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Inherent versus random variation in fitness of elephant seals: offspring quality and quantity

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Abstract

Variation in reproductive success is the basis of evolution and allows species to respond to the environment, but only when it is based on fixed individual variation that is heritable. Several recent studies suggest that observed variation in reproduction is due to chance, not inherent individual differences. Our aim was to quantify inherent versus neutral variation in fitness of northern elephant seal (*Mirounga angustirostris* (Gill, 1866)) females, including both quality and quantity of their offspring. Using 44 years of observations at Año Nuevo in California, we assembled lifetime pup production of 1065 individual females and mass at weaning for 2120 of their pups. Females varied significantly in mean lifetime mass of their pups, with 28% of the variance due to fixed individual differences among mothers. Variation was repeatable over 6 years of a mother's lifetime and heritable ($h = 0.48$). Moreover, pup mass at weaning was associated with future lifetime fitness, since larger pups had a higher chance of surviving to breed. Larger pups, however, did not produce more offspring once breeding, and lifetime pup production was not heritable. Traits related to offspring quality in elephant seals were inherently different among females, but variation in pup production was neutral.

Key words: lifetime reproductive success, fitness variation, inherent variation, neutral variation, heritability

Introduction

Individual variation is the basis of adaptation, but even Darwin recognized 160 years ago that some variation is neutral, or as he understood it, ''not... affected by natural selection'' (Darwin 1872). Neutral variation has long been a focus of debate in ecology and evolution (Kimura 1989; Hubbell 2001), and recently, a similar controversy shifted into the realm of life history (Steiner and Tuljapurkar 2012). Here, the neutralist view holds that most individual variation in lifetime reproductive output is random and not relevant to adaptation (Cam et al. 2016; Snyder and Ellner 2018). Random variation in lifetime reproductive success echoes notions that genetic variation (Kimura 1989) and species differences (Hubbell 2001) are neutral. Debate about neutral versus adaptive variation in life history continues due to the difficulty of measuring vital rates across the lifetime of individuals in wild populations under fluctuating environments.

Debate on the role of neutral variation has stimulated rigorous analyses of the causes of variation among species, individuals, and genes (Fisher and Ford 1947; Wright 1948; Condit et al. 2012; Chisholm et al. 2014). Here, we extend the analysis to the role of neutral variation in reproductive success using lifetime observations of northern elephant seals (*Mirounga angustrirostris* (Gill 1866)). We estimate lifetime fitness considering both quality and quantity of offspring of known individuals across many years while accounting for environmental variation. Lifetime records allow us to distinguish random variation in offspring quality from inherent differences among individuals, and we further consider inherent variation by estimating heritability of both offspring quality and quantity.

Long-term studies are essential for measuring lifetime differences among individuals across varying environmental conditions (Bailey 1991; Clutton-Brock and Sheldon 2010; Jenouvrier et al. 2018; Rotella 2023). Our four-decade study has tracked thousands of individual elephant seals over their lifetimes, and observations include measures of pup mass at weaning (Holser et al. 2021), a measure of offspring quality, as well as lifetime pup output (Le Boeuf et al. 2019). With these data, we ask first whether offspring mass is repeatable over lifetimes of individual females (Falconer 1960) and second whether it is heritable. We then consider variation among females in pup quality and pup quantity together, testing whether females that produce more pups in a lifetime also wean larger pups. Finally, we update the result from Le Boeuf et al. (2019) that mass at weaning leads to future reproductive success. Here, we divide it into two questions, testing whether mass at weaning correlates with the chance of reaching breeding age or with pup production after breeding.

Elephant seals are a model system for addressing lifetime fitness. Though they are pelagic predators that forage in remote oceans, they aggregate on shore to breed, and mothers and nursing pups can be observed and measured (Reiter et al. 1981; Ortiz et al. 1984; Costa et al. 1986; Le Boeuf et al. 2000; Robinson et al. 2012). Moreover, until weaning at 1-month old, pups depend solely on their mother for sustenance, first during the 8-month gestation and then for 26 days of nursing (Reiter et al. 1981; Ortiz et al. 1984; Costa et al. 1986). Pup mass at weaning is thus a measure of the mother's ability to accrue resources for her offspring, and since weaning mass correlates positively with future reproduction (Le Boeuf et al. 2019), it is an index of the mother's fitness. Females breed annually starting at age 3–5 until a maximum of 22 years, so we can assess pup mass repeatedly over a lifetime.

In earlier work, we reported high variation in lifetime pup production of individual mothers, attributed largely to variation in lifespan (Le Boeuf et al. 2019). We also examined population-level variation in weaning mass and identified pup sex, mother's age, and productivity on foraging grounds as important influences. Male pups are 4 kg heavier at weaning than females (Reiter et al. 1978; Holser et al. 2021), and mass at weaning increases by 40 kg as mothers grow from age 3 to 7 years, after which it levels off (Reiter et al. 1981; Le Boeuf et al. 2019). Marine productivity is implicated because average annual weaning mass of the entire colony fluctuates by as much as 15 kg (Le Boeuf and Crocker 2005; Holser et al. 2021). We define residual weaning mass as the observed mass minus the average predicted by those three population-wide factors. Variance in the residual mass defines differences in offspring quality and thus fitness of mothers. They are an opportunity for selection, but only if some of the variance can be attributed to lifetime differences among individuals.

Colony history

Monitoring the northern elephant seal colony at Año Nuevo Reserve (37.113°N, 122.333°W) began in 1961 when the colony was settled and the first pups produced. Censuses of the seals were conducted from 1961 to 1967, and most of the pups were tagged (Orr and Poulter 1965). After 1968, researchers at the University of California at Santa Cruz took over the study. Now in its 63rd year, it is one of the longest continuous studies of any mammal (Le Boeuf and Peterson 1969; Clutton-Brock and Sheldon 2010). Measurements of pup mass at weaning began in 1977, and to date, we have 41 years of data on mass of pups raised by identified mothers.

Field operations

Plastic cattle ear tags (mostly Dalton Jumbo Roto tags) were inserted in the interdigital webbing of the hind flippers of seals, allowing animals to be followed throughout their lifetimes (Le Boeuf et al. 1972, 2019; Le Boeuf and Reiter 1988). We searched for tagged animals throughout the year, especially during the winter breeding season, when we also marked known females and their nursing pups with bleach or dye. By tagging those pups, we had mother–pup pairs with lifetime marks. After weaning, pups were weighed by placing them in a canvas bag that could be suspended from a scale on a tripod (Ortiz et al. 1978; Reiter et al. 1978). Since pup mass could seldom be collected on the day of weaning, we back-corrected to weaning day using the formula $M = M_0e^{kt}$, where M is the mass at weaning, M_0 is the observed mass, t is the number of days since weaning, and $k = 0.00596\ \text{day}^{-1}$ is the rate constant of mass loss (Le Boeuf and Crocker 2005).

Ethics statement

Research was carried out at the University of California Natural Reserve System's Año Nuevo Reserve within Año Nuevo State Park. Permission to access the Park was granted by the California Department of Parks and Recreation. Elephant seal handling and sampling was approved by the University of California Santa Cruz Institutional Animal Care and Use Committee and follows guidelines set forth by the ethics committee of the Society for Marine Mammalogy and the Canadian Council for Animal Care. Fieldwork was carried out under National Marine Fisheries Service permits #786-1463, 87-143, 14636, 14535, and 19108.

Data analysis

Residual weaning mass

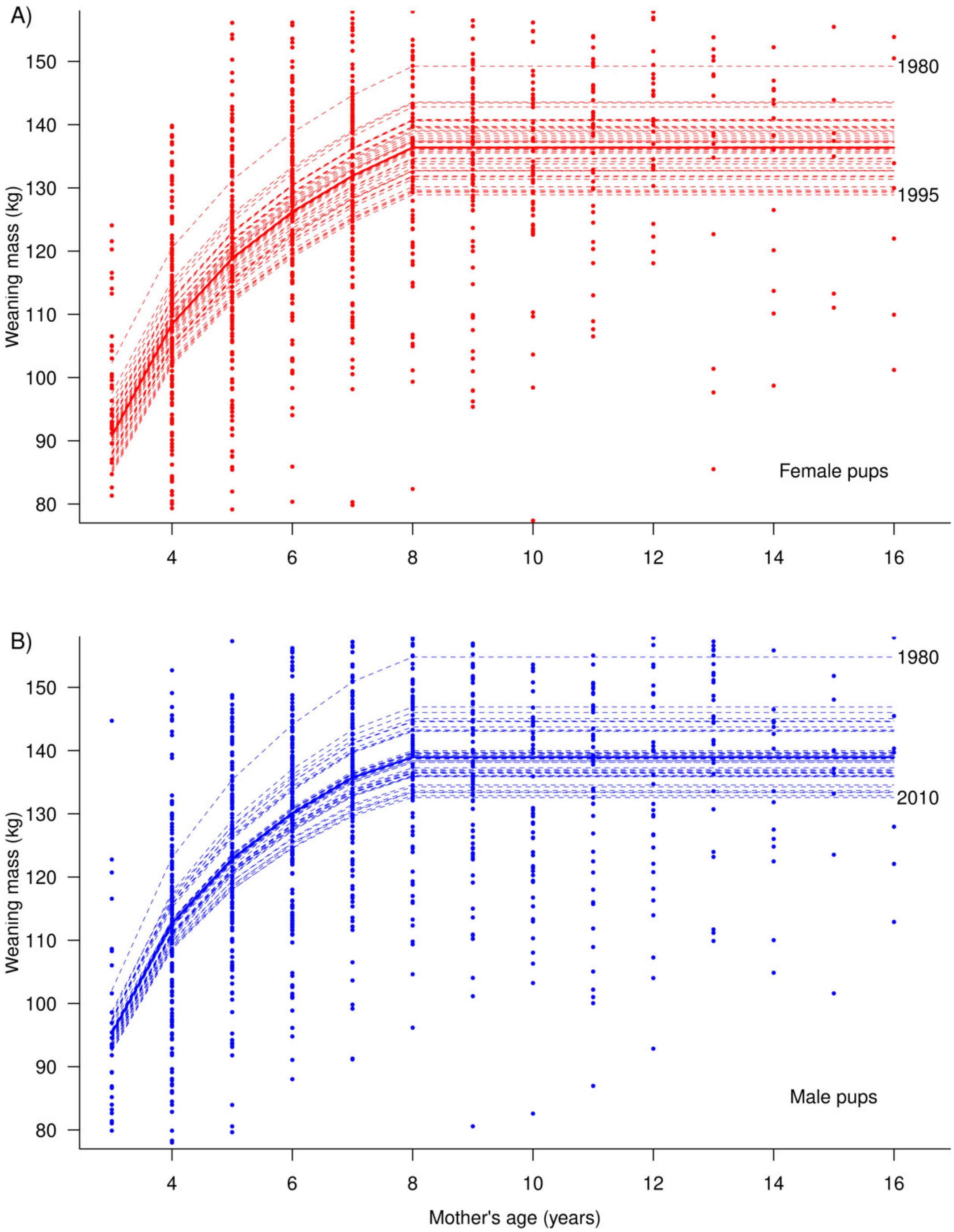
Individual mothers were assigned a residual mass for each pup produced, defined as the pup's mass at weaning minus its expected mass given the mother's age, the year, and the pup's sex. Those population-wide factors accounted for 34.2% of the overall variance around the mean weaning mass of 127.0 kg, with mother's age being most important (accounting for 26.5% of the variance), followed by year (6.5%) and pup sex (1.1%; supplemental Table S1). The variance in those residuals, what remained after accounting for those three factors, was 299.9, and it is the focus of our analysis. The total sample was 2120 residual pup masses produced by 1065 different mothers (Table S2).

