

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

Janelle Badger¹, W. Don Bowen², Cornelia den Heyer², and Greg Breed³

¹NOAA Fisheries Pacific Islands Fisheries Science Center

²Bedford Institute of Oceanography

³University of Alaska Fairbanks

September 1, 2022

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.

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

3 Janelle J. Badger^{1,2*}, W. Don Bowen³, Cornelia E. den Heyer³, Greg A. Breed^{1,4}

4 ¹ Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, Alaska, USA

5 ² Current Address: Pacific Islands Fisheries Science Center, National Oceanic and Atmospheric
6 Administration, Honolulu, Hawaii, USA

7 ³ Bedford Institute of Oceanography, Department of Fisheries and Oceans Canada, Dartmouth,
8 Nova Scotia, Canada

9 ⁴ Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska, USA

10 **Abstract**

11 An individual's size in early stages of life may be an important source of individual variation in
12 lifetime reproductive performance, as size effects on ontogenetic development can have cascading
13 physiological and behavioral consequences throughout life. Here, we explored how natal size
14 influences subsequent reproductive performance in grey seals (*Halichoerus grypus*) using repeated
15 encounter and reproductive data on a marked sample of 363 females that were measured for length
16 at ~ 4 weeks of age and eventually recruited to the Sable Island breeding colony. Two reproductive
17 traits were considered: provisioning performance (mass of weaned offspring), modeled using
18 linear mixed effects models; and reproductive frequency (rate at which a female returns to breed),
19 modeled using mixed-effects multistate mark-recapture models. Mothers with the longest natal
20 lengths produced pups 8 kg heavier and were 20% more likely to breed in a given year than
21 mothers with the shortest lengths. Correlation in body lengths between natal and adult life stages,
22 however, is weak: longer pups do not grow to be longer than average adults. Thus covariation
23 between natal length and future reproductive performance appears to be a carry-over effect, where
24 the size advantages afforded in early juvenile stages may allow enhanced long-term performance
25 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

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

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

72 and an important link between evolutionary and ecological processes (Lomnicki 1978, Cam et al.
73 2002, Bolnick et al. 2003, Vindenes et al. 2008, Bolnick et al. 2011, Stover et al. 2012, Gimenez
74 et al. 2017).

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

87 Sable Island grey seal pup production (a proxy for population size) has increased dramatically
88 over the past half century with near maximum population growth of 13% per year between the
89 1960s and late 1990s (Bowen 2011) and a reduced rate of increase of 5-7% per year since 2004
90 (den Heyer et al. 2017, den Heyer et al. 2021). Associated with declines in population growth,
91 juvenile apparent survival to reproductive recruitment has decreased by more than half from an
92 average of 74% in cohorts born 1985-1989 to 33% in cohorts born 1998-2002 (den Heyer et al.
93 2013). This decline appears to be size-selective, with recent investigations finding that heavier
94 and longer pups are more likely to recruit (Bowen et al. 2015). Apparent survival to recruitment

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

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

118 **Methods**

119 This study was conducted on Sable Island, Canada (43.93°N, 59.91°W), a partially vegetated
120 sandbar on the Scotian Shelf roughly 160 km off the coast of Nova Scotia, during the 1998-2020
121 breeding seasons. The breeding season at this colony spans early December through early February,
122 with 91.2% of pups born by mid-January (Bowen et al. 2007, den Heyer et al. 2021). Sable Island
123 supports the largest breeding colony of grey seals in the world with an estimated 87,500 pups (SE
124 = 15,100) born on the island in 2016, comprising 80% of the total grey seal pup production in the
125 Northwest Atlantic (den Heyer et al. 2021).

126 *Data Collection*

127 Our 19-year study (2002-2020) was conducted on a subset of female grey seals born on Sable
128 Island from 1998-2002 that survived to recruit to the breeding colony, as part of a larger program
129 led by the Department of Fisheries and Oceans, Canada (DFO). Individuals were marked at roughly
130 4 weeks old, shortly after weaning, with unique alpha-numeric hot-iron brands in each year 1998-2002.
131 Prior to marking, researchers recorded standard dorsal body length (to the nearest cm) of these
132 individuals while they were sedated with diazepam (~ 0.4 mg/kg body mass, Sandoz Canada,
133 Boucherville, Quebec, Canada) to ensure accurate measurement standardized across individuals
134 (Bowen et al. 2015). These permanent brands allowed reliable identification of individuals over
135 the course of their lives. Females can recruit to the breeding population as early as 4 years old,
136 but this is uncommon, and the average age of first reproduction is 6.5 ± 0.21 SE years for these
137 cohorts (den Heyer et al. 2013) with 87% of females recruited at or before age 7 (Bowen et al.
138 2015). During each breeding season since 2002, teams of researchers conducted 5-7 roughly
139 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).

163 *Statistical Analysis*

164 In this analysis, we were interested in understanding how a female's size during early life stages
165 influences subsequent reproductive success once she has matured. To do this, we analyzed the
166 effect of natal length (L_{natal} , her length after weaning, but prior to independent foraging at approximately
167 4 weeks old) on her reproductive performance in adulthood, measured two ways: annual provisioning
168 performance and reproductive frequency (both described below). We used generalized mixed-effect
169 additive and linear models to determine the effect of L_{natal} on these traits, and accounted for
170 imperfect detection in reproductive rate using a multi-state capture-recapture model in a Bayesian
171 framework (Gimenez et al. 2007, Lebreton et al. 2009, Kéry and Schaub 2012).

172 Modeling annual provisioning performance

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

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

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

183 indicator variable, and m denotes the parity group (1, 2, or 3+) of female i in year t so $m \in \{1, 2, 3\}$.
184 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,
185 where $\eta_t \sim N(0, \sigma_\eta^2)$, and $v_{i,t}$ is the error term where $v_{i,t} \sim N(0, \sigma_v^2)$.

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

192 Modeling reproductive rate

193 The second reproductive trait, reproductive rate, is defined as the probability an individual will
194 return to the island to give birth in any given year, and is the reciprocal of a female's interval
195 between births adjusted by her reproductive state the previous year and other covariates. We
196 estimated the effect of a female's natal length L_{natal} on her reproductive rate by modeling her
197 reproductive history as a Markov chain in a multi-state capture re-capture modeling framework.
198 Between her first and last sightings on the island during our study, a female transitions among
199 three reproductive states: initially a first time breeder F , then switching between a breeder state
200 B , or non-breeder state N . An individual's state transitions from year t to $t + 1$ is modeled as a
201 categorical trial with probabilities of transition ψ^{ks} from state k to state s . Reproductive frequency
202 is then defined as the probability of transition from any state k into the reproductive state B
203 (ψ^{kB}). We used mixed-effects logistic regression embedded in this multistate model to account
204 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. Beuplet 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 `Unif(0,10)` prior for σ_θ and σ_β .

