

1 Large offspring have enhanced lifetime reproductive success: long-term carry-over effects of
2 natal size in grey seals (*Halichoerus grypus*)

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Abstract

An individual's size in early stages of life may be an important source of individual variation in lifetime reproductive performance, as size effects on ontogenetic development can have cascading physiological and behavioral consequences throughout life. Here, we explored how natal size influences subsequent reproductive performance in grey seals (*Halichoerus grypus*) using repeated encounter and reproductive data on a marked sample of 363 females that were measured for length at ~ 4 weeks of age and eventually recruited to the Sable Island breeding colony. Two reproductive traits were considered: provisioning performance (mass of weaned offspring), modeled using linear mixed effects models; and reproductive frequency (rate at which a female returns to breed), modeled using mixed-effects multistate mark-recapture models. Mothers with the longest natal lengths produced pups 8 kg heavier and were 20% more likely to breed in a given year than mothers with the shortest lengths. Correlation in body lengths between natal and adult life stages, however, is weak: longer pups do not grow to be longer than average adults. Thus covariation between natal length and future reproductive performance appears to be a carry-over effect, where the size advantages afforded in early juvenile stages may allow enhanced long-term performance in adulthood.

26 **Introduction**

27 Life history theory predicts that maternal fitness is maximized by the reproductive strategy which
28 results in the greatest number of offspring surviving to maturity, and subsequently producing large
29 numbers of viable offspring themselves (Stearns 1992, Roff 1992). Variation in offspring quality
30 may be influenced by parents through a myriad of pathways including the selection of safe and
31 nutritious oviposition or birth sites, incubation behavior, food provisioning, defense of young, and
32 investment in offspring size (Mousseau and Fox 1998, Krist 2011). These behaviors are costly, and
33 reproductive strategies in long-lived species will be driven by the relationship between offspring
34 traits and environmental conditions that determines fitness (Smith and Fretwell 1974, Mousseau
35 and Fox 1998, Allen et al. 2008).

36 Offspring size is one of the most important and well-studied of these traits in evolutionary
37 ecology, as natural selection on body size and size-related traits is ubiquitous in nature (reviewed
38 in Sogard 1997, Krist 2011, Pettersen et al. 2015). Within species, larger offspring typically
39 outperform their smaller conspecifics, with higher survival rates to sexual maturity (e.g. plants:
40 Stanton 1984, marine invertebrates: Moran and Emlet 2001, Marshall et al. 2006, grey seals:
41 Bowen et al. 2015, lizards: Sinervo 1990), enhanced resistance to starvation, environmental extremes,
42 and predation (Sogard 1997), increased metabolic efficiency (Pettersen et al. 2015), and higher
43 reproductive performance found in some species (arthropods: Fox and Czesak 2000, birds: reviewed
44 in Krist 2011, marine invertebrates: Marshall and Keough 2008). Mothers may confer this advantage
45 on their young either through a heritable genetic predisposition (possibly by choosing larger mates)
46 or maternal effects such as nutrient transfer and protective behavior toward young (Bernardo 1996,
47 Mousseau and Fox 1998).

48 The advantages of natal size are often pronounced in early stages of ontogeny, but may persist

throughout life affecting reproduction and even the performance of the subsequent generation (Lindström 1999, Marshall et al. 2003, Dias and Marshall 2010). While many studies have confirmed the relationship between offspring size and survival, less is known about how the effects of natal size subsequently manifest in adults recruited to the breeding population. Even in mammals and birds where offspring are relatively large and individuals may be tracked, estimates of the effect of an individual's size when young on subsequent performance are available for only a few taxa (Clutton-Brock 1991, Festa-Bianchet et al. 2000, Fox and Czesak 2000, Crawley et al. 2017) and fewer still for natural populations. This knowledge gap is particularly apparent in long-lived iteroparous animals, where it is difficult to track individuals' reproductive performance and survival throughout an adulthood that may last decades. Offspring size effects on fitness would then be inaccurately estimated because key components of fitness are not measured at sufficient temporal scales (Marshall et al. 2003).

Reproductive and early life-history traits can be considered aspects of either offspring or maternal phenotype, and their evolution will therefore depend on selection operating through both offspring and maternal components of fitness (Mousseau and Fox 1998). Selection acts to maximize parental fitness, but offspring size also simultaneously influences offspring fitness. An individual's size when young may be an important source of individual variation in lifetime reproductive performance (individual quality), as size effects on ontogenetic development can have cascading physiological and behavioral consequences throughout life (Lindström 1999). Size may mediate the expected trade-off between growth, self-maintenance, and mortality in early stages by increasing survival probabilities (avoiding starvation, predator escapement) and/or increasing foraging efficiency, allowing individuals to mature more quickly or invest in costly physiological functions that lead to greater lifetime reproductive output. This variation in individual quality is a key driver in natural selection

and an important link between evolutionary and ecological processes (Lomnicki 1978, Cam et al. 2002, Bolnick et al. 2003, Vindenes et al. 2008, Bolnick et al. 2011, Stover et al. 2012, Gimenez et al. 2017).

The extensively studied colony of grey seals (*Halichoerus grypus*) breeding on Sable Island, Nova Scotia provides an excellent opportunity to explore the link between natal size and subsequent performance as adults. Grey seals are long-lived (~ 40 years), iteroparous capital breeders in which females invest heavily into the survival of a single offspring over the course of a relatively short, intense lactation period lasting 16-18 days (Boness and James 1979, Iverson et al. 1993). During the nursing period, mothers lose a third of their body mass on average (4.1 kg per day, Mellish et al. 1999) relying only on fat reserves to produce milk and maintain metabolism, while their pups typically more than triple their birth mass (2.8 kg per day, Bowen et al. 1992). At the end of lactation, females abruptly end care and return to the sea, which allows female reproductive expenditure to be accurately measured by the energy allocated to offspring (Bowen et al. 2007). In this system, offspring size is more variable than offspring number (twins are exceedingly rare), so offspring size (rather than litter size) is more subject to selection for maternal fitness.

Sable Island grey seal pup production (a proxy for population size) has increased dramatically over the past half century with near maximum population growth of 13% per year between the 1960s and late 1990s (Bowen 2011) and a reduced rate of increase of 5-7% per year since 2004 (den Heyer et al. 2017, den Heyer et al. 2021). Associated with declines in population growth, juvenile apparent survival to reproductive recruitment has decreased by more than half from an average of 74% in cohorts born 1985-1989 to 33% in cohorts born 1998-2002 (den Heyer et al. 2013). This decline appears to be size-selective, with recent investigations finding that heavier and longer pups are more likely to recruit (Bowen et al. 2015). Apparent survival to recruitment

increases asymptotically with mass at weaning, but monotonically with length at weaning (Bowen et al. 2015), indicating stabilizing selection for mass, but directional selection for larger natal skeletal size. The survival advantage of larger skeletal size may be due to increased swimming speed and agility allowing greater foraging ability and predator escapement (Sogard 1997, Hindell et al. 1999), though other physiological mechanisms cannot be ruled out. This size selection may be intensifying under density dependence, as young-of-the-year grey seals now must make longer foraging trips and forage farther from haul-out sites than older animals which occupy foraging areas closer to rookeries (Breed et al. 2011, Breed et al. 2013), so larger-bodied animals that can swim more efficiently may experience increased survival compared to shorter conspecifics.

