk of pup abandonment during capture. Not all measurements could be obtained on the target dates due to inclement weather. However, measurements were taken on, or within a day or two of the targets.

All procedures used on study animals followed applicable animal care guidelines of the Canadian Council on Animal Care and were approved by The Department of Fisheries and Oceans and Dalhousie University Animal Care Committees.

Data Description

The dataset included mother-pup pairs studied between 1992 and 2011 that had 5 measurements: maternal body mass on day 3 and day 10 or 12 postpartum and pup body mass on day 3 and 10 or 12 postpartum and at weaning. Two outliers with abnormally high maternal mass losses and one with unusually low mass loss were removed (having to assuming measurement recording error), resulting in a sample of 324 observations from 222 females and their pups. In addition to the multiple measurements of maternal and pup body mass, pup sex, pup age (days), maternal age, weaning date, lactation duration (difference between weaning date and birth date) and parity were recorded for each pair.

Based on previous work, we predicted maternal age and maternal mass at parturition (hereafter referred to as "postpartum mass") to influence maternal energy allocation (Mellish et al. 1999a, Pomeroy et al. 2000, Bowen et al. 2006). A female's postpartum mass was estimated by extrapolating her day-3 mass to day 0 using her measured rate of mass loss between day 3 and day 10 or 12. Total maternal mass loss (kg) during the lactation period was calculated as the difference between her estimated postpartum mass (i.e., mass on day 0) and her estimated mass at weaning, again using a female's individual rate of mass loss. This approach was warranted as Mellish et al. (1999*b*) had shown that maternal mass loss during lactation was constant over the entire lactation period. Maternal age was included in the models with a quadratic term (see Bowen et al. 2006). To illustrate changes in allocation during a female's lifetime, values for each response variable (total maternal mass loss, relative maternal mass loss, lactation duration, mass transfer efficiency, pup mass on day 3, proportional pup mass gain and pup weaning mass) were estimated for three female ages: age 6, 15 and age 25. Ages were chosen based on work form Bowen et al. (2006), which defined age 4 to early teens as a period of female growth, mid-teens to early 20's as non-growing females in their reproductive prime, and mid to late 20's as the beginning of senescence.

In addition to age, reproductive experience can influence maternal performance. Therefore, parity was also included in models. The parity of a female was estimated as the number of years she had been sighted in the breeding colony pregnant or with a pup. The first time a female was sighted in the breeding colony was considered her age at first birth. Few of the seals marked on Sable Island at weaning are known to breed elsewhere so the error in estimating the age at first birth is likely small (Bowen et al. 2015). Previous studies have identified that the effects of parity are most pronounced in young growing females, thus parity is represented in the model as a factor with three levels: primiparous females, second parity females and multiparous females (3+).

Pup growth rate was calculated as mass gain per day from day 3 to weaning. I did not extrapolate pup mass to birth, as Mellish et al. (1999*c*) found that pups gained mass at a lower rate in the first few days of lactation than later in lactation. Pup mass on day 3 will be referred to as pup birth mass hereafter. Measurement dates for pup birth mass (kg) ranged from day 3 to day 5 postpartum, so masses were standardized to day 3 postpartum using each pup's rate of gain. Pup sex was included as a covariate to account for the fact that male pups are heavier than female pups on average (Bowen et al. 2006).

Statistical Models

Mixed-effect general linear models were used to examine the relationships between the response variables and covariates in this study. Models were written using the *lme4* (Bates et al. 2015) package in R version 1.3.959 (R Core Team 2020). Each response variable was modelled with all possible combinations of the variables included in the maximum model using the package *MuMIn* (Bartón 2020). The models were evaluated by AIC value, number of parameters, and AIC weight. Goodness of fit of each model was assessed by examining the residuals from the *stats* package in R (R Core Team 2020). For model selection, continuous variables were centered and scaled to a mean of zero and standard deviation of 1. Coefficients of the covariates in the final models were estimated by re-running models using the untransformed data and the fixed effects were plotted using *effects* package (Fox 2003). Conditional and marginal R_2 were calculated for each model using the *MuMIn* package (Bartón 2020).

Response variables for the proportional models (relative maternal mass loss, relative pup mass gain and maternal mass loss) were normally distributed (Figure A1-A3) and therefore were modeled as linear mixed effects models.

Of the 222 individual females in the sample, 61 were each measured in 2 to 7 years. To account for lack of independence in repeated measures, maternal identity was included as a random effect. Study year was not included as a random effect as study year and maternal age were highly correlated, particularly during the early years of the study.

Models

There were seven response variables that were investigated to examine the different elements of maternal energy allocation. Response variables were meant to contribute to our understanding of the evolution of maternal energy allocation strategies in animals, or to examine the consequence of maternal energy allocation on pup weaning mass. Response variables and their hypothesized importance are listed in Table 1.

The first model predicted total maternal mass loss (Total Maternal Mass Loss_{ij}; where i denotes mom, j denotes pup) during lactation as a function of the female's age, her experience (parity), her postpartum mass and pup sex. Maternal mass was modeled as a random normal variable (ε_{ij} =

$N(0, \delta^2)$. Maternal ID was included as a random effect (γ_i=N(0, d^2). The maximum model was written:

Total Maternal Mass Loss $_{ij} \sim \beta_{Female\ Age}$ * Female Age$_{ij}$+ $\beta_{Female\ Age^2}$ I(Female Age$_{ij}^2$) +$\beta_{postpartum\ Mass}$ * postpartum Mass $_{ij}$ + β_{Parity} *Parity$_{ij}$ + $\beta_{Pup\ Sex}$ * Pup Sex$_{ij}$ + γ_j + ε_{ij}.

The second model predicted maternal allocation as relative postpartum maternal mass (Proportional Maternal Mass Loss$_{ij}$; where i denotes mom, j denotes pup) during lactation as a function of female age, female experience, lactation duration, pup birth mass and pup sex. Proportional maternal mass loss was calculated as total maternal mass loss / maternal postpartum mass and was modeled as a random normal variable (ε_{ij} = $N(0, \delta^2)$. Again, maternal ID was included as a random effect (γ_i=N(0, d^2). The maximum model was written:

Proportional Maternal Mass Loss $_{ij} \sim \beta_{Female\ Age}$ * Female Age$_{ij}$ + $\beta_{Female\ Age^2}$ I(Female Age$_{ij}^2$) + $\beta_{Pup\ Sex}$ * Pup Sex$_{ij}$ + $\beta_{Lactation\ Duration}$* Lactation Duration$_{ij}$ + β_{Parity} *Parity$_{ij}$ + $\beta_{Pup\ Birth\ Mass}$* Pup Birth Mass$_{ij}$ + γ_j + ε_{ij}.

The third model predicted pup birth Mass (Pup Birth Mass$_{ij}$; where i denotes mom, j denotes pup) as a function of female age, pup sex, maternal postpartum mass, and parity. Pup birth mass was modeled as a random normal variable (ε_{ij} = $N(0, \delta^2)$. To account for variation among females, maternal ID was included as a random effect (γ_i=N(0, d^2). The maximum model was written:

Pup Birth Mass$_{ij} \sim \beta_{Female\ Age}$ * Female Age$_{ij}$ + $\beta_{Female\ Age^2}$ I(Female Age$_{ij}^2$) + $\beta_{Pup\ Sex}$ * Pup Sex$_{ij}$ + $\beta_{Postpartum\ Mass}$* Postpartum Mass$_{ij}$ + β_{Parity} *Parity$_{ij}$ + γ_j + ε_{ij}.

The fourth and fifth model predicted lactation duration and mass transfer efficiency from mother to pup during the lactation period (Table A1). Mass transfer efficiency was calculated as pup mass gain / total maternal mass loss. Lactation duration and mass transfer efficiency were modeled as random normal variables.

The final objective was addressed with two models that used proportional pup mass gain and weaning mass as the response variables. Pup mass gain relative to maternal postpartum mass (Proportional Pup Mass Gain$_{ij}$; where i denotes mom, j denotes pup) was modeled as a function of female age, pup sex, maternal postpartum mass, lactation duration and parity. Proportional pup mass gain was calculated as pup mass gain / maternal postpartum mass modeled as a random normal variable ($\varepsilon_{ij} = N(0, \delta^2)$). Maternal ID was included as a random effect (γ_i=N(0, d^2)). The maximum model was written:

Proportional Pup Mass Gain$_{ij}$ ~ $\beta_{Female\ Age}$ * Female Age$_{ij}$ + $\beta_{Female\ Age^2}$ I(Female Age$_{ij}^2$) + $\beta_{Pup\ Sex}$ * Pup Sex$_{ij}$ + $\beta_{Lactation\ Duration}$* Lactation Duration$_{ij}$ + β_{Parity} *Parity$_{ij}$ + $\beta_{Postpartum\ Mass}$ * Postpartum Mass$_{ij}$ + γ_j + ε_{ij}.

Two maximum models to predict pup weaning mass were developed: one included total maternal mass loss as a covariate and the other included maternal postpartum mass. Due to the method used to calculate maternal mass loss, both covariates could not exist in the same model, so their effects were tested separately. Pup weaning mass (Weaning Mass$_{ij}$; where i denotes mom, j denotes pup) was modeled as a function of female age, pup sex, postpartum mass, lactation duration, parity, pup birth mass, and maternal postpartum mass or total maternal mass loss. Pup weaning mass was modeled as a random normal variable ($\varepsilon_{ij} = N(0, \delta^2)$). Once again, maternal ID was included as a random effect (γ_i=N(0, d^2)). The maximum models are as follows:

Weaning Mass$_{ij}$ ~ $\beta_{Female\ Age}$ * Female Age$_{ij}$ + $\beta_{Female\ Age^2}$ I(Female Age$_{ij}^2$) + $\beta_{Pup\ Sex}$ * Pup Sex$_{ij}$ + $\beta_{Lactation\ Duration}$* Lactation Duration$_{ij}$ + β_{Parity} *Parity$_{ij}$ + $\beta_{Pup\ Birth\ Mass}$ * Pup Birth Mass$_{ij}$ + $\beta_{Total\ Maternal\ Mass\ Loss}$ * Total Maternal Mass Loss + γ_j + ε_{ij}

$$\text{Weaning Mass}_{ij} \sim \beta_{\textit{Female Age}} * \text{Female Age}_{ij} + \beta_{\textit{Female Age}^2}\, \text{I}(\text{Female Age}_{ij}{}^2) + \beta_{\textit{Pup Sex}} * \text{Pup Sex}_{ij} + \beta_{\textit{Lactation Duration}} * \text{Lactation Duration}_{ij} + \beta_{\textit{Parity}} * \text{Parity}_{ij} + \beta_{\textit{Pup Birth Mass}} * \text{Pup Birth Mass}_{ij} + \beta_{\textit{Postpartum Mass}} * \text{Postpartum Mass} + \gamma_j + \varepsilon_{ij}$$

To investigate whether pup weaning mass can serve as a reasonable estimate of maternal energy allocation, the relationship between the estimates from the weaning mass model and the maternal mass loss model were compared through visual analysis and correlation coefficients.

Variation about the mean is expressed as standard deviation throughout.

Results

Residuals for all fixed effects in each model were investigated to determine that there were no underlying patterns unaccounted for (Fig A4 – A10). In all cases the models fit the data well.

Total Maternal Energy Allocation

Total maternal mass loss over lactation in 222 females (n = 324) ranged from 30.4 to 118.3 kg, with a mean of 73.1 ± 15.9 kg. The preferred model used maternal postpartum mass, maternal age, and pup sex as explanatory variables (Table 2; Table 3). However, there was some evidence for the second model that suggested pup sex as an explanatory variable of total maternal mass loss (Table 3). The fixed effects in the model explained 64.1 % of the variance ($R_2(m) = 0.641$, $R_2(c) = 0.781$). Maternal identity accounted for 14 % of the variance unexplained by fixed effects. Of the covariates included in the preferred model, maternal postpartum mass had the strongest effect on total maternal mass loss during lactation (Table 4, Figure 2). There was some evidence for an increase in variability with increasing maternal age. After accounting for maternal postpartum mass, total maternal mass loss increased with female age until about age 15, then tended to level off, before indicating a slight decline in in older females (Table 4; Table 5, Figure 3), such that larger and older mothers had greater mass loss during lactation up until about age 15. The apparent lack of fit in Figure 3 results from the fact that postpartum mass accounted for most of the variation in total allocation in young females. Although postpartum mass continued to be an important predictor, maternal age became more important as females got older. Females with female pups lost on average 2.19 kg less than females with male pups (Table 4).

Relative Maternal Energy Allocation

Maternal mass loss relative to postpartum mass ranged from 0.21 to 0.54, with a mean of 0.37 ± 0.05 (n = 324). The preferred model included maternal age, lactation duration, and pup birth mass (Table 2). There was also some evidence for the second model that included pup sex, and the third model that included maternal age, however the respective AIC and weight values supported the selected model (Table 6). The fixed effects in the model explained 32% of the variance ($R_2(m)$ = 0.32, $R_2(c)$ = 0.549). Maternal ID accounted for 22.9 % of the variance unexplained by the fixed effects in the model. All three covariates included in the selected model had a strong effect on proportional maternal mass loss. Females with longer lactation periods lost a greater proportion of their mass (Table 7, Figure 4). Although there was a slight increase in relative maternal mass loss early in a female's life, the quadratic term of maternal age was not retained in the model. The estimated relative mass loss during lactation decreased slightly with increasing maternal age (Table 5; Table 7, Figure 5). There was a slight positive relationship between relative maternal mass loss and the pup's birth mass (Table 7, Figure A11). This suggested that females with heavier newborns invested relatively more of their body mass during lactation than those with lighter newborns, however there was a large amount of variation with age (Figure A11).

Lactation Duration

Lactation duration of 222 females (n = 324) ranged from 11 to 23 days, with a mean of 16.7 ± 1.9 days. The best supported model for lactation duration included pup growth rate, maternal postpartum mass, maternal age, pup sex, and pup birth mass (Table 2; Table 8). The fixed effects in the model explained 42.8 % of the variance ($R_2(m)$ = 0.428, $R_2(c)$ = 0.651). Maternal identity accounted for 22.3 % of the variance unexplained by the fixed effects. Of the covariates in the final model, pup growth rate, maternal mass at parturition, pup birth mass and female age had the strongest effects on lactation duration. The model estimated that pups with higher growth rates had shorter lactation periods (Table 9), however the effect was small and of doubtful biological significance (Figure A12). The heavier a female was at parturition, the longer her lactation. The model predicted that for each additional kg that a female weighed at parturition, lactation was 0.05 days longer (Table 9). Heavier mothers with longer lactation periods were generally multiparous (parity 3+) females (Figure 6). The model estimated that heavier pups at birth tended to have shorter lactation periods, however there was no distinguishable biological pattern (Table 9). Lactation duration initially increased as females got older, until ~15 years (Table 5; Table 9, Figure 7). After age 15, there was a plateau in lactation duration followed by a slight decrease (Table 5; Table 9, Figure 7). Females that gave birth to female pups had lactation durations that were 0.35 days shorter than female's who gave birth to male pups (Table 9).

Mass Transfer Efficiency

Mass transfer efficiency of 222 females (n = 324) ranged from 0.13 to 0.74, with a mean of 0.36 ± 0.07. The selected model retained only maternal age and parity as a predictor (Table 2; Table 10). However, there was also reasonable evidence for the next three models, which suggested some effect of pup sex and maternal postpartum mass (Table 10). The fixed effects in the selected model explained only 5.0 % of the variance ($R_2(m)$ = 0.05, $R_2(c)$ = 0.219). Maternal ID accounted for 16.9 % of variance unexplained by the fixed effects in the model. Of the covariates included in the model, female age had the strongest effect on the mass transfer efficiency. In general, mass transfer efficiency decreased as females aged (Table 5; Table 11, Figure A13). Parity 2 and parity 3+ females had a 0.03 and 0.32 increase in mass transfer efficiency increase when compared to primiparous females (Table 11). However, measured covariates had relatively little influence on mass transfer efficiency.

Pup Birth Mass

Birth mass of pups from 222 females (n = 324) ranged from 12.3 to 32 kg, with a mean of 21.5 ± 3.6 kg. The preferred model included maternal postpartum mass, maternal age, pup sex and parity (Table 2; Table 12). There was another model with a similar AIC value that suggested maternal mass at parturition was not an important predictor of pup birth mass. However, the weight values (0.52 and 0.19, respectively) indicated that preferred model was better supported (Table 12). The fixed effects in the model explained 31.5% of the variance ($R_2(m)$ = 0.315, $R_2(c)$= 0.318). Maternal ID accounted for only 0.3 % of variance unexplained by the fixed effects in the model. Of the covariates included in the preferred model, maternal age had the strongest effect on pup birth mass. On average, pup birth mass increased by 0.6 kg as a female aged, until ~ age 15 when there was a slight plateau and then a noticeable decrease in initial pup mass in older females (Table 5; Table 13, Figure 8). Heavier mothers were capable of giving birth to larger pups, however, did not always do so (Table 13, Figure 9). Female pups weighed ~0.9 kg less than male pups at birth (Table 13). Females of both parity 2 and parity 3+ produced pups with higher birth masses than primiparous females (0.7 kg and 1.9 kg higher, respectively) (Table 13, Figure 10). However, the difference in pup birth mass between primiparous and parity 2 females was not statistically significant (Table 13).

Relative Pup Mass Gain

Proportional pup mas gain (pup mass gain / maternal mass at parturition) of pups from 222 females (n = 324) ranged from 0.04 to 0.21, with a mean of 0.13 ± 0.03. There were four competing models with similar AIC values, however the preferred model (Table 2) had a higher weight and was therefore chosen (Table 14). The fixed effects in the model explained 27.1 % of the variance ($R_2(m)$= 0.271, $R_2(c)$= 0.443). Maternal ID accounted for 17.2 % of the variance unexplained by the fixed effects. Of the covariates in the preferred model, lactation duration, maternal age, and parity had the strongest effects on proportional pup mass gain. Proportional pup mass gain increased for each day lactation continued (Table 15, Figure 11) and decreased with female age (Table 3; Table 15, Figure A14). The model estimated that parity 2 and 3+ females produced pups that gained 0.017 and 0.022 more proportional mass than primiparous females, respectively (Table 15). Female pups gained approximately 0.007 less proportional mass than did male pups (Table 15).

Weaning Mass

Weaning mass of pups from 222 females (n = 323) ranged from 26.5 to 67.0 kg, with a mean of 47.3 ± 8.4 kg. There were two preferred models that informed variation in weaning mass: one where weaning mass was a function of total maternal mass loss, and the other where weaning mass was a function of maternal mass at parturition. However, as maternal postpartum mass and total maternal mass loss are highly correlated (0.78), only the results from one model are reported below.

The preferred model was chosen among three other competing models with similar AIC values (Table 2). The next three models showed some evidence that lactation duration, pup sex and mom age quadratic did not have a detectable effect on pup weaning mass (Table 16). The fixed effects in the model explained 74.12 % of the variance ($R_2(m)$ = 0.741, $R_2(c)$ = 0.794). Maternal ID accounted for 5.3 % of the unexplained variance in the model. Of the covariates in the preferred model, pup birth mass and total maternal mass loss had the strongest influences on pup weaning mass. The model predicted a 0.8 kg increase in weaning mass for each additional kg in pup birth mass (Table 17, Figure 12). There was a linear relationship between total maternal mass loss and weaning mass, pups weighed an additional 0.25 kg at weaning for each kg lost by the female (Table 17, Figure 13). As total maternal mas loss increased, the difference between weaning mass and maternal mass loss increased (Figure 13). There was a 0.40 kg increase in weaning mass for each additional day in the lactation period (Table 17, Figure 14). The preferred model included a linear and quadratic term to describe the relationship between weaning mass and maternal age. Initially, weaning mass increased as maternal age increased, and eventually began to decline as females got older (Figure 15). The model coefficient estimates and confidence intervals suggested that maternal age only became important for weaning mass when females were > 20 years old (Table 5; Table 17, Figure 15). Primiparous females produced pups with lower weaning masses than more experienced breeders. The preferred model estimated that parity 2 females produced pups that were 2.5 kg larger than pups from primiparous females (Table 17, Figure A15). Females of parity 3 or greater produced pups 3.2 kg larger than primiparous females (Table 17, Figure A15). At weaning, female pups were on average ~ 1.1 kg lighter than male pups (Table 17).