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

226 of the parameters of interest. For each of the competing models, we ran three chains in parallel
227 using package `dclone` (Solymos 2010) with different sets of initial values. The first 10,000 MCMC
228 samples were discarded, known as the burn-in period, after having checked that convergence was
229 satisfactory. Convergence was visually assessed using sample path plots in conjunction with
230 the Brooks-Gelman-Rubin diagnostic \hat{r} (Brooks and Gelman 1998), with values close to 1.00
231 indicating adequate convergence. Chains then ran for 100,000 iterations after burn-in, and a total of
232 3,000 MCMC samples (every 100th sample of each chain) were used for inference. We determined
233 that a covariate had an effect if a 95% credible interval (CRI) of the posterior distribution of that
234 parameter did not include 0. We assessed support for inclusion of natal length using a measure
235 of out-of-sample predictive ability of each model, the Widely Applicable Information Criterion
236 (WAIC, Watanabe 2010), where a model with a smaller WAIC is judged a better fit.

237 **Results**

238 We analyzed the reproductive histories of 363 females born from 1998-2002 that gave birth to a
239 total of 3457 pups. 2.5% (9/363) of those females recruited to the breeding population at age 4,
240 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%
241 (111/363) recruited after age 6. From primiparity to the most recent year of the study, 2020,
242 females had an average of 10 pups ($SE = 4.48$, ranging 1 to 17). These females' natal lengths
243 (L_{natal}), ranged from 90-123 cm, with an average of 110.7 cm ($SE = 4.28$). We did find a cohort
244 effect on L_{natal} (ANOVA, $p = 0.003$), where females born in 2002 that recruited to the breeding
245 population had significantly longer L_{natal} than other cohorts analyzed (Tukey HSD, Figure 4).

246 *Effect of natal length on future reproductive performance*

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

249 of natal length as a covariate, though there was also modest support for a quadratic effect (Table
250 1, Appendix B: Table B2). Females who had the longest natal lengths proceeded to give birth
251 to offspring that weaned 8 kg heavier, on average, than conspecifics who had the shortest natal
252 lengths (Table 3). Though we expected natal body length to have a greater effect on early parities
253 (such that the effect weakened over time), we found no support for an interactive model between
254 L_{natal} and parity (Table 1, Appendix B: Table B3). Repeatable differences among individuals
255 accounted for 41% of the variance in pup weaning mass. Year accounted for only 10.8% of the
256 variance in weaning mass, suggesting that among-year environmental effects were small. Natal
257 length was also positively associated with a female's future reproductive rate. Model output from
258 fitted multistate Markov models estimated that natal length accounts for the spread in annual
259 reproductive probability to range from 0.715 for females who had the shortest L_{natal} to 0.916
260 for females who had the longest L_{natal} (Table 4, Figure 2). Model fits displayed no evidence of
261 inadequate convergence to stationary distributions.

262 *Cost of reproduction in breeding rate*

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

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

275 *Cohort effects in reproductive performance*

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

286 **Discussion**

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

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

304 *Implications for maternal fitness*

305 Our findings show that grey seal mothers increase maternal fitness by producing longer pups,
306 as longer pups mature to be more productive mothers. While the effect of offspring body size
307 on maternal fitness has been extensively studied (Lack 1947, Cody 1966, Smith and Fretwell
308 1974, Stearns 2000, Krist 2011, Rollinson and Hutchings 2013, Pettersen et al. 2015), mass
309 or fat reserves, and not length, are the typical measure of size. This methodological bias is
310 likely due to the difficulty of accurately measuring length; body posture can greatly impact length
311 measurements, while mass is accurately and precisely measured with a calibrated scale. Body
312 length and fat reserves of offspring, however, reflect different aspects of maternal quality; larger
313 skeletal size is more likely to have a significant heritable component while stored energy is a
314 measure of maternal effort and investment. Provisioning offspring with large energy reserves
315 requires considerable reproductive energy expenditure in both acquisition of resources (e.g. foraging
316 efficiency, prey choice, intraspecific competition) and effectively transferring resources to offspring

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

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

340 *Natal length as a source of individual variation in quality*

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

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

356 The extent to which body length, independent of mass, may offset the energetic cost of foraging
357 is, however, unknown in many systems, including grey seals. In Weddell seals, Wheatley et al.
358 (2006) found that postpartum mass of shorter females was significantly lower in years of poor
359 environmental conditions whereas the mass of longer females did not differ between years. This
360 suggested shorter females were less successful foragers than their larger conspecifics and may
361 generally be more susceptible to environmental variation (Wheatley et al. 2006). If longer females
362 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

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

389 *Carryover effects of early life morphology*

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

400 Carry-over effects linking ecological conditions experienced early in life to later performance
401 are well documented (Moore and Martin 2019, Madsen and Shine 2000, Gratton and Denno 2003,
402 Marshall et al. 2006, Nussey et al. 2007, Descamps et al. 2008, Harrison et al. 2011, O'Connor et al.
403 2014, Garcia et al. 2019), though such demonstrations are relatively rare for long-lived mammals
404 (Coltman et al. 1999, Festa-Bianchet et al. 2000, Nussey et al. 2007). Food availability during early
405 development is understood to be a key environmental factor driving carry-over effects (Descamps
406 et al. 2008, Harrison et al. 2011), with the ultimate driver being habitat quality, or less commonly
407 reported, intraspecific density.

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

419 *Implications for population dynamics*

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

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

440 Our sample of females also make up the post-selection distribution of body size, and this
441 study can perhaps be viewed as a lens into the reproductive performance of individuals growing
442 under intense selection pressure and slowing population growth (Coltman et al. 1999, Allen et al.
443 2008). In addition to our results linking natal size with reproductive success, we found that this
444 sample of females exhibited a slight cost of reproduction not detected when a larger subset of
445 the population was analyzed in Badger et al. (2020). That sample included females born in the
446 1960s, 1970s, and 1980s that were juveniles when population densities were much lower. From
447 this, we infer that ecological conditions during early stages can mediate future trade-offs and
448 shape the natural selection on life history and pace-of-life (Clutton-Brock et al. 1987, Coltman
449 et al. 1999). Intensified competition among these age groups may drive a less favorable energetic
450 trade-off between survival and supporting reproduction for individuals recruiting into an intensely
451 competitive environment.

