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Individual heterogeneity in life-history trade-offs with age at first reproduction in capital breeding elephant seals

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Abstract

Recruitment age plays a key role in life-history evolution. Because individuals allocate limited resources among competing life-history functions, theory predicts trade-offs between current reproduction and future growth, survival and/or reproduction. Reproductive costs tend to vary with recruitment age, but may also be overridden by fixed individual differences leading to persistent demographic heterogeneity and positive covariation among demographic traits at the population level. We tested for evidence of intra- and inter-generational trade-offs and individual heterogeneity relating to age at first reproduction using three decades of detailed individual life-history data of 6439 capital breeding female southern elephant seals. Contrary to the predictions from trade-off hypotheses, we found that recruitment at an early age was associated with higher population level survival and subsequent breeding probabilities. Nonetheless, a survival cost of first reproduction was evident at the population level, as first-time breeders always had lower survival probabilities than pre-breeders and experienced breeders of the same age. However, models accounting for hidden persistent demographic heterogeneity revealed that the trade-off between first reproduction and survival was only expressed in 'low quality' individuals, comprising 35% of the population. The short-term somatic costs associated with breeding at an early age had no effect on the ability of females to allocate resources to offspring in the next breeding season. Our results provide strong evidence for individual heterogeneity in the life-history trajectories of female elephant seals. By explicitly modelling hidden persistent demographic heterogeneity we show that individual heterogeneity governs the expression of trade-offs with first reproduction in elephant seals.

KEYWORDS

cost of reproduction, hidden heterogeneity, individual quality, mixture models, recruitment age

INTRODUCTION

The principle of energy allocation posits that individuals allocate limited resources among competing life-history functions, and that energy allocation to one fitness component decreases the energy available to other fitness components (Williams, 1966; Van Noordwijk & de Jong, 1986). Trade-offs (negative covariations) are thus expected to occur among competing fitness-related traits such as growth, survival and reproduction (Stearns, 1989). Because reproduction is energetically expensive, trade-offs between current reproduction and future growth, survival and/or reproduction are common across the slow-fast continuum of life histories (Hamel et al., 2010). Specifically, the costs of current reproduction are defined in terms of losses to an individual's potential future reproductive success (Jönsson, 2000). Reproductive costs play a key role in the evolution of life histories (Stearns, 1989) and

even moderate cost of reproduction trade-offs have significant effects on population dynamics (Proaktor et al., 2008).

The reproductive trade-offs predicted by life-history theory may be less detectable when resources are plentiful (Ricklefs & Cadena, 2007), when a population is composed of 'robust' and 'frail' individuals (Vaupel & Yashin, 1985), or when there is variation in resource acquisition and allocation among individuals (Van Noordwijk & de Jong, 1986; Descamps et al., 2016). For example, positive correlations among fitness components, rather than trade-offs, can emerge at the population level when the among-individual variation in resource acquisition exceeds the variation in resource allocation (Van Noordwijk & de Jong, 1986; Hamel et al., 2010). Variation in resource use may arise from numerous sources including heterogeneity in phenotypic quality (e.g., body size; MacNulty et al., 2009) and home range quality (McLoughlin et al., 2007). Variation in individual quality (i.e., "an axis of among-individual heterogeneity that is positively correlated with fitness"; Wilson & Nussey, 2010) resulting from uneven among-individual access to resources can therefore mask trade-offs measured at the population level (Van Noordwijk & de Jong, 1986; Hamel et al., 2010). While the covariance predictions of the trade-off (negative) and individual quality (positive) hypotheses are always opposed (Figure 1), these processes are not mutually exclusive and may operate simultaneously (Van Noordwijk & de Jong, 1986).

The age at which a female first reproduces (recruitment age) is a particularly important life-history trait that can vary substantially within wild populations (Caswell, 2001). In theory, recruitment at an early age benefits individuals by shortening generation time and increasing the number of possible breeding opportunities over a lifetime (McGraw & Caswell, 1996). In support of this prediction, numerous empirical studies indicate a fitness gain among individuals that recruit at an early age (Zhang et al., 2015: Fay et al., 2016; Paterson et al., 2018). However, the advantages of early breeding are often counter-balanced by elevated reproductive costs among younger first-time breeders (Millon et al., 2010; Desprez et al., 2014). Young breeders have less time available to accumulate resources and experience prior to reproduction, and in species that can reproduce before completing body growth, young breeders compound the energetic demands of growth and reproduction. This energetically demanding undertaking may depress survival probability and erode the fitness benefits of early compared to delayed recruitment (Tavecchia et al., 2001; Krüger, 2005).

Current reproduction may not only have direct influence on survival and/or subsequent probability of reproduction, but potentially affects other traits that indirectly decrease an individual's future performance. For example, current reproduction can reduce the residual reproductive value of an individual through its influence on the reproducing individual's phenotype (Hamel et al., 2010). In species with determinate growth, trade-offs between current reproduction and growth are most common

in young females that reproduce before reaching asymptotic body mass (Stamps et al., 1998; Hamel & Côté, 2009). Although the somatic costs associated with early breeding do not always translate into lower future reproductive success (Hamel et al., 2010; Martin & Festa-Bianchet, 2012), such penalties are probable in capital breeders. Capital breeding females primarily depend on body reserves accumulated at an earlier time to sustain the energetic requirements of reproduction (Jönsson, 1997). Consequently current reproduction may reduce maternal body mass so much that it lowers future reproductive success or individual fitness components of subsequent offspring (Hamel et al., 2010). The costs of reproduction can therefore be expressed both within as well as between generations. Inter-generational costs are rarely investigated in long-lived species (Moore et al., 2016; Markussen et al., 2018), even though this trade-off is as important to life history evolution as within-generational trade-offs (Stearns, 1989). Mothers can transfer some reproductive costs to their offspring (Festa-Bianchet & Jorgenson, 1998; Martin & Festa-Bianchet, 2010) and inter-generational reproductive costs occur when the costs of reproduction are detectable in offspring, but not necessarily in maternal traits. For example, reduced phenotypic quality and lower survival of offspring born to young mothers may suggest that offspring pay a cost for mothers' early age of first reproduction.

In this paper, we use 30 years of longitudinal data to assess life-history trade-offs with age at first reproduction in female southern elephant seals (*Mirounga leonina*; hereafter elephant seals). Because reproductive costs can be masked by phenotypic variations among individuals, we used finite mixture models (Pledger et al., 2003) to account for hidden individual heterogeneity related to age at first reproduction and its potential correlation with survival and subsequent breeding probabilities (e.g., Fay et al., 2016; Jenouvrier et al., 2018). Mixture models identified clusters (classes) of individuals sharing values of latent traits, and allowed us to compare how demographic processes vary across clusters and relative to what we observe at the population level (Gimenez et al., 2018; Hamel et al., 2018). The *trade-off hypothesis* (Figure 1) predicted that the costs of reproduction are highest in young female elephant seals breeding for the first time, as at Macquarie Island (Desprez et al., 2014). Elephant seals are extreme capital breeders and females do not feed at all during lactation (Jönsson, 1997). Resources are typically more limiting for young breeding females because of their smaller body size and lower blubber reserves relative to older females (Postma et al., 2013a). Young female elephant seals also reproduce before completing body growth (Bell et al., 2005), constraining the energy available for somatic maintenance and growth. According to this hypothesis young first time breeders should have lower survival and subsequent breeding probabilities than those delaying reproduction to an older age because they are constrained by, for example, their smaller body size. Alternatively, the *individual quality hypothesis* (Figure 1) predicted positive covariance between early recruitment and adult performance. High-quality individuals should reproduce at an early age, survive better, and have a greater probability of breeding in subsequent years than low-quality individuals.

To complement our analyses of the direct survival and reproductive costs associated with first breeding, we investigated inter-generational costs by determining how mothers' allocation decisions could potentially influence offspring's fitness components. Specifically, we determined whether the somatic costs of breeding at the earliest possible age compromise females' body mass and their ability to allocate resources to future offspring, if they survived and bred again in the following year. The short-term somatic costs of early reproduction are potentially important for allocation to offspring, as maternal body mass is the key determinant of weaning mass (Fedak et al., 1996; Arnbom et al., 1997) and thus offspring fitness components (Oosthuizen et al., 2018) in elephant seals.