Discussion

My study showed that maternal postpartum mass and female age had significant effects on multiple aspects of maternal energy allocation, including total maternal mass loss, lactation duration, pup birth mass and pup weaning mass. Heavier postpartum females allocated more body mass and therefore energy to offspring than lighter females. In most aspects of maternal allocation investigated in this study, female age followed the pattern of increased allocation early in life, a plateau in non-growing prime females followed by a decline in older females. Female breeding experience (i.e., parity) also affected maternal allocation, albeit less strongly, to pup birth mass, proportional pup mass gain and weaning mass. Females that lactated longer produced pups with greater proportional mass gain and weaning mass. Finally, females that gave birth to male pups experienced greater total mass loss and weaned heavier pups than those that gave birth to female pups. Maternal identity, as a random effect, accounted for some residual variance in most models, suggesting that characteristics of maternal allocation are associated with individual females. This is consistent with previous research on grey seals on Sable Island (Lang et al. 2009; Bubac et al. 2018) and in the UK (Pomeroy et al. 1999), Weddell seals (Patterson et al. 2016) and bison (Hamel et al. 2012), where variation in maternal allocation was associated with what are likely heritable physiological traits and personality of individual females. The effect of between individual variability was likely underestimated in this study because relatively few of the females were studied in multiple years.

Previous studies conducted on both aquatic (Weddell seals, *Leptonychotes wedellii* [e.g., Wheatley et al. 2006]; and southern elephant seals, *Mirounga leonina* [e.g., Fedak et al. 1996]) and terrestrial species (e.g., reindeer, *Rangifer tarandu* [Weladji et al. 2002]; polar bears, *Ursus maritimus* [Derocher & Stirling 1998]; mountain goats, *Oreanmnos americanus* [e.g., Arnbom et al. 1997]; and bison [Hamel et al. 2012]) found that many of the same traits influenced maternal allocation. Combined, these studies on diverse taxa underscore the importance of these traits in the evolution of capital breeding strategies in both terrestrial and aquatic mammals.

Despite the relatively large sample of females, there are several limitations to this study. First, a disproportionally large fraction of young females, particularly early in the study, might explain the smaller difference between male and female weaning mass. Second, the effect of environmental variation on maternal energy allocation could not be examined in detail because there were many years with too few samples, and there was a strong correlation between year and maternal age that confounded any year effect.

Total Maternal Mass Loss

Maternal postpartum mass was the most important predictor of total maternal mass loss during the lactation period, with heavier females losing more mass (Figure 2). On average, the grey seal females in this study lost 73.1 kg of their postpartum mass during the lactation period. In accordance with the results from this study, Iverson et al. (1993) concluded that maternal mass loss increased with higher mass at parturition, also evident in southern elephant seals (Arnbom et al. 1997). Furthermore, as smaller females sustain lactation for shorter periods, females with higher postpartum masses will contribute more to the pup's growth during the lactation period (Iverson et al. 1993), thereby highlighting the importance of being larger. Larger females are capable of allocating more to offspring than smaller females.

My results also showed that total maternal mass loss varied with female age and pup sex. Females with male pups lost on average 2.2 kg more than females with female pups, suggesting that female grey seals allocate more energy to male pups. This is consistent with previous research on terrestrial (e.g. red deer, *Cervus eplaphus* (Froy et al. 2016); big horn sheep, *Ovis canadensis* (Hogg et al. 1992) and aquatic (e.g., harbour seals,*Phoca vitulina* (Bowen et al. 1994) and California sea lions, *Zalophus californianus* (Ono & Boness 1996)) mammals, where male pups are allocated more resources than female pups. In contrast, total maternal mass loss was not influenced by pup sex in southern elephant seals (Arnbom et al. 1997), however females with male pups did lose more mass than those with female pups. In general, there is a repeating trend of females losing more mass with male pups than female pups in several species.

Relative Maternal Mass Loss

Relative maternal mass loss investigates maternal allocation while accounting for differences in postpartum maternal body mass (Hamel et al. 2012). I found that grey seal females to lose ~37 % of initial body mass, similar to previous data for this species (39%; Iverson et al. 1993). This is comparable to grey seals on North Rona (38-39%; Fedak & Anderson 1982, Anderson & Fedak 1987*b*), northern elephant seals (42%; Costa e al. 1986) and southern elephant seals (37%; McCann et al. 1989). By contrast, grey seals use a much higher proportion of total body energy during lactation than hooded seals (Oftedal et al. 1987); this difference is mainly a result of the remarkably short period of lactation of only 4 days in the hooded seal (Mellish et al. 1999*b*).

Gittleman & Thompson (1988) suggested that heavier mothers are capable of allocating a greater proportion of mass, however there is substantial variation among capital breeders with respect to relative allocation. In some species, greater mass leads to greater relative allocation: Weddell seals (Wheatley al. 2006; MacDonald et al. 2020**),** and mountain goats (Coté & Festa-Bianchet 2001*b*). Alternatively, studies on bison (Hamel et al. 2012) and harbour seals (Bowen et al. 2001) have concluded that lighter mothers invest more relative mass than heavier mothers, while studies on other capital breeders have found no relationship (Fedak et al. 1996). I found no evidence of maternal mass influencing relative mass loss in grey seal mothers (Table 7). My study demonstrates that grey seal mothers exhibit the same level of relative allocation regardless of postpartum body mass. Thereby supporting predictions from life history theory that in long-lived mammals, fitness of the female is more important than the fitness of the single offspring (Roff

1992). Although relative allocation was independent of postpartum mass, relative mass loss in grey seals is most influenced by lactation duration with relative allocation increasing with increasing duration.

Previous research has highlighted the importance of postpartum mass (indicative of foraging success) for maternal allocation and reproduction in many mammals (Bercovitch et al. 1998, Broussard et al. 2005; white tailed deer, *Odocoileus virginianus* (Michel et al. 2019) and northern elephant seals, *Mirounga angustirostris* (Crocker et al. 2001)), especially capital breeders, like phocids and some ungulates such as bison (Festa-Bianchet et al. 1998). Body mass is likely a good measure of body condition (Boyd 2000) and an indicator of body energy reserves (Arnould 1995, Fedak et al. 1996). Given the strong relationship between maternal postpartum mass and body protein and lipid content in grey seals (Mellish et al. 1999*c*), it is reasonable to assume that heavier mothers have more available resources to contribute to neonates (Iverson et al 1993, Mellish et al. 1999*c*). The consequence of this is that females with reduced energy stores postpartum wean lighter pups (Iverson et al. 1993, Mellish et al. 1999*c*, Pomeroy et al. 1999**)**. Females with greater postpartum masses will allocate more resources to offspring.

Female Age

Female age was an important predictor for all elements of maternal energy allocation in older females (Table 2). Furthermore, in all models except those that were presented as proportions (relative maternal mass loss, relative pup mass gain and mass transfer efficiency), the effect of female age was curvilinear with an initial increase and plateau, followed by a decline. Variation in reproductive performance with female age occurs in many mammals, such as pinnipeds (Reiter et al. 1981, Bowen et al. 2001; Patterson et al. 2016), whales (Olesiuk et al. 1990), primates and lions (Packer et al. 1998), ungulates (Clutton-Brock et al. 1982; Ericsson et al. 2001), reindeer (Weladji et al. 2002), polar bears (Derocher & Stirling 1998), Columbia ground squirrels, *Urocitellus columbianus* (Broussard et al. 2003)), in addition to birds (Robertson & Rendall 2001, Weimerskirch 1992). There are several age-related hypotheses that pertain to maternal allocation strategies. The restraint hypothesis dictates that younger females will reduce reproductive effort due to a higher risk of mortality, and the selection hypothesis states that improved breeding in older females is associated with the loss of lower quality phenotypes (Curio 1983, Forslund & Pärt 1995). A previous study has found evidence against both theories in grey seals (Bowen et al. 2006). Another such hypothesis is the reproductive constraint hypothesis, which suggests that age structured populations usually follow a pattern in which young individuals improve reproductive performance with age and experience (Curio 1983). The results from my study illustrate that female grey seals follow the same life history pattern, with an increase early in life, a plateau in the mid-teens followed by an eventual decline later in life.

The decline in several maternal and offspring traits later in life suggests decreased reproductive performance past a certain age (Table 5). Bowen et al. (2006) documented similar evidence of reduced reproductive performance later in life and furthermore highlighted that female physiology also varies with age. Reproductive senescence leads to a decline in performance later in life (McCleery et al. 2008, Rebke et al. 2010), and although senescence has been documented grey seals and other terrestrial and aquatic capital breeders (Bowen et al. 2006, Hamel et al. 2012, Festa-Bianchet et al. 2019, Condit et al. 2014, Paterson et al. 2016)**,** this dataset did not include enough females over the age of 25 to make firm conclusions about the role of senescence in all elements of maternal energy allocation. Nevertheless, my results do add evidence in favour of a decline in maternal allocation among older grey seals consistent with the previous work on this species.

Lactation Duration

I found maternal postpartum mass to be the most important predictor of lactation duration; heavier females lactated longer than lighter females (Table 9; Figure 6). This relationship has been found for other capital breeding pinnipeds (northern elephant seals; Crocker et al. 2001). In contrast, Weddell seals have much longer lactation periods (~ 45 days), so the relationship between maternal postpartum mass and lactation duration in Weddell seals was only significant in the largest females (Wheatley et al. 2006).

There was also a strong effect of female age on lactation duration, with lactation periods increasing early in a female's life and reaching a plateau at ~ age 10 (Figure 7). The age-related pattern in lactation duration found in this study has also been documented in grey seals by Bowen et al. (2006). However, Lang et al. (2009) also found that variation in lactation duration in grey seals was explained more by maternal mass than maternal age, and only a small amount of variation in lactation duration was explained (Lang et al. 2009). My study found that maternal postpartum mass was more important than female age in younger females. Furthermore, female age became the most important driver of maternal energy allocation in older females. This pattern was also demonstrated in total and relative maternal mass loss, pup birth mass and pup weaning mass. As far as I know, this is a new finding for grey seals.

Mass Transfer Efficiency

Mellish et al. (1999*a*) found that mass transfer efficiency in grey seals averaged ~ 40.1 % ± 1.62 but increased later in lactation (Mellish et al. 1999*a*). In comparison, we found an average mass transfer efficiency of ~36% ± 6.62 during the whole lactation period. These differences are likely explained by differences in the calculation of pup mass gain (Mellish et al. 1999*a* calculated pup mass gain from day 0 to weaning vs day 3 to weaning), and a narrower range of maternal postpartum masses than those available in this study. In comparison, Weddell seals have a mass transfer efficiency of 49.6% in early lactation (MacDonald et al. 2020) and southern elephant seals have a mass transfer efficiency of 45.6 ± 0.05% (Arnbom et al. 1997). Overall, this suggests that grey seals have less efficient mass transfer than other capital breeding pinnipeds. A potential explanation could be that while female grey seals are mostly idle during the lactation period, they are more mobile than the species above and therefore a greater proportion of mass loss is attributed to that greater energy expenditure.

Additionally, mass transfer efficiency varied with maternal age and parity, decreasing as the female aged (Figure A13) and increasing with parity. Grey seals in the UK had an average mass transfer efficiency 45.4 ± 1.4 % (Pomeroy et al. 1999) that was not related to pup sex or maternal postpartum mass, as was found here. In contrast, mass transfer efficiency was found to be lower in multiparous Weddell seals (MacDonald et al. 2020) and in grey seal females (Lang et al. 2011*b*) than higher parity females. Perhaps one of the reasons for difference in efficiency is that multiparous females in this study included parity 3 to parity 21, with most of the measurements coming from females with less experience, so it is possible that mass transfer efficiency also decreased with higher parity. Weddell seal mass transfer efficiency also varied with female age, following a similar pattern to what was found in this study (initial increase, plateau, and eventual decline) (MacDonald et al. 2020), suggesting that this pattern is may be common among capital breeding mammals. MacDonald et al. (2020) found heavier Weddell seal mothers to be less efficient at energy transfer. Larger females in this study did not differ in mass transfer efficiency than smaller females, and so maternal postpartum mass was not included in the model (Table 11; Figure A16**)**. There are possible explanations for this difference; the most evident being that Weddell seals have much higher postpartum masses (278-626 kg) and lose greater relative mass

(MacDonald et al. 2020). This suggests that grey seals have moderate mass transfer efficiency when compared to other capital breeding phocids.

Similar to the results for relative maternal mass loss, this could suggest that the greater resources available to larger grey seal females allow them to incur a lower cost of lactation, rather than increase allocation. Lastly, this model did not fit the data well and it is likely that there are differences in lactation efficiency (milk energy output, maternal behaviour, metabolic compensation) between females (Mellish et al. 1999*a*, Lang et al. 2012) and pup growth efficiency (Crocker et al. 2001, Hooper et al. 2019) that influence mass transfer efficiency and could not be investigated in this study.

Pup Birth Mass

Pup birth mass was influenced by maternal postpartum mass, female age, and maternal breeding experience (Table 13). Pup birth mass increased by 1 kg, on average, for each additional 50 kg of maternal post-partum mass (Figure 9). Mellish et al. (1999*a*) found that grey seal females with greater postpartum masses did not give birth to larger pups, but that study comprised a much smaller sample size with a narrower range of maternal masses such that is likely not as representative of the population as this study. However, my results were consistent to those of southern elephant seals (McMahon et al. 2017), harbour seals (Bowen et al. 1994), and the UK grey seals (Pomeroy et al. 1999) that larger females produced larger pups at birth.

Female pups were born smaller than male pups (0.9 kg smaller). Previous findings on grey seals, both on Sable Island and in the UK, found pup sex did not have an important effect on initial pup mass (Mellish et al. 1999*a*; Pomeroy et al. 1999). However, Mellish et al. (1999*a*) had a more limited dataset and there have been established differences between the UK and Sable Island grey seals (Pomeroy et al. 1999). The differences in female and male pup birth masses are small enough that presumably the large sample size is needed to detect the difference. Male pups of southern elephant seals were born ~3-8 kg larger than female pups (McMahon et al. 2017), regardless of female mass (Arnbom et al. 1997), suggesting that differences in allocation between sexes are more pronounced in larger phocids.

In addition to this study, pup birth mass has previously been shown to follow a similar pattern (initial increase, state of plateau, eventual decline) with female age (Table 5) in grey seals Bowen et al. 2006) and northern fur seals (Boltnev & York). Harbour seals, in contrast, had increased pup birth mass with increasing maternal age without a decline in later life (Bowen et al. 1994; Ellis et al. 2000). However, harbour seal females begin feeding during the lactation period (Boness et al. 1994), suggesting that the reduced reproductive effort in older females is expressed more in true capital breeders.

Pup Weaning Mass

Pup weaning mass was most affected by total maternal mass loss and initial pup mass: increased maternal mass loss and initial pup mass resulted in increased pup weaning mass. Total maternal mass loss and weaning mass were highly correlated (correlation = 0.78), suggesting that weaning mass is a reasonable estimate of maternal energy allocation. However, the relationship between weaning mass and total maternal mass loss is not constant over the range of maternal mass. At least in grey seals, weaning mass will tend to underestimate maternal allocation for larger females in comparison to smaller females. An understanding of mass transfer efficiency for the species in question should exist prior to making assumptions about the use of weaning mass as a measure of maternal allocation. Finally, since the underestimation is size dependent, a broad distribution of female sizes in the study will be necessary. The importance of maternal mass on weaning mass was also evident in other pinnipeds: Weddell seals (MacDonald et al. 2020), southern elephant seals (Arnbom et al. 1997), harbour seals (Ellis et al. 2000; Bowen et al. 2001) and northern fur seals, *Callorhinus ursinus* (Boltnev & York 2001) and in terrestrial species (e.g. Michel et al. 2019**)**.

Pups that were born larger at birth were larger at weaning. This relationship has also been recorded in Weddell seal pups (MacDonald et al. 2020) and bison calves (Green & Rothstein 1993). A study by Monclús et al. (2014) investigated maternal ability to compensate and found no evidence of maternal compensation for pups born in unfavourable conditions (i.e., later in the season or with smaller birth masses), also suggested by the results of this study. Breeding experience in this study showed an influence on pup weaning mass, with primiparous females having pups with the lowest weaning masses and multiparous females having pups with the highest masses (Figure A8). Breeding experience has a similar effect on pup weaning mass in Weddell seals (MacDonald et al. 2020). Pups from primiparous females usually have lower weaning masses in grey seals and are therefore less likely to survive (Lang et al. 2011*b*). Additionally, weaning mass varied with female age; increasing in early life and decreasing significantly in later life, which has been found to be true for grey seals (Bowen et al. 2006) and other pinnipeds (MacDonald et al. 2020; Arnbom et al. 1997). Furthermore, the relationship between female age and pup weaning mass demonstrates senescence having a more notable effect on maternal allocation in older females. Previously, mom age had an early impact on weaning mass in grey seals, but maternal postpartum mass has been shown to be more important (Bowen et al. 2006), as was reflected in this study with total maternal mass loss.

Mass at weaning of mammalian species has impacts on future survival and fitness (e.g., Wauters et al 1993, Festa-Bianchet et al. 2000, Hall et al. 2001), and in some species, pup size and weaning can have long term consequences and be closely related to adult condition (Lindström

1999). Thus, heavier and fatter pups have greater probability of survival to one year of age (Hall et al. 2001), making maternal energy allocation an important process to understand. The relationship between milk energy transfer, weaning mass and subsequent pup survival has been well studied and documented in grey seals (Lang et al. 2009). Low body mass in grey seal pups causes reduced oxygen storage capacity, leading to shorter and shallower dives and therefore less effective foraging (Noren et al. 2008).

Pup Sex

Results from my study suggest that male grey seal pups receive greater allocation than female pups, however the differences were small. Sexual dimorphism at weaning has been documented for many mammals (grey seals; Hall et al. 2001, red deer; Froy et al. 2016, big horn sheep; Hogg et al. 1992, Festa-Bianchet & Coté 2008; harbour seals (Bowen et al. 1994), California sea lions (Ono & Boness 1996). I found that maternal allocation to males was greater than to female pups on all response variables measured except for relative maternal mass loss (Table 11). Male pups were 1.1 kg heavier than female pups at weaning; in comparison, previous studies on grey seals found male pups to weigh ~2 kg more than female pups at weaning. This may be due both to the larger dataset and the increased proportion of young females included in this study. Male pups have been hypothesized to be more energetically expensive than female pups (Bowen et al. 2006; Festa-Bianchet et al. 2019), and in animals where parental allocation comes solely from the mother, allocation is usually greater when raising a male than a female offpsring (Lee & Moss 1986, White et al. 2007; Monclús et al. 2014). Studies have shown that male grey seal pups do not grow more rapidly than female pups (Bowen et al. 1992) and while my results showed that females with male pups lost more mass, male pups were also born larger than female pups; in general this suggests that differential treatments between male and female pups was minimal.

My study showed that the effect of pup sex was not as large as the effect from the female characteristics in predicting the level of maternal energy allocation to offspring. This finding is supported by various studies on other capital breeding ungulates (e.g, Hamel et al. 2012) and pinnipeds (McMahon et al. 2017, Pomeroy et al. 1999).

Maternal Breeding experience

Maternal breeding experience (parity) was an important factor in mass transfer efficiency, initial pup mass, proportional pup mass gain and pup weaning mass (Table 2). In every case, maternal energy allocation in parity 2 females was estimated to be greater than in primiparous females, and with multiparous having the highest estimates. However, the difference between parity 2 and multiparous females were minimal in the mass transfer efficiency model (Table 11). Studies on parity in capital breeders have focused on the differences between primiparous and multiparous females (Lang et al. 2009, Lang et al. 2012, Hamel et al. 2012; Festa-Bianchet et al. 2019; Michel et al. 2019); and the effect of breeding experience on maternal allocation has also been documented in pinnipeds (Trites 1991, Ellis et al. 2000), and terrestrial mammals (Coté & Festa-Bianchet 2001*a*, Fessler et al. 2005; Michel et al. 2019; Hamel et al. 2012). There are multiple theories and explanations for the reduced reproductive success in primiparous females. First, females in many species begin to reproduce before reaching full adult size, and therefore first-time breeders usually have lower offspring growth rates and weaning mass (Lang et al. 2011*b*). Previous studies on grey seals have found an increase in pup size in second and third parity females compared to primiparous females (Bowen et al. 2006), thereby supporting the effect of breeding experience on maternal energy allocation found in this study.