We estimated the residuals using a model of weaning mass as a function of mother's age. Previous analyses showed an asymptotic form for this relationship (Reiter et al. 1981; Holser et al. 2021), so we chose a function with an explicit asymptote: a linear increase of weaning mass with the logarithm of the mother's age up to a critical age, then no change until senescence:

$$(1)\qquad M(a) = \begin{cases} M_3 \log(a-2) & \text{for } \log(a-2) < K \\ M_{\max} & \text{for } K < \log(a-2) < \log(15) \\ M_{\text{sen}} & \text{for } \log(a-2) \geq \log(15), \end{cases}$$

where $M(a)$ = expected mass of a pup at weaning born to a mother whose age is a (years). Four parameters were fitted: M_3 = weaning mass of 3-year old mothers; $M_{\max}$ = weaning mass at the age asymptote; K = mother's age when the asymptotic mass is achieved; and M_{sen} = weaning mass of senescent females, assuming senescence begins at age 17 (Condit et al. 2014). The key parameters are $M_{\max}$ and M_3, and the model aims to estimate those with minimal impact of interactions with the other two, K and M_{sen}. Paterson et al. (2016)

Fig. 1. Asymptotic model of pup mass at weaning as a function of mother's age in northern elephant seals (*Mirounga angustirostris*), showing year-to-year variation. (A) Female pups ($N = 1046$). (B) Male pups ($N = 1074$). Each dashed line is the model's predicted mass in 1 year; highest and lowest years are labeled in each sex. Solid lines are fixed effects, meaning the model prediction from all years combined. The senescent phase at age ⩾17 is omitted (see supplemental Fig. S1 for senescence).



used a similar, two-threshold model for maternal age and pup mass in Weddell seals (*Leptonychotes weddellii* (Lesson 1826)) in order to include senescence. Other asymptotic models are poor in parameter interactions and do not handle senescence (Thomas 1996; Le Boeuf et al. 2019).

To control for variation in ocean productivity, we added a random year term to the model (eq. 1) for parameters M_3 and $M_{\max}$; M_{sen} and K were fixed across years. Pup sex was included by fitting the model separately for male and female pups (Fig. 1).

To calculate residual weaning mass, we found the difference between each observed pup mass and the model fit for the corresponding age, year, and sex (eq. 1, Fig. 1). Our approach is analogous to a model with individual as a random effect, sometimes called an animal model (Cam et al. 2002; Kruuk 2004; Wintrebert et al. 2005; van de Pol and Verhulst

2006; Oosthuizen et al. 2015; Paterson et al. 2016; Jenouvrier et al. 2018; Bonnet et al. 2022; Rotella 2023). All analyses were based on these residual weaning masses, and from here forth every mass we refer to is the residual mass of a pup at weaning, unless specifically stated otherwise.

Analysis of variance

In order to measure the consistency of mothers in producing high quality pups, we used an analysis of variance of weaning mass. The groups were individual mothers, each having 1–10 pups weighed in her lifetime (Table S1). Due to the small sample per group, it was necessary to fit variances using a Bayesian, multilevel approach (Condit et al. 2006, 2007; Gelman and Hill 2007). We utilized a Monte Carlo search for the two parameters of interest: σ_m^2, the variance among the lifetime means of individual mothers, and σ_r^2, the variance within mothers around their lifetime means. Since we assumed that the within-mother variance was a single constant, i.e., mothers did not differ in their among-pup variability, there were only two variance parameters to fit. Most important was the proportion of variance, $V = \sigma_m^2/\sigma_T^2$, where $\sigma_T^2 = \sigma_m^2 + \sigma_r^2$ is total variance. The model also produced a lifetime mean pup mass for every individual female, used as a measure of mean lifetime offspring quality. Details of the model can be found in the Supplementary material.

We compared the Bayesian method to a traditional analysis of variance based on sums-of-squares (Huntsberger and Billingsley 1973) using simulated data. The traditional method was unreliable because group sizes were so small (each female had few pups), but the Bayesian method yielded reliable results. We further tested the model using randomized data, reassigning every pup to a different mother. The model correctly reported no variation in the randomized data. Details of model verification can be found in the Supplementary material.

Lifetime consistency of weaning mass

The drawback of the analysis of variance is that it equates pups raised by a mother in consecutive years with those raised years apart. We addressed this topic using correlations in the mass of two pups born to the same mother at varying lag times. We had 628 cases where one mother had her pup weighed in consecutive years—a lag of 1 year—but also had pairs with lags of 2–16 years, though sample size diminished with lag length (Table S3). We ran a correlation between pup masses at each lag of 1–6 years; beyond that, we pooled all data with lag $\geqslant$7 years. These correlations included repeated measures because one mother could have several pup pairs with the same lag. For example, if a female had her pup weighed in three consecutive years, she had two different 1-year lags, from t to $t + 1$ and from $t + 1$ to $t + 2$, plus a 2-year lag from t to $t + 2$. To avoid repeated measures, correlations were based on subsamples in which each individual mother at any lag length had just one pair drawn at random. Statistical significance of the correlations was based on the subsamples, but the correlation coefficient was based on the entire samples (see Supplement for details). We then tested whether the strength of the interyear correlation diminished with time using a regression between the seven correlation coefficients and lag time (1–7 years).

Offspring quality versus offspring quantity of individual mothers

We next asked whether females who raised larger pups also produced more pups over their lifetimes. The distribution of lifetime pup production across all females born by 2005 appears in Le Boeuf et al. (2019). Here, we extend the sample to include all 593 females born up to 2009 who had at least one pup weighed. The cutoff at 2009 allowed at least 12 years (2012–2023) to observe them breeding. We ran a regression between the mean weaning mass of pups produced by those females (from the Bayesian analysis of variance) versus their lifetime pup outputs. We used a Poisson's error for the latter since it was a positive integer. Parameters were estimated using a Bayesian method (see the Supplement on the regression and the choice of 2009 as the cutoff).

Mass at weaning and future reproductive success

In Le Boeuf et al. (2019), we demonstrated that larger pups have a higher probability of returning as reproductive adults. Here, we updated the calculation with a larger sample, this time using residual mass at weaning rather than observed mass. We also extended the result by testing whether weaning mass correlated with future lifetime pup production among those who returned. The first was a logistic regression between a pup's mass at weaning and the binomial observation whether or not she was later observed breeding; it was based on 670 female pups born and weighed by 2009. The second was a Poisson's regression of lifetime pup production as a function of the same mass at weaning, but using only the 139 females who were observed breeding (omitting the 531 females in the sample that never bred). In both regressions, parameters were fitted using the Bayesian method (see the Supplement).