Here, we use a 19-year longitudinal data set of repeated reproductive measurements from individually marked, known-aged female grey seals whose lengths were measured at roughly 4 weeks of age to evaluate the influence of natal size on subsequent long-term reproductive success. As length is a better indicator than mass of overall skeletal size that may confer a more enduring advantage, we investigate whether variation in natal length is associated with increased reproductive performance as adults, measured using two traits: reproductive rate and offspring size at weaning. If natal length is positively associated with reproductive performance, we consider that support for a “bigger is better” hypothesis, in which maternal fitness is benefitted from bearing longer offspring that will subsequently have higher reproductive success. However, we discuss the probability that these effects represent a carry-over of natal size rather than a life-long size advantage, as neither natal length nor natal mass explain more than a few percent of the variation in adult length (Bowen et al. 2015), and thus larger (or smaller) pups do not necessarily grow into larger (or smaller) adults and larger pups express better lifetime reproductive performance even when they mature to be average sized adults.

Methods

This study was conducted on Sable Island, Canada (43.93°N, 59.91°W), a partially vegetated sandbar on the Scotian Shelf roughly 160 km off the coast of Nova Scotia, during the 1998-2020 breeding seasons. The breeding season at this colony spans early December through early February, with 91.2% of pups born by mid-January (Bowen et al. 2007, den Heyer et al. 2021). Sable Island supports the largest breeding colony of grey seals in the world with an estimated 87,500 pups (SE = 15,100) born on the island in 2016, comprising 80% of the total grey seal pup production in the Northwest Atlantic (den Heyer et al. 2021).

Data Collection

Our 19-year study (2002-2020) was conducted on a subset of female grey seals born on Sable Island from 1998-2002 that survived to recruit to the breeding colony, as part of a larger program led by the Department of Fisheries and Oceans, Canada (DFO). Individuals were marked at roughly 4 weeks old, shortly after weaning, with unique alpha-numeric hot-iron brands in each year 1998-2002. Prior to marking, researchers recorded standard dorsal body length (to the nearest cm) of these individuals while they were sedated with diazepam (~ 0.4 mg/kg body mass, Sandoz Canada, Boucherville, Quebec, Canada) to ensure accurate measurement standardized across individuals (Bowen et al. 2015). These permanent brands allowed reliable identification of individuals over the course of their lives. Females can recruit to the breeding population as early as 4 years old, but this is uncommon, and the average age of first reproduction is 6.5 ± 0.21 SE years for these cohorts (den Heyer et al. 2013) with 87% of females recruited at or before age 7 (Bowen et al. 2015). During each breeding season since 2002, teams of researchers conducted 5-7 roughly weekly censuses of branded females returning to the island to give birth and mate. Once sighted,

140 branded individuals with dependent pups were visited daily but generally not disturbed. Prior to
141 weaning, pups were sexed and marked with semipermanent, uniquely numbered tags in the hind
142 flipper to ensure accurate identification after the marked female ended lactation and returned to
143 sea, leaving her pup in the colony. Females attend their pups continuously throughout lactation.
144 Therefore, once a pup was sighted alone, it was considered weaned and weighed to the nearest 0.5
145 kg.

146 The probability of observing a marked female during any given year includes both the probability
147 the female is present, and the probability that she is detected given presence at the breeding colony.
148 A recent analysis of this population indicated that, if a female rears a pup on the island, there is
149 less than a 5% chance researchers will fail to detect her in at least one resighting census (Badger
150 et al. 2020). Individuals that are not rearing pups can be skittish and may flee to the water, resulting
151 in a lower sighting probability than females nursing and defending young. Grey seals are highly
152 site philopatric, and once recruited to a breeding colony, will very rarely pup elsewhere (Bowen
153 et al. 2015). Thus, we are able to reliably follow the reproductive history of individuals, and do not
154 expect permanent emigration to other colonies to be a significant source of sighting error.

155 Individual sighting histories were collected from age at first reproduction (first sighting in
156 breeding colony) until the most recent year of our study, 2020. Sighting histories of individuals
157 were scored as a 0 (not sighted) or 1 (sighted) for each year 2002 to 2020. Females sighted in only
158 one breeding season were omitted from this analysis to ensure that they had in fact recruited to the
159 Sable Island breeding population and we have adequate data to estimate reproductive performance.

160 All procedures used on study animals were in compliance with applicable animal care guidelines
161 of the Canadian Council on Animal Care and were approved by The Department of Fisheries and
162 Oceans Animal Care Committee (Protocol numbers 98-57 through 12-08).

Statistical Analysis

In this analysis, we were interested in understanding how a female's size during early life stages influences subsequent reproductive success once she has matured. To do this, we analyzed the effect of natal length (L_{natal} , her length after weaning, but prior to independent foraging at approximately 4 weeks old) on her reproductive performance in adulthood, measured two ways: annual provisioning performance and reproductive frequency (both described below). We used generalized mixed-effect additive and linear models to determine the effect of L_{natal} on these traits, and accounted for imperfect detection in reproductive rate using a multi-state capture-recapture model in a Bayesian framework (Gimenez et al. 2007, Lebreton et al. 2009, Kéry and Schaub 2012).

Modeling annual provisioning performance

During lactation, grey seal pups consume only milk provided by the female, and as capital breeders, females fast for the entire lactation period and provision pups exclusively from energy stores. Therefore, in our study, the body mass of a pup at weaning is a reasonable estimate of the energy (i.e. nutrients) transferred to young, and is of critical importance for pup survival (Hall et al. 2001, Bowen et al. 2015). We modeled the weaning mass of pup j born to female i in year t ($mass_{j,t}$) as a linear mixed-effects model with female experience (parity, i.e. par ; because this effect tends to plateau, it was discretized into 1, 2, and 3+ parities), offspring sex, and a quadratic effect of standardized female age as covariates along with random individual and year intercepts:

$$mass_{j,t} = \pi_1 \cdot age_{i,t} + \pi_2 \cdot age_{i,t}^2 + \pi_{3,m} + \pi_4 \cdot I(sex_{i,t} = female) + \alpha_i + \eta_t + v_{i,t}$$

Where linear parameters are held in the vector $\pi = \{\pi_1, \pi_2, \pi_3, \pi_4\}$ and represent linear and quadratic age effects, effect of female experience, and pup sex, respectively; and \mathbf{I} signifies an

indicator variable, and m denotes the parity group (1, 2, or 3+) of female i in year t so $m \in \{1, 2, 3\}$.

α_i is the random effect of individual such that $\alpha_i \sim N(0, \sigma_\alpha^2)$, η_t reflects the random year effect,

where $\eta_t \sim N(0, \sigma_\eta^2)$, and $v_{i,t}$ is the error term where $v_{i,t} \sim N(0, \sigma_v^2)$.

We tested the effect of L_{natal} on the history of her pup weaning masses comparing this null model to models including L_{natal} as a linear term and a quadratic term (Table 1). We also included a model in which the effect of L_{natal} on offspring size varies with parity, such that the effect may diminish over time (Dias and Marshall 2010). Models were fit using the `lmer` function in package `lme4` (Bates et al. 2015), and support for model configurations was determined via likelihood ratio tests using the `anova` function offered in R (R Core Team 2020).