Second, in some species, maternal behaviours take time to develop, and multiparous females show significant improvement in quality and intensity of maternal care behaviours than primiparous females (Gonzalez-Mariscal & Poindron 2002, Numan et al. 2006); for example in macaques, *Macaca fascicularis* (Timmermans & Vossen 1994) and prairie voles, *Microtus ochrogaster* (Wang & Novak 1994). Previous research on grey seals, however, has ruled out reduced maternal care behaviours as the cause for decreased primiparous performance (Lang et al. 2011*a*). However, primiparous females have significantly lower daily milk output than multiparous females (Lang et al. 2011*b*; Fowler et al. 1990, Miller et al. 2006, Yang et al. 1989), and it has been hypothesized that increased nursing time allows primiparous females to achieve similar energy transfer to multiparous grey seal females (Lang et al. 2011*a*) and macaques (Gomendio 1989, Tanaka 1997).

Third, primiparous females have less developed secretory cells in the mammary gland, and in general the cells may have less secretory activity throughout lactation than multiparous females (Lang et al. 2012). Repeated cycles of pregnancy and lactation play a vital role in development of the mammary gland (Wagner et al. 2002, Vonderhaar et al. 1978, Fowler et al. 1990, Wada & Turner 1959). In cattle, there has been an observed decrease in metabolic activity of mammary tissues in primiparous females compared with multiparous females (Miller et al. 2006). Growth of mammary gland structural tissues through juvenile life up to first reproductive event are correlated strongly with body size in grey seals (Cowie et al. 1980). Thus, females that are larger at their first reproductive event have larger mammary glands and larger milk output, which may explain some of the observed variation with parity (Lang et al. 2011*b*).

Table 1. Description of response variables and how each contributes to study objectives.

Response Variable	What it Measures
Total Maternal Mass Loss	Magnitude of allocation
Relative Maternal Mass Loss	Magnitude of allocation while accounting for differences in body size
Lactation Duration	Duration of allocation
Mass Transfer Efficiency	Fraction of maternal energy allocation retained by the pup
Pup Birth Mass	Prenatal allocation
Relative Pup Mass Gain	Offspring size relative to maternal postpartum mass
Pup Weaning Mass	Consequence of maternal energy allocation for offspring size

Table 2. The fixed and random effects (represented with a "+") and response variables included in each model.

	Maternal Post-partum Mass	Total Maternal Mass Loss	Maternal Age	I(Maternal Age ^2)	Parity	Lactation Duration	Pup Birth Mass	Pup Growth Rate	Pup Sex	Maternal Id
Total Maternal Mass Loss	+		+	+					+	+
Proportional Maternal Mass Loss			+			+	+			+
Lactation Duration	+		+	+			+	+	+	+
Mass Transfer Efficiency			+		+					+
Initial Pup Mass	+		+	+	+				+	+
Proportional Pup Mass Gain			+		+	+			+	+
Weaning Mass		+	+	+	+	+	+		+	+
Weaning Mass	+		+	+	+	+	+		+	+

Table 3. Top ten models from model selection of the total maternal mass loss model. Includes fixed effects from the maximum model, respective AIC, ΔAIC, weight values and number of parameters.

	Maternal Postpartum Mass	Female Age	I(Female Age^2)	Parity	Pup Sex	AICc	Δ AIC	Weight	Parameter Number
1	0.82	-0.05	-0.11	NA	+	568.59	0	0.52	6
2	0.82	-0.06	-0.1	NA	NA	570.98	2.39	0.16	5
3	0.82	-0.08	-0.09	+	+	572.07	3.48	0.09	8
4	0.9	-0.16	NA	NA	+	572.67	4.08	0.07	5
5	0.86	-0.19	NA	+	+	573.12	4.53	0.05	7
6	0.9	-0.16	NA	NA	NA	573.76	5.17	0.04	4
7	0.82	-0.1	-0.08	+	NA	574.17	5.58	0.03	6
8	0.86	-0.18	NA	+	NA	574.26	5.67	0.03	6
9	0.79	NA	NA	NA	+	579.57	10.98	0	4
10	0.78	NA	NA	NA	NA	580.35	11.76	0	3

Table 4. Coefficient estimates, standard errors and t-values for each variable included in the total maternal mass loss model (n = 324). CL = confidence limit.

Model covariates	Estimate	Std. Error	t value	2.5% CL	97.5% CL
(Intercept)	-16.04	4.42	-3.63	-24.94	-7.22
Maternal Mass at Parturition	0.44	0.03	13.97	0.38	0.51
Female Age	0.70	0.41	1.69	-0.13	1.51
I(Female Age ^2)	-0.03	0.01	-2.52	-0.05	-0.01
Pup Sex (female)	-2.19	1.03	-2.14	-4.24	-0.16

Table 5. Mean predicted values and corresponding standard deviations for each response variable by the corresponding model for three ages of females (6, 15 and 25).

	Age 6	Age 15	Age 25
Total Maternal Mass Loss (kg)	62.6 ± 7.0	80.6 ± 4.4	77.3 ± 12.6
Proportional Maternal Mass Loss	0.36 ± 0.03	0.40 ± 0.02	0.35 ± 0.04
Lactation Duration (days)	15.9 ± 1.3	17.4 ± 1.2	17.3 ± 1.3
Mass Transfer Efficiency	0.37 ± 0.02	0.35 ± 0.01	0.34 ± 0.01
Pup Birth Mass (kg)	19.5 ± 0.9	23.1 ± 0.3	22.7 ± 0.6
Proportional Pup Mass Gain	0.13 ± 0.02	0.14 ± 0.01	0.12 ± 0.01
Weaning Mass (Total Maternal Mass Loss) (kg)	42.6 ± 4.5	54.5 ± 3.10	47.9 ± 6.8

Table 6. Top ten models from model selection of the relative maternal mass loss model. Includes fixed effects from the maximum model, respective AIC, ΔAIC, weight values and number of parameters.

	Lactation Duration	Female Age	I(Female Age^2)	Parity	Pup Sex	Pup Birth Mass	AICc	Δ AIC	Weight	Parameter Number
1	0.03	-0.01	NA	NA	NA	0.02	-1162.2	0	0.34	5
2	0.03	-0.01	NA	NA	+	0.01	-1161.3	0.91	0.22	6
3	0.03	-0.01	0	NA	NA	0.02	-1160.5	1.72	0.15	6
4	0.03	-0.01	0	NA	+	0.02	-1159.4	2.84	0.08	7
5	0.03	-0.01	NA	+	NA	0.01	-1159.1	3.08	0.07	7
6	0.03	-0.02	0	+	NA	0.02	-1158.5	3.68	0.05	8
7	0.03	-0.01	NA	+	+	0.01	-1158.3	3.92	0.05	8
8	0.03	-0.02	0	+	+	0.01	-1157.2	4.99	0.03	9
9	0.02	NA	NA	NA	NA	0.01	-1141	21.17	0	4
10	0.02	NA	NA	NA	+	0.01	-1140.7	21.56	0	5

Table 7. Coefficient estimates, standard errors and t-values for each variable included in the relative maternal mass loss model (n = 324). CL = confidence limit.

Model covariates	Estimate	Std. Error	t value	2.5% CL	97.5% CL
(Intercept)	0.057	0.026	2.201	0.0106	0.108
Lactation Duration	0.015	0.001	11.548	0.012	0.017
Female Age	-0.002	0.000	-4.914	-0.002	-0.001
Pup Birth Mass	0.004	0.001	6.273	0.003	0.005

Table 8. Top ten models from model selection of the lactation duration model. Includes fixed effects from the maximum model, respective AIC, ΔAIC, weight values and number of parameters.

	Pup Growth Rate	Maternal Postpartum Mass	Female Age	I(Female Age^2)	Parity	Pup Sex	Pup Birth Mass	AICc	Δ AIC	weight	Parameter Number
1	-0.19	0.78	0.03	-0.23	NA	+	-0.39	728.16	0	0.7	8
2	-0.18	0.77	0.01	-0.21	NA	NA	-0.38	731.03	2.87	0.17	7
3	-0.19	0.78	0.01	-0.23	+	+	-0.4	732.08	3.92	0.1	10
4	-0.18	0.77	0	-0.2	+	NA	-0.38	734.87	6.71	0.02	9
5	-0.17	0.9	-0.19	NA	NA	+	-0.34	740.54	12.38	0	7
6	-0.16	0.88	-0.18	NA	NA	NA	-0.34	740.87	12.71	0	6
7	-0.19	0.87	-0.23	NA	+	+	-0.36	741.1	12.94	0	9
8	-0.18	0.85	-0.22	NA	+	NA	-0.36	741.71	13.55	0	8
9	NA	0.68	0.06	-0.2	NA	+	-0.41	742.65	14.49	0	7
10	NA	0.68	0.04	-0.18	NA	NA	-0.39	743.27	15.11	0	6

Table 9. Coefficient estimates, standard errors and t-values for each variable included in the lactation duration model (n = 324). CL = confidence limit.

Model covariates	Estimate	Std. Error	t value	2.5% CL	97.5% CL
(Intercept)	12.10	0.72	16.89	10.68	13.51
Pup Growth Rate	-0.88	0.21	-4.14	-1.30	-0.46
Maternal Postpartum Mass	0.05	0.01	9.89	0.04	0.06
Female Age	0.20	0.06	3.07	0.07	0.32
I(Female Age^2)	-0.01	0.00	-3.85	-0.01	-0.003
Pup Sex (female)	-0.35	0.15	-2.24	-0.66	-0.04
Pup Birth Mass	-0.20	0.02	-8.27	-0.25	-0.15

Table 10. Top ten models from model selection of the mass transfer efficiency model. Includes fixed effects from the maximum model, respective AIC, ΔAIC, weight values and number of parameters.

	Maternal Postpartum Mass	Female Age	I(Female Age^2)	Parity	Pup Sex	AICc	Δ AIC	Weight	Parameter Number
1	NA	-0.02	NA	+	NA	-882	0	0.23	5
2	NA	-0.02	NA	+	+	-881.95	0.05	0.23	6
3	0	-0.02	NA	+	+	-880.44	1.56	0.11	7
4	0	-0.02	NA	+	NA	-880.34	1.66	0.1	6
5	NA	-0.01	0	+	+	-879.99	2.01	0.09	7
6	NA	-0.02	0	+	NA	-879.93	2.07	0.08	6
7	NA	-0.01	-0.01	NA	+	-878.65	3.35	0.04	5
8	0.01	-0.02	NA	NA	+	-878.51	3.49	0.04	5
9	0.01	-0.02	NA	NA	NA	-878.35	3.65	0.04	4
10	0	-0.02	0	+	+	-878.33	3.67	0.04	8

Table 11. Coefficient estimates, standard errors and t-values for each variable included in the mass transfer efficiency model (n = 324). CL = confidence limit.

	Estimate	Std. Error	t value	2.5% CL	97.5% CL
(Intercept)	0.357	0.009	40.799	0.340	0.374
Female Age	-0.002	0.001	-3.483	-0.003	-0.001
Parity 2	0.030	0.014	2.153	0.003	0.058
Multiparous	0.032	0.012	2.765	0.009	0.055

Table 12. Top ten models from model selection of the pup birth mass model. Includes fixed effects from the maximum model, respective AIC, ΔAIC, weight values and number of parameters.

	Maternal Postpartum Mass	Female Age	I(Female Age^2)	Parity	Pup Sex	AICc	Δ AIC	Weight	Parameter Number
1	0.16	0.25	-0.3	+	+	807.62	0	0.52	8
2	NA	0.38	-0.36	+	+	809.64	2.02	0.19	7
3	0.18	0.4	-0.4	NA	+	810.2	2.58	0.14	6
4	0.15	0.23	-0.28	+	NA	811.56	3.94	0.07	7
5	NA	0.36	-0.33	+	NA	813.05	5.43	0.03	6
6	NA	0.57	-0.47	NA	+	813.37	5.75	0.03	5
7	0.18	0.39	-0.38	NA	NA	815.17	7.55	0.01	5
8	NA	0.55	-0.45	NA	NA	817.76	10.14	0	4
9	0.24	NA	NA	+	+	822.37	14.75	0	6
10	0.29	-0.09	NA	+	+	822.94	15.32	0	7

Table 13. Coefficient estimates, standard errors and t-values for each variable included in the initial pup mass model (n = 324).

	Estimate	Std. Error	t value	2.5% CL	97.5% C:
(Intercept)	12.63	1.42	8.91	9.84	15.42
Maternal Postpartum Mass	0.02	0.01	2.05	0	0.04
Female Age	0.6	0.16	3.88	0.3	0.91
I(Female Age^2)	-0.02	0	-4.25	-0.02	-0.01
Pup Sex (female)	-0.88	0.35	-2.51	-1.57	-0.18
Parity 2	0.68	0.74	0.92	-0.77	2.13
Multiparous	1.85	0.71	2.59	0.44	3.25

Table 14. Top ten models from model selection of the proportional pup mass gain model. Includes fixed effects from the maximum model, respective AIC, ΔAIC, weight values and number of parameters.

	Maternal Postpartum Mass	Lactation Duration	Female Age	I(Female Age^2)	Parity	Pup Sex	AICc	Δ AIC	Weight	Parameter Number
1	NA	0.01	-0.01	NA	+	+	-1533.26	0	0.5	6
2	0	0.01	-0.01	NA	+	+	-1531.34	1.92	0.19	8
3	NA	0.01	-0.01	0	+	+	-1531.33	1.93	0.19	8
4	0	0.01	-0.01	0	+	+	-1529.59	3.67	0.08	9
5	NA	0.01	-0.01	NA	+	NA	-1526.93	6.33	0.02	6
6	0	0.01	-0.01	NA	+	NA	-1525.33	7.93	0.01	7
7	NA	0.01	-0.01	0	+	NA	-1524.83	8.43	0.01	7
8	0	0.01	-0.01	0	+	NA	-1523.24	10.02	0	8
9	NA	0.01	0	0	NA	+	-1518.7	14.56	0	6
10	0	0.01	0	0	NA	+	-1516.61	16.65	0	7

Table 15. Coefficient estimates, standard errors and t-values for each variable included in the proportional pup mass gain model (n = 324). CL = confidence limit.

	Estimate	Std. Error	t value	2.5% CL	97.5% CL
(Intercept)	0.046	0.011	4.040	0.024	0.068
Lactation Duration	0.005	0.001	7.547	0.004	0.007
Female Age	-0.001	0.000	-6.304	-0.002	-0.001
Parity 2	0.017	0.005	3.281	0.007	0.027
Multiparous	0.022	0.004	5.156	0.014	0.030
Pup Sex (female)	-0.007	0.002	-2.924	-0.012	-0.002

Table 16. Top ten models from model selection of the weaning mass model. Includes fixed effects from the maximum model, respective AIC, ΔAIC, weight values and number of parameters.

	Lactation Duration	Female Age	I(Female Age^2)	Parity	Pup Sex	Pup Birth Mass	Total Maternal Mass Loss	AICc	Δ AIC	Weight	Parameter Number
1	0.09	-0.01	-0.1	+	+	0.34	0.47	482.61	0	0.44	10
2	NA	0.01	-0.11	+	+	0.3	0.54	484.8	2.19	0.15	9
3	0.11	-0.11	NA	+	+	0.37	0.48	485.02	2.41	0.13	9
4	0.09	-0.03	-0.08	+	NA	0.35	0.48	485.25	2.64	0.12	9
5	0.11	-0.11	NA	+	NA	0.37	0.49	486.01	3.4	0.08	8
6	NA	-0.01	-0.09	+	NA	0.31	0.55	487.83	5.22	0.03	8
7	NA	-0.1	NA	+	+	0.32	0.57	489.12	6.51	0.02	8
8	0.08	0.09	-0.16	NA	+	0.36	0.49	489.33	6.72	0.02	8
9	NA	-0.1	NA	+	NA	0.33	0.57	490.13	7.52	0.01	7
10	0.1	NA	NA	+	+	0.36	0.46	490.14	7.53	0.01	8

Table 17. Coefficient estimates, standard errors and t-values for each variable included in the weaning mass model (n = 323). CL = confidence limit.

	Estimate	Std. Error	t value	2.5% CL	97.5% CL
(Intercept)	2.55	3.11	0.82	-3.65	8.75
Lactation Duration	0.39	0.19	2.04	0.01	0.77
Female Age	0.33	0.21	1.57	-0.09	0.75
I(Female Age^2)	-0.01	0.01	-2.12	-0.02	-0.001
Parity 2	2.52	0.99	2.55	0.58	4.46
Multiparous	3.24	1.00	3.25	1.26	5.22
Pup Sex (female)	-1.07	0.48	-2.24	-2.00	-0.13
Pup Birth Mass	0.78	0.09	9.07	0.61	0.95
Total Female Mass Loss	0.25	0.03	9.47	0.20	0.30

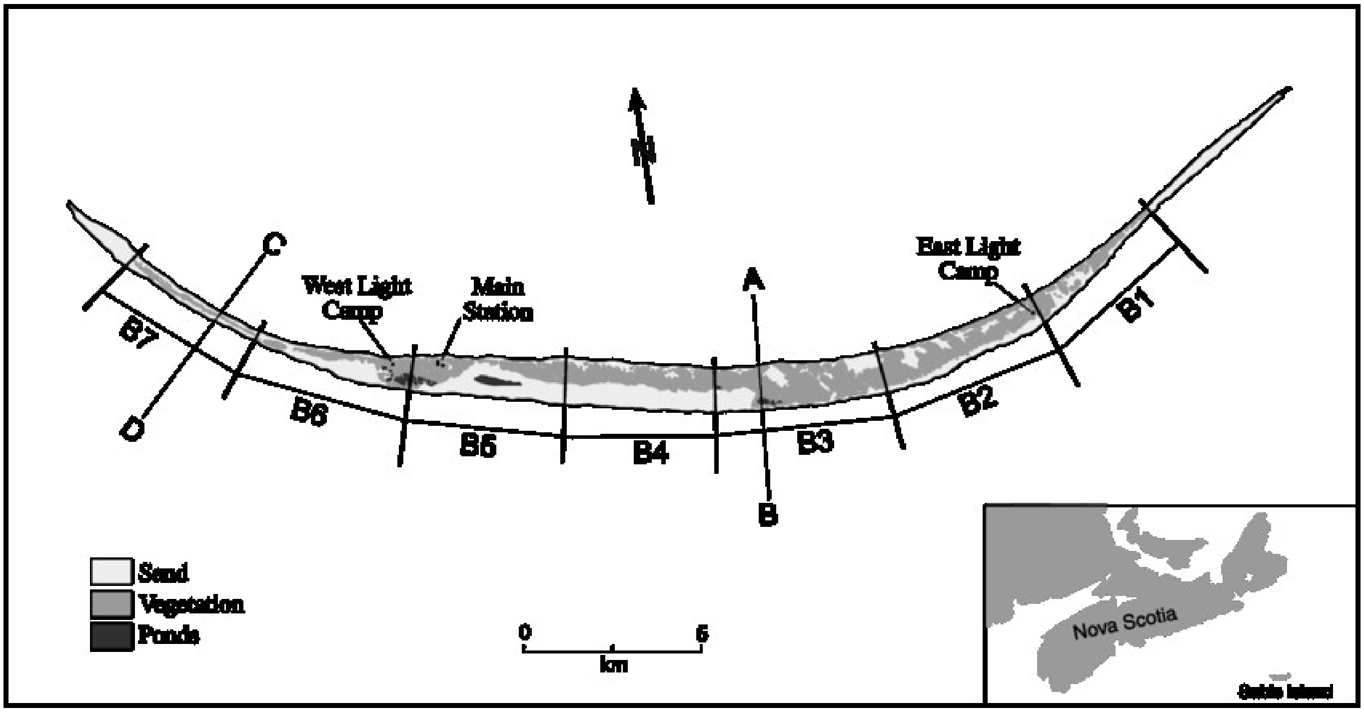

Figure 1. Map and geographic location of Sable Island, Nova Scotia.