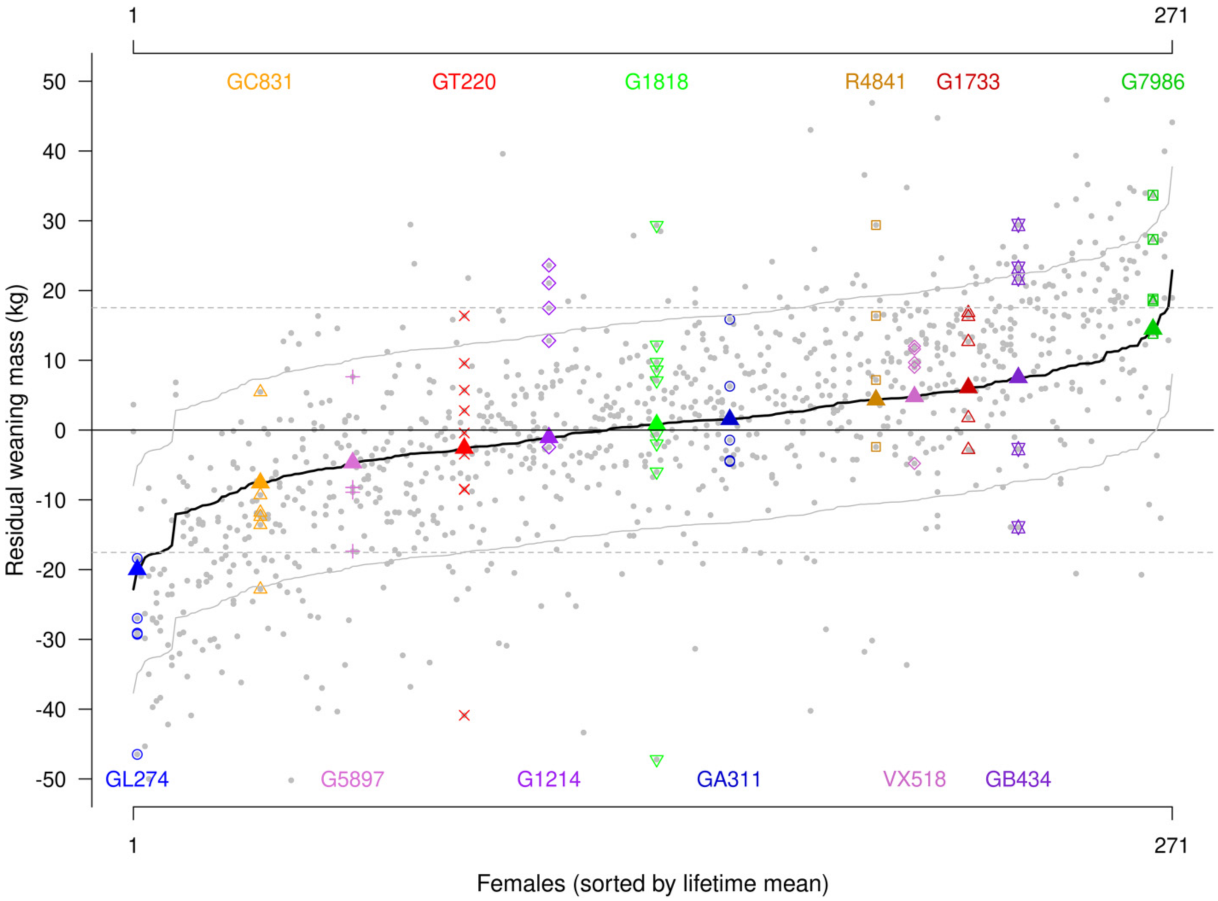
Heritability of weaning mass

Heritability was estimated as twice the slope of the regression between weaning mass of mother and offspring. Following Falconer (1960), the correlation was based on average weaning mass of all pups from one mother (from the Bayesian analysis of variance), with the average weighted by the number of pups per mother. We had 189 cases where a mother who was weighed at weaning had a pup weighed at weaning, including 97 different mothers having up to six pups each (Table S1). The regression thus had 97 individual points, each weighted by 1–6. The slope and its error were estimated with the standard formulae based on normally distributed data.

Heritability of lifetime pup production

We calculated the mother–daughter correlation in the number of pups produced over a lifetime. This required a

Fig. 2. Variation in pup mass at weaning within and among individual northern elephant seals (*Mirounga angustirostris*), based on subsets of females with larger samples. The 271 females along the *x*-axis are the subset having three or more pups weighed during their lifetimes, and their residual weaning masses are on the *y*-axis. Multiple measurements for one female appear directly above one another. The black curve connects lifetime means for the females, as estimated by the Bayesian, multilevel model; they are sorted from smallest to largest lifetime mean so the curve increases monotonically. Thin gray curves are 1 standard deviation (SD) above and below the mean of each female ($\sigma_r = 14.9$), exactly parallel to the black curve due to the assumption that within-female variance is constant across seals. The horizontal dashed lines show 1 SD of all masses ($\sigma_T = 17.5$) above and below the overall mean of zero. The among-female SD was $\sigma_m = 9.3$. Twelve mothers are highlighted with large colored points, including a large triangle for lifetime mean and smaller points at individual masses; they are identified by tag numbers at the top or bottom. The 12 females were chosen arbitrarily by sorting a refined subset, the 62 females with at least 5 pups weighed, by lifetime mean weaning mass and extracting evenly spaced ranks (ranks 1, 7, 12, 18, 23, 29, 34, 40, 45, 51, 56, 62). A few outlying masses are off the graph, such as G1214's pup when she was 18 years old (residual mass −81.7 kg). The Bayesian means are pulled toward the center, evident for GL274 and G7986. Figure S2 shows lifetime trajectories of pup masses for the females identified here. Figure S3 shows the same analysis with randomized data, when among-female variance was removed.



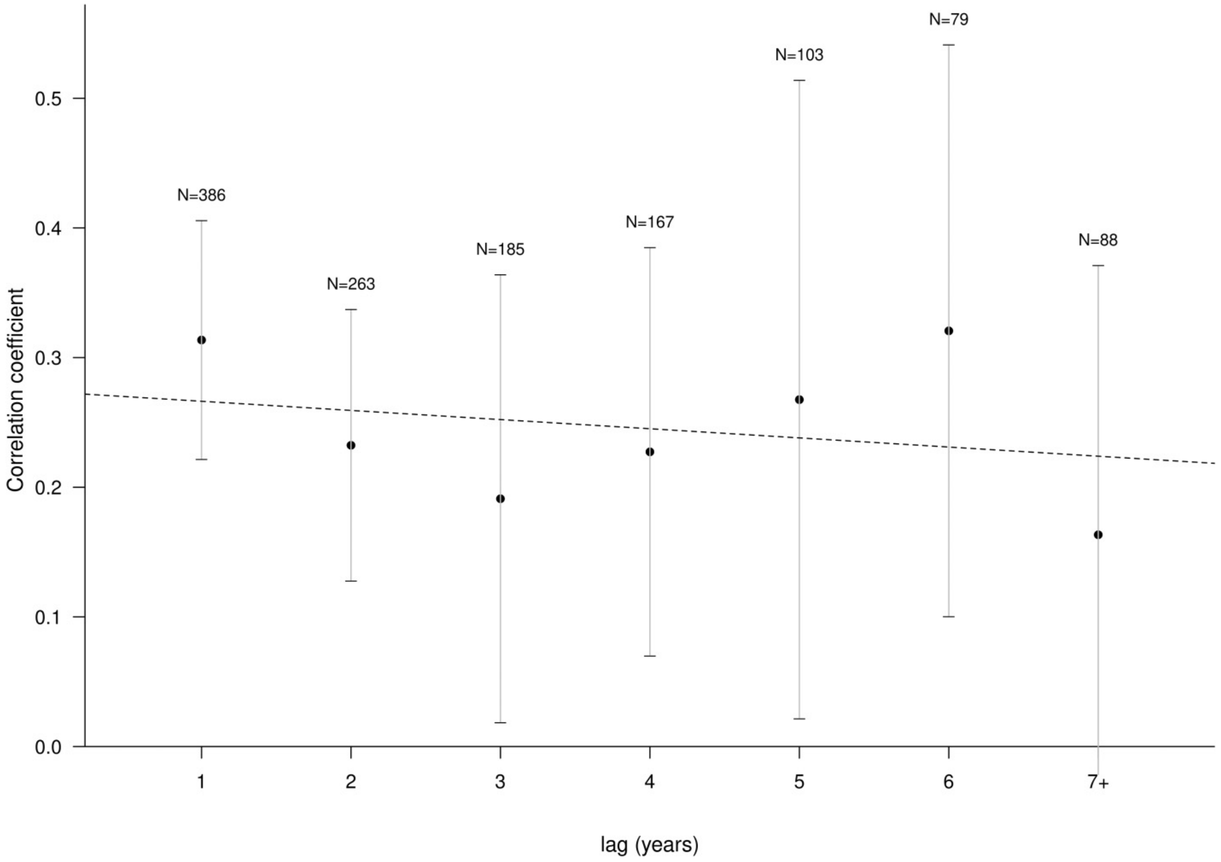
sample limited to mothers whose female pups were tagged by 2009, meaning that both mother and daughter had (near) complete observations of lifetime pup output. There were 719 daughters of 493 distinct mothers, and we estimated the correlation coefficient between lifetime pup production of mother and daughter. Unlike the other models predicting lifetime pup production, this one must include the tagged daughters never observed breeding, meaning the dependent variable had many zeroes. The distribution was thus far from Poisson (Le Boeuf et al. 2019; Bonnet et al. 2022), so the correlation was estimated using a negative binomial error (see the Supplement for details).

Results

Intrinsic female differences in offspring quality

Female elephant seals differed significantly in lifetime mean of their pup's masses, where mass was measured as the residual relative to the population average. After controlling for mother's age, pup sex, and year, 28.1% of the remaining variance in weaning mass was accounted for by differences among individual mothers (credible interval 23%–34%). The standard deviation among females was 9.3 kg, and 10% of the mothers with highest pup quality had lifetime mean pup mass >6 kg above the average of 127 kg, including some with lifetime pup mass >15 kg above average (Fig. 2). The 10% low-

Fig. 3. Correlation of pup mass at weaning with increasing lag time within northern elephant seal (*Mirounga angustirostris*) mothers. Circles show estimated correlation coefficients between pup masses of the same mother separated by exactly 1–6 years; the final point at 7+ includes all lags ⩾7 years combined. Gray vertical bars give twice the standard error above and below each estimate. Sample sizes of distinct mothers in each lag class are given above. The dashed line is the regression between correlation coefficients and lag (slope $= -0.007$, $p = 0.58$). Figure S4 illustrates the correlation within specified lags.



est in pup quality were 6.9 kg below average, with some 15 kg below. On the other hand, 20% of the females in the middle differed from the average by <1.3 kg.