452 *Implications & Conclusions*

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

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

475 density intensify, or if there is counteracting selection against extremely long adults even when
476 longer natal lengths are favored. Grey seals have particularly high and consistent survival as adults
477 (0.989 ± 0.001 for females aged 4-24, 0.901 ± 0.004 for females aged 25+, den Heyer and Bowen
478 2017), so directional selection on body length as adults is more likely to act through variation
479 in reproductive performance. Further investigation into changes in size-selective vital rates as
480 the population continues to increase would likely yield important insights into density-related
481 evolutionary changes in long-lived animals.

482 **Acknowledgements** The authors would like to acknowledge the invaluable field assistance of
483 a myriad of volunteers, employees, graduate students, and postdoctoral fellows, including: C.
484 Abraham, S. Armsworthy, D. Austin, D. Boness, C. Bubac, S. Budge, S. Heaslip, S. Iverson, W.
485 Joyce, S. Lang, E. Leadon, P. Leblanc, D. Lidgard, J. McMillan, B. Nowak, R. Ronconi, S. Smith,
486 S. Tucker, M. Wilson, K. Whoriskey, and S. Wong. **Funding:** This work is supported by the
487 National Science Foundation Graduate Research Fellowship Program under Grant No. 1839290
488 awarded to JJB. Any opinion, findings, and conclusions or recommendations expressed in this
489 material are those of the authors and do not necessarily reflect the views of the National Science
490 Foundation. Data collection was supported by the Department of Fisheries and Oceans Canada,
491 and Natural Sciences and Engineering Research Council grants to S. J. Iverson and W. D. Bowen
492 and the Department of Fisheries and Oceans Centre of Expertise for Marine Mammalogy. **Author**
493 **Contributions:** JJB and WDB conceived of the research with significant input from GAB and
494 CDH. WDB and CDH were responsible for the design and execution of data collection. JJB
495 analyzed the data and drafted the manuscript with contributions from all authors. **Competing**
496 **Interests:** We declare we have no competing interests. **Data Accessibility:** The Department of

497 Fisheries and Oceans Canada scientific data are a public resource and subject to full and open
498 access within two years of being acquired or generated. Please refer all data enquiries directly to
499 the DFO.

References

- 501 Allen RM, Buckley YM, Marshall DJ. 2008. Offspring size plasticity in response to intraspecific
502 competition: An adaptive maternal effect across life-history stages. *American Naturalist* **171**:
503 225–237. ISSN 00030147.
- 504 Badger JJ, Bowen WD, den Heyer CE, Breed GA. 2020. Variation in individual reproductive
505 performance amplified with population size in a long-lived carnivore. *Ecology* **e03024**.
- 506 Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4.
507 *Journal of Statistical Software* **67**: 1–48.
- 508 Beauplet G, Barbraud C, Dabin W, Kussener C, Guinet C, Benton T. 2006. Age-specific survival
509 and reproductive performances in fur seals: Evidence of senescence and individual quality.
510 *Oikos* **112**: 430–441. ISSN 00301299.
- 511 Bernardo J. 1996. Maternal effects in animal ecology. *American Zoologist* **36**: 83:105.
- 512 Betini GS, Griswold CK, Norris DR. 2013. Density-mediated carry-over effects explain variation
513 in breeding output across time in a seasonal population. *Biology Letters* **9**. ISSN 1744957X.
- 514 Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber
515 SJ, Urban MC, Vasseur DA. 2011. Why intraspecific trait variation matters in community
516 ecology. *Trends in Ecology and Evolution* **26**: 183–192. ISSN 01695347.
- 517 Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003. The
518 ecology of individuals: incidence and implications of individual specialization. *American*

519 *Naturalist* **161**: 1–28. ISSN 0003-0147.

520 URL <http://www.ncbi.nlm.nih.gov/pubmed/12650459>

521 Boness DJ, James H. 1979. Reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable
522 Island, Nova Scotia. *Journal of Zoology* **188**: 477–500. ISSN 09528369.

523 Bowen WD. 2011. Historical grey seal abundance and changes in the abundance of grey seal
524 predators in the Northwest Atlantic. *DFO Canadian Science Advisory Secretariat Research*
525 *Document* **2011/026**.

526 Bowen WD, den Heyer CE, McMillan JI, Iverson SJ. 2015. Offspring size at weaning affects
527 survival to recruitment and reproductive performance of primiparous gray seals. *Ecology and*
528 *Evolution* **5**: 1412–1424. ISSN 20457758.

529 Bowen WD, Iverson SJ, McMillan JI, Boness DJ. 2006. Reproductive performance in grey seals:
530 Age-related improvement and senescence in a capital breeder. *Journal of Animal Ecology* **75**:
531 1340–1351. ISSN 00218790.

532 Bowen WD, McMillan JI, Blanchard W. 2007. Reduced population growth of gray seals at Sable
533 Island: Evidence from pup production and age of primiparity. *Marine Mammal Science* **23**:
534 48–64. ISSN 08240469.

535 Bowen WD, Stobo WT, Smith SJ. 1992. Mass changes of grey seal *Halichoerus grypus* pups on
536 Sable Island: differential maternal investment reconsidered. *Journal of Zoology, London* **227**:
537 607–622.

538 Breed GA, Bowen WD, Leonard ML. 2011. Development of foraging strategies with age in a
539 long-lived marine predator. *Marine Ecology Progress Series* **431**: 267–279. ISSN 01718630.

- 540 Breed GA, Bowen WD, Leonard ML. 2013. Behavioral signature of intraspecific competition and
541 density dependence in colony-breeding marine predators. *Ecology and Evolution* **3**: 3838–3854.
542 ISSN 20457758.
- 543 Brooks SP, Gelman A. 1998. General methods for monitoring convergence of iterative simulations.
544 *Journal of Computational and Graphical Statistics* **7**: 434–455. ISSN 15372715.
- 545 Bubac CM, Cullingham CI, Fox JA, Bowen WD, den Heyer CE, Coltman DW. 2021. Genetic
546 association with boldness and maternal performance in a free-ranging population of grey seals
547 (*Halichoerus grypus*). *Heredity* **127**: 35–51. ISSN 13652540.
548 URL <http://dx.doi.org/10.1038/s41437-021-00439-4>
- 549 Cam E, Link WA, Cooch EG, Monnat JY, Danchin E. 2002. Individual covariation in life-history
550 traits: seeing the trees despite the forest. *American Naturalist* **159**: 96–105. ISSN 1537-5323.
551 URL <http://www.ncbi.nlm.nih.gov/pubmed/18707403>
- 552 Chambert T, Rotella JJ, Higgs MD, Garrott RA. 2013. Individual heterogeneity in reproductive
553 rates and cost of reproduction in a long-lived vertebrate. *Ecology and Evolution* **3**: 2047–2060.
554 ISSN 20457758.
- 555 Clutton-Brock TH. 1984. Reproductive effort and terminal investment in iteroparous animals.
556 *American Naturalist* **123**: 212–229.
- 557 Clutton-Brock TH. 1988. *Reproductive success: studies of individual variation in contrasting*
558 *breeding systems*. Chicago, IL: University of Chicago Press.
- 559 Clutton-Brock TH. 1991. *The evolution of parental care*. Princeton University Press.