METHODS

Study species and capture recapture methods

Southern elephant seals have a synchronous annual breeding season in the austral spring (September to November) (Supporting Information 1). Breeding females have high site fidelity and dispersal of experienced breeders to other islands is highly unusual (Oosthuizen et al., 2011). Females not present at their site of first reproduction are thus unlikely to be breeding elsewhere. Breeding females stay ashore continuously for the entire period of lactation (21 to 23 days) and nearly all females present at the breeding colony give birth to a single pup. Females that are not breeding (pre-breeders and non-breeders) are typically absent during the breeding season and probably mate at sea (De Bruyn et al., 2011). All elephant seals older than pups moult ashore annually for a month or more during summer (Kirkman et al., 2003). Thus, pre-breeders and non-breeders may be observed during the obligatory moult (November to February) and reproductive skipping does not necessarily constitute temporary emigration within annual capture histories. After the moult, adult seals return to and typically remain at sea to forage, up until the next breeding season. In contrast, pre-breeders frequently haul out on land during the austral winter (March to August), often remaining ashore between two to four weeks (Kirkman et al., 2001). Seals do not consume prey while hauled out on land and rely on catabolism of blubber lipids for metabolic energy during such periods.

From 1983 to 2009, 6439 recently weaned female elephant seal pups born at Marion Island were uniquely marked with two hind-flipper tags (Pistorius et al., 2011). Tag loss are known to occur at a low rate (Oosthuizen et al., 2010), and was integrated in analysis. In total, 65602 resightings of marked female elephant seals were made between 1983 and 2014. Seals were resighted throughout all years on a weekly or 10-day cycle.

Field estimation of adult female body mass and weighing of weaned pups

From 2007 to 2013, a cross-sectional sample of female elephant seals aged 3 or 4 years were photographed at the start of the breeding season and at the beginning and end of the moult. Cross-sectional data were collected by means of random sampling: the moult arrival and departure body mass of 20 3-year old females and the breeding season arrival body mass of 30 4-year old females were estimated using three-dimensional photogrammetry (De Bruyn et al., 2009; Postma et al., 2013a; Postma et al., 2013b). The detection probability of breeding females was near perfect during these years (Results) and reproductive histories could therefore be assigned to individual females with confidence. To evaluate the somatic cost of early breeding we (1) compared the moult arrival and departure body mass of age 3 pre-breeders to the moult arrival and departure body mass of age 3 first-time breeders; and (2) compared the breeding season arrival body mass of age 4 first-time and experienced breeders.

From 2006 to 2016, some of the pups born to age 3 first-time breeders and age 4 first-time- and experienced breeders were weighed at weaning (n = 108) (for mother-pup identification methods see De Bruyn et al., 2008). Pups were rolled into a net sling and weighed using a spring scale suspended from a pole resting on the shoulders of two fieldworkers (Oosthuizen et al., 2015). Estimates of maternal body mass and pup weaning mass are independent as pups weighed were not the offspring of females included in maternal body mass analysis.

General multievent model

Individual encounter histories were modelled using multievent models (Pradel, 2005). Our general model considered 11 different states underlying 15 possible field observations. In each year, a female could occupy one of the following reproductive states: (1) pre-breeder (PB), has not previously pupped; (2) first-time breeder (FTB), pupped this year for the first time; (3) experienced breeder (EB), pupped previously and in this year; (4) non-breeder (NB), pupped previously, but not in this year. All individuals entered the marked population as pups, mostly (98%) marked with two (PB2) but occasionally only one tag (PB1) at first release. Pre-breeders could remain available for recapture (PB2, PB1), or temporarily emigrate from the study area ("alive elsewhere", states PB2_AE, PB1_AE), based on the results of a goodness-of-fit test (see below). First-time breeders (FTB2, FTB1) that survived automatically transitioned to the experienced breeder (EB2, EB1) or non-breeder (NB2, NB1) states in the next year. Lastly, an absorbing state (Dead) represents death and permanent emigration.

Encounter histories summarised multiple sightings of an individual from one breeding season to the next ($\text{September}_{(t)}$ to $\text{August}_{(t+1)}$) as a single event. The observation process combined robust design recapture data collected within each breeding season with auxiliary resightings containing state uncertainty that were made outside of the breeding season sampling period. The modelling framework is described in detail in Oosthuizen et al. (2019), but we summarize the main elements here (also see

Supporting Information 2). Briefly, we aggregated alternating secondary surveys (n = 8 weekly surveys) within each breeding season (primary period) to generate two distinct capture periods (κ) per breeding season. Surveys conducted during 'uneven' survey weeks of the breeding season collapsed to generate capture period U (κ^U), whereas surveys conducted during 'even' weeks collapsed to capture period E (κ^E). Within each breeding season, a breeding female could (1) be encountered during both capture periods U and E (UE); (2) only be encountered in κ^U (U); (3) only be encountered in κ^E (E); (4) not be encountered in either capture period (NS). All recaptures made outside of the breeding season (whether during the moult, winter or both these non-breeding periods) were summarized as a single observation and assigned to capture period M (κ^M). By pooling observations over a longer period during the interval between occasion t and $t + 1$ we underestimate recapture probability outside of the breeding season, as individuals that have died since breeding are considered alive and missed (whereas they are dead) (Oosthuizen et al. 2019). The net consequence of violating the instantaneous sampling assumption is minimal, however, given that breeding season recapture probabilities are high. In total, we defined 15 composite events (Supporting Information 2) by integrating resighting data collected for every individual during all three capture periods, and by partitioning observations according to the number of flipper tags an individual was marked with. The encounter history matrix thus simply encoded the particular combination of field observations that was made, and not the underlying state of the individual at that moment (Oosthuizen et al., 2019).

Goodness-of-fit testing (Pradel et al., 2003) suggested that the encounter histories of both pre-breeders and breeders deviated systematically from the homogeneity assumptions of the Jolly-MoVe multistate model (Supporting Information 3). We accounted for Markovian temporary emigration among pre-breeders by specifying our capture-recapture model with "observable" and "unobservable" states between which pre-breeders were allowed to move (Schaub et al., 2004). Although adult capture histories revealed similar trends, model violations were smaller in magnitude and a variance inflation factor ($\hat{c} = \chi^2/df;\ \hat{c} = 1.25$) was used in the model selection procedure to account for the remaining capture heterogeneity.

Estimation of demographic parameters

Transitions between states were modelled in five steps, with each step conditioning on preceding transitions: (1) probability to lose the first tag; (2) probability to lose the second tag; (3) apparent survival probability (hereafter survival); (4) breeding probability; and (5) temporary emigration. The observation process, which conditions on the underlying states, was described via the product of three matrices, highlighting the successive processes of detection outside of the breeding season (κ^M), and within the capture periods κ^U and κ^E of the breeding season, respectively (Supporting Information 4). Models were fitted using E-SURGE 2.1.2 (Choquet et al., 2009).

Various models with different plausible constraints on recapture, tag loss and migration parameters were considered (Supporting Information 5). Our interest was centred on life-history trade-offs with age at first reproduction, and our model set and parameter constraints reflected this aim. Survival probability (φ) was initially modelled as being dependent on reproductive state and age. We considered seven age classes for pre-breeders (0, 1, 2, 3, 4, 5, ≥ 6), four age classes for first-time breeders (3, 4, 5, ≥ 6) and three age classes for experienced- and non-breeders (4, 5, ≥ 6). The survival cost of first reproduction was estimated by comparing the survival probability of first-time breeders to that of pre-breeders and experienced breeders of the same age. The transition $\psi_i^{k \to k'}$ is the conditional probability that an individual i makes a transition between states k and $k'(k, k'$= PB, FTB, EB, NB) between occasion t and $t + 1$. Elephant seals give birth from 3 years of age, and in our dataset, it was unusual to observe pre-breeders older than age 5 (n = 35). The transition probability from pre-breeder to first-time breeder was fixed to zero at age ≤ 2, and first-time breeders could only transition to experienced- or non-breeders. Experienced- and non-breeders could not return to the pre-breeder or first-time breeder states, but could move between these two states. We included age dependence in the transitions of pre-breeders up to age class ≥ 6 and in first-time-, experienced- and non-breeders up to age class ≥ 7. Transition into the non-breeder state denotes probabilities of skipping reproduction; higher transition probabilities to the non-breeder state at $t + 1$ for individuals breeding at t relative to those that did not reproduce at t corresponds to a cost of reproduction. To prevent over-parameterization of models, we did not investigate temporal variation in survival and breeding probabilities.