Lifetime consistency of female differences

Differences among mothers in mass of their pups at weaning were consistent over at least 6 years, as demonstrated by the correlation of the mass of two pups born to the same mother. The correlation remained positive at all lags and did not decline with lag (Fig. 3). The correlation coefficient after pooling all lags of 1–6 years was 0.27 (credible intervals 0.20–0.34), close to the repeatability calculated from the among-female portion of the analysis of variance. Repeatability is illustrated with lifetime trajectories of pup mass for a selection of individual mothers (Fig. S2).

Weaning mass and pup production of females

Mothers who weaned larger pups did not also have high pup production. There was a positive trend, but it was slight and credible intervals broadly overlapped zero (Fig. 4).

Mass at weaning and future reproductive success

Pups larger at weaning had a higher probability of returning later as breeding adults (Fig. 5A, updating the result in Le Boeuf et al. 2019). For low quality females, those one standard deviation below mean lifetime pup mass (Fig. 2), the probability that a pup reached breeding age was 0.178, while for those one standard deviation above, it was 0.229 (Fig. 5A). Of those that returned, however, there was no correlation between mass at weaning and their future lifetime pup production (Fig. 5B). In the latter case, there was a positive relationship, but it was non-significant (Fig. 5B).

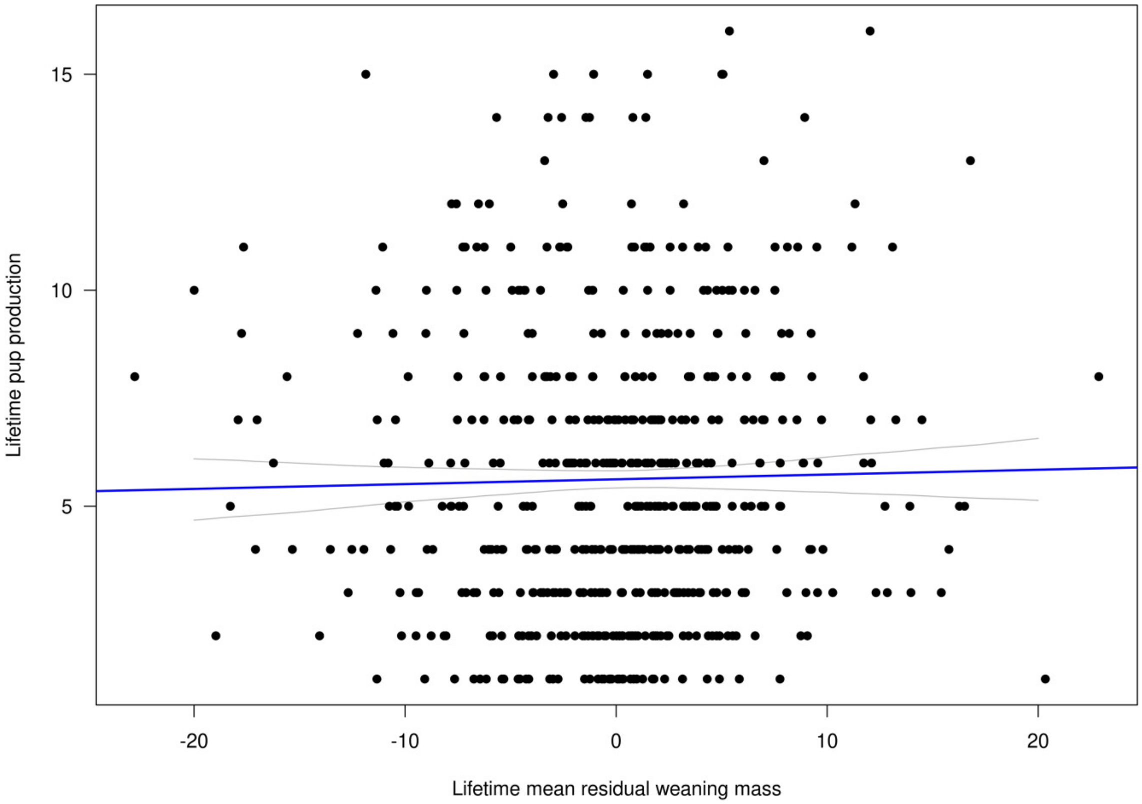
Heritability of weaned pup mass

The ability of mother elephant seals to wean large pups was passed on to their daughters. The correlation between mass of the mother (when she herself was a pup) and her pup was 0.24 and significantly different from zero; heritability was thus $h = 0.48$ (Fig. 6).

Heritability of lifetime pup production

The ability to produce a high number of pups in a lifetime was not passed from mother to daughter. The mother–pup

Fig. 4. Correlation between quality and quantity of individual mothers' lifetime reproductive output in northern elephant seals (*Mirounga angustirostris*). Pup quality is measured by lifetime mean pup mass at weaning (*x-axis*); quantity by lifetime pup output (*y-axis*); each point is a single female ($N = 593$). The solid blue line is the regression curve, fitted using a Poisson's error in y. Thin gray lines show estimated 95% credible intervals at each mass, calculated from post-burn-in draws of the regression coefficients. The regression is slightly positive but not significantly different from zero (slope =0.0111, 95% credible intervals −0.021 to 0.046).



correlation coefficient was negligible and credible intervals broadly overlapped zero (Fig. 7).

Discussion

Mother elephant seals maintained consistent differences in the size of pups they weaned over at least 6 years. Since the median breeding life span is less than 6 years (Le Boeuf et al. 2019), these differences in pup quality meant fixed, lifetime variation in a fitness-related trait. Lifetime consistency meant that highly successful mothers weaned pups 30 kg larger than the least successful, averaged over a lifetime. Our results demonstrate that the extra 30 kg, almost 25% of the mean weaning mass, has a large impact on the pup's future breeding success. Weddell seals are similar, having a 24 kg difference between females of the highest and lowest quality pups, and large pups had higher juvenile survival (Proffitt et al. 2008; Paterson et al. 2016). We demonstrated that differences among females were not a result of short-term environmental fluctuations, because we controlled for year-to-year variation in marine productivity. Other studies of maternal differences in offspring quality in marine birds and mammals also accounted for environmental variation, but none included a test of whether variation was maintained over many years (Oosthuizen et al. 2015; Paterson et al. 2016; Jenouvrier et al. 2018).

We also discovered that fitness quality, measured by weaned pup size, is heritable in elephant seals. The component of the variance due to inheritance was 48%, higher than repeatability within females, which was 27%–28% based on analysis of variance and lag correlations. Heritability should not be higher than repeatability, but confidence limits of both measures overlapped substantially, so elevated heritability can be attributed to sampling error. In a review of wild populations, Postma (2014) reported 30%–60% heritability for many traits, with an average for fitness-related traits of 32%.

On the other hand, lifetime pup production, which is largely a function of how long a female lives, was not heritable, nor did a female's ability to raise large pups correlate with her lifetime output. Moreover, while mass of a female when she was weaned predicted her probability of returning to breed, it did not predict her pup output after that. Our conclusion is that high mass at weaning helps young females survive the first 1–3 years, but not beyond. We also suggest that heritability of weaning mass arises from traits different from those associated with adult survival. Traits that relate to nursing success, and how these relate to the ability to wean fit

Fig. 5. Mass at weaning as a predictor of future reproductive success in northern elephant seals (*Mirounga angustirostris*). In both panels, the *x*-axis is residual mass at weaning of individual females and the *y*-axis is a measure of future lifetime reproduction of those individuals. (A) Reproduction measured as the probability each female was observed reproducing at least once in her lifetime, as in Le Boeuf et al. (2019) but updated. The points are observed proportions in eight categories defined by quantiles ($N = 670$, each category has 83–84 individuals). The regression curve is solid blue and was estimated by logistic regression with the full sample. It is significantly positive (slope = 0.0169, 95% credible intervals 0.004–0.029). Vertical lines indicate mean lifetime pup mass of females one standard deviation below the mean versus one standard deviation above (one SD is $\sigma_m = 9.3$ kg). (B) Reproduction measured as lifetime pup production of each animal, including only those seen reproducing ($N = 139$). Each point represents one animal. The regression curve is solid blue and is not significantly different from zero (slope = 0.0127, 95% credible intervals −0.017 to 0.043). The *y*-axis is log-transformed for display purposes; the regression used untransformed integers and was based on a Poisson's error in *y*. In both panels, thin gray lines show estimated 95% credible intervals at each mass, calculated from post-burn-in draws of the regression coefficients.

