

Phenotypic selection and covariation in the life - history traits of elephant seals: heavier offspring gain a double selective advantage

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Abstract

Early developmental conditions contribute to individual heterogeneity of both phenotypic traits and fitness components, ultimately affecting population dynamics. Although the demographic consequences of ontogenic growth are best quantified using an integrated measure of fitness, most analyses to date have instead studied individual fitness components in isolation. Here, we estimated phenotypic selection on weaning mass in female southern elephant seals (*Mirounga leonina*) by analyzing individual-based data collected between 1986 and 2016 with capture-recapture and matrix projection models. In support of a hypothesis predicting a gradual decrease of weaning mass effects with time since weaning (the replacement hypothesis), we found that the estimated effects of weaning mass on future survival and recruitment probability was of intermediate duration (rather than transient or permanent). Heavier female offspring had improved odds of survival in early life and a higher probability to recruit at an early age. The positive link between weaning mass and recruitment age is noteworthy, considering that pre-recruitment mortality already imposed a strong selective filter on the population, leaving only the most 'robust' individuals to reproduce. The selection gradient on asymptotic population growth rate, a measure of mean absolute fitness, was weaker than selection on first-year survival and recruitment probabilities. Weaker selection on mean fitness occurs because weaning mass has little impact on adult survival, the fitness component to which the population growth of long-lived species is most sensitive. These results highlight the need to interpret individual variation in phenotypic traits in a context that considers the demographic pathways between the trait and an inclusive proxy of individual fitness. Although variation in weaning mass do not translate to permanent survival differences among individuals in adulthood, it explains heterogeneity and positive covariation between survival and breeding in early life, which contribute to between-individual variation in fitness.

Introduction

Animal populations consist of individuals that are heterogeneous in both phenotypic traits and fitness components. Individual heterogeneity is of great interest, as the eco-evolutionary changes of a population depend on the selection pressure that acts on individual phenotypic and genetic variation (Stearns 1989a, Tuljapurkar et al. 2009, Plard et al. 2012, Chambert et al. 2014). For quantitative traits, the phenotypic distribution of individuals in a population typically varies along a continuous gradient that depends on genotypes and the conditions that individuals experience during pre- and post-natal development, either through direct environmental effects or indirect parental effects (Lynch and Walsh 1998, Monaghan 2008, Maestripieri and Mateo 2009). The phenotypic variation induced by early development conditions can have short-term fitness consequences that diminish over time (Lindholm et al. 2006), but may also have long-term consequences on the phenotypic quality and demographic performance of individuals, even in adulthood (Lindström 1999, Cam and Aubry 2011, Allen and Marshall 2013, Kruuk et al. 2015).

Adult survival strongly influences the lifetime reproductive success of long-lived iteroparous species (Gaillard et al. 2000). However, individuals must first survive the juvenile stage and then, upon reaching the age of maturity, recruit to the breeding population. Factors that influence juvenile survival and/or recruitment probability thus contribute significantly to between-individual variation in fitness components such as lifetime reproductive success (Clutton-Brock 1988). Juvenile survival depends strongly on structural size or body mass at independence (and even size before independence, e.g., Krist [2011], Hadfield et al. [2013]), and persistent positive selection on juvenile growth rate and size is observed in a wide range of taxa (Rollinson and Rowe 2015, Armstrong et al. 2017). Mothers that do not allocate sufficient energy to their offspring thus risk reducing their own fitness through lower offspring survival (Marshall and Keough 2008, Ozgul et al. 2010). However, juvenile survival only represents one fitness component and the age at which females first reproduce is another prominent life-history trait that may correlate with early growth (Day and Rowe 2002). Reproductive parameters typically impact fitness less than survival in iteroparous species, but still influences the

dynamics of populations through ensuing effects on other traits (e.g., trade-offs between reproduction and survival, Stearns 1989b). In growing populations, however, early reproduction increases fitness, indicating the importance of taking the timing of reproduction within the life cycle of an organism into account (Houston and McNamara 1999). Because selection strengths can differ for survival and reproduction (Kingsolver et al. 2001), early body growth may not necessarily affect survival and reproduction equally, especially in species with delayed maturity. The demographic consequences of early body growth are therefore best quantified using an integrated measure of fitness, instead of only studying individual fitness components in isolation (Muniz Dias and Marshall 2010).

The extent to which phenotypic differences in growth, structural size or body mass during early development translate into individual variation in fitness components such as lifetime reproductive success is of primary importance in evolutionary ecology (Sterns 1992, Lindström 1999). However, the benefits or disadvantages of size at independence is frequently only expressed as short-term effects, for example in terms of juvenile survival, even though this may lead to the large underestimation of fitness consequences in long-lived species (van de Pol et al. 2006, Cam and Aubry 2011). To better understand how body mass and mass gain during early development correlate with fitness, it is instead necessary to estimate both on the magnitude and duration of impacts on survival and fecundity (e.g., Festa-Bianchet et al. 2000, Garant et al. 2004, van de Pol et al. 2006, Pelletier et al. 2007).

In this study, we estimate phenotypic selection (the relationship between fitness and a phenotype, Endler 1986) on weaning mass in a large marine predator, the southern elephant seal (hereafter elephant seal, *Mirounga leonina*). We achieved this by analyzing individual-based data collected over a 30-year period using capture-recapture models that accounted for observed phenotypic variation in weaning mass and unobserved (latent) differences across individuals caused by unmeasured factors. Maternal effects have strong phenotypic influence on elephant seal offspring and the high within-year variation in weaning mass (up to 100 kg differences between individuals, Oosthuizen et al. 2015) provides a good opportunity to study the life-history consequences of phenotypic variation during

early development. Our first set of objectives was 1) to test competing hypotheses about the duration (short, medium or long-term) of weaning mass impacts on age-specific survival and recruitment probabilities (where recruitment is defined as the permanent transition from the juvenile/pre-breeder to breeder state, *sensu* Pradel and Lebreton 1999); 2) to evaluate the relative support for directional or stabilizing selection on weaning mass; and 3) to ascertain whether latent individual heterogeneity, which may obscure patterns of selection, had any effects on selection coefficients. We compared three hypotheses of effects (Figure 1) to a null hypothesis that predicted no significant influence of weaning mass on survival or recruitment ($\beta = 0$). The frailty hypothesis predicts that weaning mass only affects first-year survival ($\beta > 0$). First-year mortality acts as a selective filter that removes frail individuals from the population (Nevoux et al. 2010). Individuals that survive the first year acquire adequate resources or develop sufficient foraging skills so that weaning mass has no further influence on survival, and never influences recruitment ($\beta = 0$). The replacement hypothesis predicts a gradual decrease of weaning mass effects with time since weaning (Proffitt et al. 2008). Current conditions increasingly replace the effects of weaning mass as individuals age, which weakens the relationship between weaning mass and fitness components. The replacement hypothesis therefore assumes that $\beta > 0$ beyond the first year, but that $\beta = 0$ at some age (but not necessarily the same age) for both survival and recruitment. Lastly, the silver spoon hypothesis predicts that weaning mass continues to influence fitness components throughout life ($\beta > 0$). Individuals with a better start to life (a ‘silver spoon’, Grafen 1988) always perform better, leading to persistent fitness differences among individuals (‘fixed heterogeneity’, Cam et al. 2016). Conversely, poorly provisioned young face greater mortality risk at all ages and experience delayed maturation: a ‘lead spoon’ effect (Grafen 1988).