560 Clutton-Brock TH, Albon SD, Guinness FE. 1987. Interactions between population density and
561 maternal characteristics affecting fecundity and juvenile survival in red deer. *Journal of Animal*
562 *Ecology* **56**: 857–871.

563 Cody ML. 1966. A general theory of clutch size. *Evolution* **20**: 174–184.

564 Coltman DW, Smith JA, Bancroft DR, Pilkington J, MacColl AD, Clutton-Brock TH, Pemberton
565 JM. 1999. Density-dependent variation in lifetime breeding success and natural and sexual
566 selection in Soay rams. *American Naturalist* **154**: 730–746. ISSN 00030147.

567 Costa DP. 1993. The relationship between reproductive and foraging energetics and the evolution
568 of the Pinnipedia. *Symposia of the Zoological Society of London* **66**: 293–314.

569 Crawley JA, Mumby HS, Chapman SN, Lahdenperä M, Mar KU, Htut W, Thura Soe A, Aung HH,
570 Lummaa V. 2017. Is bigger better? The relationship between size and reproduction in female
571 Asian elephants. *Journal of Evolutionary Biology* **30**: 1836–1845. ISSN 14209101.

572 den Heyer CE, Bowen WD. 2017. Estimating changes in vital rates of Sable Island grey seals using
573 mark-recapture analysis. *Canadian Science Advisory Secretariat Research Document* **2017/054**.

574 den Heyer CE, Bowen WD, Dale J, Gosselin JF, Hammill MO, Johnston DW, Lang SL, Murray
575 KT, Stenson GB, Wood SA. 2021. Contrasting trends in gray seal (*Halichoerus grypus*) pup
576 production throughout the increasing northwest Atlantic metapopulation. *Marine Mammal*
577 *Science* **37**: 611–630. ISSN 17487692.

578 den Heyer CE, Bowen WD, Mcmillan JI. 2013. Long-term changes in grey seal vital rates at
579 Sable Island estimated from POPAN mark-resighting analysis of branded seals. *DFO Canadian*
580 *Science Advisory Secretariat Research Document* **2013/021**.

581 den Heyer CE, Lang SLC, Bowen WD, Hammill MO. 2017. Pup production at Scotian shelf
582 grey seal (*Halichoerus grypus*) colonies in 2016. *DFO Canadian Science Advisory Secretariat*
583 *Research Document* **2017/056**.

584 Descamps S, Boutin S, Berteaux D, McAdam AG, Gaillard JM. 2008. Cohort effects in red
585 squirrels: the influence of density, food abundance, and temperature on future survival and
586 reproductive success. *Journal of Animal Ecology* **77**: 305–314.

587 Dias GM, Marshall DJ. 2010. Does the relationship between offspring size and performance
588 change across the life-history? *Oikos* **119**: 154–162. ISSN 00301299.

589 Festa-Bianchet M, Jorgenson JT, Realé D. 2000. Early development, adult mass, and reproductive
590 success in bighorn sheep. *Behavioral Ecology* **11**: 633–639.

591 Fox CW, Czesak ME. 2000. Evolutionary ecology of progeny size in arthropods. *Annual Review*
592 *of Entomology* **45**: 341–369.

593 Garcia TS, Bredeweg EM, Urbina J, Ferrari MC. 2019. Evaluating adaptive, carry-over, and plastic
594 antipredator responses across a temporal gradient in Pacific chorus frogs. *Ecology* **100**: 1–11.
595 ISSN 00129658.

596 Gearty W, McClain CR, Payne JL. 2018. Energetic tradeoffs control the size distribution of aquatic
597 mammals. *Proceedings of the National Academy of Sciences of the United States of America*
598 **115**: 4194–4199. ISSN 10916490.

599 Gimenez O, Cam E, Gaillard JM. 2017. Individual heterogeneity and capture–recapture models:
600 what, why and how? *Oikos* **127**: 664–686. ISSN 16000706.

- 601 Gimenez O, Rossi V, Choquet R, Dehais C, Doris B, Varella H, Vila JP, Pradel R. 2007. State-space
602 modelling of data on marked individuals. *Ecological Modelling* **206**: 431–438. ISSN 03043800.
- 603 Glazier DS. 2005. Beyond the '3/4-power law': Variation in the intra- and interspecific scaling
604 of metabolic rate in animals. *Biological Reviews of the Cambridge Philosophical Society* **80**:
605 611–662. ISSN 14647931.
- 606 Gratton C, Denno RF. 2003. Inter-year carryover effects of a nutrient pulse on *Spartina* plants,
607 herbivores, and natural enemies. *Ecology* **84**: 2692–2707. ISSN 00129658.
- 608 Green WCH, Rothstein A. 1991. Trade-offs between growth and reproduction in female bison.
609 *Oecologia* **86**: 521–527.
- 610 Hall AJ, McConnell BJ, Barker RJ. 2001. Factors affecting first-year survival in grey seals and
611 their implications for life history strategy. *Journal of Animal Ecology* **70**: 138–149. ISSN
612 0021-8790.
- 613 Hammill MO, den Heyer CE, Bowen WD, Lang SLC. 2017. Grey seal population trends in
614 Canadian waters, 1960-2016 and harvest advice. *DFO Canadian Science Advisory Secretariat*
615 *Research Document* **2017/052**: 1–35.
- 616 Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S. 2011. Carry-over effects as drivers of
617 fitness differences in animals. *Journal of Animal Ecology* **80**: 4–18. ISSN 00218790.
- 618 Hernández-Matías A, Real J, Pradel R, Ravayrol A, Vincent-Martin N. 2011. Effects of age,
619 territoriality and breeding on survival of Bonelli's Eagle *Aquila fasciata*. *Ibis* **153**: 846–857.
620 ISSN 00191019.