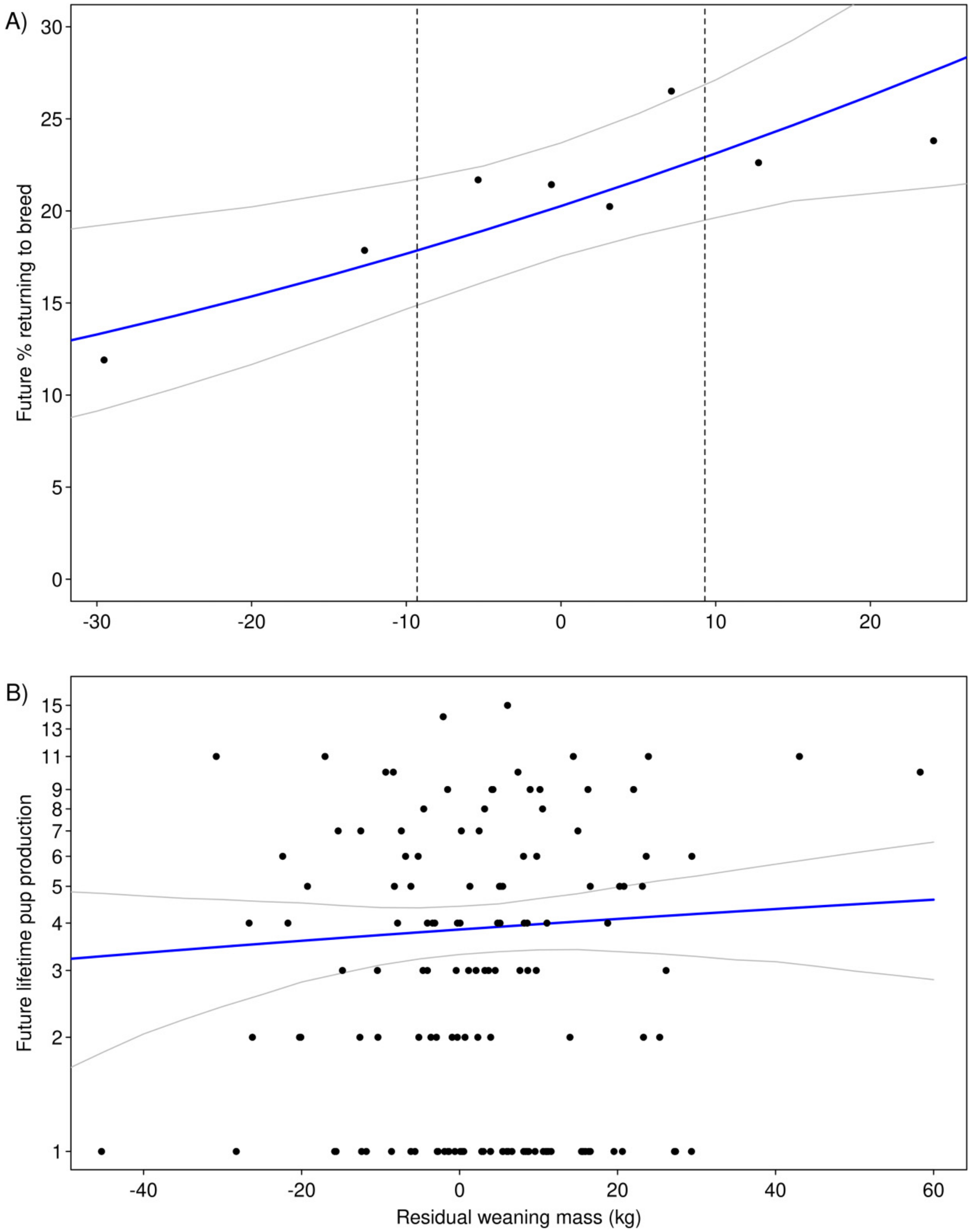
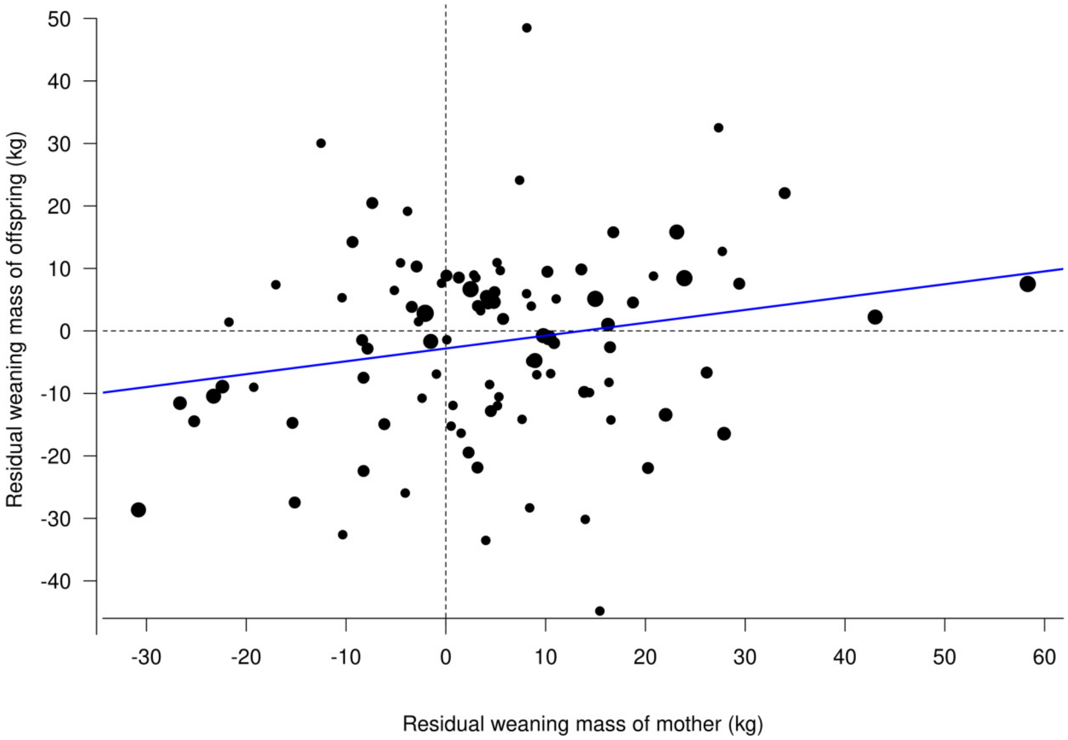


Fig. 6. Correlation between a mother's mass at weaning and the mean mass of her pups ($N = 92$) in northern elephant seals (*Mirounga angustirostris*). The solid blue line is the regression; dashed lines are at $x = 0$ and $y = 0$. The size of each point is scaled with $\log N_w$, where $N_w \in [1–6]$ is the number of pups per female (Table S3). The regression is highly significant ($p = 0.00002$, slope $\rho = 0.2396$). Heritability h is twice the slope ($h = 0.48$, 95% confidence intervals 0.26–0.70).



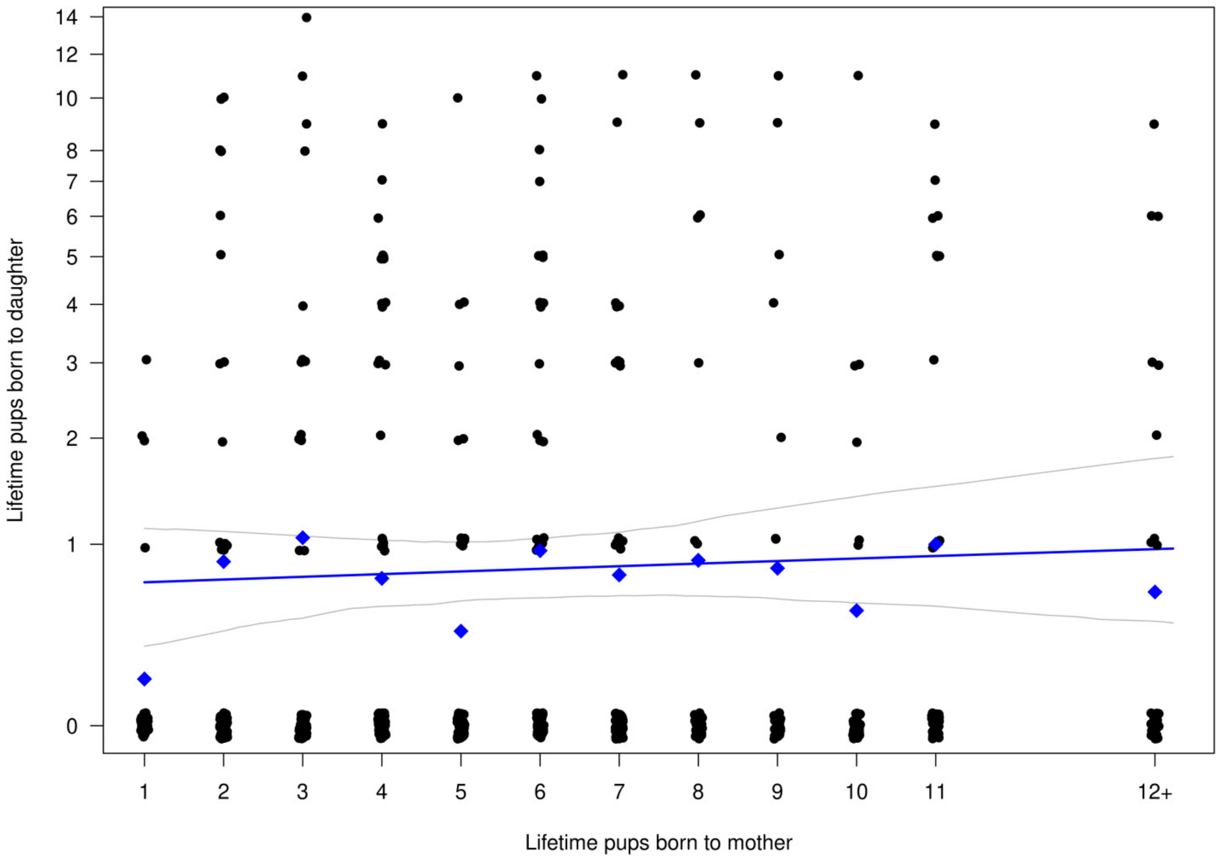
pups, include behavior on the colony, such as ability to maintain close contact with the pup (Reiter et al. 1981; Riedman and Le Boeuf 1982) and lactation physiology (Ortiz et al. 1984; Costa et al. 1986), neither of which relates to survival. On the other hand, traits related to foraging success do associate with both nursing success and survival (Crocker et al. 2001; Robinson et al. 2010; Beltran et al. 2023).

We believe our current observations favor some genetic basis for traits affecting the size of pups that females wean. We found strong evidence that the ability to raise high-quality pups lasted throughout a mother's adulthood, and that the ability was passed on to her daughters. The phenotypic maternal influence ends when pups are only 1 month old, and mass at weaning affected subsequent survival as juveniles but not later. Together, these lines of evidence suggest that the ability to raise high quality pups is an adult trait, whereas the maternal influence is important only for pups and juveniles. Confirming the genetic influence, however, will require developing technologies in genomics that can identify loci associated with nursing success or survival (Jones et al. 2012).