We considered two principal modes of selection: directional selection, i.e., a linear relationship characterizing a consistent change in survival or recruitment probability with weaning mass; and stabilizing selection, a nonlinear fitness function potentially selecting against extreme phenotypes

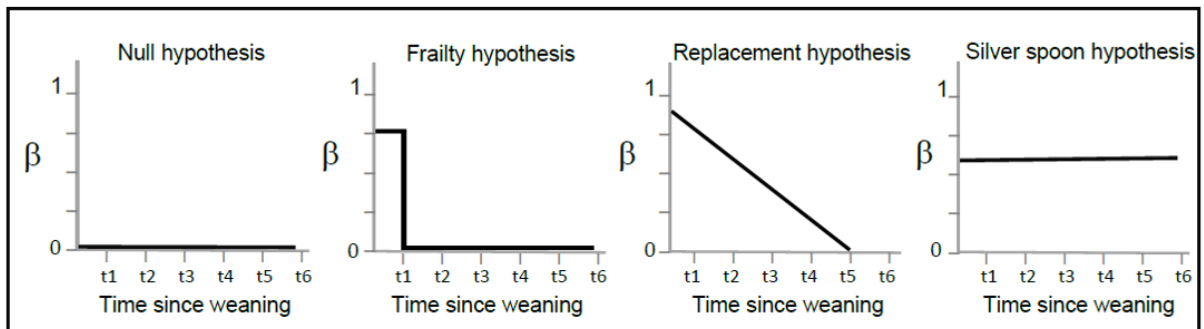


Figure 1. Conceptualization of hypotheses describing weaning mass effects on survival and recruitment. Recruitment may take place at any time step after t_1 . The y-axis represents the slope parameter β , which describes the strength of the effect of weaning mass on either survival or recruitment. Weaning mass has an important influence on survival or recruitment when the slope parameter differs from zero.

(Brodie et al. 1995, Kingsolver and Pfennig 2007). Both modes of selection have received support in studies that investigated the association between weaning mass and survival in phocid seals (elephant seals, McMahon et al. 2003; Weddell seals *Leptonychotes weddellii*, Proffitt et al. 2008; gray seals *Halichoerus grypus*, Bowen et al. 2015). Less is known about the consequences of weaning mass on reproduction, but increased body growth during early life are expected to reduce age at maturity in many taxa (Day and Rowe 2002). However, reproductive maturity does not occur for several years in elephant seals, which may decouple age-specific recruitment probability and weaning mass (as Bowen et al. 2015 suggested for gray seals). If present, we expected selection on weaning mass through age-specific recruitment probability to be positive and directional.

Our final objective was to estimate the strength of phenotypic selection on weaning mass. We first estimated the selection gradient on weaning mass separately for each of the fitness components (survival and recruitment, respectively) linked to weaning mass. Secondly, we used matrix projection models to derive an estimate of the selection gradient on weaning mass that integrated fitness components throughout the life-cycle (Van Tienderen 2000, Coulson et al. 2003, van de Pol et al. 2006, Gamelon et al. 2011). Specifically, we estimated the selection gradient on weaning mass through changes in the asymptotic population growth rate, a measure of mean absolute fitness (Fisher 1930, Lande 1982, McGraw and Caswell 1996).

Methods

Elephant seal breeding biology

Southern elephant seals are wide-ranging mesopredators with a circumpolar Southern Ocean distribution (Hindell et al. 2016). The annual cycle of adult seals is typically characterized by only two terrestrial periods: the breeding phase and the molt haulout. Elephant seals are extreme capital breeders in the sense that seals do not consume prey while hauled out on land. Instead, females from as young as three years of age fast ashore for the entire lactation period of 21 to 23 days, relying on

catabolism of blubber lipids and body protein for metabolic energy (Fedak et al. 1996, Boyd 2000). Adult females, with a mean mass at parturition around 500 kg (range 300 - 800 kg), arrive at the breeding colony in September and October and give birth to a single pup weighing approximately 40 kg a few days after arrival (Fedak et al. 1996, Postma et al. 2013). Four weeks after arrival at the colony, a female will mate with the dominant male and wean her pup abruptly by returning to sea.

Field methods

Our study is based on long-term life-history data of individually marked female elephant seals at Marion Island, in the southern Indian Ocean (Bester et al. 2011). Since 1983, virtually all recently weaned elephant seal pups born at Marion Island were sexed and uniquely marked with two tags attached to the interdigital webbing of each rear flipper (see Pistorius et al. 2011 for details). During 19 years between 1986 and 2012, a sub-sample of the pups born were weighed at weaning (see Oosthuizen et al. 2015 for details). Female pups averaged 114 kg at weaning ($n = 746$), but weaning mass were highly variable within and among years (standard deviation [SD] = 22 kg, range 57 – 176 kg) (Supplementary material Appendix 1 Fig. A1). Resights of elephant seals were made throughout all years on a systematic 7- or 10-day cycle. Although seals spend extensive periods foraging at sea they have high philopatry and typically return to natal sites during winter (mostly pre-breeders), breeding and molt haulouts (Hofmeyr et al. 2012).

Model design

Because we did not have sufficient information on the influence of weaning mass on male reproduction, and seeing that female numbers limit reproduction in this highly polygynous species, we limit our inference to the female segment of the population. The encounter histories of 746 females weighed as weaned pups between 1986 and 2012, and resighted from 1986 to 2016, were analyzed. Of those marked, 477 individuals were resighted 6762 times following their year of birth. The annual sample size of weaned pups tagged and the total number of resightings each year are shown in

Supplementary material Appendix 1 Table A1. Multiple sightings of an individual within a seal year (September to August) were treated as a single observation, yielding a capture-history matrix with 30 occasions. We used multievent capture-recapture models (Pradel 2005) to estimate three demographic parameters: apparent survival probability (φ) (hereafter survival), recruitment probability (ψ), and recapture probability (p). In addition, we incorporated tag loss (τ^{21} and τ^{10}) within the multievent framework, avoiding pitfalls associated with post-hoc correction of survival estimates (Laake et al. 2014). This parameter was needed given that seals may lose both the tags they were marked with at weaning, at which time they become unidentifiable and appear ‘dead’ within the capture-recapture context (Oosthuizen et al. 2010).

Five mutually exclusive field observations (events) were encoded in the individual capture histories. At every occasion, individuals could not be seen (0), be seen as pre-breeder marked with two tags (1), be seen as pre-breeder marked with one tag (2), be seen as breeder marked with two tags (3), or be seen as breeder marked with one tag (4). We defined pre-breeders as all females not yet sighted in a breeding season with a pup and breeders as females sighted with a pup during the current or any previous breeding season. Events modelled the imperfect observation process by relating, in a probabilistic framework, to the underlying state that an individual occupied at each sampling occasion (Pradel 2005). We did not include uncertainty in state assignment, assuming that the number of tags that an individual was marked with, as well as the reproductive state of an individual was correctly observed. Events therefore corresponded to five states: ‘pre-breeder, two tags’, ‘pre-breeder, one tag’, ‘breeder, two tags’, ‘breeder, one tag’ and ‘dead’. The ‘dead’ state corresponds to an absorbing state representing death and permanent emigration from the study area. Given that the monitoring design at Marion Island allows numerous opportunities for encounter, most breeders are observed in this population (de Bruyn et al. 2011, Results section). However, if we incorrectly assigned individuals to the pre-breeder state because of imperfect detection during a previous breeding season, our estimates of recruitment probability will be underestimated. Nevertheless, we are very confident that any uncertainty in reproductive state assignment would be random with regard to weaning mass. A low

frequency of state misclassification could thus occur, but will not bias the relationship between weaning mass and survival or recruitment, the objective of our study.