- 621 Hindell MA, McConnell BJ, Fedak MA, Slip DJ, Burton HR, Reijnders PJ, McMahon CR. 1999.
622 Environmental and physiological determinants of successful foraging by naive southern elephant
623 seal pups during their first trip to sea. *Canadian Journal of Zoology* **77**: 1807–1821. ISSN
624 00084301.
- 625 Iverson SJ, Bowen WD, Boness DJ, Oftedal OT. 1993. Effect maternal size and milk energy
626 output on pup growth in grey seals (*Halichoerus grypus*). *Physiological Zoology* **66**: 61–88.
- 627 Johns ME, Warzybok P, Bradley RW, Jahncke J, Lindberg M, Breed GA. 2018. Increased
628 reproductive investment associated with greater survival and longevity in Cassin’s auklets.
629 *Proceedings of the Royal Society B* **285**. ISSN 14712954.
- 630 Kemper KE, Visscher PM, Goddard ME. 2012. Genetic architecture of body size in mammals.
631 *Genome Biology* **13**: 244. ISSN 1465-6906.
- 632 Kéry M, Schaub M. 2012. *Bayesian Population Analysis using WinBUGS: a hierarchcial*
633 *perspective*. Elsevier.
- 634 Kleiber M. 1947. Body size and metabolic rate. *Physiological Reviews* **27**: 511–541.
- 635 Krist M. 2011. Egg size and offspring quality: A meta-analysis in birds. *Biological Reviews* **86**:
636 692–716. ISSN 14647931.
- 637 Lack D. 1947. The significance of clutch size. *Ibis* : 302–352.
- 638 Lebreton JD, Nichols JD, Barker RJ, Pradel R, Spendelov JA. 2009. Modeling individual
639 animal histories with multistate capture-recapture models. In *Advances in Ecological Research*,

640 volume 41. Burlington, VT: Academic Press, 1 edition. ISBN 9780123749253, 87–173.
641 URL [http://dx.doi.org/10.1016/S0065-2504\(09\)00403-6](http://dx.doi.org/10.1016/S0065-2504(09)00403-6)

642 Lindström J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology and*
643 *Evolution* **14**: 343–348. ISSN 01695347.

644 Lloyd KJ, Oosthuizen WC, Fay R, Bester MN, de Bruyn PJ. 2019. Selective disappearance of frail
645 juveniles: consequences for understanding social dominance in adult male elephant seals. *Oikos*
646 **129**. ISSN 16000706.

647 Lomnicki A. 1978. Individual differences between animals and the natural regulation of their
648 numbers. *Journal of Animal Ecology* **47**: 461–475.

649 Madsen T, Shine R. 2000. Silver spoons and snake body sizes: Prey availability early in life
650 influences long-term growth rates of freeranging pythons. *Journal of Animal Ecology* **69**:
651 952–958. ISSN 00218790.

652 Marshall DJ, Bolton TF, Keough MJ. 2003. Offspring size affects the post-metamorphic
653 performance of a colonial marine invertebrate. *Ecology* **84**: 3131–3137. ISSN 00129658.

654 Marshall DJ, Cook CN, Emler RB. 2006. Offspring size effects mediate competitive interactions
655 in a colonial marine invertebrate. *Ecology* **87**: 214–225. ISSN 00129658.

656 Marshall DJ, Keough MJ. 2008. The relationship between offspring size and performance in the
657 sea. *American Naturalist* **171**: 214–224. ISSN 00030147.

658 Mellish JE, Iverson SJ, Bowen WD. 1999. Variation in milk production and lactation performance

659 in grey seals and consequences for pup growth and weaning characteristics. *Physiological and*
660 *Biochemical Zoology* **72**: 677–690. ISSN 1522-2152.

661 Moore MP, Martin RA. 2019. On the evolution of carry-over effects. *Journal of Animal Ecology*
662 **88**: 1832–1844. ISSN 13652656.

663 Moran AL, Emlet RB. 2001. Offspring size and performance in variable environments: Field
664 studies on a marine snail. *Ecology* **82**: 1597–1612. ISSN 00129658.

665 Mousseau TA, Fox CW. 1998. The adaptive significance of maternal effects. *Trends in Ecology &*
666 *Evolution* **13**: 403–407. ISSN 01695347.

667 Norris DR. 2005. Carry-over effects and habitat quality in migratory populations. *Oikos* **109**:
668 178–186. ISSN 00301299.

669 Nussey DH, Kruuk LEB, Morris A, Clutton-Brock TH. 2007. Environmental conditions in early
670 life influence ageing rates in a wild population of red deer. *Current Biology* **17**: 1000–1001.
671 ISSN 09609822.

672 O'Connor CM, Norris DR, Crossin GT, Cooke SJ. 2014. Biological carryover effects: Linking
673 common concepts and mechanisms in ecology and evolution. *Ecosphere* **5**: 1–11. ISSN
674 21508925.

675 Partridge L, Harvey PH. 1988. The ecological context of life history evolution. *Science* **241**:
676 1449–1455.

677 Peters RH. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge
678 edition.

679 Pettersen AK, White CR, Marshall DJ. 2015. Why does offspring size affect performance?
680 Integrating metabolic scaling with life-history theory. *Proceedings of the Royal Society B:*
681 *Biological Sciences* **282**. ISSN 14712954.

682 Plummer M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs
683 sampling.

684 Plummer M. 2018. rjags: Bayesian graphical models using MCMC. R package version 4-8.

685 R Core Team. 2020. R: A language and environment for statistical computing.
686 URL <https://www.r-project.org/>

687 Roff DA. 1992. *The evolution of life histories*. New York: Chapman and Hall.

688 Rollinson N, Hutchings JA. 2013. The relationship between offspring size and fitness: integrating
689 theory and empiricism. *Ecology* **94**: 315–324. ISSN 0036-5505 (Print).

690 Sinervo B. 1990. The evolution of maternal investment in lizards: an experimental and comparative
691 analysis of egg size and its effects on offspring performance. *Evolution* **44**: 279–294.

692 Smith CC, Fretwell SD. 1974. The optimal balance between size and number of offspring.
693 *American Naturalist* **108**: 499–506.

694 Sogard SM. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. *Bulletin*
695 *of Marine Science* **60**: 1129–1157. ISSN 00074977.

696 Solymos P. 2010. dclone: Data cloning in R. *The R Journal* **2**: 29–37.

697 Stanton ML. 1984. Seed variation in wild radish: effect of seed size on components of seedling
698 and adult fitness. *Ecology* **65**: 1105–1112.