We found that some variation in fitness of elephant seals is not neutral, because females were inherently different in the quality of the pups they raised and passed that ability on to their daughters. Some variation is neutral, however, since 73% of the observed variance in weaning mass remained within individual mothers and remains unexplained, and variation in pup production was entirely unexplained. Our results underscore the need to quantify neutral versus non-neutral variation in order to understand how selection operates. Progress with neutral theories in ecology arose from rigorous partitioning of variation (Chisholm and Pacala 2011; Kalyuzhny et al. 2015; Fung et al. 2016). Several recent studies about neutrality in lifetime fitness did not partition variation among individuals, settling for comparisons of observed variance with that expected from stochastic models (Tuljapurkar et al. 2009; Steiner et al. 2010; Chambert et al. 2013; Snyder and Ellner 2018). This indirect method fails to distinguish short-term and long-term individual variation and is weak at separating stochastic variation from individual differences (van de Pol and Verhulst 2006; Bonnet and Postma 2016). Lifetime observations, on the other hand, allow clear-cut partitioning of individual variation (Oosthuizen et al. 2015; Jenouvrier et al. 2018; Rotella 2023).

Inherent differences among individuals in the fitness of their offspring allow flexibility across the population and dampens demographic stochasticity (Fox and Kendall 2002; Vindenes et al. 2008; Vindenes and Langangen 2015; Barabás and D'Andrea 2016). We identified inherent differences in elephant seals' ability to raise high fitness pups, and traits related to those differences provide a source of adaptive flexibility. We did not, however, identify adult survival as a trait inherently different among individuals. These results add to our understanding of how elephant seals might respond to unanticipated variation in oceanographic conditions.

Fig. 7. Correlation of lifetime pup production between mothers and daughters of northern elephant seals (*Mirounga angustirostris*). Black points are the $N = 719$ cases where a known mother had her daughter tagged and followed throughout life. Some of the mothers had more than one daughter. Included among the daughters are those never seen, thus having zero pups produced. Because all points are integers, they are jittered to show where many overlap. Blue diamonds are the observed mean production of daughters within each x; all data with $x \in [12, 16]$ were pooled. The blue line is the regression, fitted by a Bayesian method using a negative binomial error; it is not significantly different from zero (slope $= 0.0183$, 95% credible intervals -0.040 to 0.103). Thin gray lines show estimated 95% credible intervals at each x, calculated from post-burn-in draws of the regression coefficients.



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Data availability

All data can be downloaded from public archives: weights of northern elephant seal weanlings from Año Nuevo Reserve (https://doi.org/10.7291/D1D973); Elephant seal female breeding histories at Año Nuevo (https://doi.org/10.7291/D18084).

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Competing interests

The authors have none to declare.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjz-2023-0166.

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Inherent versus random variation in fitness of elephant seals: Supplemental material

by

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Bayesian model to partition variance

We used a multi-level model (Gelman & Hill, 2007) to estimate the variance of residual weaning masses within and among mothers. This mass is a residual because it is the difference between the observed mass of a pup and the model prediction for the given pup sex, mother age, and year. Define m_{ij} as the residual mass of pup j born to mother i. At a lower level, the model estimated a lifetime mean of weaning mass for every mother, $\widehat{m_i}$. Since there were 1065 mothers, this requires 1065 parameters in the model. The upper-level of the model added three hyper-parameters: $\widehat{M}$, the overall mean mass; σ_m^2, the variance among the $\widehat{m_i}$; and σ_r^2, the variance within m_{ij} of each mother. Because m_{ij} was defined as a model residual, $\widehat{M}$ should be zero, but it was not constrained and was fitted as a free parameter, though the result was not used. Every female was assumed to have the same residual variance, hence there was just a single σ_r^2.

We assumed Gaussian distributions for both m_{ij} within females and $\widehat{m_i}$ among females, so

$$m_{ij} \sim \mathbf{Norm}(\widehat{m_i}, \sigma_r^2) \tag{1}$$

$$\widehat{m_i} \sim \mathbf{Norm}(\widehat{M}, \sigma_m^2) \tag{2}$$

provide likelihood functions for each of the parameters. We used a Markov Chain Monte Carlo sampling method (MCMC) based on the Metropolis algorithm (Metropolis *et al.*, 1953) to generate posterior distributions. This meant repeated draws of all parameters, with the likelihood recalculated each time; a non-informative prior was utilized for all parameters (for means, any value had equal prior probability; for σ, any > 0 had equal probability). All individual female means, the $\widehat{m_i}$, were updated first, given observations m_{ij} and the current values of other hyper-parameters (Eqs. 1 and 2 together repeated 1065 times), then hyper-parameters were updated given those female means (σ_r^2 from Eq. 1, σ_m^2 and $\widehat{M}$ each from a Eq. 2). The Metropolis algorithm is a tool for keeping the MCMC parameter draws in the vicinity of the maximum, producing precisely a posterior distribution for every parameter; it is a standard Bayesian method that we have used in many contexts (Condit *et al.*, 2006, 2014, 2022). It would also be possible with Gaussian distributions to use draws from conjugate distributions, without Metropolis, but we chose Metropolis MCMC because we use it often; the conjugate method would yield identical results.

Parameter searches were run 4000 steps, with the first 1000 discarded as burn-in; the chains were well-mixed and rapidly converged. Credible intervals for each variance, as well as the proportion $V = \sigma_m^2/(\sigma_m^2 + \sigma_r^2)$, were calculated as 95^{th} percentiles of post-burn-in chains. The 1065 individual female means, $\widehat{m_i}$, were calculated as the means of each post-burn-in posterior distribution; they were used in subsequent analyses (see Fig. 2, main text).

Verification of variance partition

We compared results of the Bayesian analysis-of-variance to the traditional method based on sums-of-squares (Huntsberger & Billingsley, 1973) using simulated data from the R function *rnorm* (R Core Team, 2021). We created a dataset having group sample sizes matching our data (pup masses per female), assigning within- and among-group means and variances arbitrarily. Our Bayesian method produced reasonable estimates of the among-group variance, while observed sums of squares overestimated it by two-fold.

We also checked model results from the original data against a randomized dataset. To randomize, the entire table of mothers and their pup masses was shuffled, so each mother was assigned one of the masses at random, without replacement. The randomized table thus had all the same mothers and same pup masses, with unchanged sample sizes for each mother, but multiple pups of the same mother were divided among several mothers. Our Bayesian model correctly reported low variation among females in the randomized data (Fig. S3).

Lag regressions

For the regressions between two pup masses of the same mother separated by a lag of L years, we needed to address the concern with repeated measures. This arose because one individual mother could have multiple cases where two of her pups were weighed L years apart. To remove repeated measures, we created subsamples of any one lag sample by drawing each individual female just once. For example, there were 628 cases where the same mother had two pups weighed one year apart (lag one), but this included only 386 individual mothers (Table S3). Thus a subsample at lag 1 had 386 data points created by randomly choosing a single pair (pup masses in two years) from each mother. From each, we calculated the correlation coefficient ρ between the two pup masses, along with its standard error (σ_ρ) and p-value from the t-statistic of ρ. Subsamples were repeated using 50 different random draws for each lag, and σ_ρ and p were averaged across the replicates (each differed slightly due to the random draws). The correlation coefficient itself, ρ, was not averaged in this way, but was calculated from the full sample. because it would not be biased by repeated measures.

Baysian regression of mean lifetime pup mass versus lifetime pup production of individual mothers

We fit a linear regression between offspring quality and offspring quantity of individual mothers. The sample included all 593 females born up to 2009 who had at least one pup weighed. The cutoff of 2009 meant lifetime observations of pup production were near complete. In fact, 17 of the 593 were still alive in 2023, and thus we have not yet observed their full lifetimes; however, each is already in the upper echelons of lifetime reproductive success, so the few births missing should not change results.

Define lifetime pup output of female i as n_i (an integer), and the Bayesian estimate of mean lifetime mass at weaning of her pups as $\widehat{m_i}$ (as in Eq. 1). The linear model is

$$\widehat{n_i} = \rho\widehat{m_i} + \beta, \tag{3}$$

where $\widehat{n_i}$ is the predicted (non-integer) number of pups born to a female whose pups had mass $\widehat{m_i}$; ρ is the regression slope and β the intercept. The range of n_i was 1-16; there were no zeroes because females had to reproduce to be included. The distribution of n_i was near Poisson, so we used a Poisson error in the regression. The parameters $\{\rho, \beta\}$ were updated with the Metropolis Markov Chain method described above, and credible intervals taken as 95^{th} percentiles of the post-burn-in chain. The regression was considered significant if the credible intervals of ρ did not overlap zero.

Baysian regression of a pup's mass at weaning versus her future lifetime breeding

We fit two regressions predicting future lifetime breeding success as a function of female i's mass when she was weaned (w_i). The first measure of reproductive success is the probability of breeding at least once, b_i; the second is the number of pups born in a lifetime, n_i. The sample included all 670 females who were weighed at weaning through 2009, again providing near complete breeding lifetimes. The first regression was logistic, since the observations were binomial: each female either bred once or did not.

$$\mathbf{L}(b_i) = \rho w_i + \beta, \tag{4}$$

where $\mathbf{L}$ means the logit transformation and $\{\rho, \beta\}$ are the slope and intercept. The error was binomial. The second regression was Poisson, exactly as in Equation 3, but based only on the 139 females that bred (as for Equation 3, there were no zeroes). Parameters for both regressions were estimated using the Metropolis Markov Chain method described above, and credible intervals for the slopes were 95^{th} percentiles of post-burn-in chains.