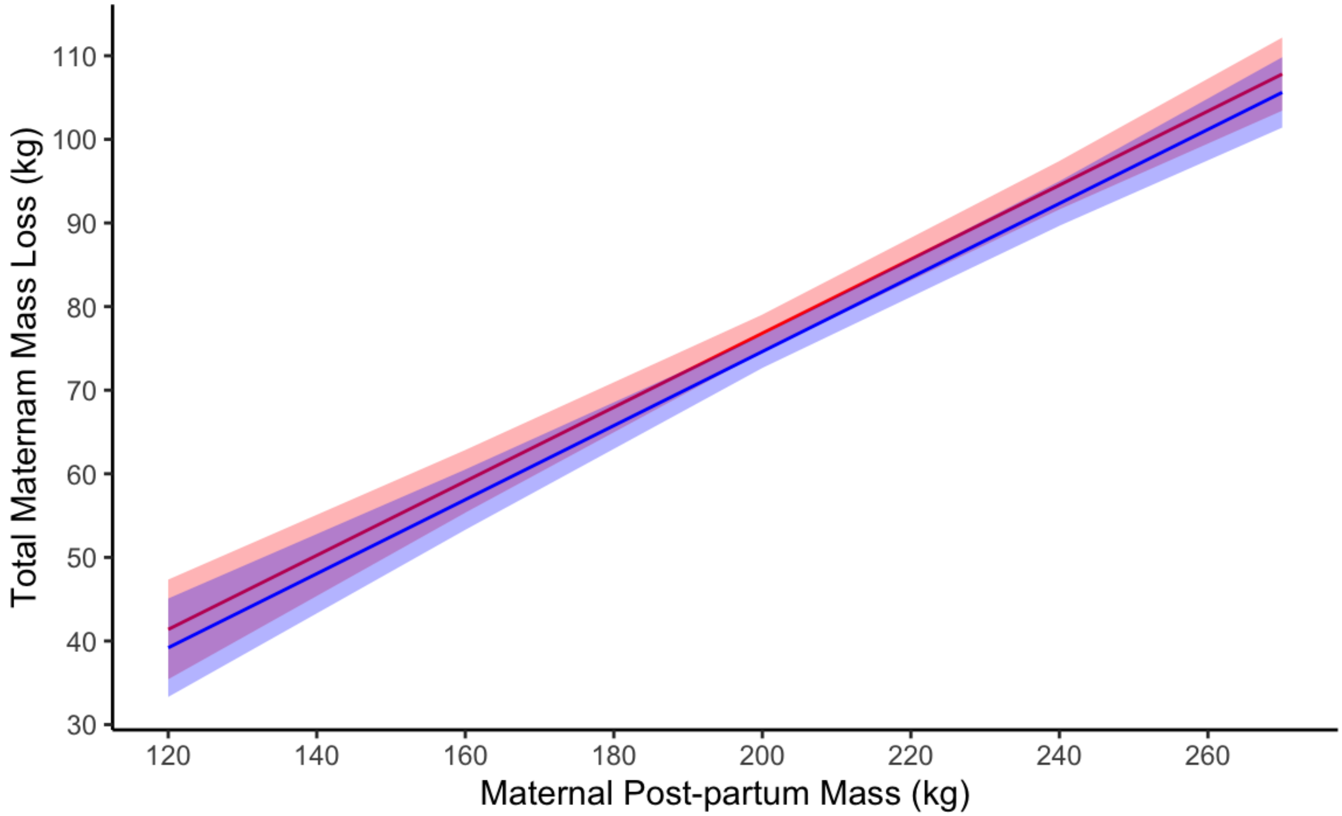

Figure 2. Predicted total maternal mass loss with 95% confidence intervals (shaded bands) for 324 observations of 222 females plotted against maternal postpartum mass. Separate lines for male (red) and female (blue) pups.

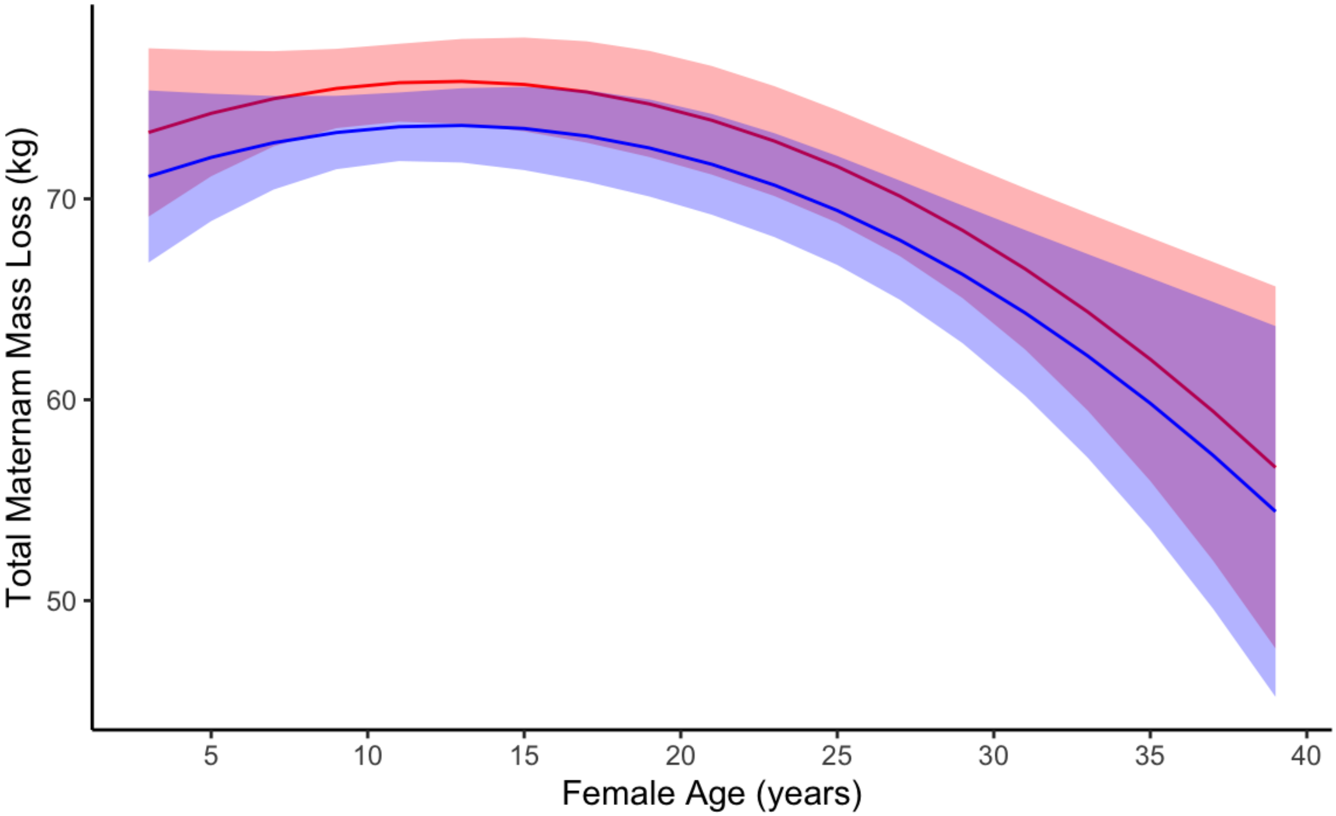

Figure 3. Total maternal mass loss model predictions and 95% confidence intervals (shaded bands) for 324 observations of 222 females plotted against female age with predictions for male (red) and female (blue) pups .

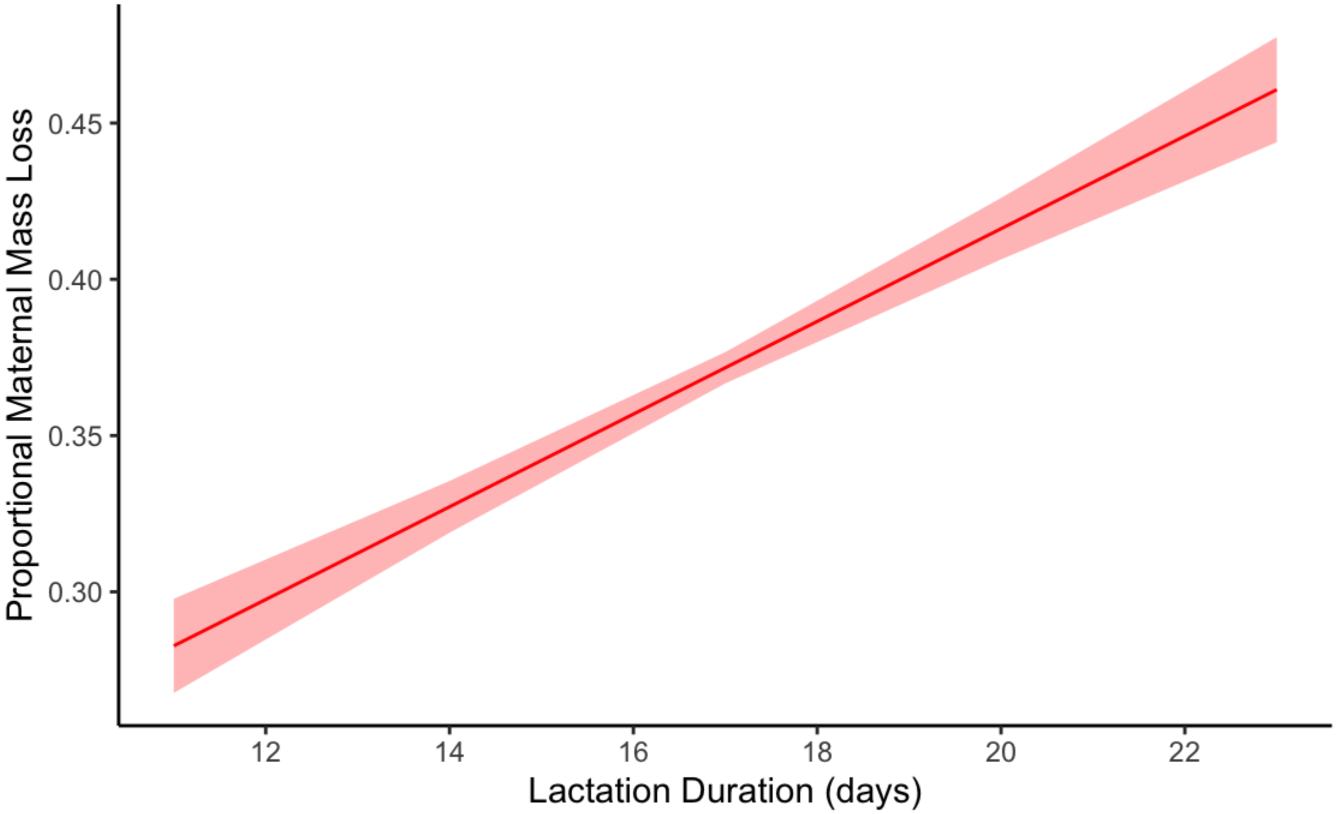

Figure 4. Proportional maternal mass loss model predictions and 95% confidence intervals (shaded band) for 324 observations of 222 females plotted against lactation duration .

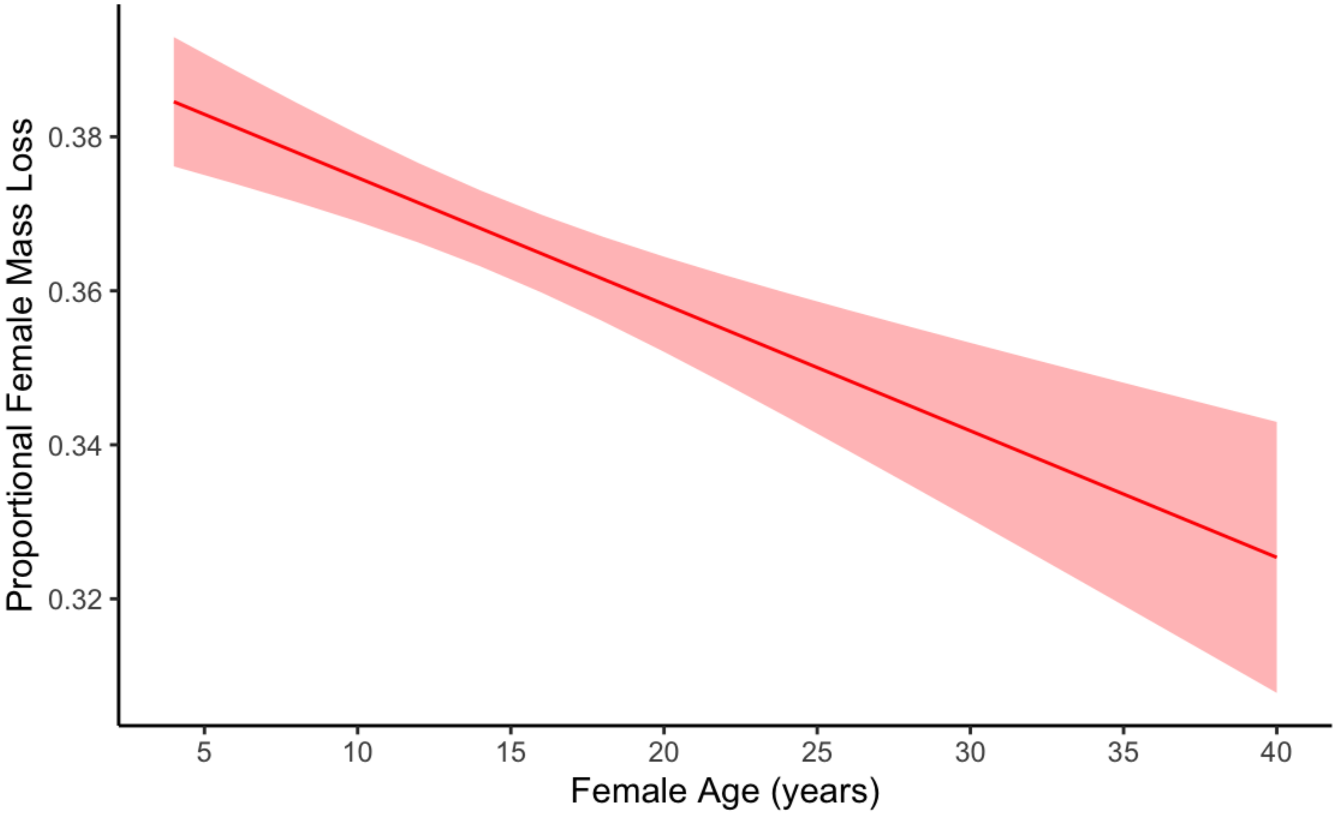

Figure 5. Proportional maternal mass loss model predictions and 95% confidence intervals (shaded band) for 324 observations of 222 females plotted against female age .

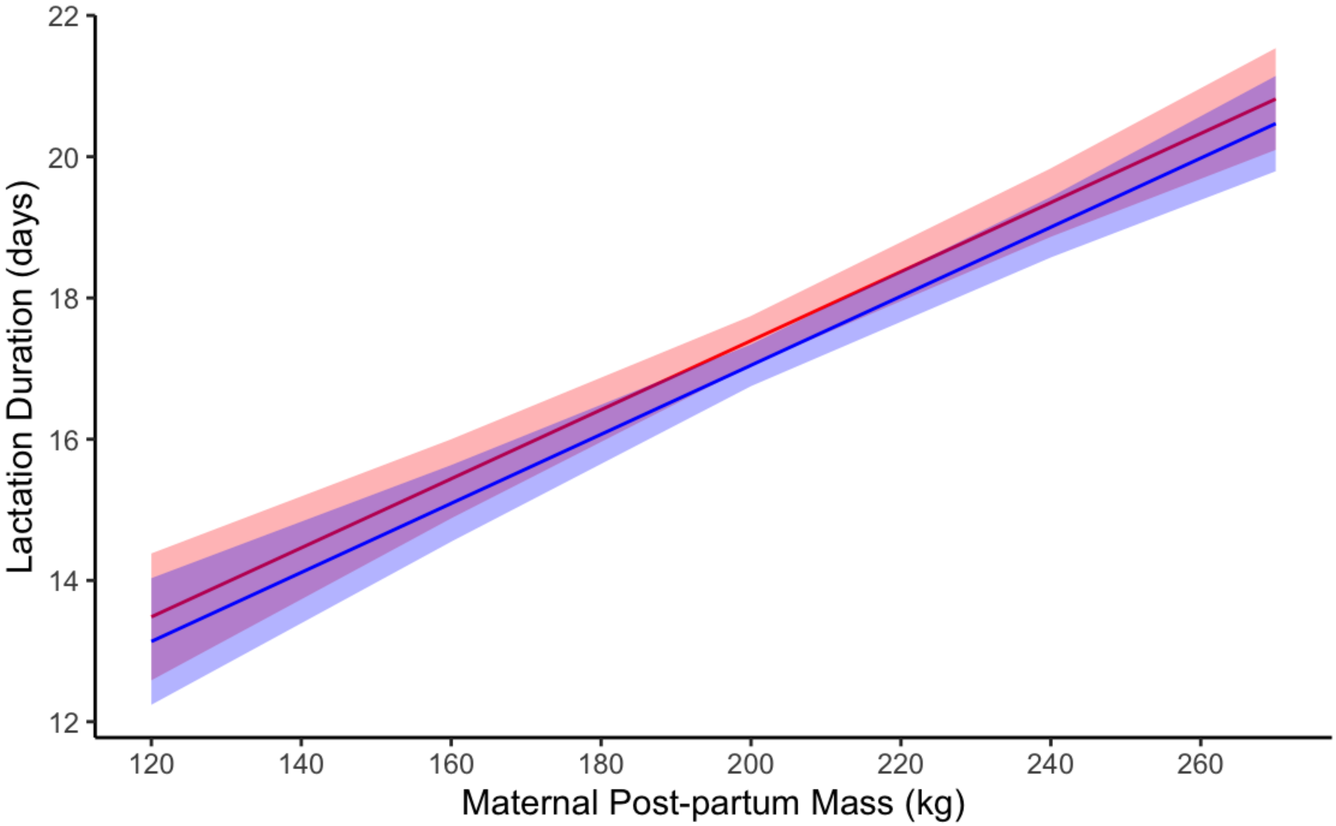

Figure 6. Lactation duration model predictions and 95% confidence intervals (shaded bands) for 324 observations of 222 females plotted against maternal postpartum mass. Separate lines for male (red) and female (blue) pups .

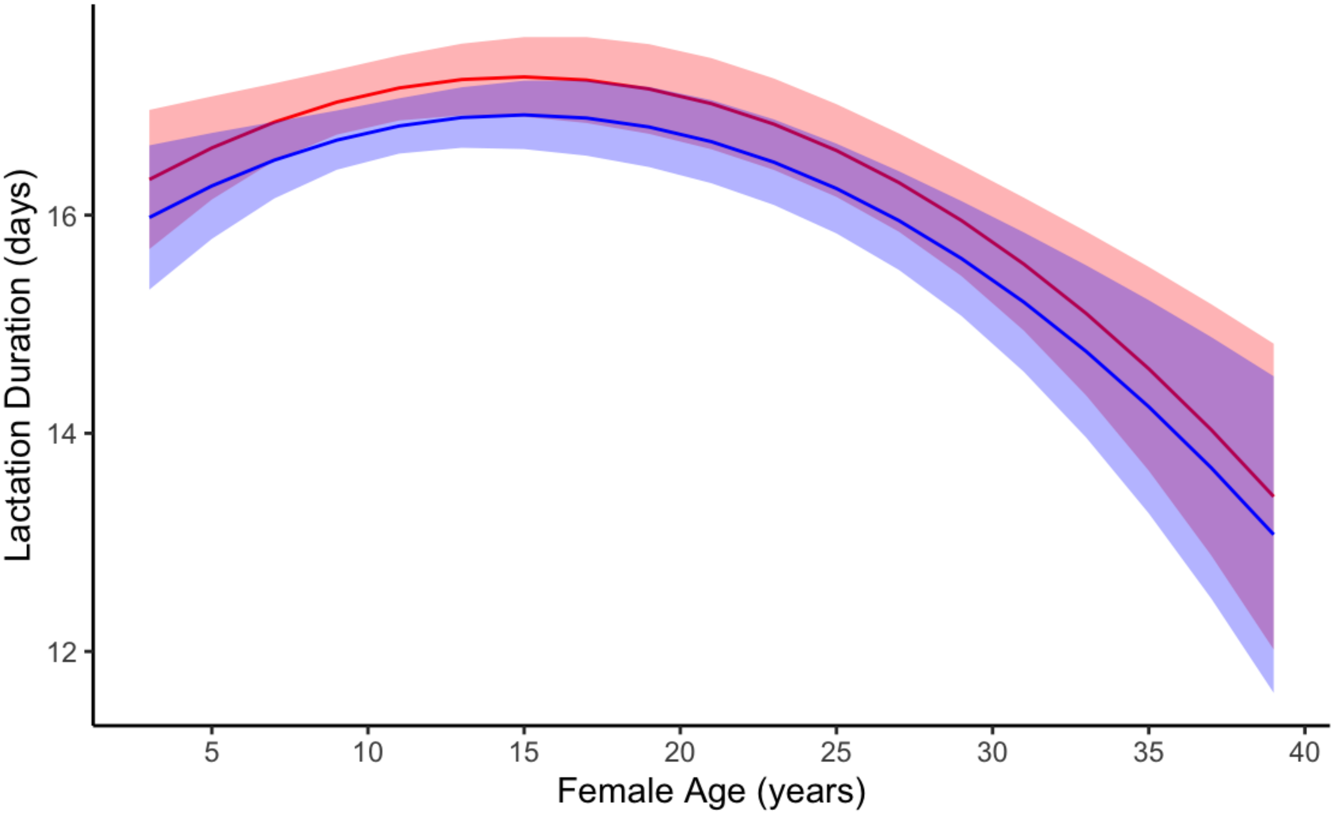

Figure 7. Lactation duration model predictions and 95% confidence intervals (shaded bands) for 324 observations of 222 females plotted against female age for male (red) and female (blue) pups .