Modelling individual heterogeneity

We used finite mixture models (Pledger et al., 2003; Gimenez et al. 2018) with two hidden classes of individuals to investigate individual heterogeneity and covariation between recruitment probability and adult demographic traits. Mixture models assume that populations comprise a mixture of several types of individuals, and that the demographic parameters can be described with two or more discrete distributions (Pledger & Schwarz, 2002). Mixture models with two classes are generally sufficient to account for hidden between-individual heterogeneity (Pledger & Schwarz, 2002). Transitions between classes were not considered, and thus each heterogeneity class represents fixed or hidden persistent demographic heterogeneity (i.e., permanent inter-individual differences in demographic parameters corresponding to "individual quality"; Wilson & Nussey, 2010) that we partly captured with our model through two classes (Cam et al., 2016; Authier et al., 2017). Each state of the general model was duplicated (e.g., $FTB2^A$, $FTB2^B$, $FTB1^A$, $FTB1^B$ for first-time breeders) to create two heterogeneity states (A, B) which may assume state-specific survival, breeding transition and recapture probabilities (Supporting Information 6). Individuals were not assigned *a priori* to a particular class; instead, the proportion of individuals in heterogeneity classes A and B was estimated by the model according to

their pattern of state transition. The initial state parameter π (respectively $1 - \pi$) defined the proportion of individuals in class A (respectively class B). Modelling individual heterogeneity as a latent effect allowed us to detect positive or negative covariation between survival and breeding processes at the individual level.

The most parsimonious model with no heterogeneity served as a benchmark for modelling hidden persistent demographic heterogeneity. We considered heterogeneity in survival, breeding probability and recapture probabilities in the most general heterogeneity model. We modelled both adult survival ($\varphi_{a*h}^{FTB}, \varphi_{h}^{EB}, \varphi_{h}^{NB}$) and breeding probabilities ($\psi_{a*h}^{PB,FTB}, \psi_{a*h}^{FTB,EB}, \psi_{h}^{EB,EB}, \psi_{h}^{NB,EB}$) with interactive age (a) and heterogeneity (h) effects. We assumed that each individual had an intrinsically high or low recapture probability and therefore modelled time-variation in recapture probabilities with an additive effect (on the logit scale) between the two mixture classes. Recapture probabilities of the two heterogeneity classes thus fluctuated over time in parallel.

Model selection

Model selection was based on quasi-likelihood Akaike's Information Criterion (QAIC). Akaike weights (w_i) were used to scale models and relative model support was based on differences in QAIC values (ΔQAIC). Models with ΔQAIC < 2 received approximately equivalent support from the data, but all models with ΔQAIC < 7 have some support as plausible hypotheses (Burnham & Anderson, 2002). To ensure that models converged to the lowest deviance, we used the Expectation Maximization (EM) algorithm combined with Quasi-Newton minimization methods implemented in E-SURGE (Choquet et al., 2009), and ran the same models multiple times using different randomly chosen starting values. Numerical methods implemented in E-SURGE indicated that models were not parameter redundant, and therefore at least locally identifiable (Choquet & Cole, 2012). Because of the large number of parameters involved, model selection was structured into successive steps, with each parameter initially included in the model as generally as possible. An appropriate model structure for recapture probabilities was selected first, keeping all other parameters fixed at high dimensionality. The next two steps involved modelling tag loss probabilities (τ^{21} and τ^{10}), followed by temporary emigration, survival and finally breeding probabilities, at every step retaining the most parsimonious structure for the parameter evaluated. Finally, by adding discrete classes of heterogeneity to the most parsimonious population level model selected we tested for individual heterogeneity in adult survival, breeding transitions and recapture probabilities.

Analysis of adult female body mass and pup weaning mass

We quantified somatic costs of early reproduction in three ways. First, we compared the body mass of early breeders (age 3) to pre-breeders of the same age during the moult haulout that follows first reproduction. Secondly, we compared the breeding season body mass of early breeders breeding for the second time at age 4, to same age first-time breeders. If significant somatic costs of early reproduction were carried over to the next breeding season, we expect early breeding females to have lower body mass at age 4 compared to females that were first-time breeders at age 4. Lastly, we directly quantified the potential costs of early reproduction on subsequent offspring phenotype by comparing the weaning mass of offspring born to early breeders (at age 3 and 4, i.e., at their first and second breeding attempts) to the weaning mass of offspring born to first-time breeders at age 4. Again, if early breeding had carry-over effects to the next year, we expected offspring born to age 4 first-time breeders to be heavier than those born to age 4 females that also reproduced at age 3. We tested for differences in the mean body mass of females and the weaning mass of pups as a function of female reproductive state using two-sample t-tests and analysis of variance (ANOVA) in R 3.0.2 (R Core Team, 2013). Mean body mass ± one standard deviation (SD) is given.

RESULTS

Population level demographic performance

Female elephant seal recruitment and the subsequent breeding probabilities of first-time breeders varied by age (Table 1). Overall, recruitment probability averaged 32% (95% CI: 30 – 34%) at age 3 and 67% (95% CI: 63 – 71%) at age 4 (model 10, Table 1). Few individuals delayed first reproduction to after age 4 and, at older ages, pre-breeders had lower probabilities to start breeding (Figure 2). First-time breeders had lower population level survival than pre-breeders, experienced breeders and non-breeders at all ages, indicating a direct short-term survival cost associated with breeding for the first time (Figure 3). Unexpectedly, first-time breeder survival was highest for young first-time breeders (age 3) and progressively declined with every year that recruitment was delayed (Figure 3). First-time breeders that survived to the next breeding season, in contrast, did not incur an immediate cost to future reproduction. Instead, these females were more likely to breed again than pre-breeders of similar age. For example, age 3 first-time breeders that were alive at age 4 had a more than 10% higher probability to reproduce (at age 4) compared to females that were pre-breeders at age 3 (Figure 2). Breeding probabilities in adulthood also did not point to short-term costs of current reproduction as experienced breeders (0.86 [95% CI: 0.84 – 0.88]) had distinctly higher subsequent breeding probabilities than non-breeders (0.66 [95% CI: 0.61 – 0.71]). The complete model selection results and estimates of recapture, tag loss and migration probabilities are provided online (Supporting Information 7).

Hidden persistent demographic heterogeneity

Finite mixture models provided strong evidence of individual heterogeneity in survival and reproduction that was not explained by models including only age effects and Markovian state transition probabilities (Table 2, Figure 4, Figure 5). Adding heterogeneity classes to survival and breeding parameters decreased QAIC values considerably, confirming the presence of demographic heterogeneity, provided that heterogeneity in recapture probability were also accounted for in the model (Table 2). . We found positive covariation between early recruitment probabilities and adult fitness components. On average, 35% (95% CI: 32 - 38%) of females belonged to mixture class A. Individuals from this class had low recruitment and subsequent breeding probabilities, associated with low survival probability as first-time breeders in particular. In contrast, individuals from mixture class B had high recruitment and subsequent breeding probabilities, and high survival probability, particularly as first-time breeders. Individuals from class A thus exhibited demographic rates indicative of 'low quality individuals' whereas the demographic performance of individuals from class B suggested that they perform well in terms of both survival and reproduction (i.e., 'high quality individuals'). An immediate survival cost of first reproduction was present among 'low quality individuals' only, with the majority (65%) of females in the population having high survival probability after breeding for the first time (Figure 5). Recapture probabilities during the breeding season were high for all individuals. In contrast, individuals from class A had lower recapture probabilities outside of the breeding season than those from class B (Supporting Information 8).