Baysian model for heritability of pup production

We fit a linear regression between mother pup production and daughter pup production. This was based on 719 mothers having a daughter born up to 2009, here applying the year cutoff to assure near-complete lifetime observations of both mother and daughter. In this case, the dependent variable, daughter production, had many zeroes because non-reproductives were included, and the distribution was far from Poisson. To accommodate this we used a negative binomial error. For each pair, mother i and daughter j, let n_i be the number of pups born to the mother over her lifetime and d_{ij} the number born to the daughter; $n \geq 1$ and $d \geq 0$. Individual mothers appeared one or more times, but each daughter only once; to allow the negative binomial, we needed integers and could not average d over each mother (as we did for heritability of pup mass). Define the linear regression as

$$\widehat{d_i} = \rho n_i + \beta, \tag{5}$$

where $\widehat{d_i}$ is the predicted (non-integer) number of pups born to a daughter whose mother had n_i pups. The likelihood of observing the data is

$$d_{ij} \sim \mathbf{NegBinom}(\widehat{d_j}, k). \tag{6}$$

Parameter k is the clumping parameter of the negative binomial, akin to a standard-deviation; it was needed to fit the model but the value was not used. The parameters $\{\rho, \beta, k\}$ were updated with the Metropolis Markov Chain method described above, and credible intervals for ρ taken as 95^{th} percentiles of the post-burn-in chain.

Supplemental references

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Supplemental Tables

Table S1: Variance partitioning of weaning mass in northern elephant seals (*Mirounga angustirostris* [Gill 1866]), covering the three population-wide factors known to be important. The mean mass of all pups at weaning was 127.0 kg; the first row gives the total variance around that mean. The next three rows give the variance within groups defined by pup sex, mother age, and year, and finally the remaining variance after removing each. These were calculated using the standard approach based on sums of squares. The variance after removing these factors, 299.9, is the residual variance, and it is the basis for our analysis of variation among and within females.

	Between group variance (percent of total)		Remaining variance
Total			454.6
Sex	4.8	(1.1)	449.8
Age	125.3	(26.5)	329.3
Year	154.7	(6.5)	299.9

Table S2: Sample sizes for the number of northern elephant seal (*Mirounga angustirostris*) mothers with pups weighed N times. The count under 'All mothers' is the total number of individuals who had N pups weighed throughout their lives; under 'Weighed mothers' is the total of mothers who were themselves weighed, then had N pups weighed in a lifetime. Since elephant seal females have a single pup per year, the number of pups weighed equals the number of years.

N pups weighed	All mothers	Weighed mothers
1	532	44
2	262	33
3	129	7
4	80	8
5	37	4
6	13	1
7	7	0
8	1	0
9	3	0
10	1	0
Total	1065	97

Table S3: Sample sizes of mothers with two pups weighed at given lag times in northern elephant seals (*Mirounga angustirostris*); the last row combines all lags ≥ 7 years. The first count, under 'Individual mothers', is the number of unique individual mothers with at least one pair of pups at each lag. 'Full sample' shows the total number of mother-pup pairs, including multiple pairs with the same lag within a single mother.

Lag (years)	Individual mothers	Full sample
1	386	628
2	263	413
3	185	269
4	167	217
5	103	137
6	79	106
7+	88	252

Supplemental Figures

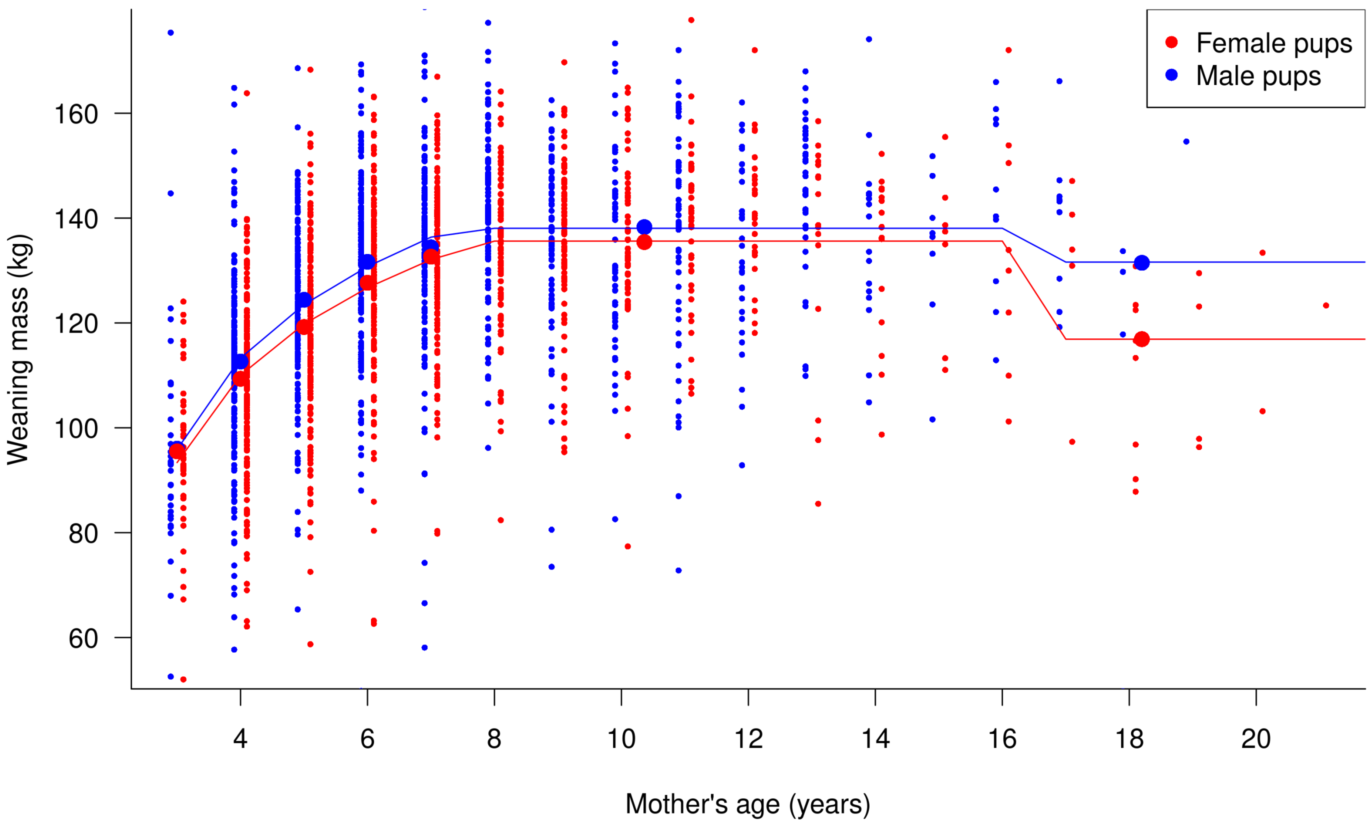

Figure S1: Asymptotic model of pup mass at weaning as a function of mother's age in northern elephant seals (*Mirounga angustirostris*), comparing male and female pups. Small points are individual masses; large circles are observed mean masses at ages 3-7 separately, ages 8-16 and 17-21 grouped. Solid lines are fixed effects, meaning the estimated overall average mass of each sex, including all years, as a function of mother's age (main text Eq. 1).

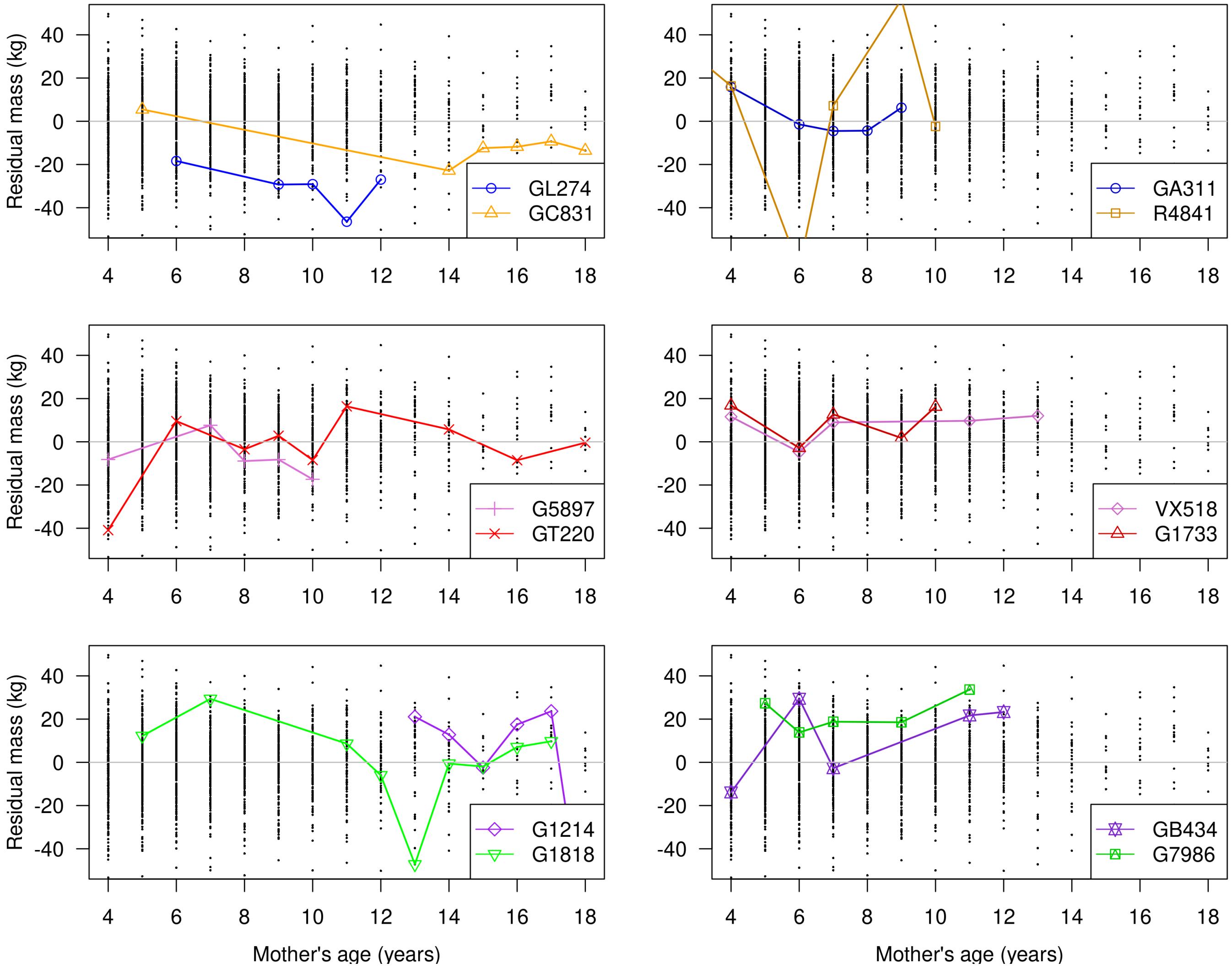

Figure S2: Examples of variation in residual weaning mass over the lifetime of individual northern elephant seal (*Mirounga angustirostris*) mothers as they aged. Small black points show the entire sample of all pups of all mothers. The 12 mothers highlighted match those in Figure 2 (main text), ordered from low lifetime mean (top left) to high (bottom right). For example, female GL724's pups were always below average, while G7986's were always above-average; G1818 was inconsistent, near average in many years, but well above at age 7 and below at age 13.