We specified elementary matrices corresponding to initial state probabilities (π), transition probabilities ($\tau^{21}, \tau^{10}, \varphi, \psi$) and event probabilities (p), respectively (Supplementary material Appendix 2). Transitions between states were modelled as four successive matrices, with each step conditioning on preceding transitions. Models were fitted by maximum likelihood using E-SURGE 1.9.0 (Choquet et al. 2009).

Estimation of parameters and model constraints

Initial state probabilities: All individuals entered the marked population as weaned pups (age 0) and nearly all seals were marked with two tags at first release. This parameter was kept constant in all models.

Recapture probabilities: A null model which assumed constant detection (i) was compared to models specifying time-dependent variation (t) in recapture, between pre-breeders and breeders ($state$), and between individuals marked with two or one remaining tag(s) (n) (those with zero tags are never observed). Because haulout behavior (breeding season attendance) depends more on life stage (pre-breeder or breeder) than age, we did not consider age effects for recapture probabilities.

Tag loss probabilities: We estimated unique tag loss probabilities from two to one tag (τ^{21}) as well as from one to zero tags (τ^{10}), even though individuals with zero tags are unobservable, by assuming that the number of tags (two or one) an individual is marked with does not influence its survival. Estimates of τ^{21} and τ^{10} were obtained from two consecutive matrices and the transition from two tags to zero tags (τ^{20}) was derived as the product of τ^{21} and τ^{10} . For τ^{21} , we compared two parameterizations of age-specific tag loss (“full” age dependence ($\tau_0, \tau_1, \tau_2, \tau_3, \tau_4, \tau_{\geq 5}$) and first-year

loss different from subsequent loss ($\tau_0, \tau_{\geq 1}$) to an age-independent model. A two-level factor (“group”, g) allowed seals marked in the inner and outer webbing of the rear flipper respectively, to have different tag loss rates. Because estimates of τ^{10} were based on a smaller sample of individuals (113 of the 746 seals were known to have lost one tag at some stage), we did not consider the “full” age dependent parameterization for τ^{10} . Individuals did not gain tags at any stage (seals were not remarked).

Survival probabilities: Our starting model corresponded to the silver spoon hypothesis: weaning mass influencing survival throughout life. Survival was always age-structured ($\varphi_0, \varphi_1, \varphi_2, \varphi_3, \varphi_4, \varphi_{\geq 5}$), assuming constant adult survival after the age of 5 (Pistorius and Bester 2002, Pistorius et al. 2004). Alternative hypotheses were tested by modifying the effect that weaning mass (fitted as an individual covariate – see below) had on parameter estimates.

Recruitment probabilities: Recruitment is the probability of giving birth for the first time, conditional on being alive. Recruitment is age-dependent in elephant seals (Pistorius et al. 2001, Desprez et al. 2014) and we estimated age-specific recruitment for all ages where variation in this parameter existed (ψ_2, ψ_3, ψ_4). In elephant seals, there is no recruitment to the breeding population prior to age three, and in our dataset, all surviving females were breeding by age 6. The transition probability from pre-breeder to breeder was therefore fixed to zero at age < 2 (ψ_0 and $\psi_1 = 0$), whereas the transition probability to breeder at age class ≥ 5 was set to unity ($\psi_5 = 1$). Alternative hypotheses were tested by modifying the weaning mass individual covariate; as for survival, the starting model assumed a lasting influence of weaning mass on female elephant seals’ age-specific probability of recruitment.

Observable individual covariates and latent individual effects: Directional selection was modelled using weaning mass, standardized to a mean of zero and unit variance prior to analyses, as an individual covariate (Lande and Arnold 1983). Models of variance selection additionally included quadratic (squared) terms for weaning mass; the resulting coefficients represent the strength of

disruptive selection (when positive) or stabilizing selection (when negative). However, simple quadratic regressions may not capture asymmetry in fitness surfaces (Gimenez et al. 2006). Therefore, where results of the quadratic regression suggested nonlinear fitness surfaces, we used a penalized spline regression with two knots (Crainiceanu et al. 2005) to explore the form of selection without constraining the regression to an *a priori* parametric function.

Unexplained residual variance can induce bias in the magnitude of β that may lead to an inflated type I error rate, i.e., detecting an effect of the individual covariate when there is no effect (Gimenez and Choquet 2010, Cam et al. 2013). To verify that our estimates of β were robust, we refitted the best-supported model(s) with additive individual random effects that accounted for unobserved between-individual heterogeneity (Gimenez and Choquet 2010). Our emphasis was not on the heterogeneity distribution as an interpretable property of the population (Tuljapurkar et al. 2009, Cam et al. 2013), but instead we used individual effects as a means of accounting for unexplained residual heterogeneity in the data (Pradel et al. 2012). We tested for significant individual effects in survival (σ_ϕ), recruitment (σ_ψ) and recapture probabilities (σ_p).

Model selection

Model selection was structured into successive steps. First, an appropriate model for recapture probabilities was selected by constraining p , while maintaining other parameters fixed at high dimensionality. Once a suitable recapture probability structure was selected, it was retained for modelling the transition probabilities. The next two steps involved modelling tag loss probabilities (τ^{21} and τ^{10}), followed by survival probabilities and finally recruitment probabilities, retaining the most parsimonious structure for the parameter evaluated at every step. Models were ranked using Akaike's Information Criterion adjusted for small sample sizes (AICc). The model with the minimum AICc value is the most parsimonious model among those considered in the model set, representing the structure in the data with a minimal number of parameters (Burnham and Anderson 2002). Relative

model support was based on differences in AICc values (ΔAICc). The ratios of model probabilities (Akaike weights, w_i) for any two models a and b (termed the evidence ratio) were used to gauge the relative likelihood of model a versus model b (Burnham and Anderson 2002). Model selection based on AICc assumes that the model set includes an umbrella model that fits the data (Burnham and Anderson 2002). Goodness-of-fit testing (Pradel et al. 2005) suggested that the encounter histories of both pre-breeders and breeders provided adequate fit to the Cormack-Jolly-Seber capture-recapture model if age structure was incorporated in the survival parameter (see Supplementary material Appendix 3 and Table A2 for details).

Selection gradients

Selection gradients represent the steepness of the fitness landscape; the proportional change in fitness (or a fitness component) resulting from a proportional change in a phenotypic trait (Lande and Arnold 1983, Kingsolver et al. 2001). Coefficients of single traits (β) describe changes in trait means, their quadratic terms (γ) the importance of variance selection (Brodie et al. 1995). We standardized the selection gradient relative to the standard deviation of weaning mass. In this case, the standardized selection gradient β_{SD} is the change in relative fitness that results from a one standard deviation change in weaning mass. Thus, if $\beta_{SD} = 0.1$, relative fitness increases by 10% when moving one standard deviation away from the population mean. This allows for a direct comparison of selection intensity measured in different studies and for different fitness components (Kingsolver and Pfening 2007). Because survival and recruitment are dichotomous outcomes, the regression coefficients obtained from the capture-recapture analyses were logistic in nature. Coefficients were therefore transformed to linear selection gradients (β_{avggrad}) following Janzen and Stern (1998).