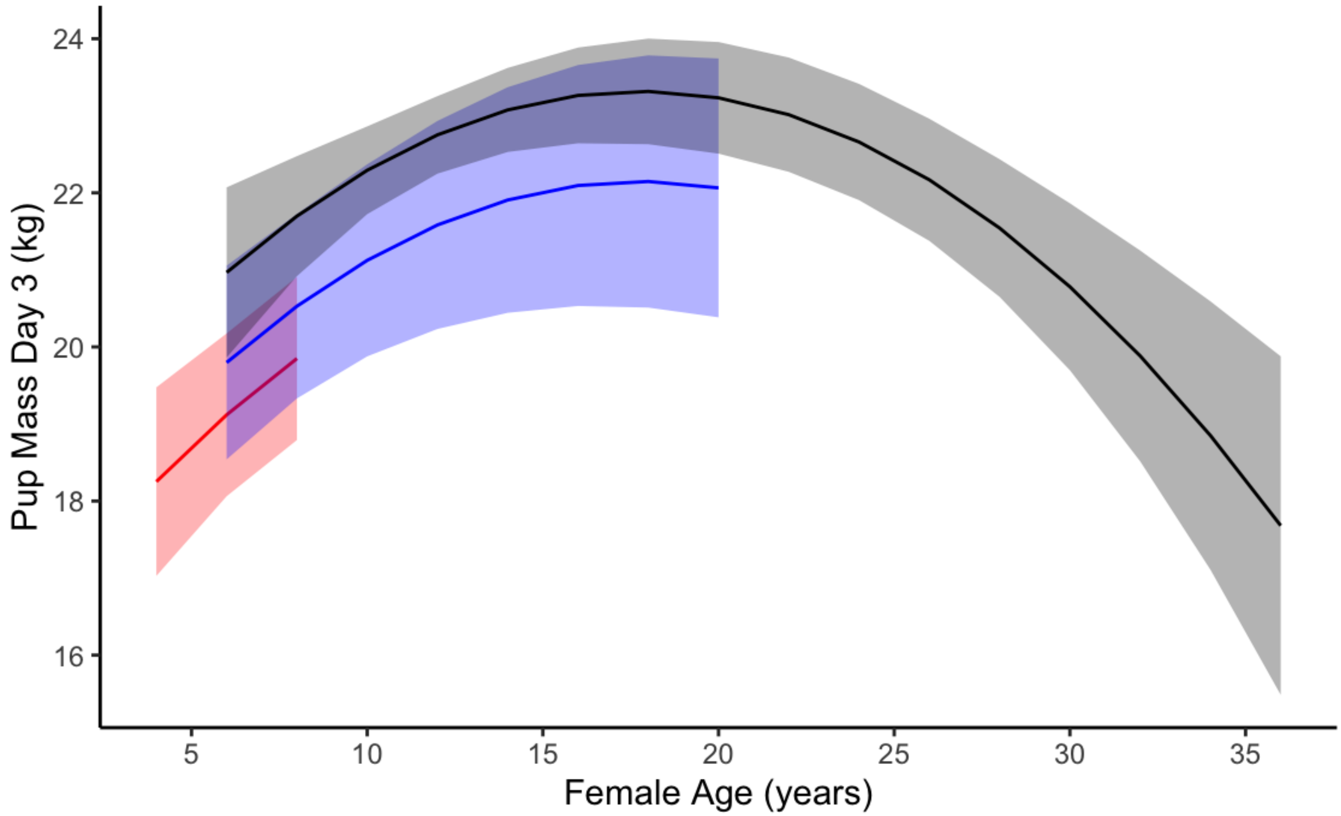

Figure 8. Birth mass model predictions and 95% confidence intervals (shaded bands) for 324 observations of for pups from 222 females plotted against female age with predictions for primiparous (red), parity 2 (blue) and multiparous 3+ (black) females.

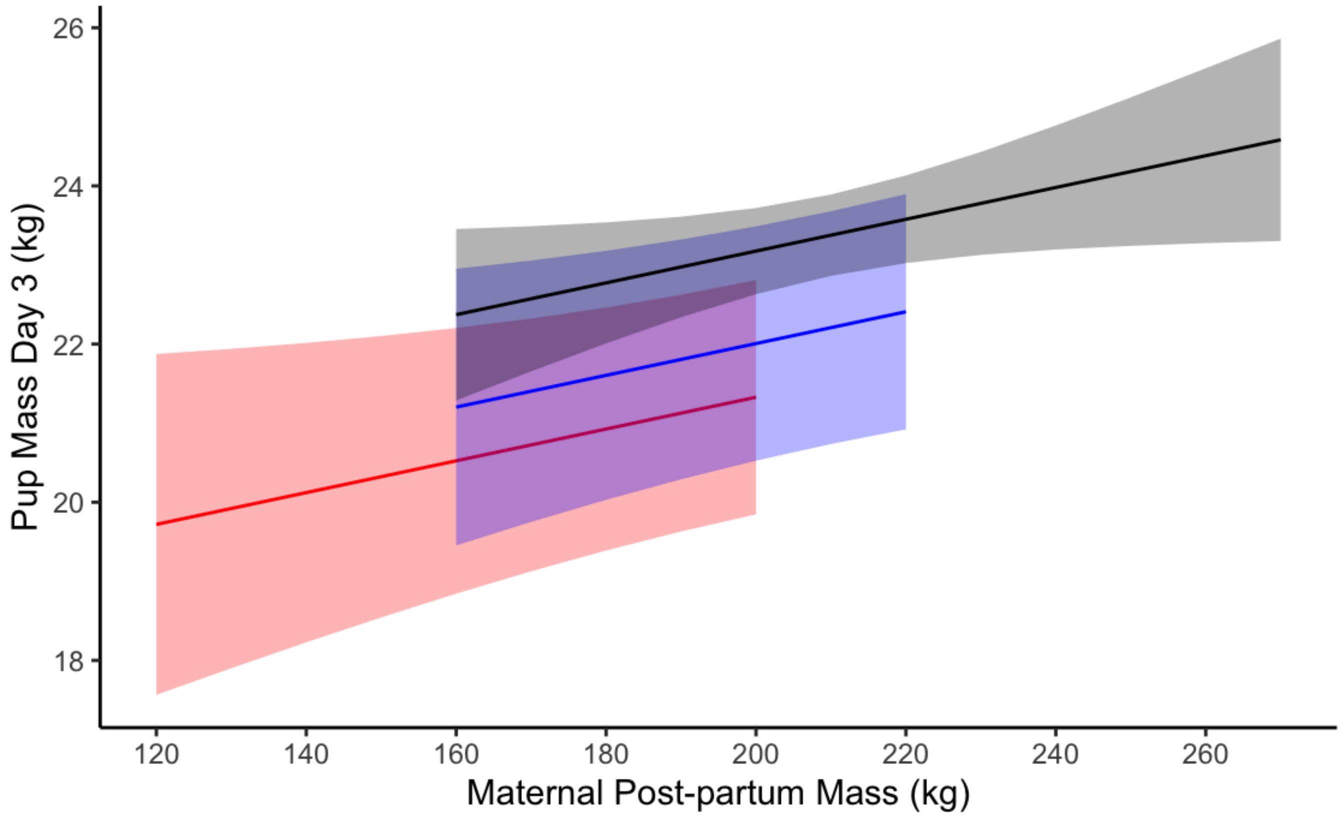

Figure 9. Birth mass model predictions and 95% confidence intervals (shaded bands) for 324 observations of pups from 222 females plotted against maternal postpartum mass with predictions for primiparous (red), parity 2 (blue) and multiparous 3+ (black) females .

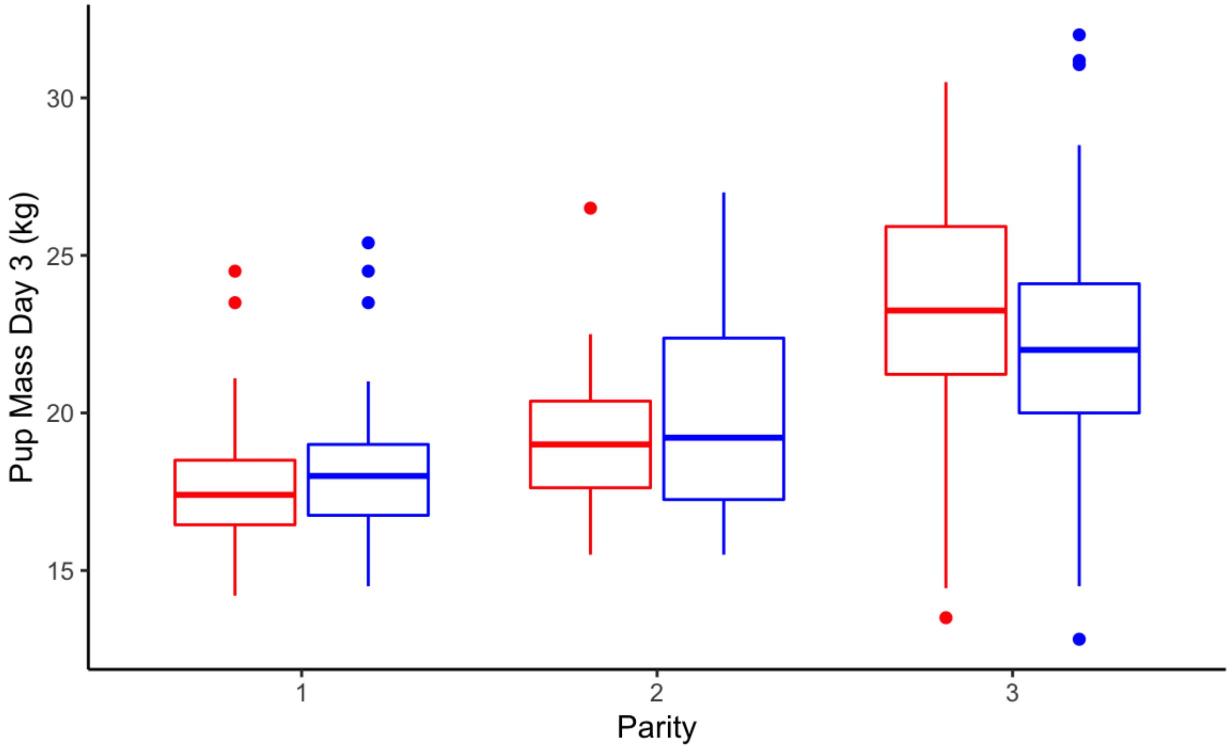

Figure 10. Box and whisker of birth mass of 324 pups from 222 females plotted against parity with pup sex (red: male pups; blue: female pups),. Median is represented by the heavy horizontal line.

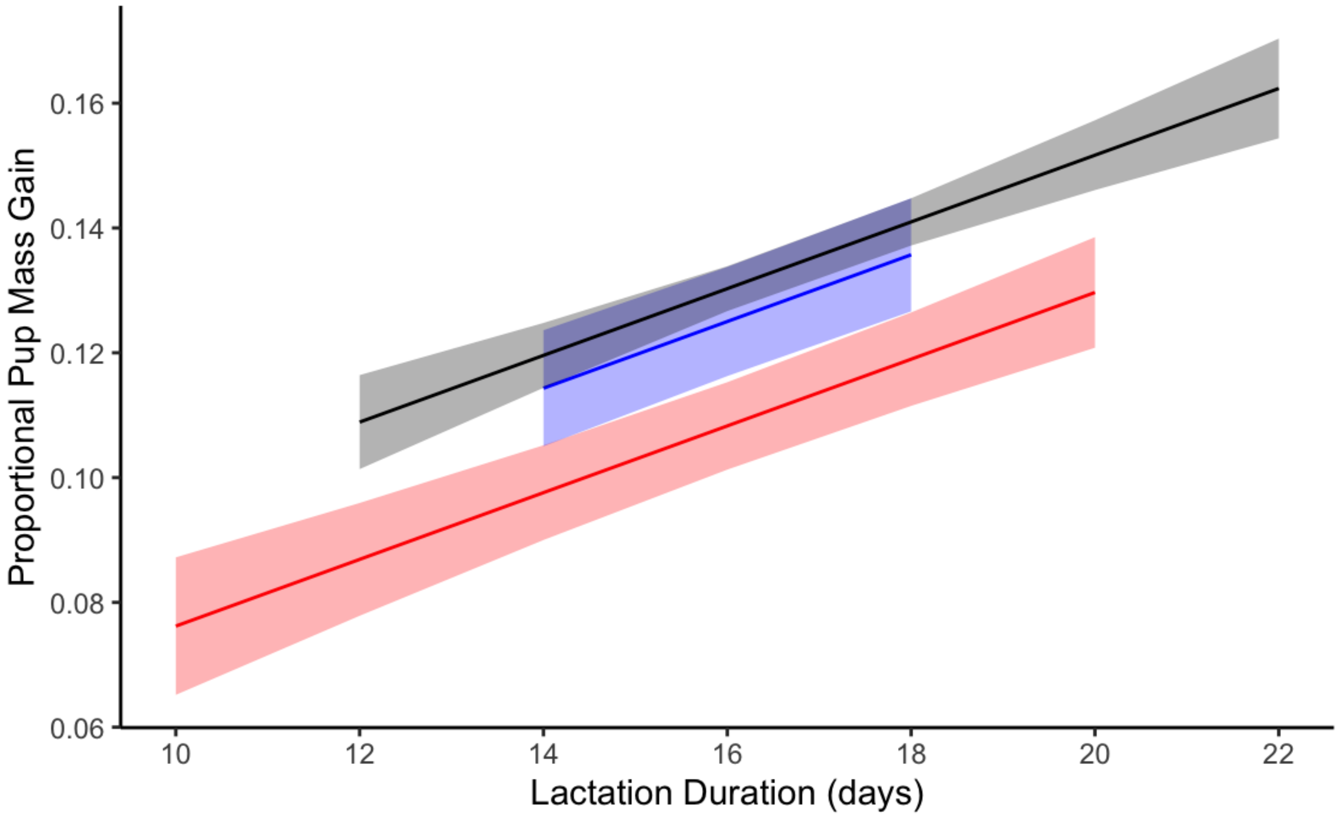

Figure 11. Proportional pup mass gain model predictions and 95% confidence intervals (shaded bands) for 324 observations of pups from 222 females plotted against lactation duration with predictions for primiparous (red), parity 2 (blue) and multiparous (black) females .

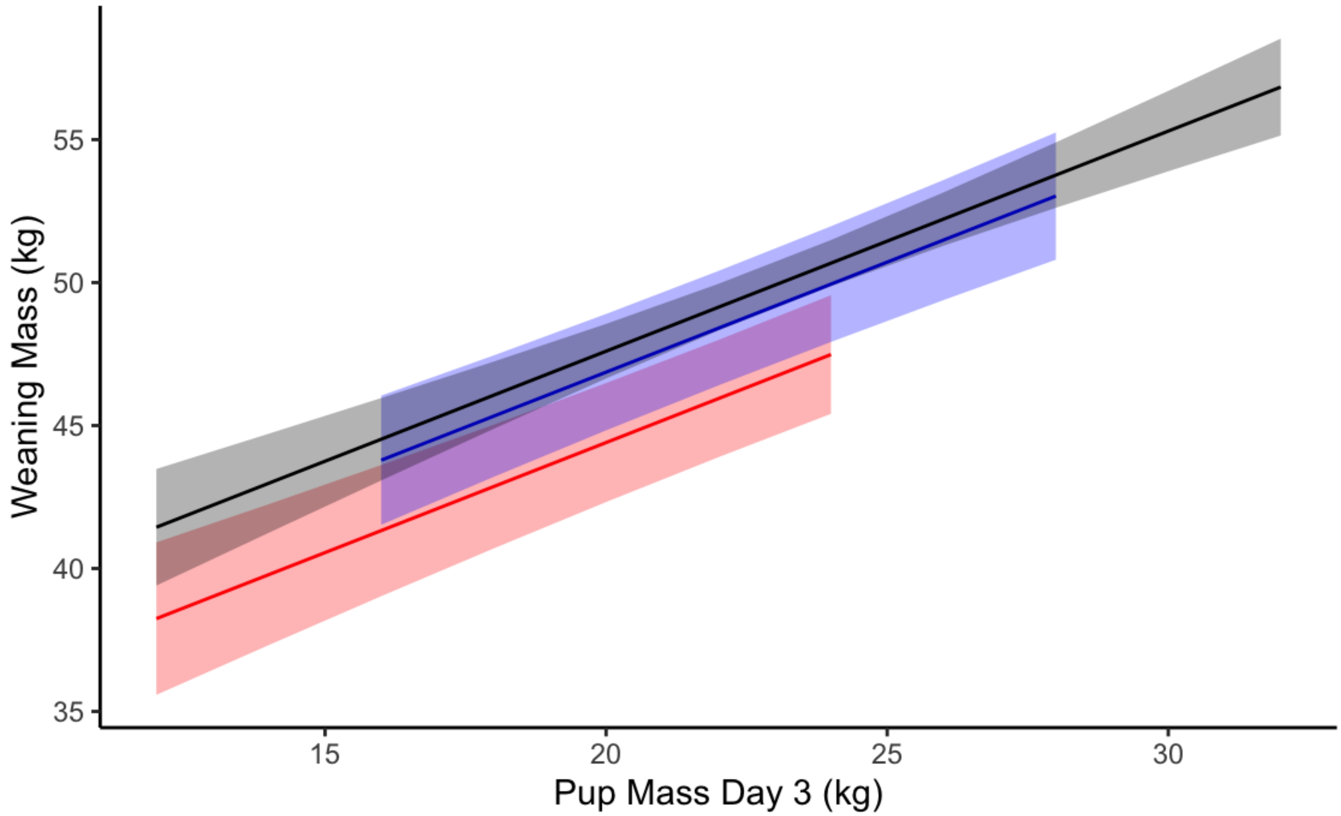

Figure 12. Weaning mass model predictions and 95% confidence intervals (shaded bands) for 324 observations of pups from 222 females plotted against pup birth mass with predictions for primiparous (red), parity 2 (blue) and multiparous (black) females .