Modeling reproductive rate

The second reproductive trait, reproductive rate, is defined as the probability an individual will return to the island to give birth in any given year, and is the reciprocal of a female's interval between births adjusted by her reproductive state the previous year and other covariates. We estimated the effect of a female's natal length L_{natal} on her reproductive rate by modeling her reproductive history as a Markov chain in a multi-state capture re-capture modeling framework. Between her first and last sightings on the island during our study, a female transitions among three reproductive states: initially a first time breeder F , then switching between a breeder state B , or non-breeder state N . An individual's state transitions from year t to $t + 1$ is modeled as a categorical trial with probabilities of transition ψ^{ks} from state k to state s . Reproductive frequency is then defined as the probability of transition from any state k into the reproductive state B (ψ^{kB}). We used mixed-effects logistic regression embedded in this multistate model to account for standardized female age, previous breeding state, and random individual and year effects in

205 probability of breeding (ψ^{kB}):

$$\psi_{i,t}^{kB} = \mu + \lambda_1 \cdot age_{i,t} + \lambda_2 \cdot age_{i,t}^2 + \lambda_{3,k} + \beta_i + \theta_t + \omega_{i,t}$$

206 Where parameters $\lambda = \{\lambda_1, \lambda_2, \lambda_3\}$ represent the quadratic age effect and the effects of the
207 previous breeding state k , respectively, where parameters $\lambda_{3,k}$ sum to zero. β_i is the random effect
208 of individual such that $\beta_i \sim N(0, \sigma_\beta^2)$, θ_t reflects the random year effect, where $\theta_t \sim N(0, \sigma_\theta^2)$, and
209 $\omega_{i,t}$ is the error term where $\omega_{i,t} \sim N(0, \sigma_\omega^2)$.

210 Similar to above, we tested the effect of natal length L_{natal} on a female's reproductive rate by
211 comparing this null model to models including L_{natal} as a linear term and a quadratic term (Table
212 2). Further, we included a model in which the effect of L_{natal} on offspring size varies with parity,
213 such that the effect may diminish over time.

214 Multistate models can also be used to detect a cost of reproduction (e.g. Beauplet et al. 2006,
215 Hernández-Matías et al. 2011, Chambert et al. 2013, Stoelting et al. 2015, Johns et al. 2018, Badger
216 et al. 2020). A common approach is to determine whether breeding at time t negatively affects an
217 individual's probability of surviving from time t to $t + 1$ or its probability of breeding at time $t + 1$.
218 In the model used here, one way in which a cost of reproduction may be observed as a higher
219 probability of transition ψ into a breeding state B from a nonreproductive state N , i.e. $\psi^{NB} > \psi^{BB}$.

220 A Bayesian approach was used for estimation and implemented in the software program JAGS
221 4.2.0 using the R interface `rjags` (Plummer 2003, R Core Team 2020, Plummer 2018). Parameters
222 λ were assigned diffuse normal prior distributions $N(0, 1000)$. Random year term θ was specified
223 hierarchically following a normal distribution, $\theta_t \sim N(0, \sigma_\theta^2)$, and individual terms β_i were pulled
224 from a $N(0, \sigma_\beta^2)$. We specified a $\text{Unif}(0, 10)$ prior for σ_θ and σ_β .

225 Markov chain Monte Carlo (MCMC) methods were used to sample the posterior distributions

of the parameters of interest. For each of the competing models, we ran three chains in parallel using package `dclone` (Solymos 2010) with different sets of initial values. The first 10,000 MCMC samples were discarded, known as the burn-in period, after having checked that convergence was satisfactory. Convergence was visually assessed using sample path plots in conjunction with the Brooks-Gelman-Rubin diagnostic \hat{r} (Brooks and Gelman 1998), with values close to 1.00 indicating adequate convergence. Chains then ran for 100,000 iterations after burn-in, and a total of 3,000 MCMC samples (every 100th sample of each chain) were used for inference. We determined that a covariate had an effect if a 95% credible interval (CRI) of the posterior distribution of that parameter did not include 0. We assessed support for inclusion of natal length using a measure of out-of-sample predictive ability of each model, the Widely Applicable Information Criterion (WAIC, Watanabe 2010), where a model with a smaller WAIC is judged a better fit.

Results

We analyzed the reproductive histories of 363 females born from 1998-2002 that gave birth to a total of 3457 pups. 2.5% (9/363) of those females recruited to the breeding population at age 4, 31.4% (114/363) had their first birth at the age of 5, 24.5% (89/363) at the age of 6, and 30.5% (111/363) recruited after age 6. From primiparity to the most recent year of the study, 2020, females had an average of 10 pups ($SE = 4.48$, ranging 1 to 17). These females' natal lengths (L_{natal}), ranged from 90-123 cm, with an average of 110.7 cm ($SE = 4.28$). We did find a cohort effect on L_{natal} (ANOVA, $p = 0.003$), where females born in 2002 that recruited to the breeding population had significantly longer L_{natal} than other cohorts analyzed (Tukey HSD, Figure 4).

Effect of natal length on future reproductive performance

L_{natal} was positively associated with a female's future provisioning performance ($p < 0.001$, Table 1). The best supported model describing pup weaning masses included an additive, linear effect

of natal length as a covariate, though there was also modest support for a quadratic effect (Table 1, Appendix B: Table B2). Females who had the longest natal lengths proceeded to give birth to offspring that weaned 8 kg heavier, on average, than conspecifics who had the shortest natal lengths (Table 3). Though we expected natal body length to have a greater effect on early parities (such that the effect weakened over time), we found no support for an interactive model between L_{natal} and parity (Table 1, Appendix B: Table B3). Repeatable differences among individuals accounted for 41% of the variance in pup weaning mass. Year accounted for only 10.8% of the variance in weaning mass, suggesting that among-year environmental effects were small. Natal length was also positively associated with a female's future reproductive rate. Model output from fitted multistate Markov models estimated that natal length accounts for the spread in annual reproductive probability to range from 0.715 for females who had the shortest L_{natal} to 0.916 for females who had the longest L_{natal} (Table 4, Figure 2). Model fits displayed no evidence of inadequate convergence to stationary distributions.

Cost of reproduction in breeding rate

In this analysis fit to the reproductive data of individuals from the 1998-2002 cohorts, the fitted multistate model estimated somewhat ($\sim 2\%$) higher reproductive probabilities for individuals that did not breed in the previous year (Table 4). However, previous analyses on a larger subset of this population including individuals born in the 1960s - 1980s, did not find evidence for a cost of reproduction expressed in reproductive rate. In one of these previous analyses, individuals that reproduced in the current year were on average 11% more likely to breed the next year than those that skipped reproduction (Badger et al. 2020, den Heyer and Bowen 2017, Figure 3). Importantly, females born in the 1960s-1980s recruited during a period of exponential growth with population densities much lower than the females recruiting in the present study (den Heyer and

Bowen 2017). The result of this current analysis, indicating a slight cost under higher population densities, contrasting with the previous studies indicating no cost when population densities were lower suggest that the cost of reproduction may only be expressed at higher population densities.

Cohort effects in reproductive performance

After detecting a cohort effect in (L_{natal}), we incorporated cohort effects into reproductive performance models of breeding rate and offspring mass. Individuals from the 2002 cohorts had lighter pups on average than individuals from other cohorts (Appendix B: Table B4), though this model performed worse in out-of-sample predictive accuracy than models without cohort effects (Table 1). In reproductive rate, our multistate models also estimated a lower breeding rate of individuals born in the 2002 cohort (Appendix B: Table B4) relative to other cohorts analyzed. However, this model also performed poorly relative to models not including cohort as a covariate (Table 2). We further caution the interpretation of the result of this multistate model including cohort effects as we were not able to control for the effects of maternal age due to issues with convergence likely stemming from multicollinearity of the age, cohort, and parity variables.

Discussion

We found positive covariation between an individual's natal length and subsequent adult reproductive performance measured by two traits from a large sample of grey seals observed for over 20 years. Mothers with the longest natal lengths produced pups nearly 8 kg heavier and were 20% more likely to breed in a given year than mothers with the shortest natal lengths. This result is consistent with a "bigger is better" hypothesis (Bowen et al. 2006), in which longer offspring mature to have higher reproductive success. However, as natal length is only weakly correlated with adult length, the pattern is not simply the result of larger adults being more fit. Instead, natal length appears to act as a carry-over effect of juvenile morphology on lifetime reproductive success.