Linking selection gradients with elasticities of fitness components

We measured fitness as the average rate of increase of individuals possessing a particular phenotype (Fisher 1930). In this context, fitness can be taken as the asymptotic population growth rate λ (the rate of propagation of an individual's genes into the future) of a collection of individuals with a common probability to survive and reproduce (Metz et al. 1992, McGraw and Caswell 1996, Caswell 2001). Fitness is thus a demographic parameter determined by age- or stage-specific fitness components. We estimated λ using a stage-structured projection matrix that included separate stages for pre-breeders, first-time breeders and experienced breeders (Figure 2). We parameterized the matrix with estimates of age-specific pre-breeder survival and recruitment probabilities obtained from this study, and allowed these to vary with weaning mass where model selection results suggested meaningful effects. Matrix parameters which we did not estimate here (first-time breeder survival, experienced breeder survival and annual breeding probability after recruitment) were derived from another study (Oosthuizen 2016) based on the entire population of females ($n = 6439$) and not only those weighed at weaning ($n = 746$). The matrix model separated first-time breeders from experienced breeders to account for a possible trade-off between early recruitment and high reproductive costs to survival. The population projection matrix for females corresponding to the stage structure in Figure 2 is given online (Supplementary material Appendix 4). We assumed a post-breeding census and an annual projection interval. We used elasticity analysis to identify to which fitness components λ was most sensitive. The elasticity (e_{ij}) of the element at row i and column j of a matrix is the proportional sensitivity of λ (change in λ) resulting from changes in individual matrix elements and represents the relative contributions of different matrix elements to fitness (Caswell 2001).

The asymptotic population growth rate λ computed when all fitness components are set to the population mean gives a measure of mean fitness (Metz et al. 1992). If λ_{SD} is the adjusted growth rate of individuals that differ in weaning mass from the population mean by one standard deviation, $\lambda - \lambda_{SD}$ is a measure of selection (β') equivalent to the selection gradient on individual traits, but using a fitness measure that is integrated over the life cycle (Van Tienderen 2000, Caswell 2001, Coulson et al. 2003, Altwegg et al. 2007, Roulin et al. 2010, Gamelon et al. 2011). Parametric

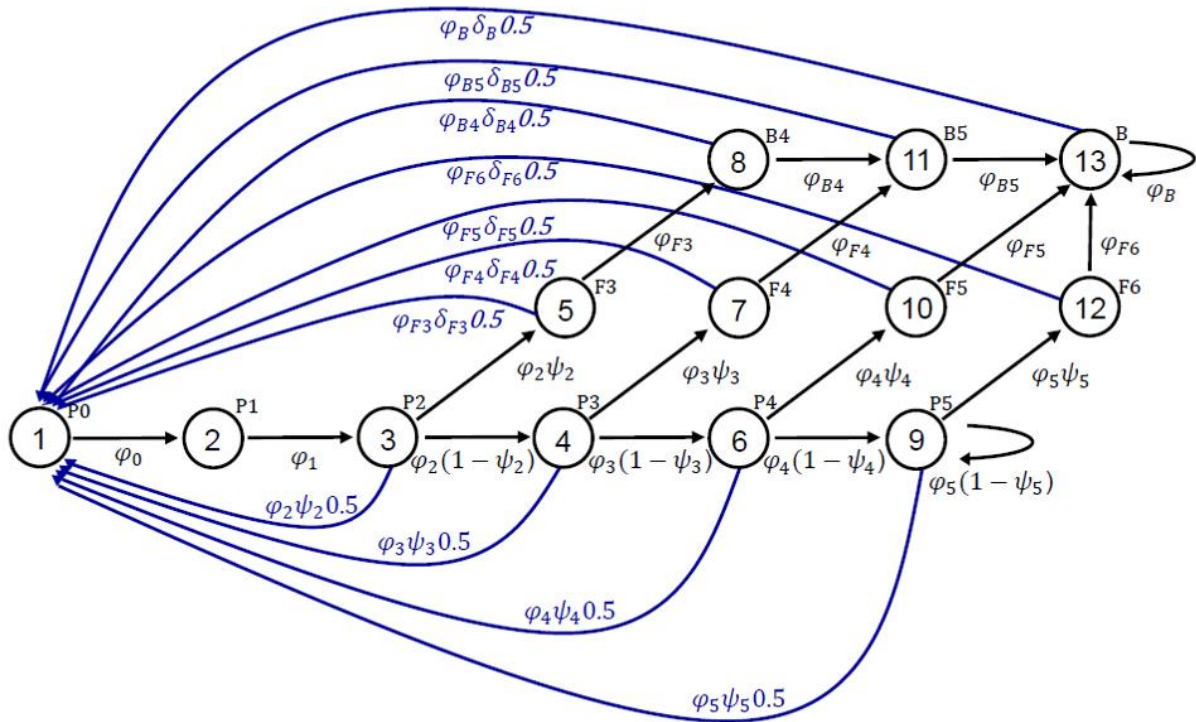


Figure 2. Life-cycle graph of a stage-based population model for female southern elephant seals. Black arrows indicate transitions between age- and stage classes (pre-breeders (P), first-time breeders (F) and breeders (B), with superscripts denoting the age group). Curved blue arrows extending back to the first node represent the contribution of each stage to female offspring. Transitions occur over an annual time step. Node 1 refers to offspring, nodes 2, 3, 4, 6 and 9 to pre-breeders, nodes 5, 7, 10 and 12 to first-time breeders, and nodes 8, 11 and 13 to experienced breeders. The parameter φ refers to survival probability, ψ to recruitment probability, and δ to breeding propensity subsequent to recruitment. Female elephant seals typically give birth to a single pup and therefore fecundity, the number of female pups born to breeding female, is 0.5 when a 50:50 sex ratio at birth is assumed.

bootstrap methods were used to calculate confidence intervals (CI) for β' . We drew 10 000 random values from a normal distribution (on the logit scale for survival and recruitment probabilities) with mean and variance equal to the observed values. With these values, we reconstructed 10 000 matrices and calculated λ_{SD} for each of them. The limits of the 95% CI are the 2.5th and 97.5th percentiles of $\lambda - \lambda_{SD}$. Matrix analysis was performed in R 3.0.2 (R Core Team 2013).

Data deposition

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.6275j> (Oosthuizen et al. 2018).

Results

Survival and age-specific recruitment probability

We detected important phenotypic correlations between weaning mass and both survival and recruitment probabilities. First-year survival of elephant seal pups was positively related to weaning mass, but model selection was tied (i.e., the difference in AICc negligible) between linear, quadratic and penalized spline regressions of weaning mass on first-year survival (Table 1, Table 2). The structure in the data could therefore be represented by any of these models, and the hypotheses of directional (S6) or stabilizing selection (S12) on weaning mass through first-year survival were equally plausible for this dataset. This result indicates that size-selective mortality strongly selected against pups with below-average weaning mass, but that any conclusion regarding the relationship between weaning mass and survival at the upper part of the weaning mass distribution contains considerable model selection uncertainty (Figure 3). Whereas survival probability was predicted to increase consistently with weaning mass in the linear model, the negative quadratic term of model S12 indicated stabilizing selection, with lower first-year survival for individuals at either extreme of the weaning mass distribution. The regression of the penalized spline model showed a rapid decrease in first-year survival probability for pups with a weaning mass below 100 kg. Above this apparent