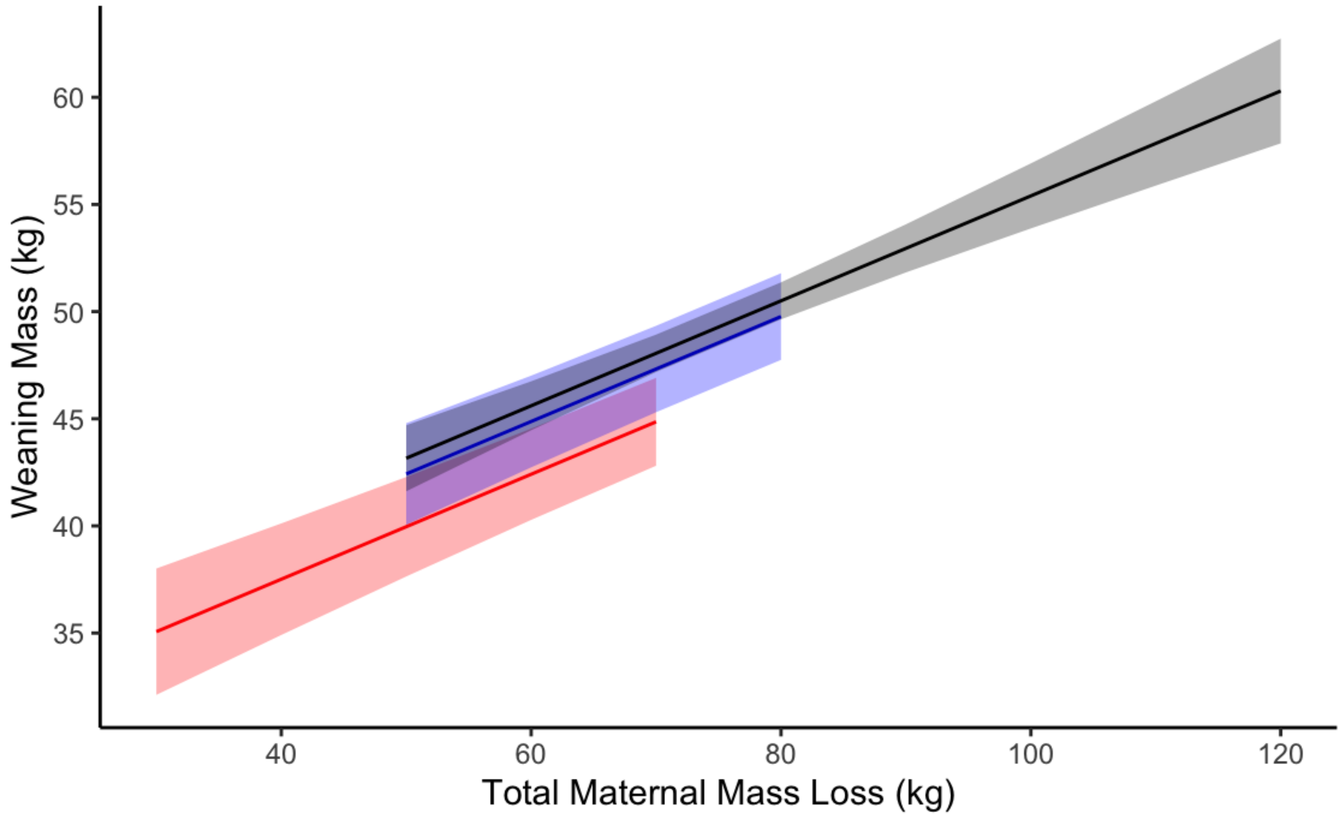

Figure 13. Weaning mass model predictions and 95% confidence intervals (shaded bands) for 324 observations of pups from 222 females plotted against total maternal mass loss with predictions for primiparous (red), parity 2 (blue) and multiparous (black) females .

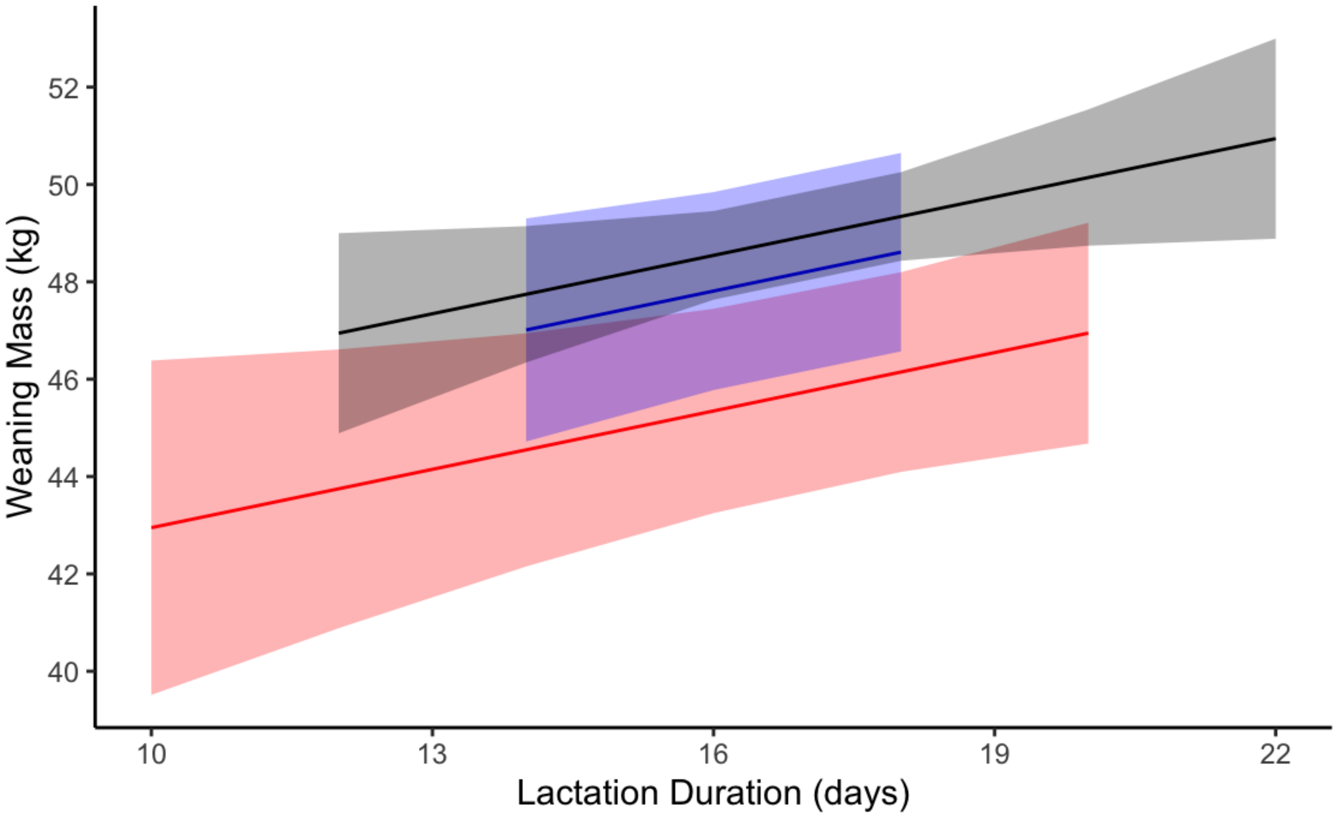

Figure 14. Weaning mass model predictions and 95% confidence intervals (shaded bands) for 324 observations of pups from 222 females plotted against lactation duration with predictions for primiparous (red), parity 2 (blue) and multiparous (black) females .

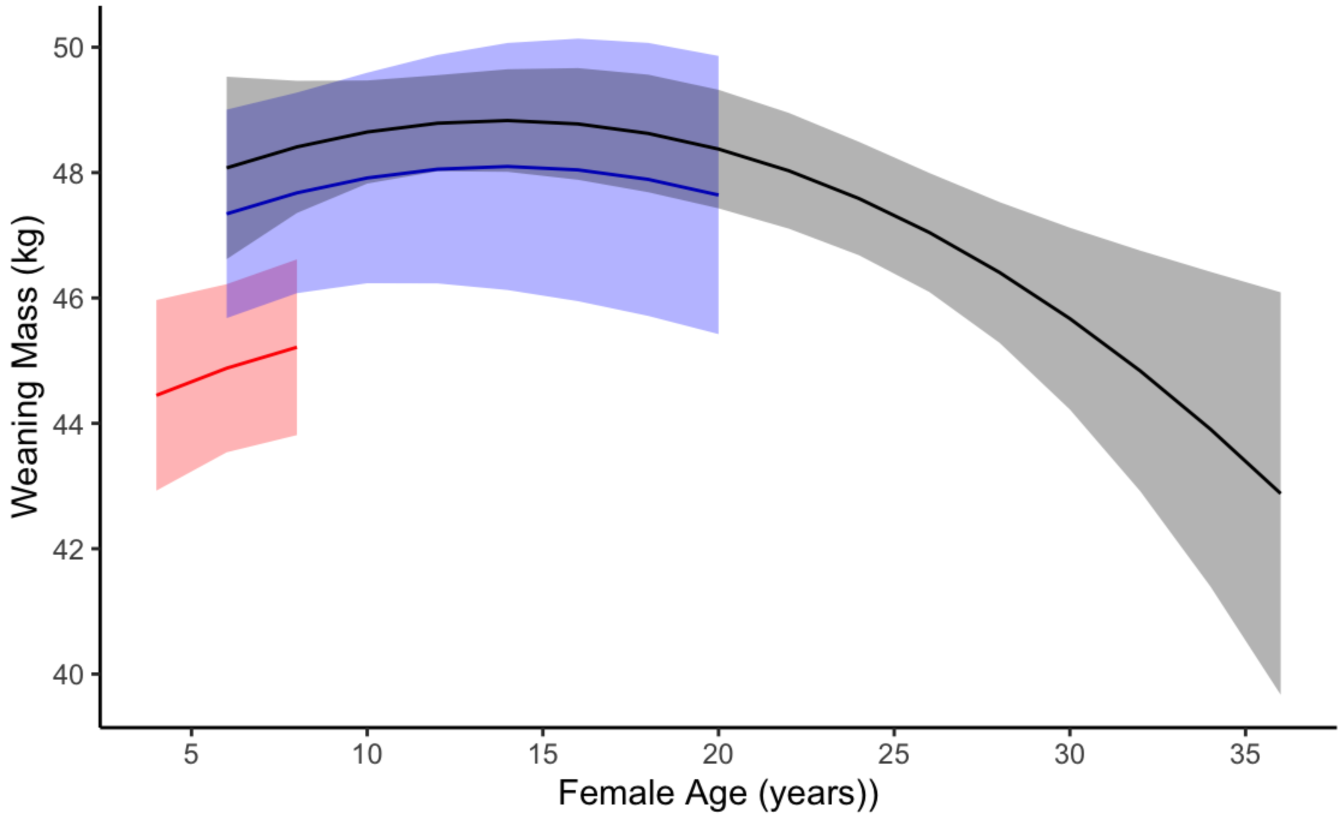

Figure 15. Weaning mass model predictions and 95% confidence intervals (shaded bands) for 324 observations of pups from 222 females plotted against female age with predictions for primiparous (red), parity 2 (blue) and multiparous (black) females.

Chapter 3: Conclusion

My study investigated how maternal and offspring characteristics influenced maternal allocation in a capital breeding phocid, the grey seal. Allocation was measured though six response variables related to measures of maternal energy allocation. Given that offspring weaning mass is commonly used to infer the magnitude of maternal energy allocation in capital breeders (e.g., Fedak et al. 1996**,** Arnbom et al. 1997, Lang et al. 2009**)**, my study examined the relationship between total maternal mass loss and weaning mass to evaluate this hypothesis.

My study highlighted that maternal postpartum mass is the major influence of the magnitude and duration of maternal energy allocation in grey seals. This was an expected finding given previous research on the importance of maternal resource availability (expressed as maternal mass) in capital breeders (Millar 1977, Eisenberg 1981, Calder 1984, Millar 1984, Schmidt-Nielson 1984, Gittleman 1986, Martin & Festa-Bianchet 2010). My study also revealed that maternal energy allocation varies with female age. In almost all aspects of maternal allocation investigated in my study, female age followed the same pattern of increase early in life, reaching a plateau in the mid-teens and an eventual decline later in life. The effect of breeding experience has been examined thoroughly in pinnipeds and most significant differences have been found between primiparous and multiparous females, which is supported by the results of this study.

Multiple aspects of maternal energy allocation were explained by lactation duration, suggesting that energy allocation to offspring is a function of resource availability and duration of allocation. There were several pup characteristics found to be important to predicting maternal allocation. Namely, pup sex revealed that male pups receive greater allocation than female pups and the effect of pup birth mass illustrated that pups with greater prenatal allocation would receive greater postnatal allocation.

Finally, there was a strong correlation between weaning mass and total maternal mass loss suggesting that weaning mass is a reasonable estimate of maternal allocation. However, the difference between total maternal mass loss and pup weaning mass increased with larger females. Future studies aiming to use weaning mass as a measure of allocation should have suitable female mass distributions and understand that allocation will be underestimated in larfer females.

It is important to note that while females spend most of lactation idle, there is energy being used by females for body maintenance, movement and increased aggressive encounters with males and other females, especially in late lactation (Boness et al. 1995, Haller et al. 1996). Thus, not all energy lost by the female during the lactation period can be strictly defined as allocation to offspring.

Significance

Maternal allocation represents a trade-off between weaning mass (future survival and fitness of the offspring) and consequences of maternal cost (Rogowitz 1996). Therefore, understanding the predictors and consequences of maternal energy allocation are important for several reasons. First, studies on capital breeders can offer an understanding of reproductive strategies employed by other terrestrial and aquatic capital breeders. Second, because large-non captive mammals are difficult to study in their own environment, the energetics of such animals are poorly understood (Iverson et al. 2010). Therefore, existing and current research that offers insight into the energetic costs of life history strategies of such animals is important. Finally, the consequence of maternal energy allocation is represented in the offspring weaning mass. Offspring weaning mass is tightly correlated with fitness and survival in adult life (Coté et al. 2001*b,* Ellis et al. 2000). Additionally, in long-lived mammals and birds, the period of maternal allocation is especially crucial because offspring mortality is much higher than adult mortality (Gaillard et al. 2000). Since offspring survival often drives population dynamics of long-lived species, it is important to understand the factors influencing offspring survival (Ozgul et al. 2010, Hamel et al. 2012).

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Appendix A: Supplementary Tables

Appendix B: Supplementary Figures

Table A 1 The maximum models for the lactation duration model and the mass transfer efficiency model. Where i is mom and j is pup. The response variables were modeled as random normal variables ($\varepsilon_{ij} = N(0, \delta^2)$). To account for variation among females, maternal ID was included as a random effect (γ_i=N(0, d^2).

Maximum Model	
Lactation Duration	Lactation Duration$_{ij}$ ~ $\beta_{Female\ Age}$ * Female Age$_{ij}$+ $\beta_{Female\ Age^2}$ I(Female Age$_{ij}^2$) +$\beta_{Maternal\ Mass\ at\ Parturition}$ * Maternal Mass at Parturition$_{ij}$ + $\beta_{Pup\ Birth\ Mass}$ *Pup Birth Mass + $\beta_{Pup\ Sex}$ * Pup Sex$_{ij}$ + $\beta_{Pup\ Growth\ Rate}$ *Pup Growth Rate ++ γ_j +
Mass Transfer Efficiency	Mass Transfer Efficiency$_{ij}$ ~ β_{Parity} * Parity$_{ij}$+ $\beta_{Female\ Age}$ * Female Age$_{ij}$+ $\beta_{Female\ Age^2}$ I(Female Age$_{ij}^2$) ++ γ_j + ε_{ij}

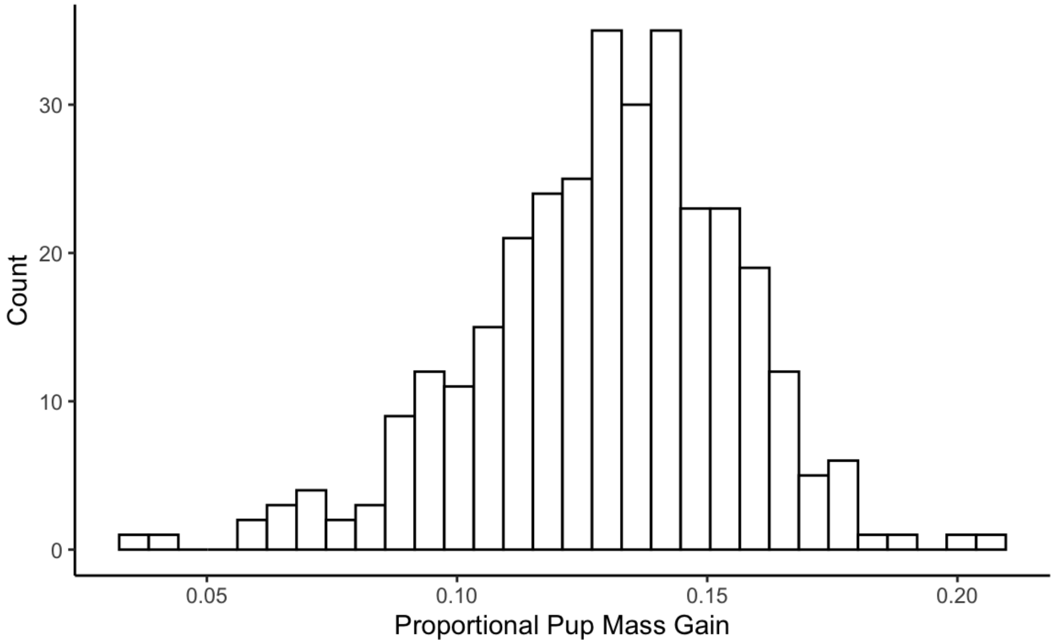

Figure A1. Distribution of proportional mass gain of pups from 222 females (n = 325).

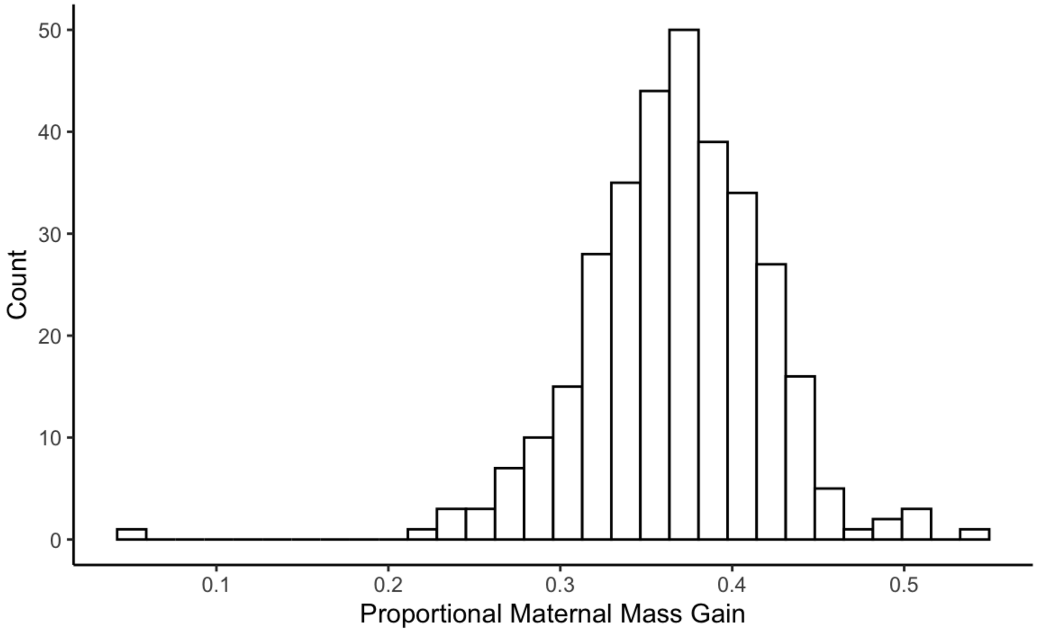

Figure A2, Distribution of proportional maternal mass gain of 222 females (n = 325).

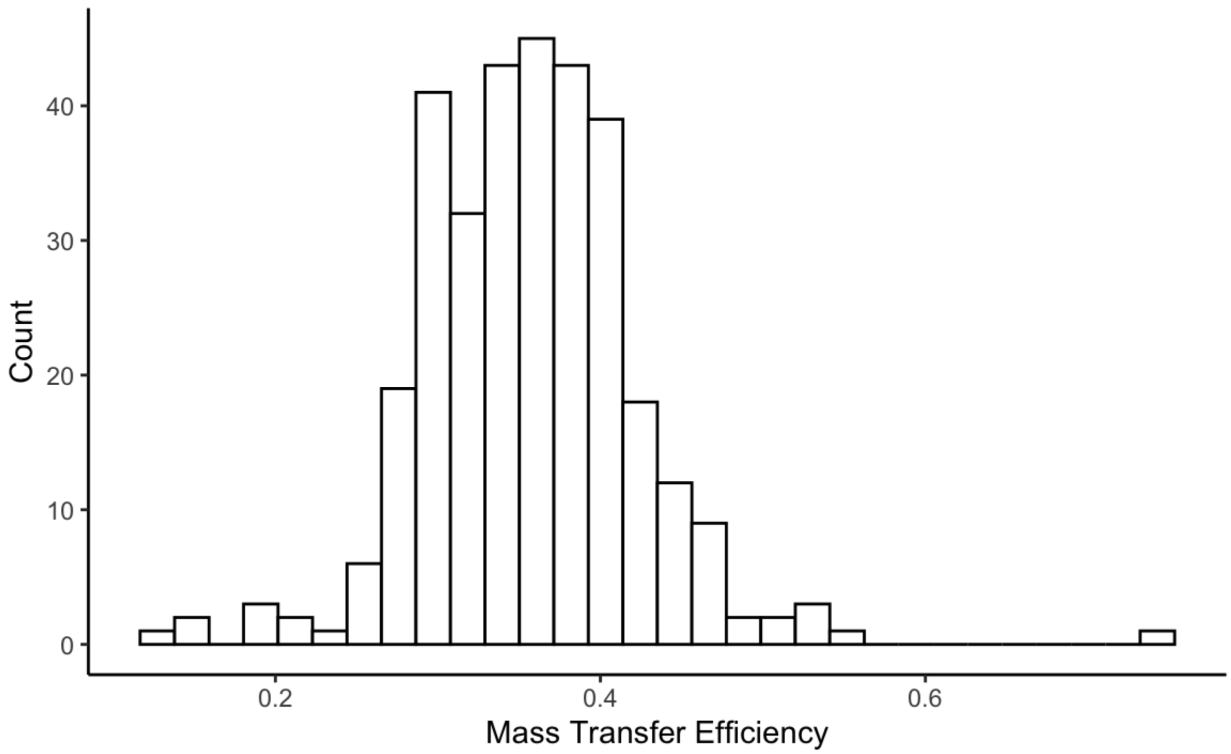

Figure A3. Distribution of mass transfer efficiency from 222 females (n = 325).