Adult female body mass and offspring weaning mass

Females that deferred breeding at age 3 (i.e., pre-breeders) were heavier at the start of the moult (424.07 ± 44.07 kg) than age 3 females that produced their first offspring in the preceding breeding season (379.09 ± 25.38 kg) (Welch's t-test, $t_{(14.38)} = -2.80$, $p < 0.02$). But, age 3 moulting pre-breeders commonly remained longer ashore (33.3 ± 13.4 days) than moulting females that bred at age 3 (26.4 ± 9.8 days) and the mean post-moult departure mass of age 3 pre-breeders and first-time breeders did not differ ($t_{(17.93)} = -0.58$, $p = 0.57$; Figure 6). Likewise, the breeding season arrival mass of age 4 experienced breeders was comparable to that of age 4 first-time breeders ($t_{(26)} = -0.57$, $p = 0.58$; Figure 6). A somatic cost associated with early reproduction was therefore detected at the start of the moult, but not at its end, and meaningfully, not in the subsequent breeding season.

Weaning mass differed significantly ($F_{(2,105} = 18.17$, $p < 0.001$) as a function of maternal age, but not according to reproductive experience. Post-hoc Tukey's HSD tests showed that the mean weaning mass of pups born to age 3 females (91.77 ± 14.77 kg) was significantly lower than those born to age 4 females (Figure 7). The weaning mass of pups born to experienced breeders at age 4 (109.65 ± 17.21 kg) were similar to those born to age 4 first-time breeders (108.75 ± 13.73 kg) (Figure 7).

DISCUSSION

Our results provide strong evidence for individual heterogeneity in the life-history trajectories of female elephant seals after accounting for age effects and Markovian state dependence. Life-history trajectories quantified at the population and individual level suggested that early recruitment is associated with superior demographic traits, which may correlate with individual quality. A survival cost of first reproduction was evident at the population level, as elephant seal females breeding for the first time always had lower survival probabilities than pre-breeders and experienced breeders of the same age. However, by modelling hidden persistent demographic heterogeneity with finite mixture models, we were able to statistically partition individual life-history trajectories into two classes that represent life-history tactics that differ from the mean trajectory of the population (Authier et al., 2017; Hamel et al., 2018). This partitioning enabled us to show that individual heterogeneity governs the expression of trade-offs with first reproduction in elephant seals, with an immediate survival cost of first reproduction present among 'low quality' individuals only, comprising 35% of the population (class A). The life-history trajectories of the majority (65%) of females in the population were instead characterized by a high probability of recruitment, and high survival and breeding probabilities after reproducing for the first time. This structured life-history differences among individual females from the same population would have gone undetected had we not accounted for hidden demographic heterogeneity in our analyses. Although correlative in nature, the positive covariation (instead of trade-offs) we observed between survival and breeding at the individual level in models accounting for unobserved heterogeneity is best explained by the individual quality hypothesis. Our population-level analyses, which indicated a deterioration in survival and future breeding probabilities with increasing recruitment age also fits the predictions of the individual quality hypothesis. Younger first-time breeders had the highest population level post-breeding survival rates, with progressively lower survival probability after first reproduction for females that delayed breeding. Breeding probabilities measured at the population level also indicated that younger breeders were less likely to skip reproduction in the subsequent breeding season than females that delayed breeding. Furthermore, independent measures of indirect or inter-generational costs of reproduction (adult female body mass and offspring weaning mass) suggested that breeding at an early age did not compromise the ability of females to allocate resources to offspring in the next breeding season. Individuals that begin to reproduce earlier in life are seemingly of higher inherent quality, perhaps due to genetic or ontogenetic factors such as conditions experienced during early development (Oosthuizen et al., 2018).

Recruitment age and resource acquisition

Contrary to the predictions from the trade-off hypothesis, we found that recruitment at an early age was associated with higher population level survival and subsequent breeding probabilities. An immediate survival cost of first reproduction was detected among 'low quality' individuals, but the majority of the population had positive covariation among life-history traits at the individual level. Positive correlations among fitness components, rather than trade-offs, can emerge because of within-cohort selection (Vaupel et al., 1979; Cam et al., 1998; Cam et al., 2002; Sanz-Aguilar et al., 2008) or due to individual variation in resource acquisition and/or utilization (Van Noordwijk & de Jong, 1986). Female elephant seals recruiting at a young age are not a random subgroup of the population. Age-specific recruitment probabilities are strongly affected by weaning mass, with females heavier as weaned pups more likely to start breeding at an earlier age (Oosthuizen et al., 2018). Variation in weaning mass does not translate to permanent survival differences among individuals during adulthood, but it leads to positive covariation between juvenile survival probability and breeding in early life (Oosthuizen et al., 2018). Here, we show that breeding in early life also correlates with higher first-time breeder survival and higher subsequent breeding performance compared to those that delay recruitment to older ages. Conditions that individuals experience during ontogeny may therefore contribute strongly to variation in individual quality, where individual quality represents the underlying characteristics and prospect of an individual to contribute to the evolutionary trajectory of the population (Bergeron et al., 2011).

Besides the nutritional conditions that individuals experience during ontogeny, variation in individual quality may also result from variation in foraging behaviour and uneven among-individual access to resources subsequent to weaning (Van Noordwijk & de Jong, 1986). Individual fidelity to foraging strategies, but variation across individuals, has been observed in both northern and southern elephant seals (Bradshaw et al., 2004; Robinson et al., 2012). For example, adult female southern elephant seals from the Western Antarctica Peninsula are specialised foragers (as inferred from stable isotope variability), with a rather limited individual niche width relative to the total available niche (Hückstädt et al., 2012). This suggests that individuals were exploiting different habitats and prey resources. Substantial individual variation in body condition has also been observed throughout foraging migrations of Marion Island southern elephant seals, suggesting individual heterogeneity in foraging success and energy assimilation (McIntyre et al., 2015). Similarly, Robinson et al. (2012) found that the mass gain of female northern elephant seals during post-breeding foraging migrations showed little annual variation but wide inter-individual variation. Such inter-individual differences in foraging behaviour may lead to variation in resource acquisition and allocation among individuals.

Variation in the cost of first reproduction

Life-history trade-offs with age at first reproduction are especially important in long-lived iteroparous species at the late-maturing and slow-reproducing end of the slow-fast continuum of life histories (Fay

et al., 2016). These species have high residual reproductive value at the onset of adulthood, meaning that reproductive costs leading to the death of first-time breeders are especially detrimental to fitness. This may explain why delaying reproduction beyond the age of sexual maturity is commonly observed in long-lived iteroparous species (Curio, 1983; Forslund & Pärt, 1995). Costs of reproduction are often more pronounced when environmental conditions deteriorate, such as when food resources are limited (Barbraud & Weimerskirch, 2005), under high density (Festa-Bianchet et al., 1998), harsh weather (Tavecchia et al., 2005) or in the presence of disease (Descamps et al., 2009). For elephant seals at Marion Island, population level survival costs associated with first reproduction are significantly less than that at Macquarie Island, where first-time breeders have survival probabilities that are 31%, 19% and 17% lower than that of pre-breeders at age 3-, 4- and 5, respectively (Desprez et al., 2014). The difference in reproductive costs between the Marion- and Macquarie Island populations is most pronounced among young breeders. At Macquarie Island, few females recruit at age 3 ($\psi^{PB\text{-}FTB} = 0.1$) and those that do, face large survival costs (Desprez et al., 2014). At Marion Island, recruitment probability is three times higher at age 3 ($\psi^{PB\text{-}FTB} = 0.34$) and breeding costs are low for young compared to old first-time breeders. This suggests comparatively favourable conditions for reproduction at Marion Island, perhaps related to per capita food availability in their marine habitat or because of the small population (and low density) of elephant seals that haul out to breed here. Declines of elephant seals at both Marion Island (in the south Indian Ocean) and Macquarie Island (in the south Pacific Ocean) have been attributed to decreases in food availability (McMahon et al., 2005), but while time-series data suggest continued decreases at Macquarie Island (Van den Hoff et al., 2014), seal numbers have increased in recent years at Marion Island (Pistorius et al., 2011). Temporal and spatial variation in food availability is difficult to quantify for each of these populations (Oosthuizen et al., 2015), but population sizes undoubtedly differ, with the Macquarie Island elephant seal population (~20 000 breeding females) many times larger than the Marion Island population (~550 breeding females).