- 699 Stearns SC. 1992. *The evolution of life histories*. Oxford: Oxford University Press.
- 700 Stearns SC. 2000. Life history evolution: Successes, limitations, and prospects.
701 *Naturwissenschaften* **87**: 476–486. ISSN 00281042.
- 702 Stoelting RE, Gutiérrez RJ, Kendall WL, Peery MZ. 2015. Life-history tradeoffs and reproductive
703 cycles in Spotted Owls. *The Auk* **132**: 46–64. ISSN 0004-8038.
- 704 Stover JP, Kendall BE, Fox GA. 2012. Demographic heterogeneity impacts density-dependent
705 population dynamics. *Theoretical Ecology* **5**: 297–309. ISSN 18741738.
- 706 van Noordwijk AJ, de Jong G. 1986. Acquisition and allocation of resources: their influence on
707 variation in life history tactics. *American Naturalist* **128**: 137–142.
- 708 Vindenes Y, Engen S, Sæther BE. 2008. Individual heterogeneity in vital parameters and
709 demographic stochasticity. *American Naturalist* **171**: 455–467. ISSN 0003-0147.
710 URL <http://www.journals.uchicago.edu/doi/10.1086/528965>
- 711 Watanabe S. 2010. Asymptotic equivalence of Bayes cross validation and Widely Applicable
712 Information Criterion in singular learning theory. *Journal of Machine Learning Research* **11**:
713 3571–3594.
714 URL <http://arxiv.org/abs/1004.2316>
- 715 Wauters L, Bijmens L, Dhondt AA. 1993. Body mass at weaning and juvenile recruitment in the
716 red squirrel. *Journal of Animal Ecology* **62**: 280–286.
- 717 Wheatley KE, Bradshaw CJ, Davis LS, Harcourt RG, Hindell MA. 2006. Influence of maternal

718 mass and condition on energy transfer in Weddell seals. *Journal of Animal Ecology* **75**: 724–733.
719 ISSN 00218790.

720 Williams TM, Davis RW, Fuiman LA, Francis J, LeBoeuf BJ, Horning M, Calambokidis J, Croll
721 DA. 2000. Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* **288**:
722 133–136. ISSN 00368075.

723 Wilson AJ, Pemberton JM, Pilkington JG, Clutton-Brock TH, Coltman DW, Kruuk LE. 2007.
724 Quantitative genetics of growth and cryptic evolution of body size in an island population.
725 *Evolutionary Ecology* **21**: 337–356. ISSN 02697653.

726 Wilson AJ, Réale D. 2006. Ontogeny of additive and maternal genetic effects: Lessons from
727 domestic mammals. *American Naturalist* **167**. ISSN 00030147.

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

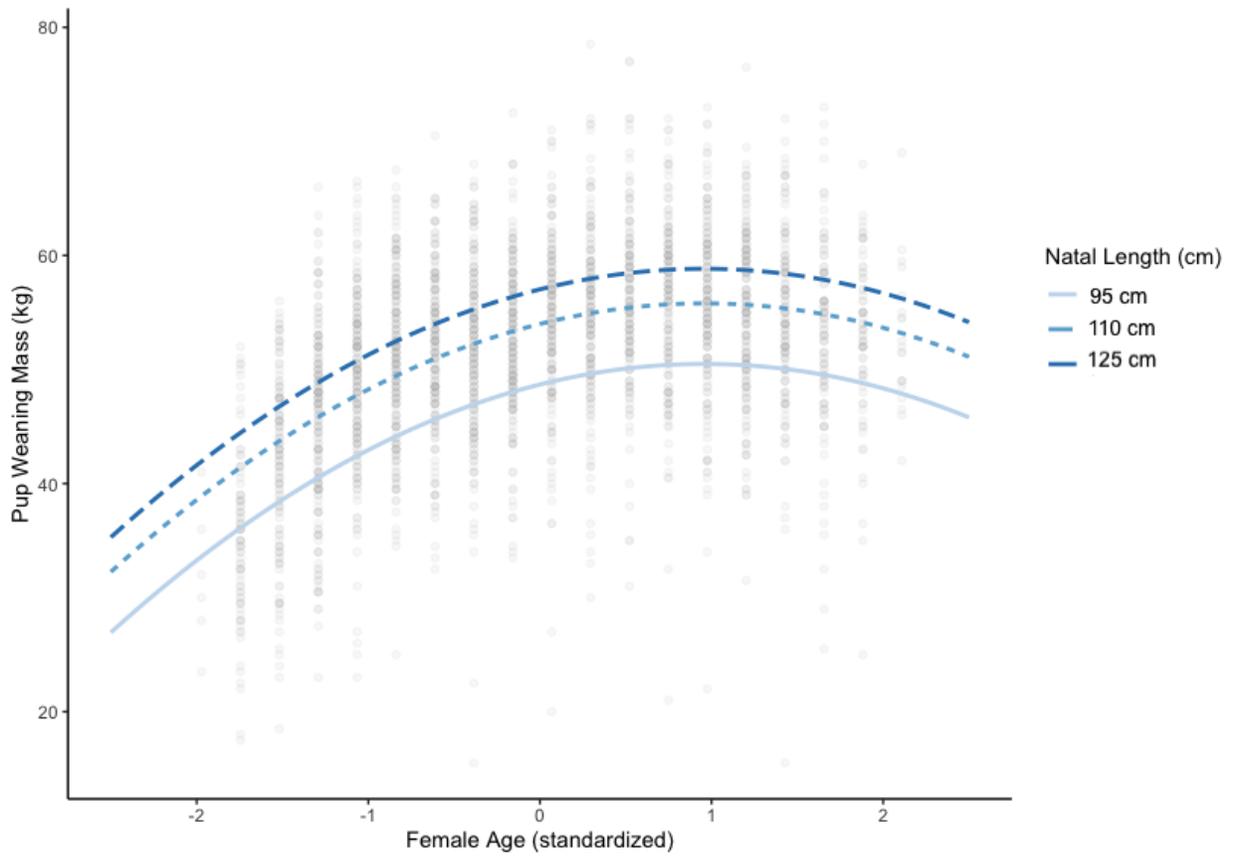


Figure 1: The estimated effect of natal length on provisioning performance as a female ages. Lines are 0.025%, 50%, and 97.5% quantiles of natal lengths corresponding to 95 cm, 110 cm, and 125 cm.