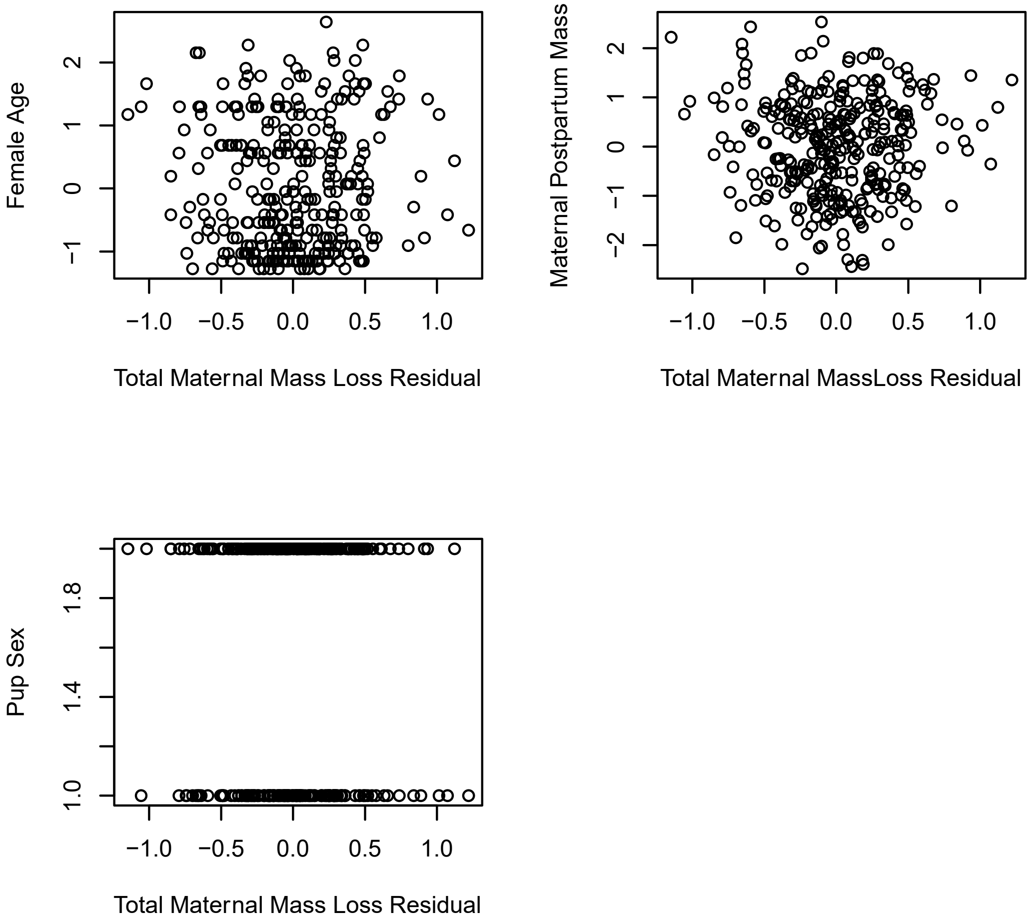

Figure A4. Total maternal mass loss model residuals plotted against the fixed effects (female age, maternal postpartum mass, pup sex) in the model (n = 324).

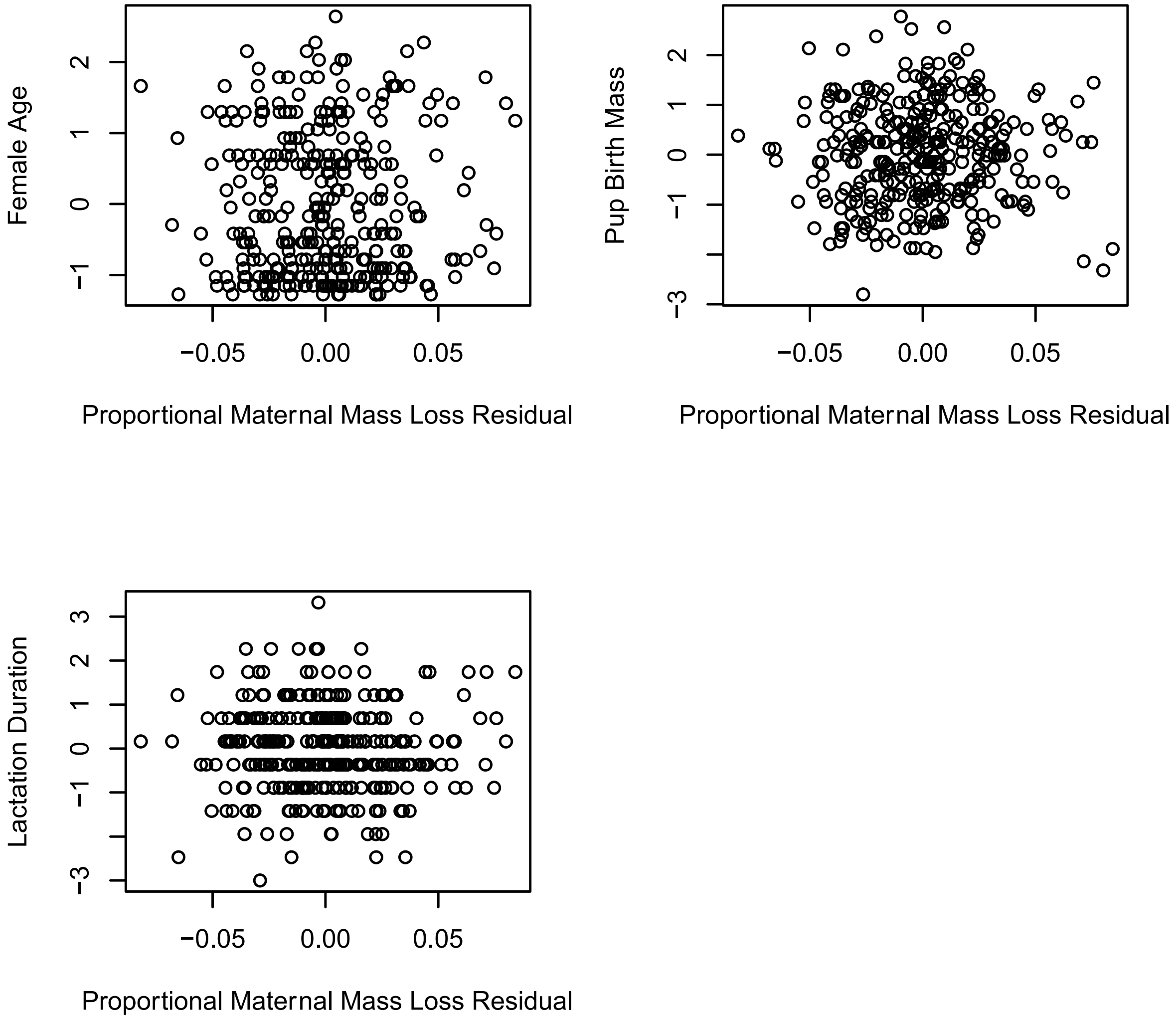

Figure A5. Proportional maternal mass loss model residuals plotted against the fixed effects (female age, pup birth mass, and lactation duration) in the model (n = 324).

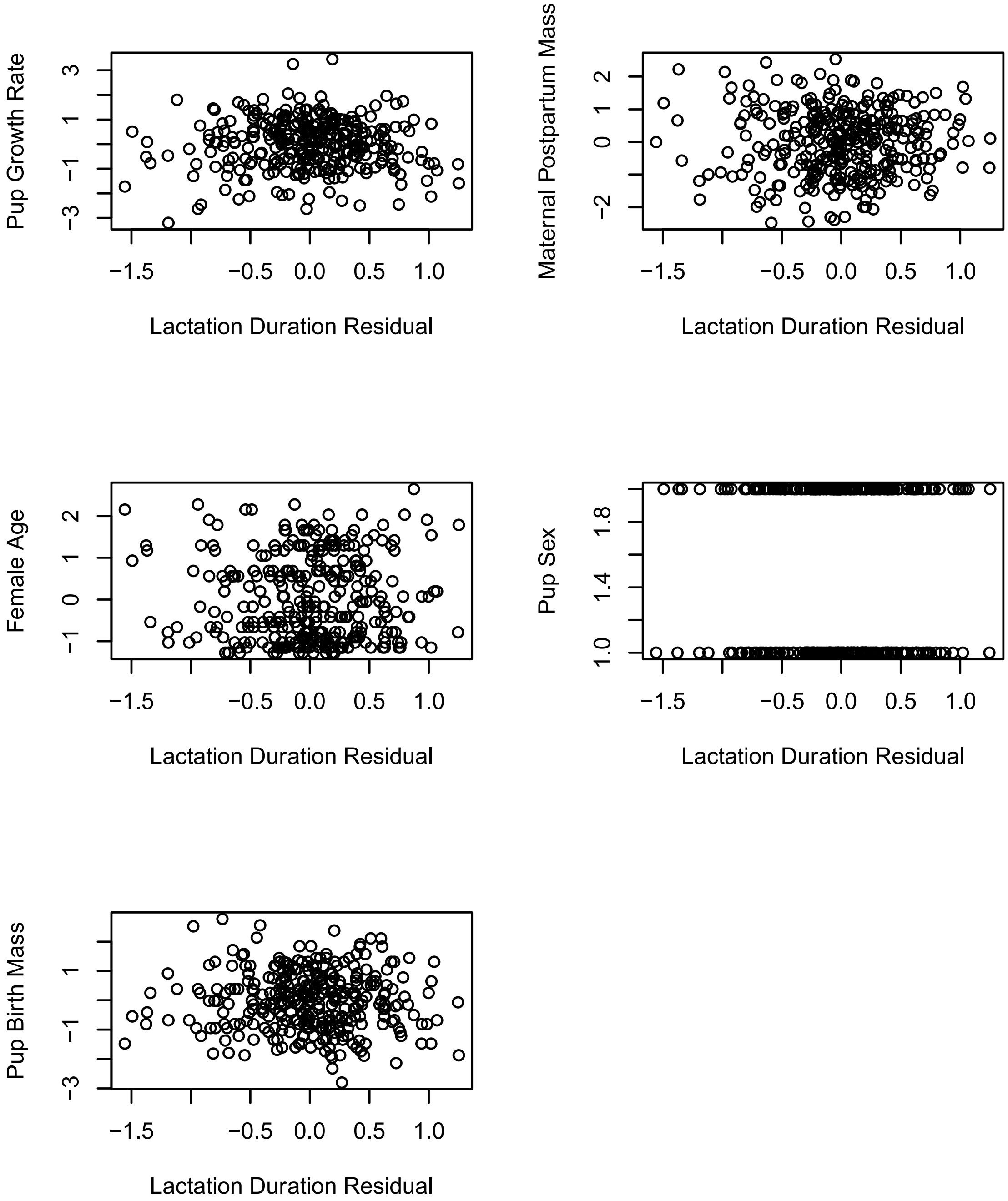

Figure A6. Lactation duration model residuals plotted against the fixed effects (pup growth rate, maternal postpartum mass, female age, pup sex, pup birth mass)) in the model (n = 324).

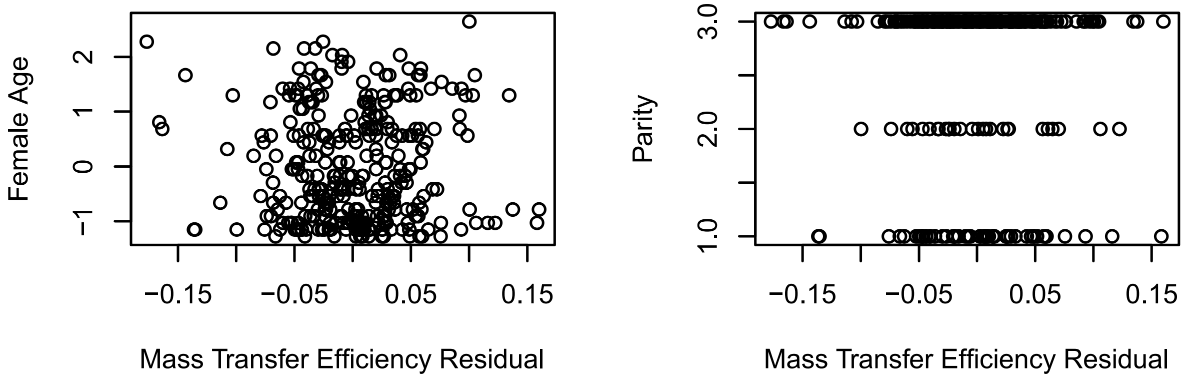

Figure A7. Mass transfer efficiency model residuals plotted against the fixed effects (female age, and parity) in the model (n = 324).

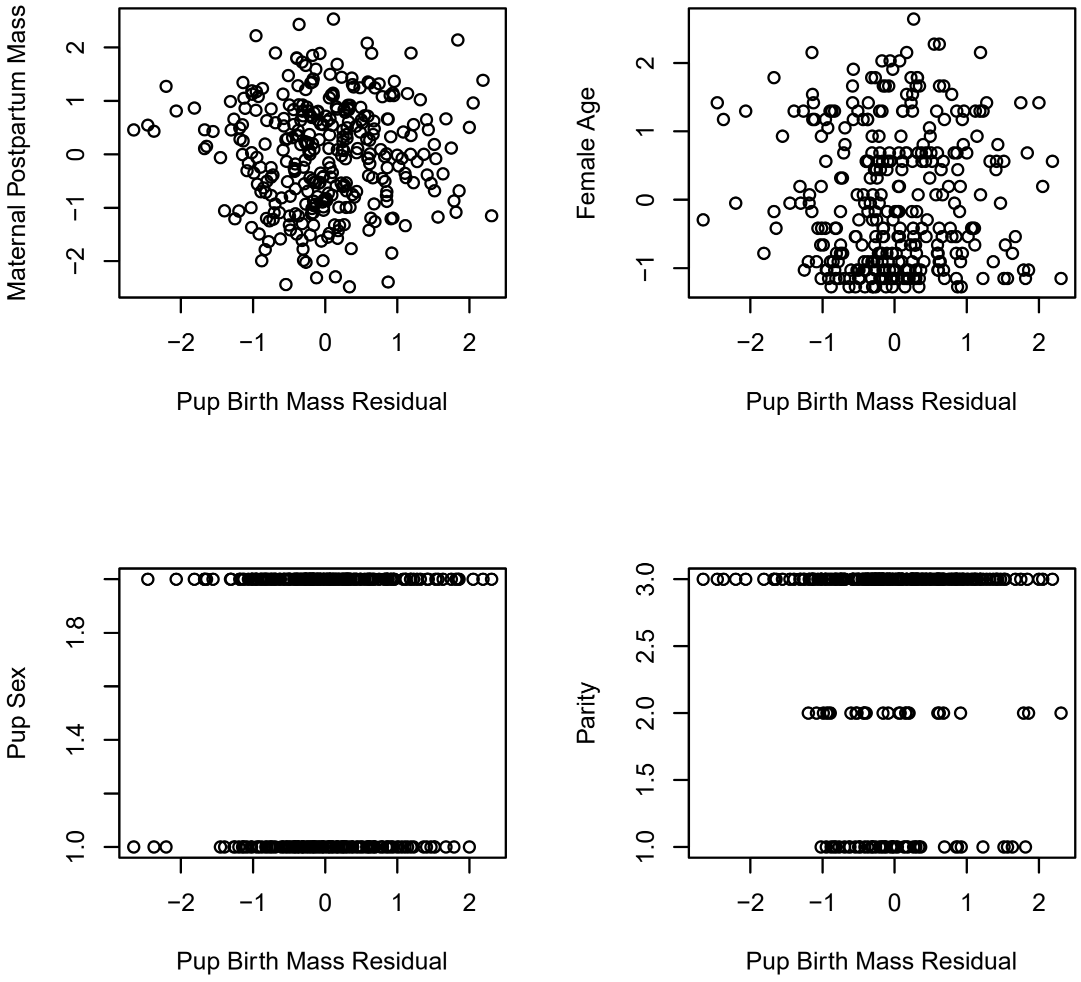

Figure A8. Pup birth mass loss model residuals plotted against the fixed effects (maternal postpartum mass, female age, pup sex and parity)) in the model (n = 324).

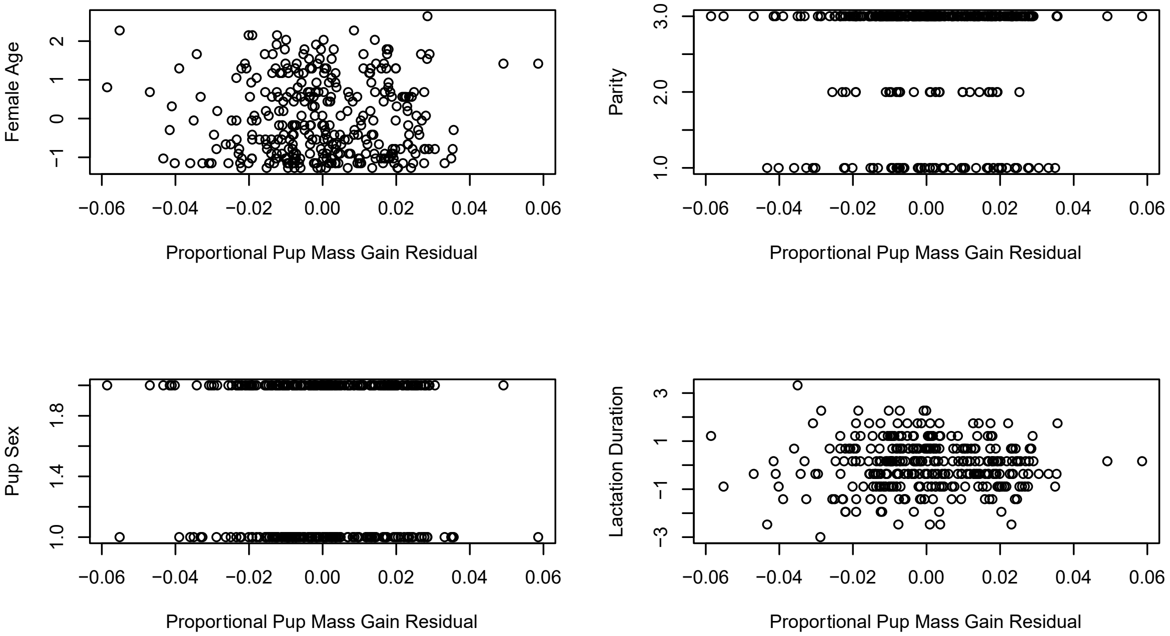

Figure A9. Proportional pup mass gain model residuals plotted against the fixed effects (female age, parity, pup sex and lactation duration) in the model (n = 324).