An earlier study of female elephant seals at Marion Island advocated no reduced survival following breeding at any age (Pistorius et al., 2004); however, their analysis did test for reduced survival following first breeding specifically. Pistorius et al. (2008) indicated that first-time breeders had lower post-breeding survival than experienced breeders. However, Pistorius et al. (2008) ignored age effects and unobserved individual heterogeneity, and did not compare individuals that reproduced (first-time- or experienced breeders), to those that faced no costs (pre-breeders). Our results provide strong evidence of age-specific survival of first-time breeders estimated at the population level. Additionally, our analysis accounting for hidden persistent demographic heterogeneity revealed that the trade-off between first reproduction and survival was only expressed in the part of the population (35%) with demographic rates indicative of 'low quality' individuals.

Heterogeneity modelling choices and limitations

We chose finite mixture models to cluster individuals into discrete heterogeneity classes with life-history trajectories that differ from each other and the mean trajectory of the population (Authier et al., 2017; Hamel et al., 2018). We found strong model support for individual heterogeneity in demographic parameters over homogeneity (i.e., a single cluster, the population level) when heterogeneity in recapture probability was also accounted for in the model. A limitation of our modelling approach is that heterogeneity in demographic parameters, when included in the model, was linked with heterogeneity in recapture probability (i.e., individuals in mixture class A had to be in that class for the survival, breeding and recapture probability parameters). Separating heterogeneity (allowing individuals to be in mixture class A for demographic parameters and mixture class B for recapture probability, for example) would have required four hidden groups and such models are likely to present identifiability problems (Lindberg et al., 2013). We also chose not to allow individuals to transition from one heterogeneity class to another (e.g., Pradel, 2009). This is a common assumption when modelling heterogeneity with mixture models with a specific interpretation: each heterogeneity class represents fixed or hidden persistent demographic heterogeneity (Cam et al., 2016; Authier et al., 2017). Though individual improvement is not permitted in such models by allowing transition from a "low quality" to a "high quality" mixture class, improvements (or deterioration) with age is allowed within a mixture class. Our results should, however, not be interpreted as evidence of the existence of two explicit classes of individuals (Pledger et al., 2003). Rather, individual heterogeneity is a continuous latent variable that we partly captured in our model through two classes. Two heterogeneity classes are generally considered sufficient to capture hidden heterogeneity (Pledger et al., 2003; Péron et al., 2010; Lindberg et al., 2013; Fay et al., 2016; Guéry et al., 2017; Desprez et al., 2018), but more flexible mixture structures can also be modelled, and selected (e.g., three classes; Jenouvrier et al., 2018). Here, we chose to limit our investigation of individual heterogeneity to two mixtures, but acknowledge that we could also have modelled a larger (but finite) number of classes of heterogeneity, or alternatively have accounted for heterogeneity through fitting individual random effect models that consider individual heterogeneity (e.g., "frailty" in survival) as a random variable with a continuous distribution (Cam et al., 2002, Gimenez et al., 2018).

Somatic and inter-generational costs of early breeding

Mass loss during the breeding season is inherent to extreme capital breeders like elephant seals and, when taking the underlying breeding tactic into consideration, mass loss alone should not immediately be interpreted as evidence of a cost of reproduction (Moreno, 1989). Rather, to be costly, mass loss associated with reproduction must have detrimental consequences on the residual reproductive value of an individual. In breeding female elephant seals, the energetic demands of lactation is compounded by a four week fast. Pre-breeders, in contrast, do not allocate energy to offspring and forage uninterruptedly

during the breeding season to increase their blubber reserves. Breeding females only have a relatively short (eight to 10 week) post-breeding pelagic foraging trip to rebuild their fat reserves, prior to the moult. It is therefore unsurprising that females that bred at age 3 had lower body mass than same-aged pre-breeders when they returned to land to moult.

In the moult, elephant seals remain ashore without feeding. Although the shedding and replacement of hair and the top layers of the epidermis takes about four weeks to complete, some individuals stay ashore several weeks after completing the moult (Ling & Bryden, 1981). The ability to fast is determined by a seal's available energy stores, which is directly related to total body fat. The duration of the adult female (breeder) moult haulout is the shortest of any age/sex class (Ling & Bryden, 1981), reflecting the limited ability of breeding females to rebuild energetic reserves during the relatively short foraging phase between breeding and moulting. At Marion Island, moulting 3-year old pre-breeders typically remain ashore one week longer than same aged females that bred in the preceding breeding season (MRI unpublished data, 1986 - 2013). The longer moult haulout of pre-breeders reflects their larger energy stores at the start of the moult, and contributes to the similarity of departure body mass of pre-breeders and first-time breeders at the end of the moult. Moulting females therefore appear to remain ashore until they reach an energetic or body mass 'threshold', at which point they return to sea.

Age 4 experienced breeders had comparable body mass to age 4 first-time breeders at the start of a breeding season, despite the major somatic cost incurred by the former when breeding at age 3. Thus, while females breeding at age 3 were not able to acquire sufficient energy resources prior to the moult to fully recover body mass from the breeding effort, we detected no carry-over effect on body mass of females that survived to the subsequent breeding season. This is important, given that most of the variation in weaning mass of elephant seal pups derives directly from variation in maternal body mass (Fedak et al., 1996; Arnbom et al., 1997; Postma et al., 2013a) and because weaning mass significantly correlates with juvenile survival and female recruitment age in elephant seals (McMahon et al., 2000; Oosthuizen et al., 2018). Our sample size for female body mass was small, but the larger sample of offspring weaning mass independently confirmed that early reproduction did not affect the ability of females to allocate resources to offspring in the next year.

Although we detected no difference in the breeding season arrival body mass of age 4 experienced breeders compared to age 4 first-time breeders, these comparisons strictly refer to surviving females, and do not necessarily mean that somatic costs play no role in reproductive costs of elephant seals. Young females in particular are energy-deprived when their pups are weaned (Fedak et al., 1996; Postma et al., 2013a). Mortality risk during the post-breeding foraging migration exceeds that of the post-moult foraging migration (Pistorius et al., 2008), and part of this mortality may be linked to the extreme reduction in body mass during the breeding season. Survival costs associated with reproduction

may thus be partially attributed to a failure to recuperate depleted energy reserves. The risks associated with body mass loss are not restricted to mortality. In mammals, conception is generally dependent on body condition (e.g., Cameron et al., 1993). The occurrence of pregnancy in pinniped capital breeders is especially sensitive to body reserves (Boyd, 2000) and the somatic cost of current reproduction could therefore contribute to lower breeding probabilities at $t + 1$. We did not find any evidence for such a reduction in breeding probabilities of either first-time breeders or experienced breeders.

CONCLUSION

We tested for evidence of intra- and inter-generational trade-offs and individual heterogeneity relating to age at first reproduction using multi-decadal data on individually marked female southern elephant seals. Our rigorous multi-model approach allowed us to directly compare models that included age effects, Markovian state dependence and persistent demographic heterogeneity in survival and reproduction to those that did not. We found that individual heterogeneity governs the expression of trade-offs with first reproduction in elephant seals, with an immediate survival cost of first reproduction present among 'low quality' individuals only. Although we cannot exclude long-term costs of early reproduction, our study suggests that fixed individual differences may be an important factor explaining variations in recruitment age and positive covariation among demographic traits subsequent to first reproduction. Elephant seals at Marion Island display comparatively limited flexibility in age at first reproduction, with recruitment essentially occurring between the ages of 3 to 6 in this population. This narrow window contrasts strongly with flexibility (age 4 to 16 years) in the age at first reproduction in another large phocid, the Weddell seal (*Leptonychotes weddellii*) (Paterson et al., 2018). Nonetheless, plasticity in age at first reproduction permits individuals of long-lived species to delay reproduction until sufficient somatic development allows them to at least partially mitigate costs of reproduction (Descamps et al., 2006; Paterson et al., 2018). Female elephant seals recruiting at a young age are not a random subgroup of the population, but mostly those that experienced favourable conditions during early development (Oosthuizen et al., 2018). Our finding that individuals that recruit earlier in life survive and reproduce better than delayed breeders supports the hypothesis that recruitment age is an indicator or proxy of individual quality (Fay et al., 2016; Paterson et al., 2018).