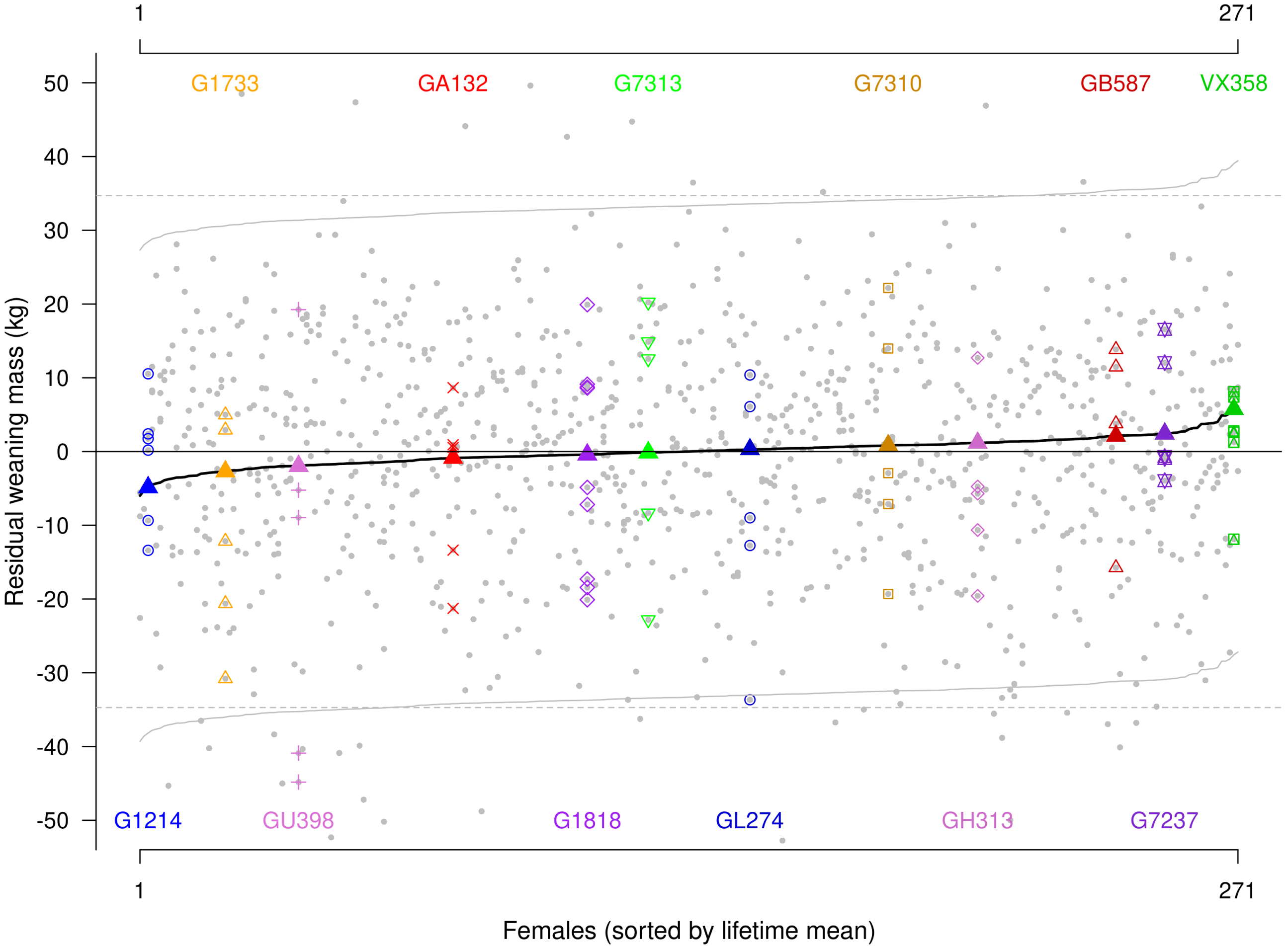

Figure S3: Lifetime residual weaning mass within and among females of northern elephant seals (*Mirounga angustirostris*) when data were randomized. The model reported 8.0% of variance between females, compared to 28.1% in the original data. Compare to main text Figure 2; highlighted females were chosen by the same ranking system. By chance, three of the females appear in main Figure 2 and here; randomization is evident for GL274, whose real pups were all below average.

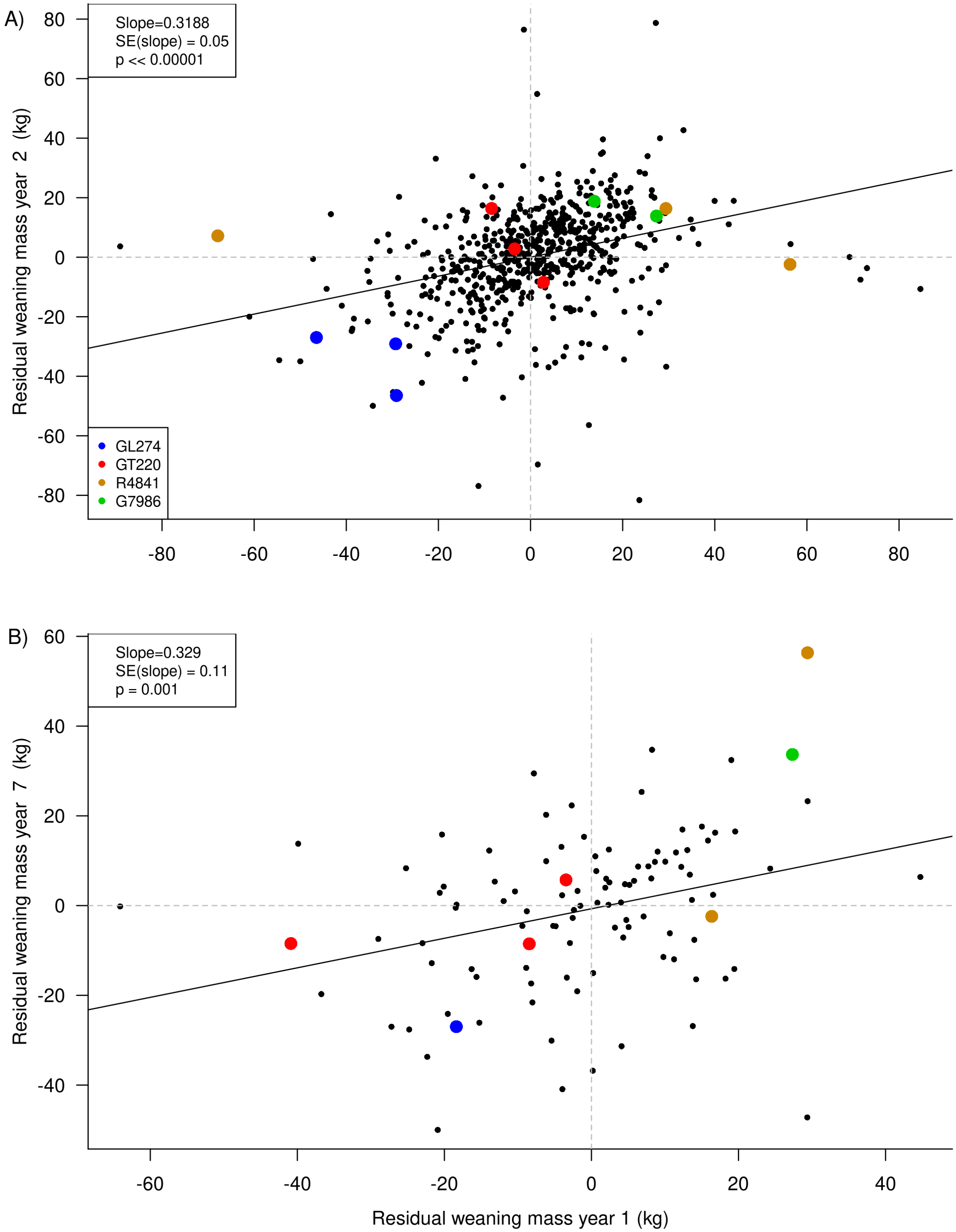

Figure S4: Residual weaning mass of two pups born to a single northern elephant seal (*Mirounga angustirostris*) mother in different years. The sloping line is the regression; vertical and horizontal lines are at $x = 0$ and $y = 0$. A) Consecutive years. Multiple pairs within the same mother are all included, $N = 628$. B) Six years apart, $N = 106$. Colored points identify four of the females highlighted in Figures 2 and S2; colors match in A) and B).