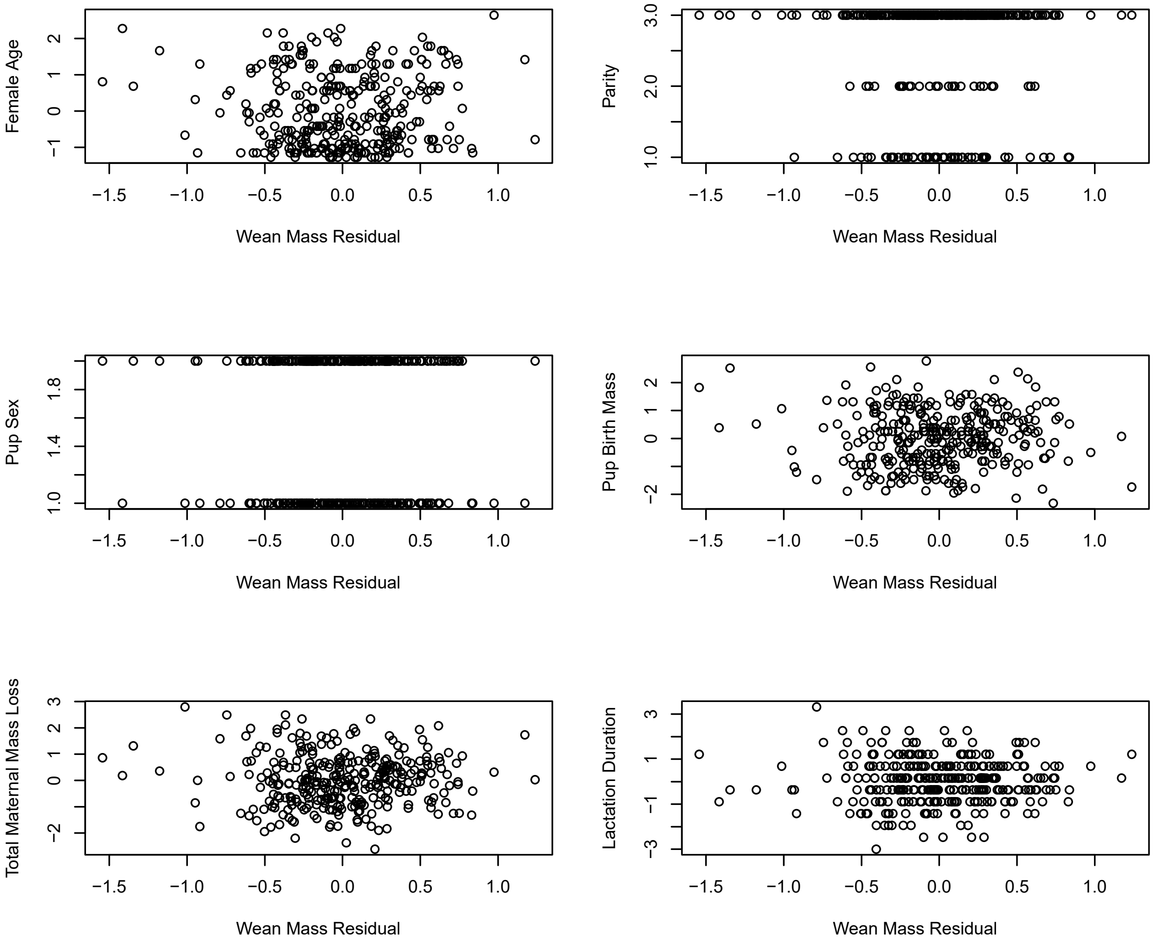

Figure A10. Weaning mass model residuals plotted against the fixed effects (female age, parity, pup sex, pup birth mass, total maternal mass loss, and lactation duration) in the model (n = 324).

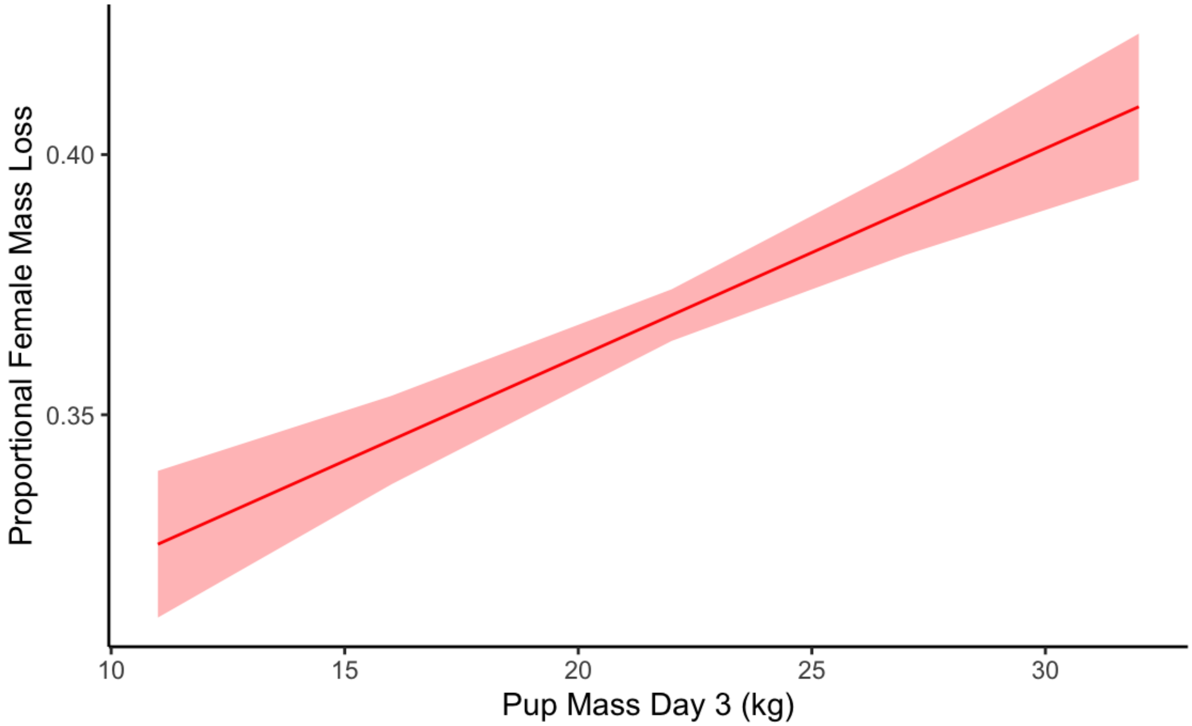

Figure A11. Proportional maternal mass loss model predictions and 95% confidence intervals (shaded bands) for 324 observations of pups from 222 females plotted against pup birth mass.

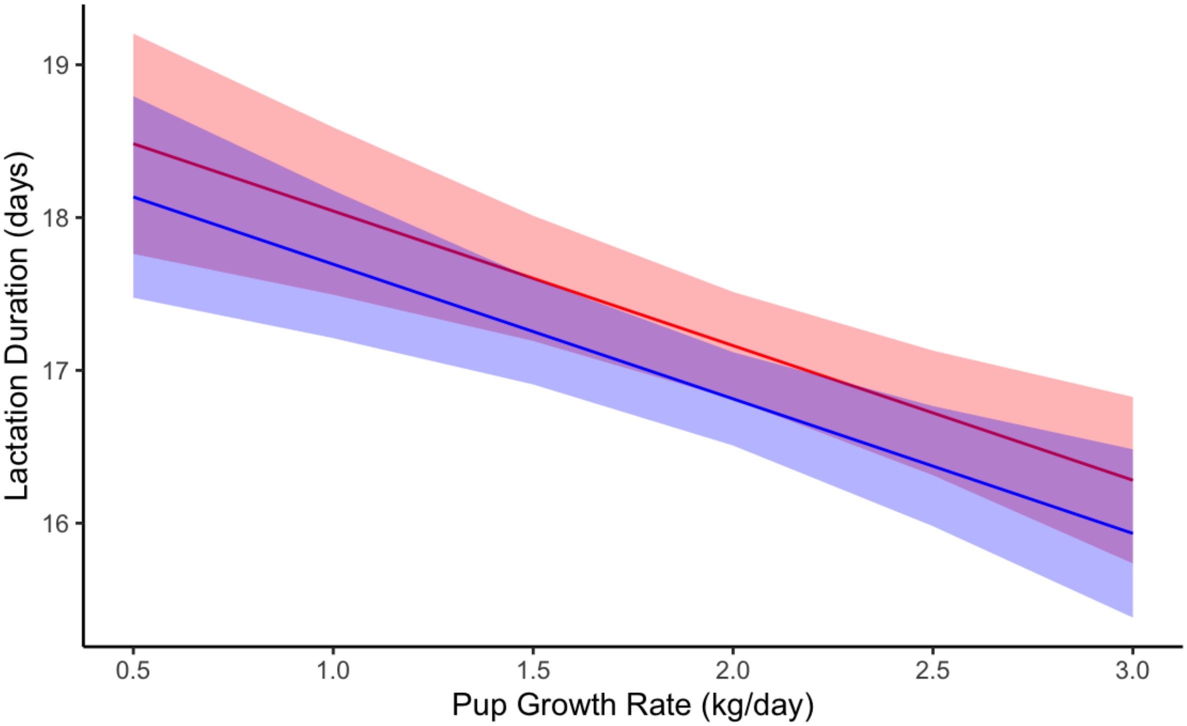

Figure A12. Lactation duration model predictions and 95% confidence intervals (shaded bands) for 324 observations of pups from 222 females plotted against pup growth rate with predictions for male (red) and female (blue) pups.

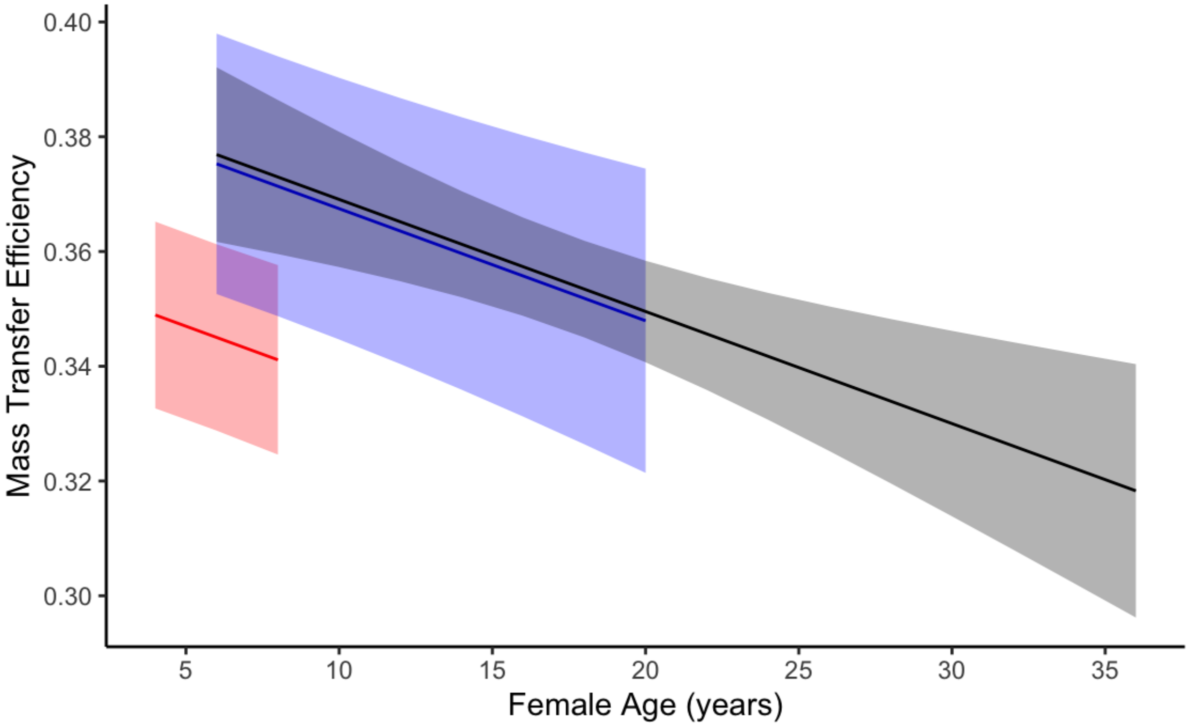

Figure A13. Mass transfer efficiency model predictions and 95% confidence intervals (shaded bands) for 324 observations of pups from 222 females plotted against female age with predictions for primiparous (red), parity 2 (blue) and multiparous (black) females.

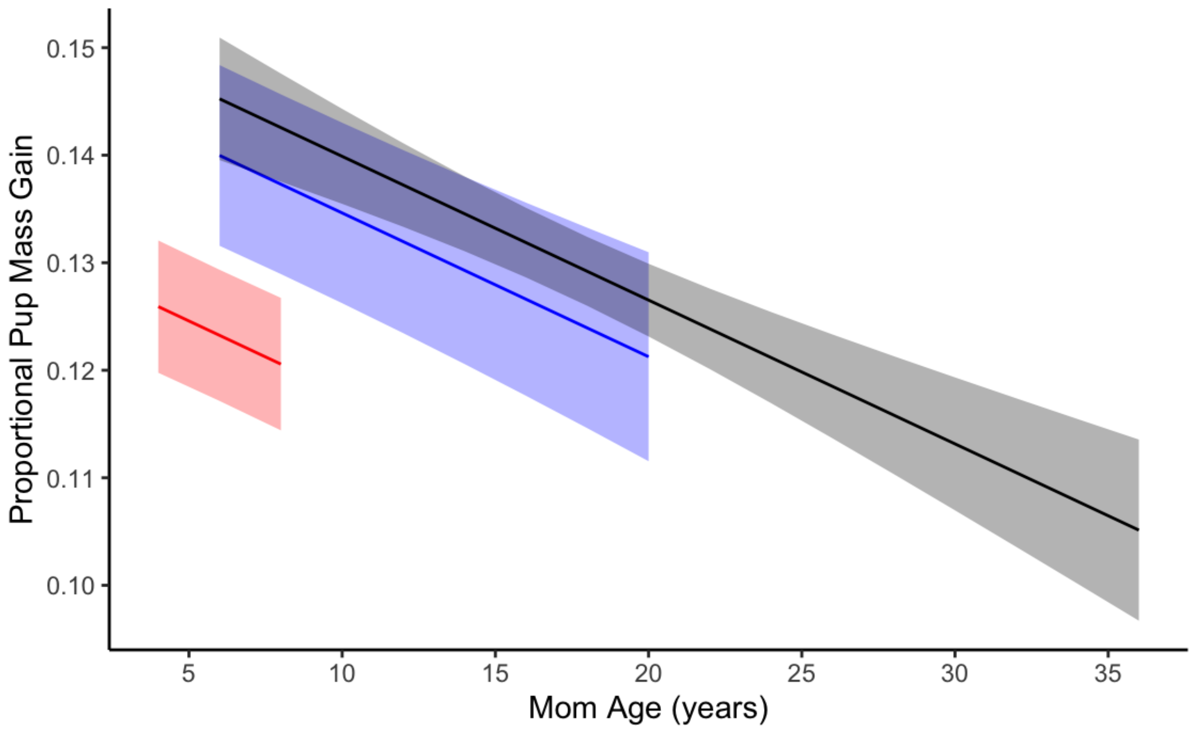

Figure A14. Proportional mass gain model predictions for pups from 222 females plotted against female age with predictions for primiparous (red), parity 2 (blue), and multiparous (black) females (n = 324).

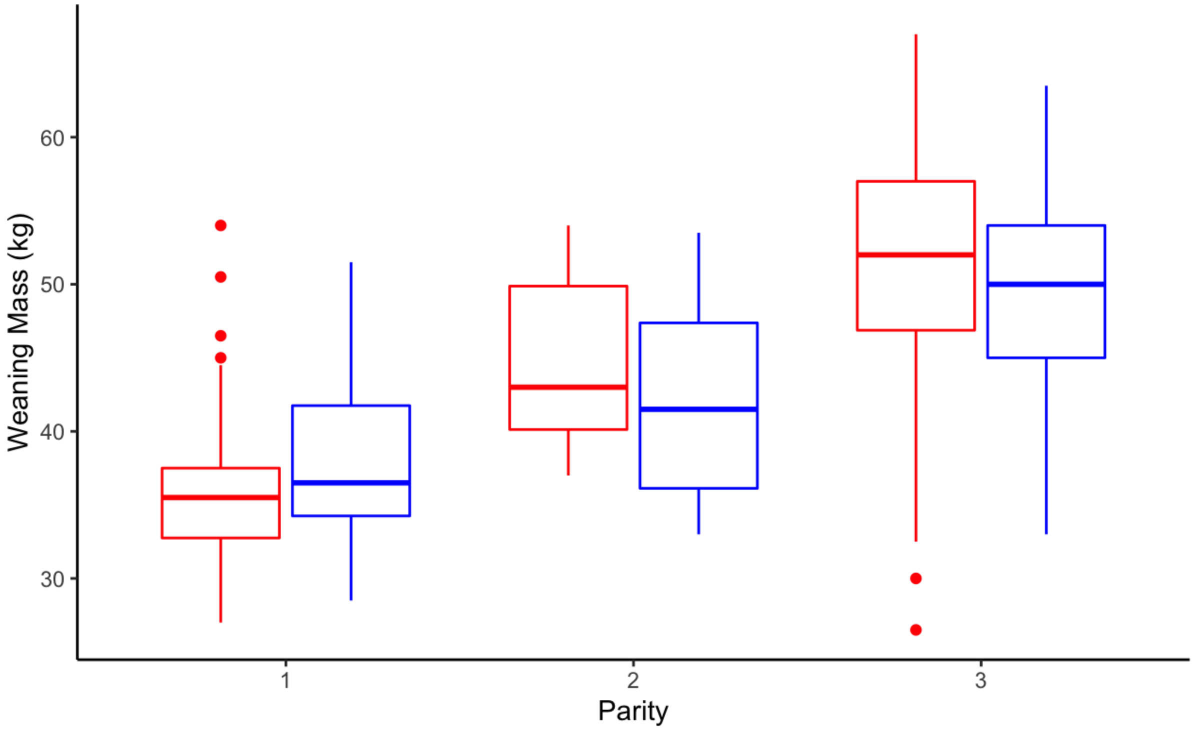

Figure A15. Weaning mass of pups from 222 females with parity (males: red; females: blue) (n = 323).

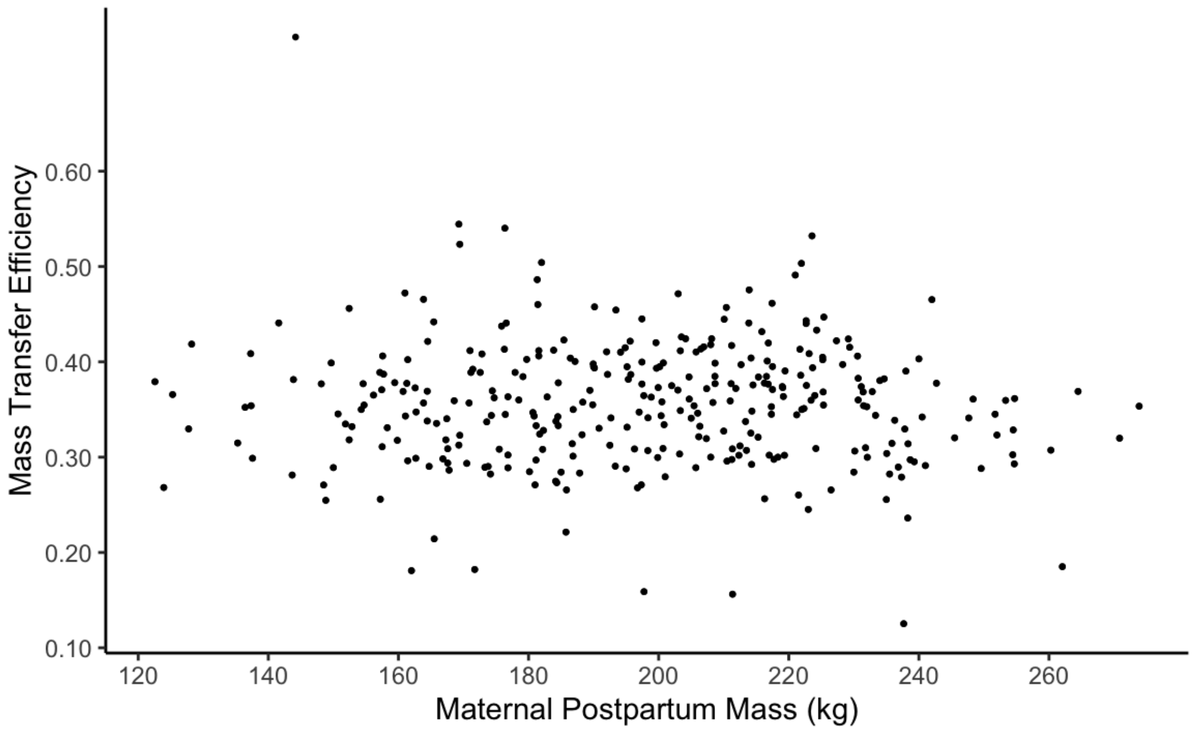

Figure A16. Mass transfer efficiency of 222 females plotted against maternal postpartum mass (n = 325).