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Ethical approval

All applicable institutional and/or national guidelines for the care and use of animals were followed. All protocols were approved by the Animal Ethics Committee of the Faculty of Veterinary Science, University of Pretoria, South Africa.

Conflict of Interest

None declared.

Author Contributions

WCO originally formulated the idea with input from RA, MN, MNB and PJNdB. WCO analysed the data with input from RP and wrote the manuscript. MP conducted photogrammetric estimation. All authors provided intellectual and editorial advice.

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TABLE 1 Candidate models representing hypotheses of the costs of first reproduction in southern elephant seals at Marion Island. The parameters of the model are tag loss (τ^{21} and τ^{10}), survival (φ), breeding (ψ), migration ($\psi^{OU,UO}$) and recapture (p_{κ^M} and $p_{\kappa^{U,E}}$). The effects of time (t), age (a), position of flipper tag (g) and reproductive state (PB, FTB, EB, NB) were considered. Numerical superscripts indicate variation in specific age classes. The structure of the umbrella model (model 1) was:

$\tau^{21}.g.a^{0,1-4,\geq 5}\ \tau^{10}.g\ \varphi^{PB,FTB,EB,NB}.a\ \psi^{PB\rightarrow FTB}.a\ \psi^{FTB\rightarrow EB}.a\ \ \psi^{EB\leftrightarrow NB}.a\ \ \psi^{OU,UO}a^{0,1,2,>3}$
$p_{\kappa^M}.t^{PB,FTB=EB,NB}\ \ p_{\kappa^{U,E}}.t^{FTB=EB}$. The number of parameters (np), model deviance, ΔQAICc and the QAICc weight (w_i; the relative support by the data of a model, in relation to the other models), are given. Models in bold font were selected.

Model	Assumption of model	np	Deviance	Δ QAICc	w_i
Survival (φ)					
1	$\varphi^{PB,FTB,EB,NB}.a$	187	59653.81	8.37	0.01
2	$\varphi^{PB,FTB=EB,NB}.a$	184	59706.98	44.90	0.00
3	$\varphi^{PB,FTB=EB=NB}.a$	181	59711.67	42.66	0.00
4	$\boldsymbol{\varphi^{PB,FTB}.a\ \varphi^{EB,NB}}$	**183**	**59659.95**	**5.28**	**0.06**
5	$\varphi^{PB}.a\ \varphi^{FTB,EB,NB}$	180	59691.05	24.16	0.00
6	$\varphi^{PB}.a\ \varphi^{FTB=EB=NB}$	178	59713.03	37.74	0.00
7	$\varphi.a$	177	59723.38	44.03	0.00
Transition between reproductive states ($\psi^{k,k'}$)					
8	$\psi^{PB\rightarrow FTB}.a\ \psi^{FTB\rightarrow EB}.\ \ \psi^{EB\leftrightarrow NB}.a$	180	59673.19	9.88	0.01
9	$\psi^{PB\rightarrow FTB}.a\ \psi^{FTB\rightarrow EB=EB\rightarrow EB}.a\ \psi^{NB}.a$	180	59669.06	6.57	0.03
10	$\boldsymbol{\psi^{PB\rightarrow FTB}.a\ \psi^{FTB\rightarrow EB}.a\ \psi^{EB\leftrightarrow NB}}$	**179**	**59663.35**	**0.00**	**0.87**
11	$\psi^{PB\rightarrow FTB}.\ \ \psi^{FTB\rightarrow EB}.\ \ \psi^{EB\leftrightarrow NB}.a$	177	59918.34	199.99	0.00

TABLE 2 Modelling individual heterogeneity (*h*) in female southern elephant seal survival, breeding, and recapture probabilities with two-class finite mixture models. Model H1 is the most parsimonious model without heterogeneity (model 10, Table 1). The structure of this model was $\varphi^{PB,FTB}.a\ \varphi^{EB,NB}$ for survival, $\psi^{PB\rightarrow FTB}.a\ \psi^{FTB\rightarrow EB}.a\ \psi^{EB\leftrightarrow NB}$ for breeding and $p_{\kappa^M}.t^{PB,FTB=EB,NB}$ $p_{\kappa^{U,E}}.t^{FTB=EB}$ for recapture probabilities. The number of parameters (np), model deviance, ΔQAICc and the QAICc weight (w_i; the relative support by the data of a model, in relation to the other models), are given. The model in bold font was selected.

	Model	np	Deviance	Δ QAICc	w_i
H1	$\varphi.\ \psi.\ p.$	179	59663.23	1140.33	0.00
H2	$\varphi^h\ \psi.\ p.$	185	59659.84	1149.62	0.00
H3	$\varphi.\ \psi^h\ p.$	190	59643.56	1146.60	0.00
H4	$\varphi.\ \psi.\ p^h$	185	58593.15	296.27	0.00
H5	$\varphi^h\ \psi^h\ p.$	193	59637.30	1147.59	0.00
H6	$\varphi^h\ \psi.\ p^h$	191	58399.76	153.56	0.00
H7	$\varphi.\ \psi^h\ p^h$	195	58264.13	53.05	0.00
H8	$\boldsymbol{\varphi^h\ \psi^h\ p^h}$	**201**	**58182.81**	**0.00**	**1.00**

FIGURES

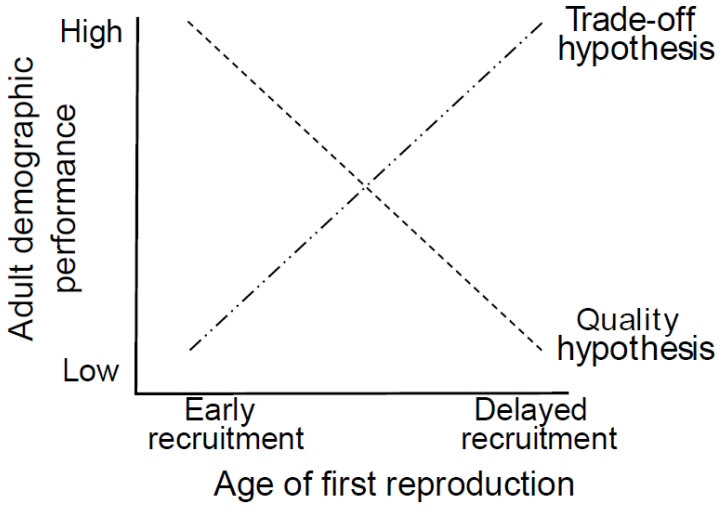

FIGURE 1 Variation in adult demographic performance (e.g., survival and breeding probability) as a function of age of first reproduction as predicted by the trade-off hypothesis and the individual quality hypothesis, respectively