The observed spread in offspring size and reproductive frequency should drive substantial variation in lifetime reproductive output. Badger et al. (2020) found reproductive frequency and the probability of weaning a viable pup were highly correlated within individual grey seal females, and over their lifetimes higher performing females will average 1.83 times more successful pups than poorer performers. Further, for weaning masses below the population mean (51.5 kg), pup survival is dependent on mass (Hall et al. 2001, Bowen et al. 2015), with each 1 kg decrease below average corresponding to a 0.12 decrease in survival to reproductive recruitment (on the logit scale). Consequently, an 8 kg spread would have a large impact on the probability a female's offspring will reach sexual maturity, affecting both maternal and offspring fitness.

Implications for maternal fitness

Our findings show that grey seal mothers increase maternal fitness by producing longer pups, as longer pups mature to be more productive mothers. While the effect of offspring body size on maternal fitness has been extensively studied (Lack 1947, Cody 1966, Smith and Fretwell 1974, Stearns 2000, Krist 2011, Rollinson and Hutchings 2013, Pettersen et al. 2015), mass or fat reserves, and not length, are the typical measure of size. This methodological bias is likely due to the difficulty of accurately measuring length; body posture can greatly impact length measurements, while mass is accurately and precisely measured with a calibrated scale. Body length and fat reserves of offspring, however, reflect different aspects of maternal quality; larger skeletal size is more likely to have a significant heritable component while stored energy is a measure of maternal effort and investment. Provisioning offspring with large energy reserves requires considerable reproductive energy expenditure in both acquisition of resources (e.g. foraging efficiency, prey choice, intraspecific competition) and effectively transferring resources to offspring

(e.g. lactation efficiency, nursing behavior). Some maternal behaviors are likely to have a genetic basis (Bubac et al. 2021), but increasing an offspring's skeletal size likely has a relatively larger heritable genetic component. The genetic basis of skeletal architecture is unknown for pinnipeds, but divergent selection experiments in domestic mammals suggest that dozens to thousands of loci underlie variation in structural body size (Kemper et al. 2012).

Allocation theory predicts an asymptotic relationship on an offspring's size and its survival because parents receive decreasing returns on investment in offspring fitness after a certain point (Smith and Fretwell 1974). Previous analyses of this population suggest stabilizing selection on weaning mass, where offspring survival to recruitment levels out near the average weaning mass and slowly decreases at increasingly higher weaning masses (Bowen et al. 2015). In contrast, body length appears to be subject to directional selection (at least in the current ecological environment), evidenced by a monotonically increasing relationship between body length and offspring survival to reproductive recruitment (Bowen et al. 2015). Early growth rate will vary among individuals as a function of their genetic makeup, environmental conditions, and an individual's foraging success in those conditions (Madsen and Shine 2000, Harrison et al. 2011). While fat reserves provide crucial resources during the transition to independent foraging, fatter pups are likely more buoyant, which in diving animals would result in less efficient foraging and greater vulnerability to predation (Sogard 1997, Hindell et al. 1999). Longer individuals, however, may gain a tangible benefit throughout early stages due to greater swimming speed, diving ability, and less vulnerability to predators, which may be accentuated in the current highly competitive foraging environment (Breed et al. 2013). The possible mechanisms driving relationships between early traits and survival remain to be tested, but results from this analysis indicate benefits of length have a persistent effect on fitness and potential for strong transgenerational effects on reproductive output.

Natal length as a source of individual variation in quality

Recent analyses of this population indicate substantial differences in quality (i.e. lifetime reproductive success) among individuals (Badger et al. 2020). Though it is expected that maternal effects on offspring size are most significant in early life (Dias and Marshall 2010), with compensatory growth or other factors reducing impact later in life (e.g., domestic sheep, Wilson and Réale 2006, red squirrels, Wauters et al. 1993), our results suggest variation in natal body length may explain some of the observed variation in individual quality across an individual's lifetime. Individuals that were longer as young juveniles consistently outperform those of shorter lengths in both survival to sexual maturity (Bowen et al. 2015) and reproductive success once recruited (this study).

Effective acquisition and conservation of food energy is impacted by morphological traits such as body length, and potentially drive substantial variation in reproductive success. Although larger animals have higher absolute metabolic requirements, larger individuals exhibit lower mass-specific rates of metabolism which confers a suite of physiological and ecological benefits at greater body sizes (Kleiber 1947, Glazier 2005, Gearty et al. 2018). These advantages include a low cost of transport, enhanced fasting ability, and, for animals such as seals, the ability to make longer and deeper foraging dives (Peters 1983, Costa 1993).

The extent to which body length, independent of mass, may offset the energetic cost of foraging is, however, unknown in many systems, including grey seals. In Weddell seals, Wheatley et al. (2006) found that postpartum mass of shorter females was significantly lower in years of poor environmental conditions whereas the mass of longer females did not differ between years. This suggested shorter females were less successful foragers than their larger conspecifics and may generally be more susceptible to environmental variation (Wheatley et al. 2006). If longer females are more successful foragers, or more robust to environmental variation, they would have a distinct

363 advantage in accumulating and storing energy needed for reproduction.

364 Alternatively, length may be advantageous in growing juvenile stages for grey seals, but attenuate
365 over time as they grow. Large skeletal size as an adult could also be subject to stabilizing selection,
366 where longer individuals experience different physical constraints and energetic costs that cause
367 impairment relative to shorter animals (Williams et al. 2000). Increasing body size will increase
368 costs to sustaining body condition and maintaining buoyancy in the water column. Though smaller
369 animals have a higher mass-specific metabolism, their absolute energy requirements are lower
370 (Peters 1983, Costa 1993) and so could be less vulnerable to food scarcities. Smaller prey items
371 are relatively unprofitable to larger individuals than smaller individuals, requiring additional costly
372 prey captures to reach energy requirements, decreasing the efficiency of a foraging bout (Costa
373 1993) and competitive ability under resource limitation (Clutton-Brock 1988). The size spectra
374 of prey of some ecological environments may be distinctly unfavorable to the largest individuals;
375 profitably sized prey may not be available to larger individuals, where smaller individuals can
376 forage efficiently on smaller prey that are more abundant.

377 Our finding that longer pups do not necessarily mature into longer adults suggests the such
378 selection against very large size in adult females may be present. Bowen et al. (2015) found
379 a positive, but weak correlation between body length of these female pups and their length at
380 primiparity (age at first reproduction), and length data collected sporadically since suggests the
381 relationship between natal and adult length is weak through adulthood. Natal body length accounted
382 for 6% of the variation in primiparous length ($n = 325$, Bowen et al. 2015), 4.6% of variation
383 in body length of adult females during early adulthood (5-10 yrs, $n = 268$, unpublished data)
384 and 4.3% of the variation in body length of older females (10+ years, $n = 29$, unpublished data).
385 Consequently, it is unlikely our results are due simply to longer juveniles remaining long throughout

life. Growth and reproduction are involved in a classic physiological trade-off, and further somatic investment during reproductive years may not maximize fitness (Partridge and Harvey 1988, Green and Rothstein 1991, Stearns 1992, Clutton-Brock 1984, van Noordwijk and de Jong 1986).