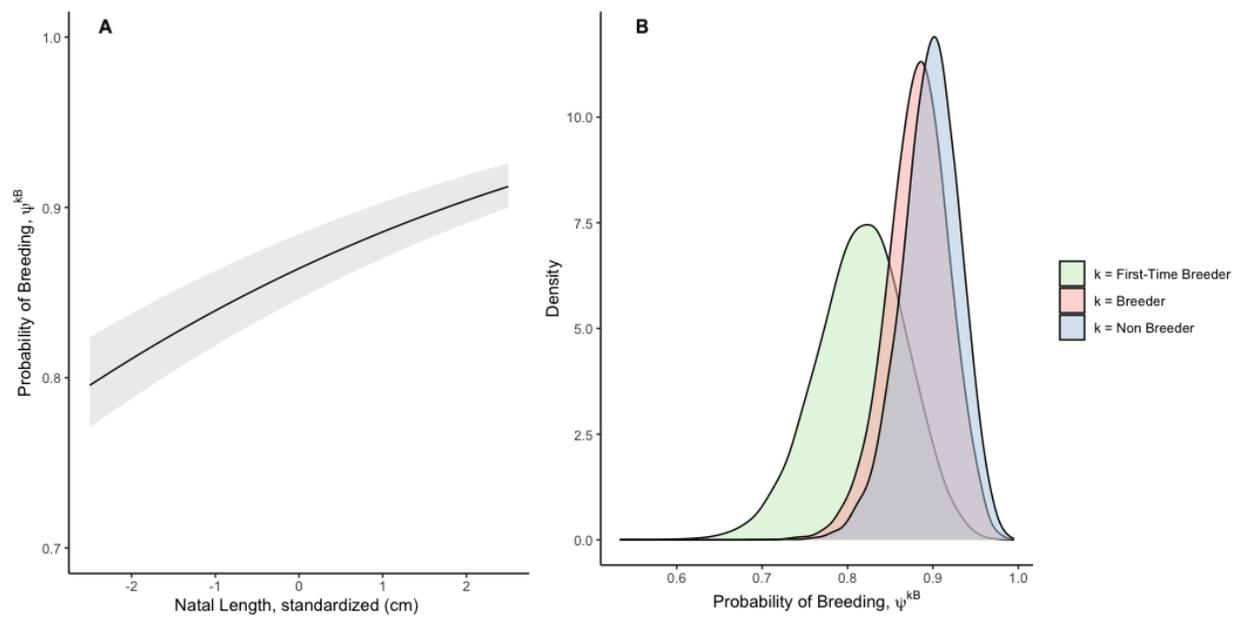


Figure 2: Results from the Markov chain multi-state model describing probability of breeding, ψ^{kB} , as a function of (A) natal length, and (B) the female's previous state in year $t-1$.

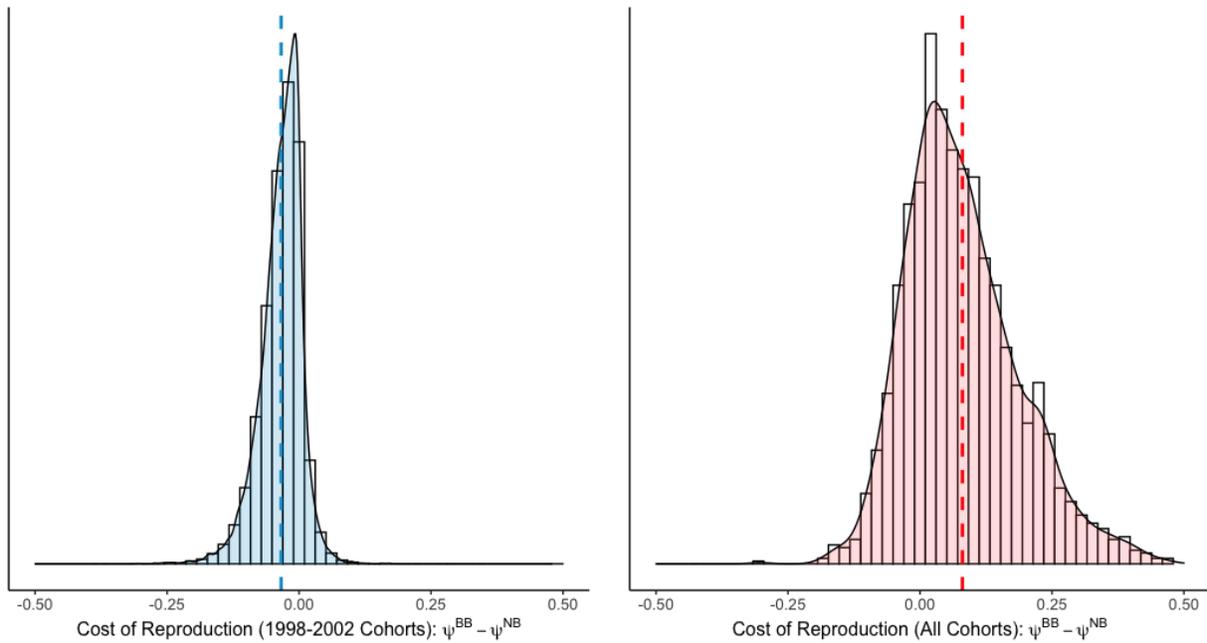


Figure 3: The cost of reproduction is estimated by finding the difference between reproductive probabilities of non-breeders and breeders: panels depict posterior distribution of ψ^{BB} minus posterior distribution of ψ^{NB} for (A) output of the preferred model reported here, estimating reproductive 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.