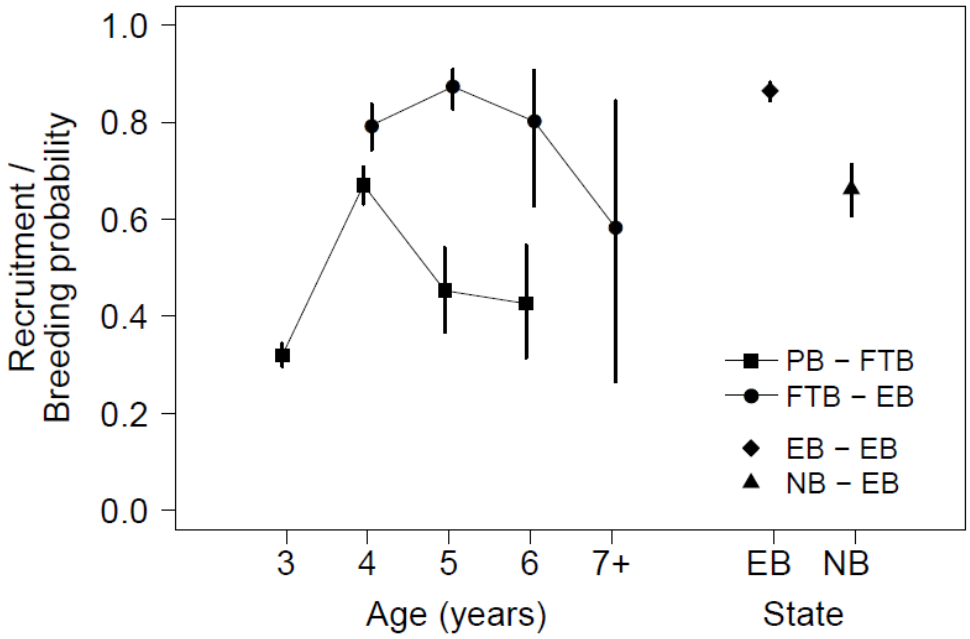

FIGURE 2 Age- and state-specific probability of breeding in year $t + 1$ given that an individual was a pre-breeder (PB), first-time breeder (FTB), experienced breeder (EB) or non-breeder (NB) in year t for southern elephant seals at Marion Island (1986 to 2013). Black squares represent recruitment probabilities (the probability to breed for the first time). Population level mean estimates and 95% confidence intervals were derived from model 10 (Table 1)

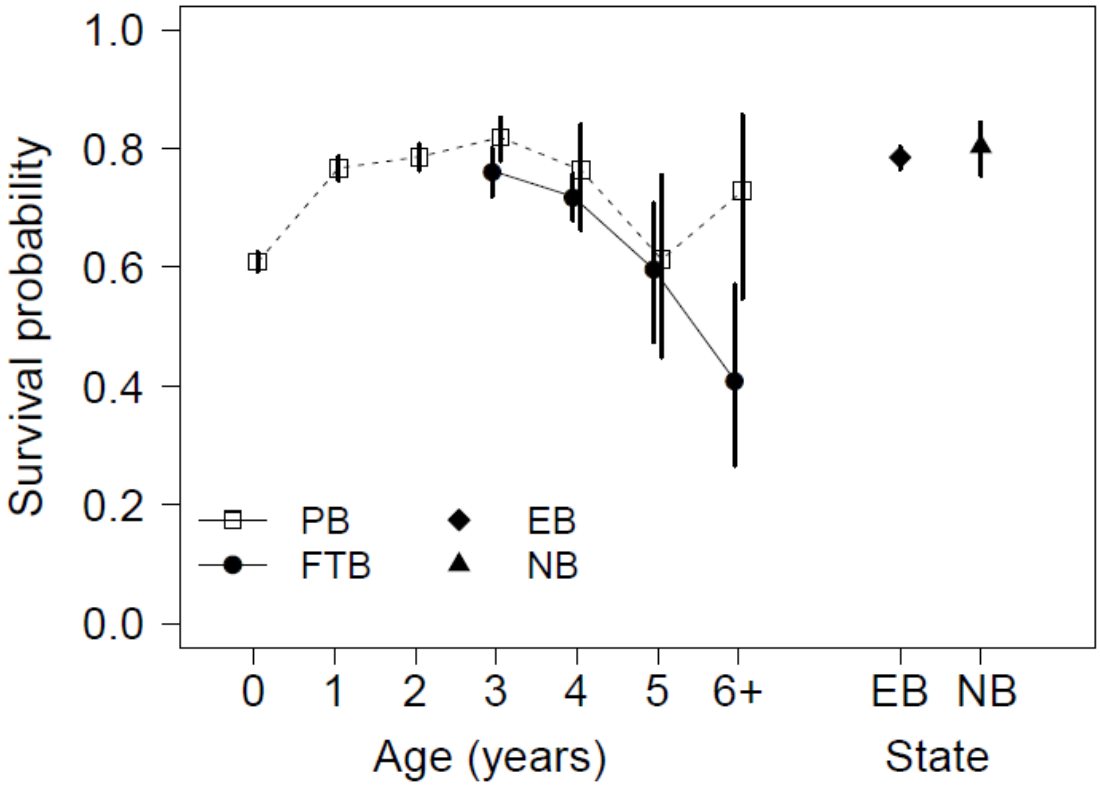

FIGURE 3 Age- and state-specific survival probabilities ($\varphi_{t,t+1}$) and 95% confidence intervals of pre-breeder (PB), first-time breeder (FTB), experienced breeder (EB) and non-breeder (NB) female southern elephant seals at Marion Island (1984 to 2013). Population level mean estimates and 95% confidence intervals were derived from model 10 (Table 1). Parameters are indexed based on the age a ($a = 0, 1, 2, ... \geq 6$) of individuals at time t

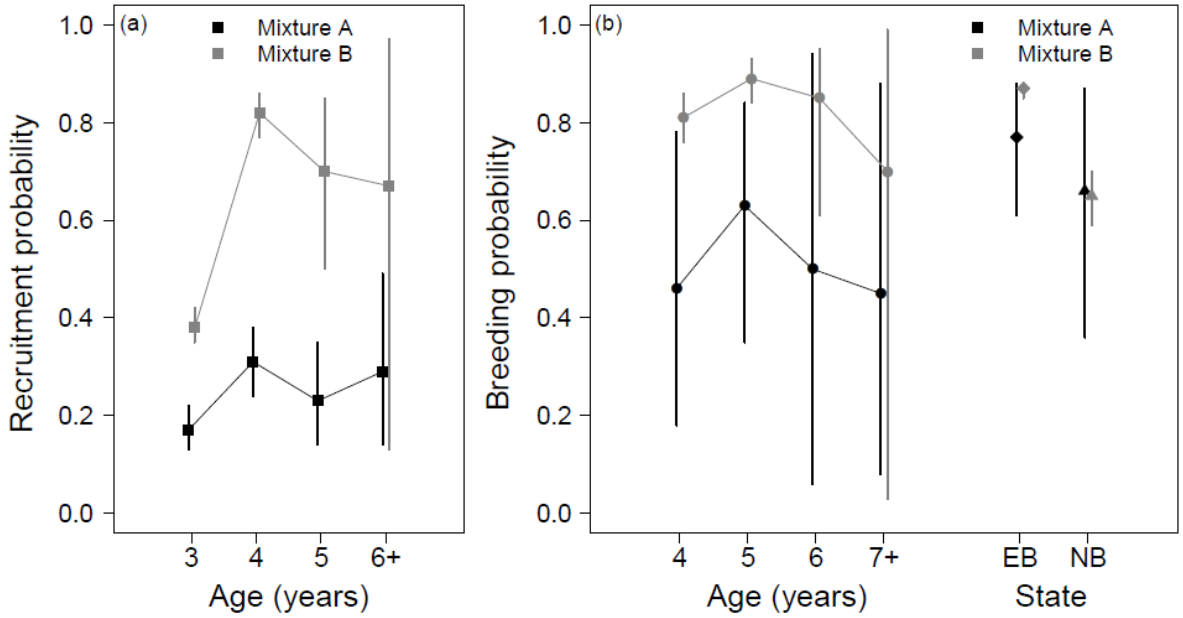

FIGURE 4 Mean estimates and 95% confidence intervals of recruitment and breeding probabilities for female southern elephant seals at Marion Island (1986 to 2013) in relation to age, reproductive state, and the two heterogeneity groups selected by mixture model analyses (model H8, Table 2). Each heterogeneity group is represented by a different colour; on both panels individuals included in mixture A is represented by black points, those in mixture B by grey points. PB, Prebreeder; FTB, first-timebreeder; EB, experienced breeder; NB, nonbreeder.