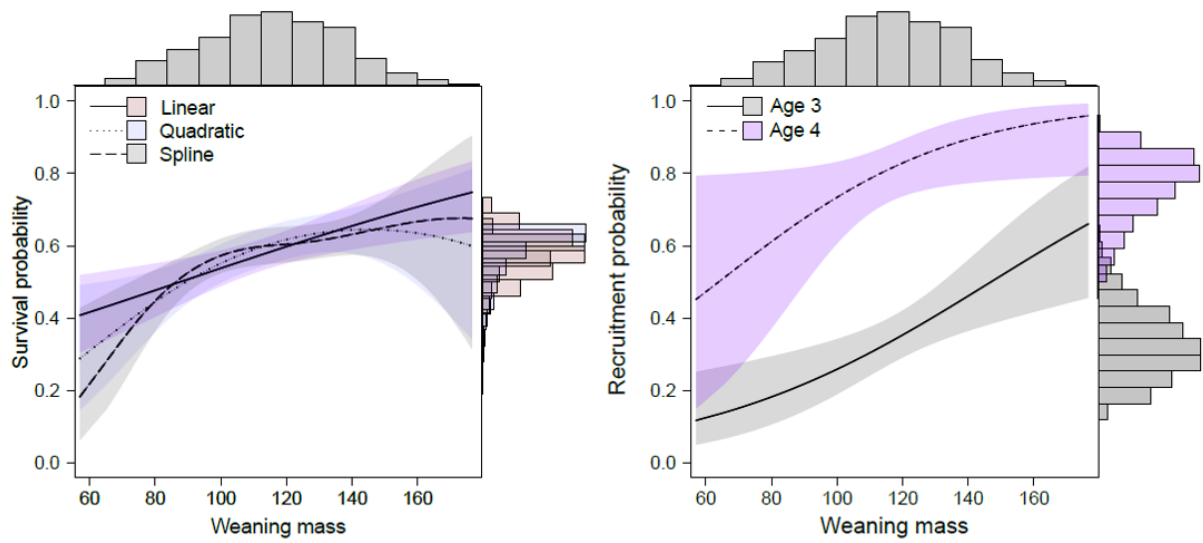


Figure 3. The relationship between weaning mass and probability of survival and recruitment of female southern elephant seals at Marion Island. Uncertainty about predicted values is given by 95% confidence intervals (shading). The distributions of observations and parameter estimates are indicated by the histograms. The three survival regressions are given as separate figures in the online material (Supplementary material Appendix 5 Fig. A2).

Table 1. Model selection for survival and recruitment probabilities of southern elephant seals, incorporating weaning mass as an individual covariate. The number of parameters (np), model deviance, ΔAICc (the difference in AICc between the model with the lowest AICc value and the relevant model) and the relative support by the data of a model, in relation to the other models (AICc weight, w_i), is given. Models within two AICc units of the best-ranked model are in boldface.

Model		np	Deviance	ΔQAICc	w_i
Null models					
N1	$\varphi \cdot a$; $\psi^{\text{PB}} \cdot a_{3,4,5}$	17	4564.29	21.30	0.00
N2	$\varphi \cdot \text{Mass} \cdot a^0 + a^{1,2,3,4,\geq 5}$; $\psi^{\text{PB}} \cdot a_{3,4,5}$	18	4553.76	12.80	0.00
N3	$\varphi \cdot a$; $\psi^{\text{PB}} \cdot \text{Mass} \cdot a^{2,3,4}$	20	4545.37	8.49	0.00
Survival probability - directional selection					
S1	Mass. a	26	4531.47	6.85	0.01
S2	Mass. $a^{0,1,2,3,4} + a^{\geq 5}$	25	4531.77	5.11	0.02
S3	Mass. $a^{0,1,2,3} + a^{4,\geq 5}$	24	4532.35	3.63	0.03
S4	Mass. $a^{0,1,2} + a^{3,4,\geq 5}$	23	4533.82	3.05	0.04
S5	Mass. $a^{0,1} + a^{2,3,4,\geq 5}$	22	4533.84	1.04	0.12
S6	Mass. $a^0 + a^{1,2,3,4,\geq 5}$	21	4534.85	0.00	0.19
Survival probability - stabilizing selection					
S7	Mass ² . a	32	4523.04	10.76	0.00
S8	Mass ² . $a^{0,1,2,3,4} + a^{\geq 5}$	30	4523.52	7.12	0.01
S9	Mass ² . $a^{0,1,2,3} + a^{4,\geq 5}$	28	4524.09	3.58	0.03
S10	Mass ² . $a^{0,1,2} + a^{3,4,\geq 5}$	26	4531.17	6.55	0.01
S11	Mass ² . $a^{0,1} + a^{2,3,4,\geq 5}$	24	4531.77	3.05	0.04
S12	Mass². $a^0 + a^{1,2,3,4,\geq 5}$	22	4532.85	0.04	0.19
Recruitment probability - directional selection					
R1	Mass. $a^{2,3} + a^4$	20	4537.73	0.84	0.13
R2	Mass. $a^2 + a^{3,4}$	19	4543.00	4.08	0.03
Recruitment probability - stabilizing selection					
R3	Mass ² . $a^{2,3,4}$	24	4530.87	2.15	0.07
R4	Mass ² . $a^{2,3} + a^4$	22	4534.97	2.16	0.07
R5	Mass ² . $a^2 + a^{3,4}$	20	4541.33	4.44	0.02

Note: Candidate models contained combinations of the following variables: intercept only (i), breeding state ($state$), six age classes (0, 1, 2, 3, 4, ≥ 5) (a), subsets of age classes (e.g., a^1), and weaning mass as an individual covariate (Mass). Mass² signifies a quadratic term for weaning mass (i.e., stabilizing selection). The starting model (S1) was $\tau^{21} \cdot g \cdot a^{0,\geq 1}$; $\tau^{10} \cdot i$; $\varphi \cdot \text{Mass} \cdot a$; $\psi^{\text{PB}} \cdot \text{Mass} \cdot a_{3,4,5}$; $p \cdot state$ where τ^{21} and τ^{10} are tag loss

parameters, φ is apparent survival probability, ψ^{PB} is recruitment probability and p is recapture probability (see Methods for details).

Table 2. Testing for latent individual heterogeneity, temporal variability in the direction of selection, and asymmetry in the fitness surface of first-year survival of southern elephant seals. Models are ranked (ΔQAIC_c) relative to models in Table 1.

Model	np	Deviance	ΔQAIC_c
Test for asymmetry in the fitness surface of first-year survival			
H1 $\text{Mass}^{\text{spline}} \cdot a^0 + a^{1,2,3,4,\geq 5}$	22	4532.87	0.07
Test for latent individual effects			
H3 Model S6 + r(survival)	22	4534.85	2.00
H4 Model S6 + r(recruit)	22	4534.85	2.00
H5 Model S6 + r(recapture)	22	4502.01	-30.79

Note: spline is for a 2-knot spline; r() is for an individual random effect. All other terms as in Table

1.

inflection point, survival probability of female offspring increased more slowly with increasing weaning mass, with no decrease at the upper end of the weaning mass distribution (Figure 3).

Although the models with the lowest AICc values suggested that weaning mass influences on survival did not persist to the second year of life, there was competitive model support ($\Delta\text{AICc} = 1.04$, model S5) for directional selection acting on weaning mass through both first- and second-year survival. The positive influence of weaning mass on second year survival was lower and more imprecise than during the first year, indicating that the amount of variance in survival explained by weaning mass decreased over time (Table 3, Supplementary material Appendix 5 Fig. A3). There was no clear evidence for selection on weaning mass through survival beyond the second year (Table 1, Table 3). The relative empirical support (evidence ratio) for the hypothesis of weaning mass affecting survival at age 1 only (S6) was 70 times that of weaning mass having no effects on survival (N3), 1.7 times that of weaning mass influencing survival during the first two years (S5), and 31 times that of weaning mass affecting survival at all ages (S1, Table 1). We continued to model weaning mass effects on recruitment while maintaining the linear regression on first-year survival only. The linear model was preferred over the quadratic model because it is simpler (more parsimonious). However, we do not completely discount the potential effects of weaning mass on survival after age 1, and included variation in second-year survival probability as a function of weaning mass in the matrix population modelling.