Carryover effects of early life morphology

The covariation between natal length and future reproductive performance likely acts as a carry-over effect, with larger natal size permitting better growth and self-maintenance as a juvenile. This better performance as a juvenile translates into greater adult performance, rather than larger size granting the same relative advantage throughout life. Carry-over effects describe how the environment experienced early in life affect the expression of traits in subsequent life stages or in habitats (O'Connor et al. 2014, Moore and Martin 2019). Carry-over effects that occur at the individual level can affect a wide range of fitness parameters. They result in long-term, large scale consequences on a population's dynamics and composition and so influence multiple levels of biological organization from individuals, populations, and even community structures (Norris 2005, Betini et al. 2013, O'Connor et al. 2014, Moore and Martin 2019).

Carry-over effects linking ecological conditions experienced early in life to later performance are well documented (Moore and Martin 2019, Madsen and Shine 2000, Gratton and Denno 2003, Marshall et al. 2006, Nussey et al. 2007, Descamps et al. 2008, Harrison et al. 2011, O'Connor et al. 2014, Garcia et al. 2019), though such demonstrations are relatively rare for long-lived mammals (Coltman et al. 1999, Festa-Bianchet et al. 2000, Nussey et al. 2007). Food availability during early development is understood to be a key environmental factor driving carry-over effects (Descamps et al. 2008, Harrison et al. 2011), with the ultimate driver being habitat quality, or less commonly reported, intraspecific density.

Our results suggest female grey seals experience a carry-over effect of their early life morphology on future reproductive performance, that may ultimately be driven by negative density dependence. In a competitive environment, longer individuals outperform shorter conspecifics early in life, and the advantages of this early life performance persist through life, even where the actual size differences do not. Breed et al. (2013) documented that juvenile grey seals may be competitively excluded from key foraging grounds by adult females in the current highly competitive environment, potentially contributing to the stark decline in juvenile apparent survival in the 1998-2002 cohorts (den Heyer et al. 2013). This exclusion may continue into adulthood, such that there is further intense competition to secure ideal foraging grounds. Longer juveniles may be more able to compete with adults and secure better foraging habitat, which carry over into reproductive years affecting their reproductive fitness traits (Lloyd et al. 2019).

Implications for population dynamics

The Sable Island grey seal colony has increased dramatically over the past 60 years with near maximum population growth of 13% per year between the 1960s and late 1990s (Bowen 2011) and a reduced rate of increase of 4% from 1997 to 2016 (den Heyer et al. 2017, den Heyer et al. 2021). Female grey seals born during the exponential growth of the 1980s and 1990s had apparent survival probabilities of 0.7–0.8 (den Heyer et al. 2013). By contrast, in the late 1990s to early 2000s, when our study animals were born, the population had entered a period of reduced population growth as it seemingly approached carrying capacity (Bowen et al. 2007, Bowen 2011, den Heyer et al. 2017, den Heyer et al. 2021), with drastically reduced apparent juvenile survival probabilities ranging from 0.26 to 0.39. Previous analyses suggest a size-selective mortality, where individuals with longer natal lengths were more likely to reach sexual maturity (Bowen et al. 2015).

In the analysis presented here, our sampling scheme and modeling framework likely yield a conservative estimate of the relationship between natal length and reproductive performance, as we only included individuals that survived to breeding age and (1) were observed in at least 2 breeding seasons and (2) nursed their pup long enough to be recorded by our research teams. These constraints result in a sample that explores the relatively better performing regions of the spectrum of reproductive investment. Inexperienced or low quality mothers may frequently flee or abandon pups, and these reproductive attempts would not be recorded in our observations (though this is not a major source of bias, see Hammill et al. 2017). For these reasons, the poorest performers are less likely to be observed, resulting in a slightly larger proportion of high quality females in our sample than present in the Sable Island breeding population.

Our sample of females also make up the post-selection distribution of body size, and this study can perhaps be viewed as a lens into the reproductive performance of individuals growing under intense selection pressure and slowing population growth (Coltman et al. 1999, Allen et al. 2008). In addition to our results linking natal size with reproductive success, we found that this sample of females exhibited a slight cost of reproduction not detected when a larger subset of the population was analyzed in Badger et al. (2020). That sample included females born in the 1960s, 1970s, and 1980s that were juveniles when population densities were much lower. From this, we infer that ecological conditions during early stages can mediate future trade-offs and shape the natural selection on life history and pace-of-life (Clutton-Brock et al. 1987, Coltman et al. 1999). Intensified competition among these age groups may drive a less favorable energetic trade-off between survival and supporting reproduction for individuals recruiting into an intensely competitive environment.

Implications & Conclusions

Here we found that natal size was positively associated with two measures of reproductive performance later in life, and because natal size is only weakly related to adult size, this relationship appears to be acting as a carry-over effect. Our findings underscore the multiple lines of evidence before us that have demonstrated that maternal fitness depends on attributes of offspring size and their cascading effects on offspring fitness, and constitute the first documentation of size carry-over effects of early ontogeny on adult performance in marine mammals. In this case, natal size appears to be acting as a carry-over effect coinciding with shifting population dynamics and increasing negative density dependence.

Our findings prompt further investigation into how negative density dependence shapes the evolution of life histories and morphology in a long-lived, iteroparous animal. Phenotypic selection across life stages will vary according to how fitness is maximized in a given environment, and will have large-scale consequences in ecological and evolutionary time scales. As long-lived iteroparous mammals must allocate their reproductive effort over many years to maximize fitness, parental genotypes that produce longer natal lengths may provide a fitness advantage. Significant heritability of length traits have been estimated in many systems (e.g. hindleg length Soay sheep, Wilson et al. 2007) though the extent of heritability in body length in grey seals (and indeed seals and marine mammals generally) has not been tested. In the grey seal cohorts we studied, there is evidence for positive selection for natal length in recruitment (Bowen et al. 2015), and the results reported here indicate that natal length continues to correlate with markers of fitness after recruitment in more frequent breeding and higher investment in pups. Though this directional selection is predicted to, if heritable, cause longer natal body lengths to evolve over time, it remains untested whether the population overall is getting longer as selection pressures from increasing seal

density intensify, or if there is counteracting selection against extremely long adults even when longer natal lengths are favored. Grey seals have particularly high and consistent survival as adults (0.989 ± 0.001 for females aged 4-24, 0.901 ± 0.004 for females aged 25+, den Heyer and Bowen 2017), so directional selection on body length as adults is more likely to act through variation in reproductive performance. Further investigation into changes in size-selective vital rates as the population continues to increase would likely yield important insights into density-related evolutionary changes in long-lived animals.

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497 Fisheries and Oceans Canada scientific data are a public resource and subject to full and open
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Table 1: Four competing linear mixed effects models to describe the effect of natal length on her reproductive performance, measured as offspring mass.

Model	Form	AIC	LRT p value
Mod 0: Null	$mass_{j,t} = \pi_1 \cdot age_{i,t} + \pi_2 \cdot age_{i,t}^2 + \pi_{3,m} + \pi_4 \cdot I(sex_{i,t} = female) + \alpha_i + \eta_t + v_{i,t}$	17713	-
Mod 1: Linear effect of natal length	Mod 0 + $\pi_5 \cdot L_{M,i}$	17702	$p < 0.001$
Mod 2: Quadratic effect of natal length	Mod 0 + $\pi_5 \cdot L_{M,i} + \pi_6 \cdot L_{M,i}^2$	17702	$p = 0.176$
Mod 3: Interactive effect with maternal experience	Mod 0 - $\pi_{3,m} + \pi_5 \cdot L_{M,i} + \pi_6 \cdot L_{M,i} \cdot I(par_{i,t} = 2) + \pi_7 \cdot L_{M,i} \cdot I(par_{i,t} = 3)$	17705	$p = 0.602$
Mod 4: Cohort effects	Mod 0 + $\pi_5 \cdot L_{M,i} + \pi_c$, where $c \in \{1998, 1999, 2000, 2001, 2002\}$	17707	$p = 0.631$

Where $mass_{i,t}$ is the mass of the weaned pup born to female i in year t . Parameters $\pi = \{\pi_1, \pi_2, \pi_3, \pi_4\}$ reflect the quadratic age effect, effect of female experience, and pup sex, respectively, and $\pi \in \{\pi_5, \pi_6, \pi_7\}$ describe the effect of maternal natal length, L_{natal} under different models. α_i is the random effect of individual such that $\alpha_i \sim N(0, \sigma_\alpha^2)$, η_t reflects the random year effect, where $\eta_t \sim N(0, \sigma_\eta^2)$.