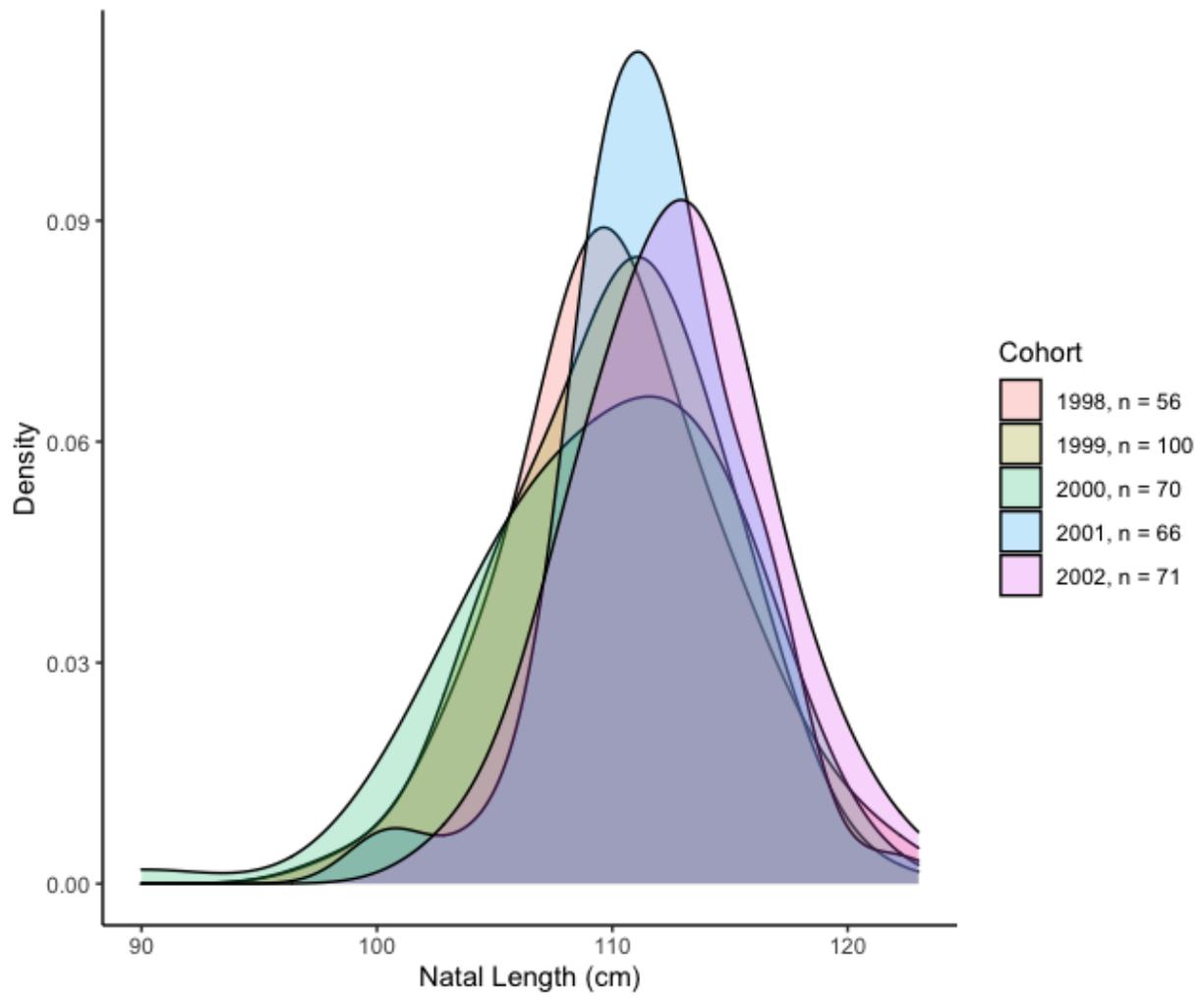


Figure 4: Density plots of the distribution of natal lengths of our sample of females by cohort, 1998-2002.

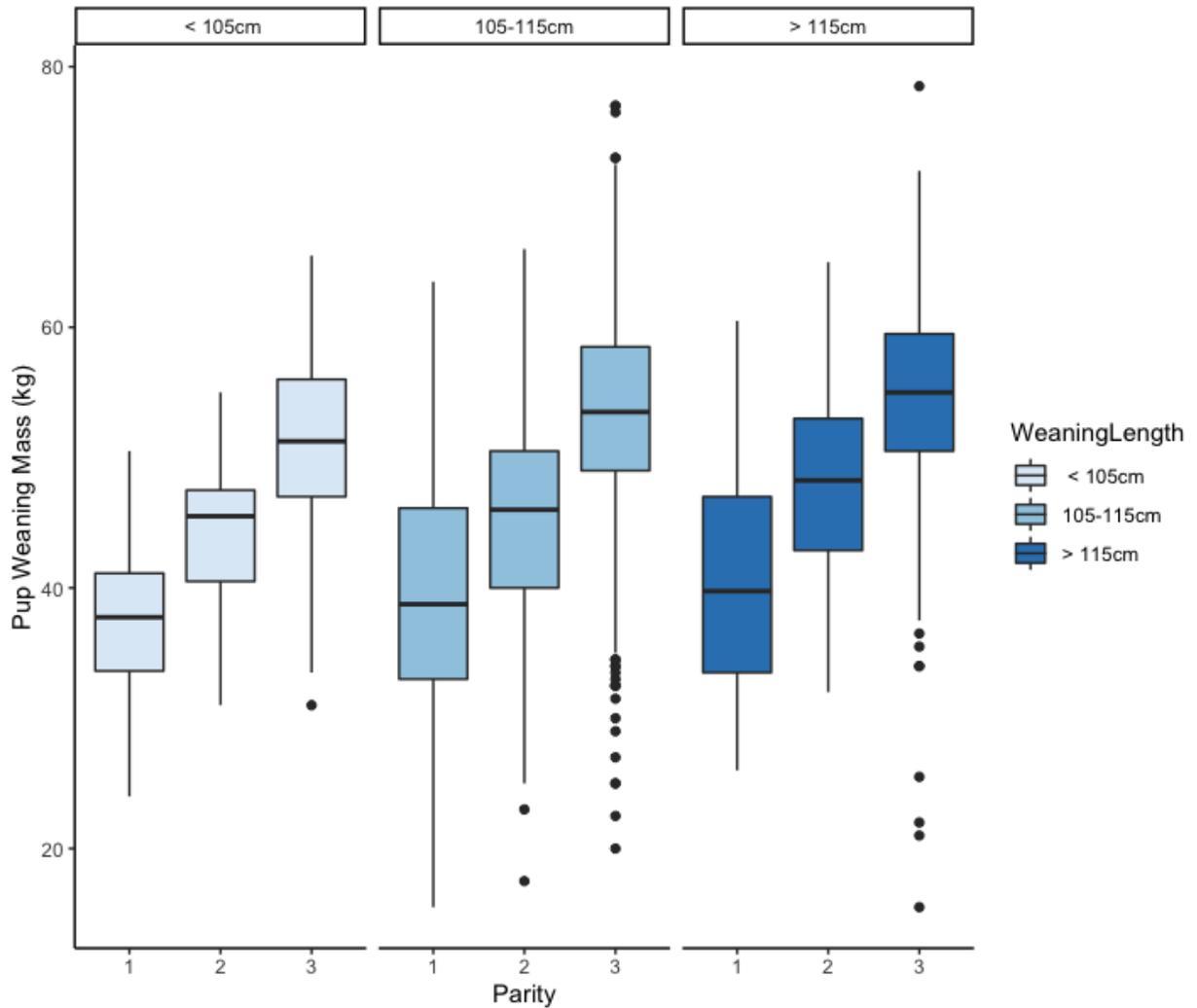


Figure 5: There is no evidence for an interactive effect of natal length and parity— effect of natal length on pup weaning mass does not taper off ($p > 0.05$, Table 1). Boxplots of pup weaning masses for individuals with short (90 - 105 cm), average (105 cm - 115 cm), and tall (115 - 125 cm) natal lengths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