Weaning mass was under positive directional selection through recruitment probability at ages 3 and 4 (Table 1, Figure 3). The influence of weaning mass on recruitment at age 5 was also present in the model with the lowest AICc value, but its exclusion from this model ensued in an unimportant increase in AICc (R1, $\Delta\text{AICc} = 0.84$). The point estimate of this parameter had large uncertainty associated with it (Table 3), as most of the surviving females had already recruited to the breeding population at an earlier age. The phenotypic distribution of weaning mass prior to, and after selection, clearly illustrated that recruits were more likely to originate from the upper part of the weaning mass distribution through the joint positive selection pressure of survival and recruitment (Figure 4).

Table 3. Relationship between weaning mass and fitness components in southern elephant seals, and the selection gradient on overall fitness.

Parameter	Mean trait		$\beta_{\text{avggrad}} / \beta'$	SE	
		value			SE
Survival probability	φ_0	0.58	0.02	0.06	0.02
	φ_1	0.76	0.03	0.03	0.03
	φ_2	0.78	0.03	0.005	0.03
	φ_3	0.76	0.03	0.04	0.03
	φ_4	0.77	0.04	-0.03	0.04
	$\varphi_{\geq 5}$	0.79	0.03	-0.01	0.02
Recruitment probability	ψ_2	0.32	0.03	0.10	0.03
	ψ_3	0.80	0.04	0.10	0.05
	ψ_4	0.55	0.14	0.19	0.12
		0.93		0.03	
Overall selection gradient	λ	(0.91/0.96)		(0.01-0.06)	

Note: The mean trait value in the population and the partial regression coefficients of weaning mass on each fitness component are shown with standard errors (SE). The last line of the table shows the estimated selection gradient on weaning mass, integrated over the life cycle, along with 95% confidence intervals (CI). Values in boldface are significantly different from zero at the 0.05 level of significance.

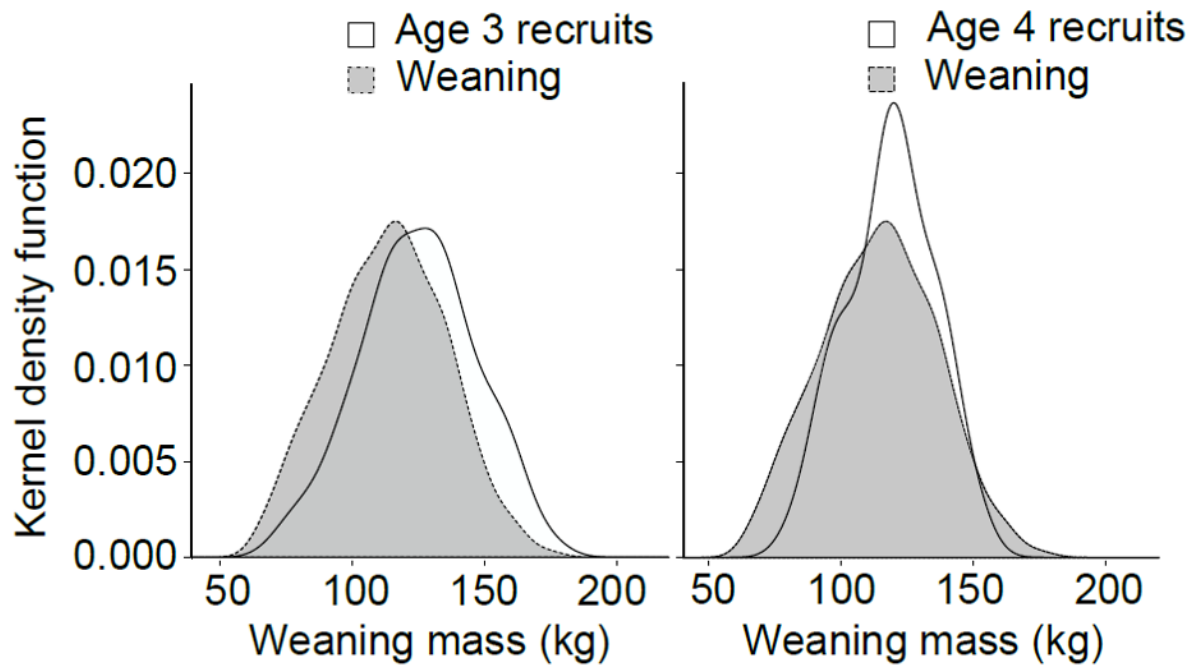


Figure 4. Phenotypic distribution of weaning mass of female southern elephant seals prior to, and after selection. The post-selection phenotype is the product of selection through pre-breeder survival and age-specific recruitment probabilities. The phenotypic distribution of age 3 recruits show the largest shift towards higher values.

Whereas the 746 female pups weighed at weaning averaged 114.03 kg (SD = 21.76), the sample of females observed to pup for the first time at age 3 had an average weaning mass of 123.25 kg (SD = 21.82, n = 80), while those observed giving birth for the first time at age 4 and age 5 averaged 118.70 kg (SD = 17.31, n = 90) and 116.10 kg (SD = 20.43, n = 10) at weaning, respectively.

We observed no change in the deviance of models including individual random effects in survival or recruitment. In each case, σ was estimated close to zero ($\sigma_\phi = -0.001$; $\sigma_\psi = 0.085$). In contrast, heterogeneity in recapture was present ($\sigma_p = 1.35$, SE = 0.14, Table 2), and accounting for this between-individual variation had some influence on the on the maximum likelihood estimates and standard errors of survival, recruitment, and their relationship with weaning mass. Consequently, the parameter estimates we report were derived from the model including an individual random effect on recapture probability. Recapture probability was time-invariant, but depended on breeding state. Both pre-breeders ($p = 0.91$ [95% CI: 0.86 - 0.94]) and breeders ($p = 0.97$ [0.94 - 0.98]) had high annual recapture probabilities. Tag loss probability (τ^{21}) during the first year of life was 6% ($\tau^{21} = 0.06$ [0.03 – 0.11]) for seals tagged in the inner interdigital webbing of the hind-flipper and 17% (12 – 22%) for those tagged in the outer interdigital webbing of the hind-flipper. At older ages $\tau^{21} = 0.07$ (0.05 – 0.10), regardless of where tags were placed. The annual probability of losing the second tag (τ^{10}) was 4% (1 – 22%). Model selection results for recapture and tag loss parameters are given online (Supplementary material Appendix 5 Table A3).

Linking selection gradients with elasticities of fitness components

Selection gradients gave the relative change in fitness components, or the relative change in λ , resulting from a proportional change in weaning mass. The selection gradient through first-year survival was lower ($\beta_{\text{avggrad}_{\phi_0}} = 0.06$, SE = 0.02) than through recruitment at age 3 ($\beta_{\text{avggrad}_{\psi_2}} = 0.10$, SE = 0.03) and recruitment at age 4 ($\beta_{\text{avggrad}_{\psi_3}} = 0.10$, SE = 0.05). The stage structured matrix population model projected an asymptotic growth rate of $\lambda = 0.93$ (95% CI: 0.91 – 0.94) when matrix

Table 4. Elasticities of the asymptotic population growth rate λ of southern elephant seals at Marion Island. Parameters a_{ij} correspond to the age-specific matrix elements of pre-breeders, first-time breeders and experienced breeders, respectively.