Table 2: Four competing multistate mixed effects mark-recapture models to describe the effect of natal length on her reproductive performance, measured as reproductive rate.

Model	Form	WAIC	δ WAIC
Mod 0: Null	$\psi_{i,t}^{kB} = \mu + \lambda_1 \cdot age_{i,t} + \lambda_2 \cdot age_{i,t}^2 + \lambda_{3,k} + \beta_i + \theta_t + \omega_{i,t}$	2503.1	14.8
Mod 1: Linear effect	Mod 0 + $\lambda_5 \cdot L_{M,i}$	2488.3	0
Mod 2: Quadratic effect	Mod 0 + $\lambda_5 \cdot L_{M,i} + \lambda_6 \cdot L_{M,i}^2$	2489.7	1.4
Mod 3: Interactive effect with maternal experience	Mod 0 + $\lambda_5 \cdot L_{M,i} + \lambda_6 \cdot L_i \cdot I(par_{i,t} = 1)$	2498.0	9.7
Mod 4: Cohort effects	Mod 0 + $\lambda_5 \cdot L_{M,i} + \lambda_c$, where $c \in \{1998, 1999, 2000, 2001, 2002\}$	2497.44	9.14

Where $\psi_{i,t}^{kB}$ is the probability that female i will be in a breeding state in year t . Parameters $\lambda = \{\lambda_1, \lambda_2, \lambda_3, \lambda_4\}$ reflect the quadratic age effect and the effect of previous states, respectively, and $\lambda \in \{\lambda_5, \lambda_6\}$ describe the effect of maternal natal length, L_{natal} under different models. β_i is the random effect of individual such that $\beta_i \sim N(0, \sigma_\beta^2)$, θ_t reflects the random year effect, where $\theta_t \sim N(0, \sigma_\theta^2)$.

Table 3: Parameter estimates for favored linear mixed effects model describing variation in pup weaning mass as a function of maternal age, experience (parity), pup sex, natal length L_{natal} , and random effects of year and individual.

Parameter	Mean	St. Error
Intercept	49.22	0.791
π_1	14.46	1.26
π_2	-11.88	1.19
$\pi_3 par_{i,t} = 2$	4.01	0.55
$\pi_3 par_{i,t} = 3$	6.23	0.63
π_4	-2.26	0.22
π_5	1.07	0.29
σ_{ID}^2	4.67	
σ_{year}^2	1.29	
$\sigma_{residual}^2$	5.45	

Table 4: Posterior mean, SD, 2.5%, 50%, and 97.5% quantiles, and convergence diagnostic \hat{r} of parameters for preferred multistate model, describing variation in reproductive rate ($\psi_{i,t}^{kB}$) as a function of previous reproductive state, quadratic effect of maternal age (λ_1, λ_2), linear maternal length as young L_{natal} (λ_5), and random effects of individual and year. The effect of previous state is reported here as transition rates among F, B, and N for ease of interpretation.

Parameter	\hat{r}	Mean	SD	2.5%	50%	97.5%
$\psi_{i,t}^{BB}$	1.003	0.861	0.038	0.784	0.861	0.935
$\psi_{i,t}^{FB}$	1.003	0.779	0.056	0.665	0.780	0.888
$\psi_{i,t}^{NB}$	1.003	0.878	0.037	0.803	0.879	0.950
λ_1	1.016	0.385	0.083	0.125	0.412	0.463
λ_2	1.016	-0.355	0.083	-0.440	-0.380	-0.096
λ_5	1.001	0.549	0.020	0.513	0.549	0.594
p	1.007	0.975	0.021	0.924	0.980	0.999
σ_β^2	1.006	0.895	0.151	0.673	0.869	1.269
σ_θ^2	1.001	1.310	0.695	0.371	1.169	3.036

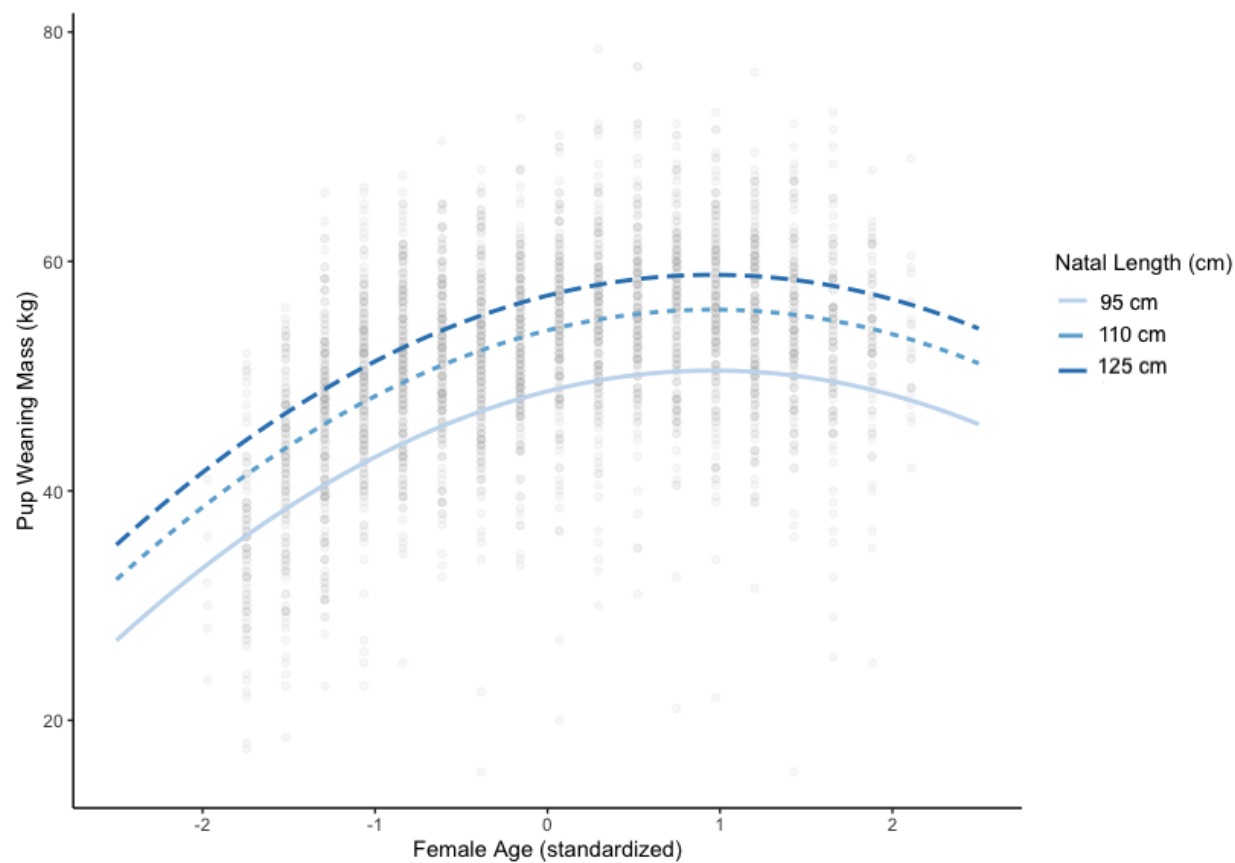


Figure 1: The estimated effect of natal length on provisioning performance as a female ages. Lines are 0.025%, 50%, and 97.5% quantiles of natal lengths corresponding to 95 cm, 110 cm, and 125 cm.