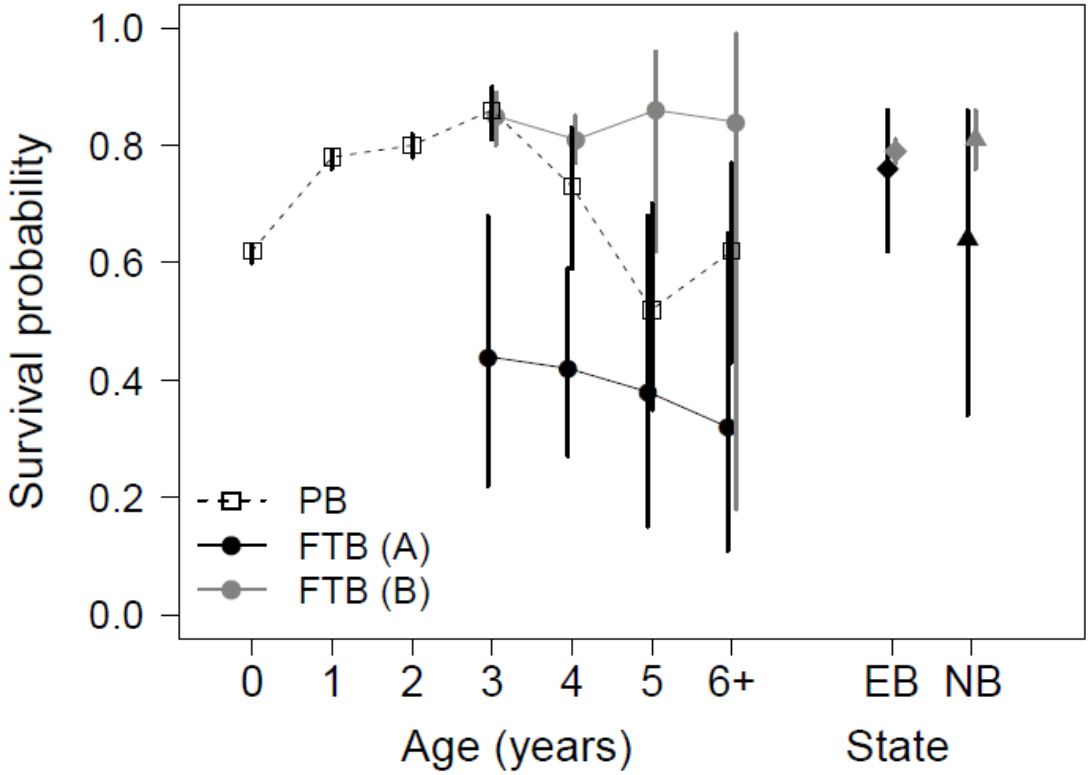

FIGURE 5 Mean estimates and 95% confidence intervals of survival probabilities ($\varphi_{t,t+1}$) for female southern elephant seals at Marion Island (1984 to 2013) in relation to age, reproductive state, and the two heterogeneity groups selected by mixture model analyses (model H8, Table 2). Each heterogeneity group is represented by a different colour; as in Figure 4, individuals included in mixture A are represented by black points, those in mixture B by grey points. Pre-breeder survival did not include heterogeneity

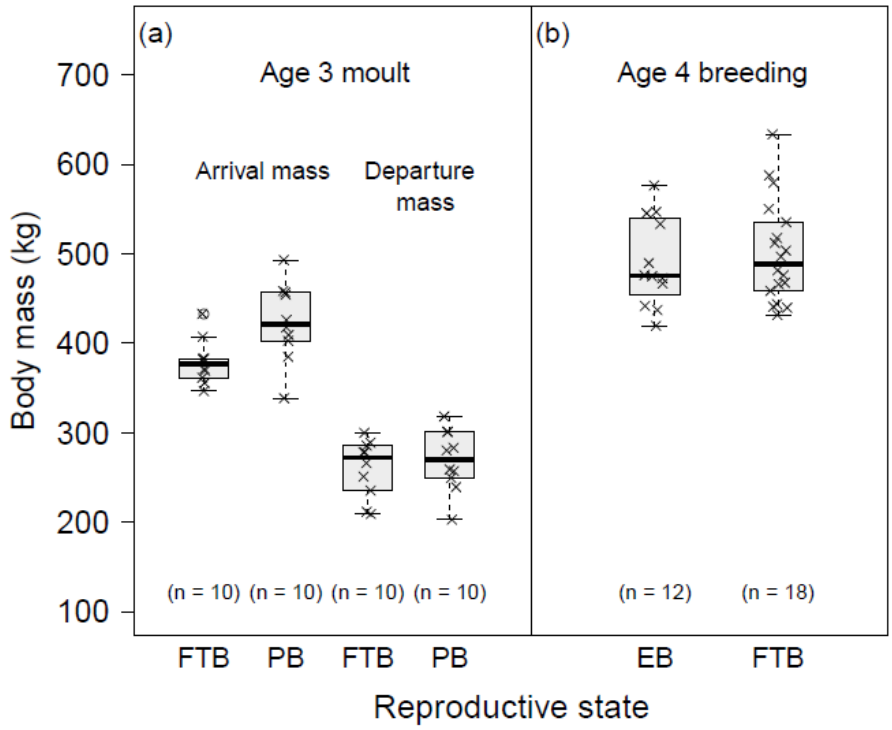

FIGURE 6 Variation in body mass as a function of reproductive state for female southern elephant seals at Marion Island. (a) The moult arrival and departure body mass of age 3 females that were first-time breeders (FTB) in the preceding breeding season is compared to the body mass of pre-breeders (PB) (i.e., individuals that deferred breeding at age 3). (b) The breeding season arrival body mass of age 4 experienced breeders (EB, i.e., females that were FTB at age 3) relative to age 4 females with no previous breeding experience (FTB). Horizontal boxplot lines show the median mass and boxes represent the 25th and 75th percentiles, respectively. Individual observations (×) are superimposed on boxplots

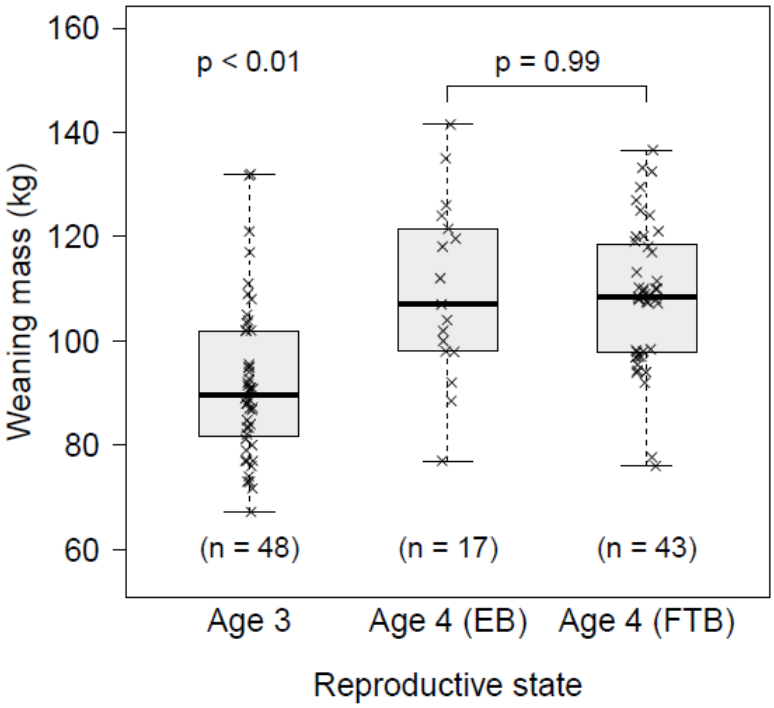

FIGURE 7 Southern elephant seal offspring weaning mass as a function of maternal age and reproductive state. All females breeding at age 3 are first-time breeders (FTB). Weaning mass did not differ between females that were experienced breeders at age 4 (EB) and those that were first-time breeders at age 4 (FTB). Individual observations (×) are superimposed on boxplots