Life stage	Parameter		Parameter	
	a_{ij}	Elasticity	a_{ij}	Elasticity
Pre-breeder	φ_0	0.114		
	φ_1	0.114		
	$\varphi_2(1 - \psi_2)$	0.069	$\varphi_2\psi_2R$	0.008
	$\varphi_2\psi_2$	0.037		
	$\varphi_3(1 - \psi_3)$	0.008	$\varphi_3\psi_3R$	0.011
	$\varphi_3\psi_3$	0.049		
	$\varphi_4(1 - \psi_4)$	0.002	$\varphi_4\psi_4R$	0.001
	$\varphi_4\psi_4$	0.005		
	$\varphi_5(1 - \psi_5)$	0.002	$\varphi_5\psi_5R$	0.001
	φ_5	0.002		
	ΣP	0.402		0.021
First-time breeder	$\varphi F3$	0.031	$\varphi F3\delta R$	0.005
	$\varphi F4$	0.042	$\varphi F4\delta R$	0.008
	$\varphi F5$	0.004	$\varphi F5\delta R$	0.001
	$\varphi F6$	0.001	$\varphi F6\delta R$	0.000
		ΣF	0.078	
Experienced breeder	$\varphi B4$	0.027	$\varphi B4\delta R$	0.005
	$\varphi B5$	0.057	$\varphi B5\delta R$	0.011
	φB	0.322	$\varphi B\delta R$	0.063
		ΣE	0.406	
Total		0.886		0.114

entries were set to describe fitness components associated with the population mean weaning mass. The adjusted growth rate for individuals that differed in weaning mass from the population mean by one standard deviation was $-\lambda_{SD} = 0.90$ (0.88 – 0.92) and $+\lambda_{SD} = 0.95$ (0.93 – 0.97), respectively. The change in λ resulting from a one standard deviation change in weaning mass corresponds to a selection gradient of $\beta' = 0.03$ (0.01 - 0.06) estimated over the whole life cycle (Table 3).

The asymptotic growth rate λ was several times more sensitive to changes in experienced breeder survival ($\sum e_{\varphi_B} = 0.41$) than an equivalent change in first-year survival ($e_{\varphi_0} = 0.11$) or recruitment probability ($e_{\psi} < 0.02$) (Table 4). However, the combined elasticity of juvenile survival across all ages ($\sum e_{\varphi} = 0.40$) nearly equaled that of experienced breeders, indicating that widespread changes to juvenile survival may also have important consequences for λ . Overall, λ was insensitive to changes in reproductive parameters compared to equivalent changes in survival (Table 4).

Discussion

We used long-term individual-based data and matrix projection models to provide the first estimate of phenotypic selection on weaning mass in elephant seals that integrate multiple fitness components throughout the life-cycle. This approach allowed us to not only consider the direct influence of weaning mass on survival and age at first breeding, but also the potential trade-offs between early recruitment and reproductive costs which are expected to occur at the individual level. Weaning mass correlated positively with first-year survival and to a lesser extent second-year survival, but its influence was unimportant for survival of older pre-breeders and breeders. Although the relationship between weaning mass and survival weakened to negligible levels before the age of sexual maturity, a strong positive link persisted between weaning mass and the age of first reproduction. Weaning mass was linearly related to recruitment probability at ages three and four; the relative fitness of these traits increased by 10% for every 22 kg (one standard deviation) increase in body mass accrued by weaning. The average strength of selection via recruitment was stronger than selection via survival

($\beta_{\text{avggrad}_{\phi_0}} = 0.06$; $\beta_{\text{avggrad}_{\phi_1}} = 0.03$), a pattern that appears to hold for numerous taxa (median selection via survival $|\beta| = 0.09$; median selection via fecundity $|\beta| = 0.16$; Kingsolver et al. 2001). Taken together, the selection gradient on mean fitness (λ) was weaker ($\beta' = 0.03$) than the selection gradients acting on individual fitness components. This is explained by the relative contributions of different fitness components to λ . Elephant seals and other long-lived iteroparous species have life histories that are characterized by low elasticities for juvenile survival and reproductive parameters (Gaillard and Yoccoz 2003). Fitness is instead strongly dependent on adult survival, which we found to be independent of body mass at weaning. While individual phenotypic variation can contribute substantially to variation in fitness (Pelletier et al. 2007), our results highlight the importance of interpreting individual variation in phenotypic traits in a context that considers the demographic pathways between the trait and an integrated measure of mean individual fitness.

Selection on weaning mass

Our results show that weaning mass influenced the life history trajectories of individuals over the medium term, but that the duration and strength of selection varied among individual fitness components. The slope of the relationship between weaning mass and survival diminished with age, indicating that the amount of variance in survival explained by weaning mass decreased over time. This result agrees with previous studies that considered the influence of weaning mass on juvenile survival of elephant seals (McMahon et al. 2000, 2003, McMahon and Burton 2005, Postma et al. 2013). While weaning mass weakly predicted survival beyond the second year, recruitment probability at ages 3 and 4 was strongly correlated with weaning mass. Taken together, these results best conform to the replacement hypothesis. If weaning mass had set the stage for persistent fitness differences among individuals (as predicted by the silver spoon hypothesis) we expected permanent differences in fitness components, including survival. Alternatively, if weaning mass had no influence on fitness beyond the first year (as predicted by the frailty hypothesis), we would not have detected clear relationships between weaning mass and age-specific recruitment probabilities.

Parametric regression did not unambiguously disentangle directional and stabilizing selection on weaning mass through first-year survival. The penalized spline model, which captured variability in the data using a nonparametric smoothing function without *a priori* constraints on the weaning mass-survival relationship, suggested that the first-year survival function may be asymmetric. According to this model, pups weaning at low weaning mass (< 100 kg) suffered a drastic reduction in survival during their first year. In contrast, there was a more gradual increase in first-year survival probability for seals weaning between 100 and 176 kg. Theoretical models for the evolution of offspring size predict such asymptotic relationships between offspring size and survival (Smith and Fretwell 1974). Flexible non-parametric analysis previously suggested that asymptotic relationships exist between measures of body size and first-year survival of other phocid seals (Hawaiian monk seals *Monachus schauinslandi*, Baker 2008; gray seals, Bowen et al. 2015). One advantage of non-parametric approaches is that it avoids potential caveats associated with constraining the fitness function to linear or quadratic regressions (Gimenez et al. 2006). For example, special caution should be exercised when interpreting quadratic relationships, which in our case suggested a decline in survival for the heaviest weaned pups, as there is a danger that the curve may depend largely on the shape of the weaning mass-survival relationship nearer to the mean.

We accounted for hidden individual heterogeneity in recapture probability as a precaution to avoid bias in the magnitude of β , which represents the sign and magnitude of selection on weaning mass. However, models that ignored individual heterogeneity led to a similar conclusion as most individuals in this population have a high encounter probability. We did not investigate temporal variability in the direction of selection, but acknowledge that the sign, strength and mode of selection may vary through time depending on how fitness components respond to environmental variation (Coulson et al. 2003, Marshall et al. 2010, Allen and Marshall 2013). In this study, the number of females weighed in each year was too small to adequately separate demographic and sampling variance on an annual time scale. A partial solution to this problem may be to analyze male and female life histories together, and asking whether fluctuating selection operates on the combined first-year survival of male and female

seals. Varying ecological and social pressures associated with temporal variation in the environment and population density may impact the manner in which selection shapes the population mean age at first reproduction in particular. Reiter and Le Boeuf (1991), for example, found strong selection against breeding early in life under conditions of high density in northern elephant seals (*M. angustirostris*). Although data from only 35 females were available, female northern elephant seals also appear to recruit at an earlier age if they were heavier at weaning (Reiter and Le Boeuf 1991).

For elephant seals, the risk of mortality is highest in the first year of life, and under-yearling mortality can exceed 40% (Pistorius et al. 1999, McMahon et al. 2015). Generous allocation of maternal energy during lactation is valuable for offspring as the transition from nutritional dependence to independence is abrupt, requiring offspring to adjust to a sudden, complete change in nutrient availability. In elephant seals, most of the increase in body mass between birth and weaning is due to deposition of high-energy blubber that provides crucial fuel reserves for pups between weaning and nutritional independence (Carlini et al. 2001). Larger body size confers clear advantages for recently weaned pups. Heavier pups have an energetic advantage over lighter conspecifics by being able to spend more time searching for food before becoming energy limited, while larger body mass may confer additional advantages in thermal regulation and scaled metabolic costs (McMahon et al. 2000). Larger pups also dive deeper and longer during their first foraging trips, perhaps improving their foraging success relative to that of smaller pups (Hindell et al. 1999).