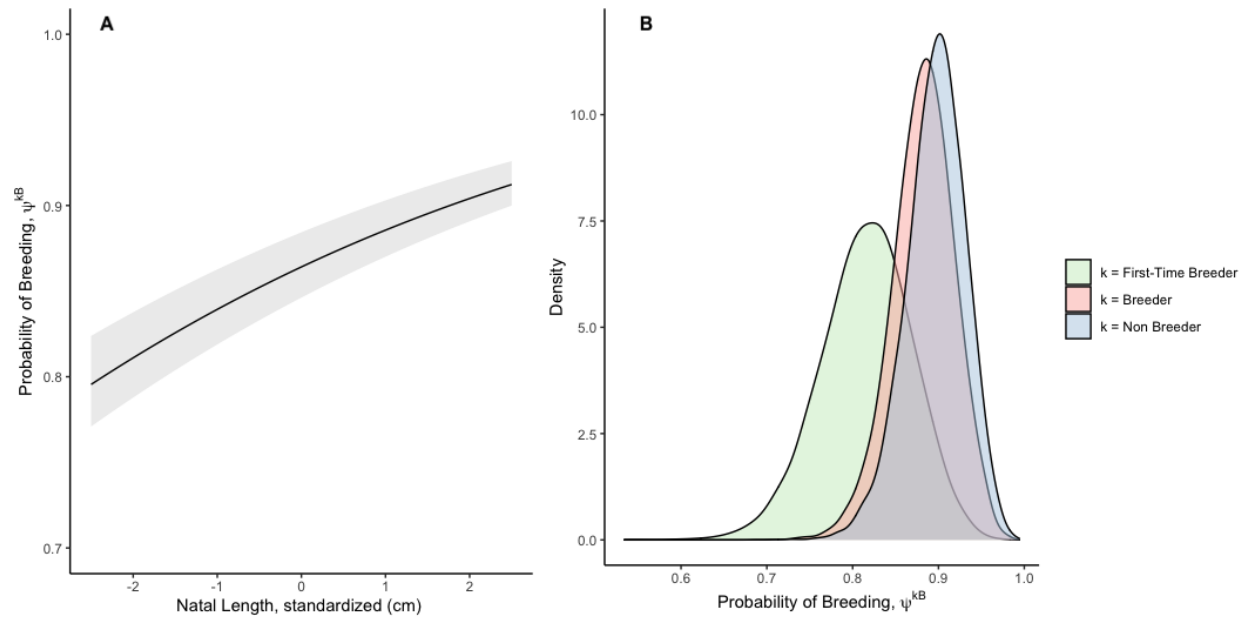


Figure 2: Results from the Markov chain multi-state model describing probability of breeding, ψ^{kB} , as a function of (A) natal length, and (B) the female's previous state in year $t-1$.

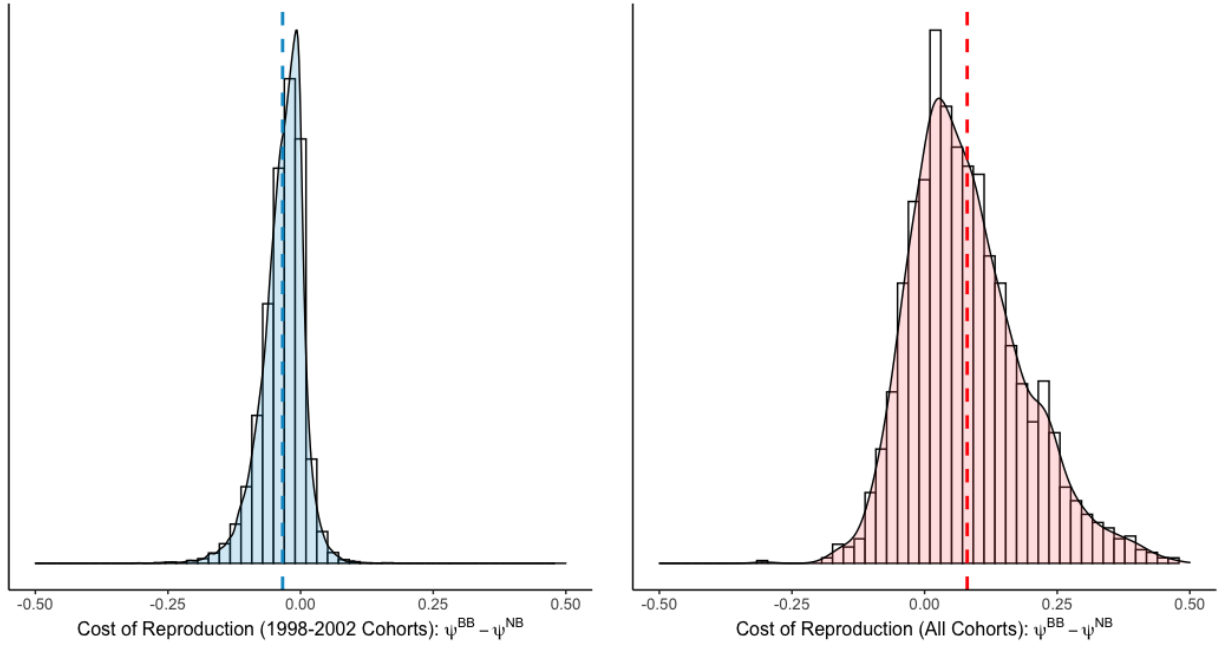


Figure 3: The cost of reproduction is estimated by finding the difference between reproductive probabilities of non-breeders and breeders: panels depict posterior distribution of ψ^{BB} minus posterior distribution of ψ^{NB} for (A) output of the preferred model reported here, estimating reproductive probabilities for females born from 1998-2002, and (B) the output from Badger et al. 2020, a similar model estimating reproductive probabilities for females born 1962, 1969, 1970, 1973, 1974, 1985-87, 1989, and 1998-2002. Note that for (B), the models did not estimate a cost of reproduction in terms of reproductive rate, where $\psi^{BB} > \psi^{NB}$, i.e. current reproduction does not incur a “penalty” to future reproduction. By contrast, our sample of females (A) show a slight cost of reproduction $\psi^{BB} < \psi^{NB}$, where individuals are slightly more likely to breed in a given year if they had skipped reproduction previously.

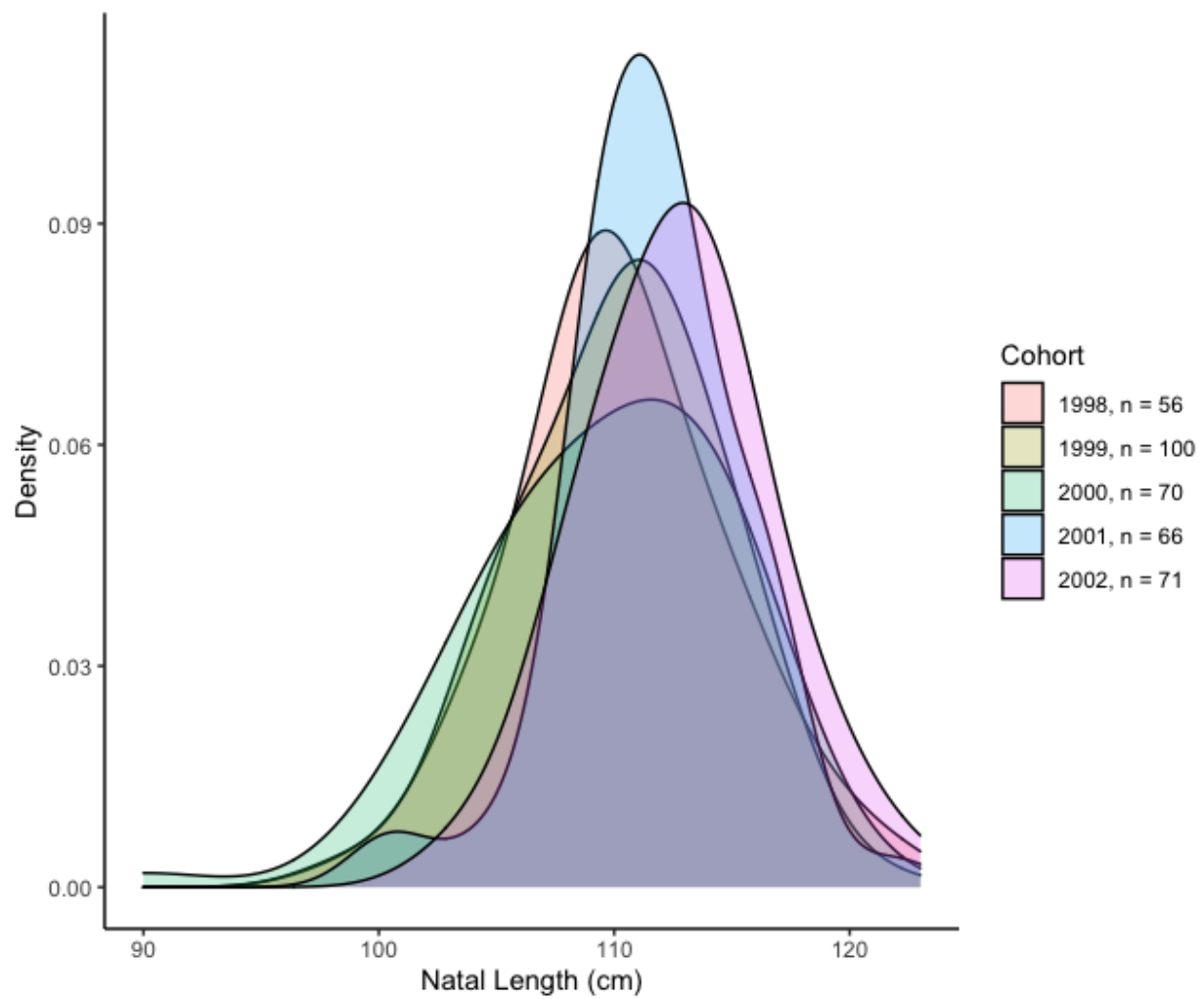


Figure 4: Density plots of the distribution of natal lengths of our sample of females by cohort, 1998-2002.

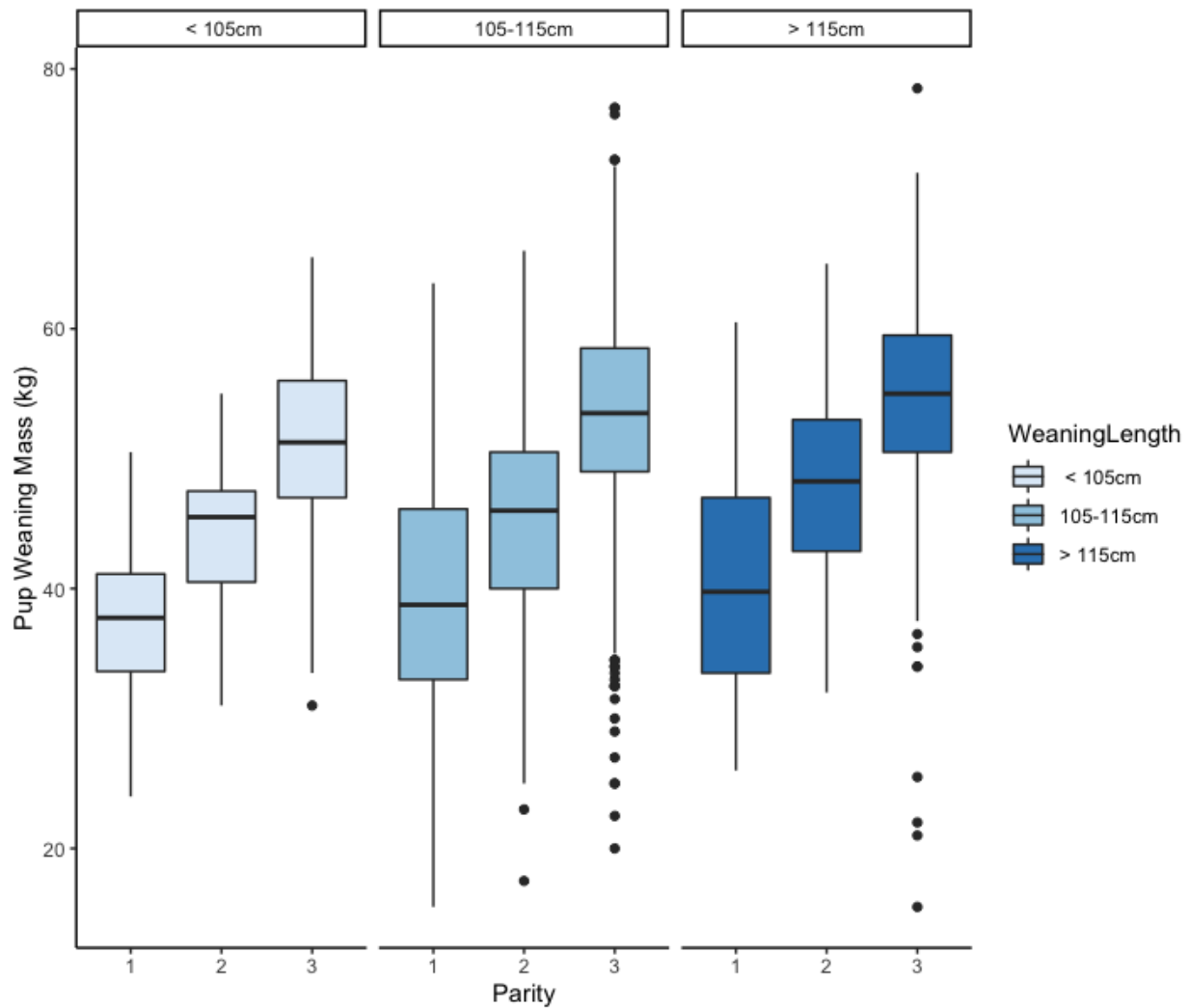


Figure 5: There is no evidence for an interactive effect of natal length and parity— effect of natal length on pup weaning mass does not taper off ($p > 0.05$, Table 1). Boxplots of pup weaning masses for individuals with short (90 - 105 cm), average (105 cm - 115 cm), and tall (115 - 125 cm) natal lengths (panels) over the 1st, 2nd, and 3+ parities.