Strong, positive directional selection on body size is widespread in nature (Kingsolver et al. 2001), but often fails to result in microevolution (Gotanda et al. 2015). Selection requires among-individual heterogeneity in both a phenotypic trait and in fitness, but only heritable traits are expected to evolve. While part of the variation in offspring mass may be heritable (e.g., Merilä et al. 2001, Ozgul et al. 2009), elephant seal weaning mass is largely determined by the amount of maternal energy transfer to pups (Fedak et al. 1996). In elephant seals, allocation of maternal resources to offspring primarily depends on female mass at parturition (Arnbom et al. 1993, Postma et al. 2013), itself a function of maternal age (Arnbom et al. 1994) and temporal and spatial fluctuations in environmental conditions

that influence foraging success of females (McMahon and Burton 2005). Because ecological processes contribute significantly to offspring phenotype, positive selection for larger body mass may have little or no effect in determining the phenotypic trajectory, even if there is a genetic component to variation in weaning mass. Therefore, any change in weaning mass over time (Oosthuizen et al. 2015) most probably reflects an ecological (plastic) response to environmental variation, which may be in the opposite direction to a genetic response to selection (Garant et al. 2004, Ozgul et al. 2009).

Offspring phenotype affects the fitness of both mothers and offspring simultaneously, and its evolution depends on selection operating through offspring and maternal components of fitness (Wolf and Wade 2001, Wilson et al. 2005). While fitness typically increases with juvenile size, upward selection on body size is balanced by the maternal trade-off that exists between current investment in offspring phenotypes and opportunities for future reproductive success (Williams 1966), which may result in no net selection gradient on offspring body size (Rollinson and Rowe 2015). Optimal offspring and maternal fitness may occur at different phenotypic values, leading to parent–offspring conflict (Trivers 1974, Wilson et al. 2005). Offspring should always demand more resources (under positive directional selection) than mothers are willing to invest, whereas mothers are selected to invest in current reproduction only to the point where the cost (e.g., through reduced survival or future fecundity) will exceed the benefit of investing in her current offspring (Trivers 1974, Wilson et al. 2005, Rollinson and Rowe 2015). Selection for larger size from the perspective of offspring is therefore balanced by selection against over-investment per offspring from the parental perspective (Rollinson and Rowe 2015).

Age at first breeding

Age-specific recruitment probabilities were strongly affected by weaning mass. Among surviving females, those that were heavier as weaned pups were more likely to start breeding at a younger age. This is noteworthy, considering that pre-recruitment mortality already imposed a powerful selective filter on individuals, leaving only the most ‘robust’ individuals in the population. The onset of reproduction is often size- and condition dependent (Sæther 1997, Boyd 2000, Day and Rowe 2002).

Capital breeding female elephant seals, like some ungulates (Gaillard et al. 2000, Servanty et al. 2009) and long-lived seabirds (Weimerskirch 1992), need to reach a threshold body mass to breed (Arnbom et al. 1994). Although animals exposed to poor developmental conditions can compensate for a poor start by increasing growth rates above the levels of non-deprived individuals, individuals in natural, resource-restricted environments may rarely get an opportunity to do so (Lummaa and Clutton-Brock 2002). Adverse early conditions, including inclement weather, high post-natal population densities or insufficient maternal care, can therefore postpone recruitment through adjustments in body growth trajectories (Stearns and Koella 1986). Prior to reproducing for the first time, female elephant seals have to invest a lot of energy into growth to increase from an average weaning mass of 114 kg to over 300 kg, the breeding threshold body mass. If heavier-weaned pups can maintain a growth or body condition advantage not only during their first foraging trip (as shown by Bell et al. 1997), but throughout the pre-breeder state, it may enable them to reproduce earlier (as in Norwegian moose *Alces alces*, Sæther and Heim 1993). Conversely, females weaning at low mass may take longer to recruit because they are too small to conceive at two years of age.

Even if individuals exposed to poor developmental conditions are able to employ compensatory strategies such as catch-up growth, it may come at a cost to reproduction, such as lower size-specific fecundity (Auer et al. 2010, Lee et al. 2012). A complementary explanation of delayed breeding among pups weaned at lower weaning mass is that energetic restrictions during early development has led to a more conservative life-history strategy favoring somatic maintenance and growth.

Experimental studies on female laboratory rats have shown that relationships exist between females' in utero nutritional status, their maturation age, and subsequent ovarian function (Sloboda et al. 2009). The nutritional conditions that individuals experience during their early development can therefore program different developmental pathways which may accelerate or delay pubertal timing. For example, environmental perturbations during early development lock female roe deer (*Capreolus capreolus*) within a growth trajectory, to directly determine the body mass of individuals in later-life, independent of the postnatal environment which was encountered (Douhard et al. 2013).

Phenotypic variance and the contribution of traits to mean fitness

Elasticity analysis of our age- and stage-structured population model supported the general life-history theory principle that the asymptotic growth rates of long-lived iteroparous species are most sensitive to changes in adult survival (Sæther and Bakke 2000). This result contrasts the sensitivity analysis results of Leslie-matrix models which previously identified pre-breeder survival as the fitness component to which the growth of elephant seal populations is most sensitive (McMahon et al. 2005). Stage-structured approaches are preferred to age-based (Leslie) matrix models when recruitment probability is one of the parameters of interest (Cooch et al. 2012) and the importance of juvenile survival was overestimated by McMahon et al. (2005) given that they considered all females up to and including age four to be juveniles. While variable pre-breeder survival undoubtedly contributes to fluctuations in population growth of long-lived species (e.g., asp vipers *Vipera aspis* [Altwegg et al. 2005] and elephant seals [McMahon et al. 2015]), our results suggest that a small change in adult survival will have the greatest impact on λ . The actual contribution of pre-breeder and adult survival to observed temporal variation in the asymptotic growth rate at Marion Island will require a retrospective population analysis, which asks how much the observed variance in pre-breeder or adult survival contributed to variance in λ (e.g., Altwegg et al. 2005). Notably, even the population projection using the most optimistic estimate of weaning mass associated vital rates ($+\lambda_{SD}$) predicted population decline. Although this population was declining at 4% per year during the initial years of the study (McMahon et al. 2009), recent population counts have shown an increase in the number of breeding females (Pistorius et al. 2011). The discrepancy between annual breeding female population counts (which has a low error margin) and modelled population growth rates may suggest significant immigration to the population, and deserves further study.

Conclusion

Body mass is a key phenotypic trait that strongly impacts life-history evolution. Elephant seal pups vary greatly in body mass at weaning and this heterogeneity influences individual life-history trajectories and population dynamics. The importance of weaning mass on early survival has been reported previously, but here we illustrated that selection on weaning mass may operate via multiple fitness components. This broadening perspective provides a more complete demographic estimate of the consequences of phenotypic variation in weaning mass on individual fitness. From a demographic point of view, our results are consistent with the hypothesis that individuals vary in early survival and recruitment probabilities, and that weaning mass influences this variation. Although variation in weaning mass do not translate to permanent survival differences among individuals during adulthood (i.e., fixed or persistent demographic heterogeneity, Cam et al. 2016), it explains inter-individual differences and positive covariation between survival and breeding in early life which contribute to between-individual variation in fitness.

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Supplementary material (available online). Appendix 1–4.