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Positive early-late life-history trait correlations in elephant seals

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Abstract

Correlations between early- and late-life performance are a major prediction of life-history theory. Negative early-late correlations can emerge because biological processes are optimized for early but not late life (e.g., rapid development may accelerate the onset of senescence; “developmental theory of ageing”) or because allocation to early life performance comes at a cost in terms of late-life performance (as in the disposable soma theory). But, variation in genetic and environmental challenges that each individual has to cope with during early life may also lead to positive early-late life-history trait correlations (the “fixed heterogeneity” or “individual quality” hypothesis). We analyzed individual life-history trajectories of 7,420 known-age female southern elephant seals (Mirounga leonina) monitored over 36 years to determine how actuarial senescence (a proxy for late-life performance) correlate with age at first reproduction (a proxy for early-life performance). As some breeding events may not be detected in this field study, we used a custom “multievent” hierarchical model to estimate the age at first reproduction and correlate it to other life-history traits. The probability of first reproduction was 0.34 at age 3, with most females breeding for the first time at age 4, and comparatively few at older ages. Females with an early age of first reproduction outperformed delayed breeders in all aspects we considered (survival, rate of senescence, net reproductive output) but one: early breeders appeared to have an onset of actuarial senescence one year earlier compared to late breeders. Genetics and environmental conditions during early-life likely explain the positive correlation between early- and late-life performance. Our results provide the first evidence of actuarial senescence in female southern elephant seals.

Key-words: actuarial senescence, age at first reproduction, breeding age, imperfect detection, theory of ageing, hidden Markov model, life-history covariation, Mirounga leonina

Introduction

Covariation among life-history traits is integral to the evolution of life-history tactics and a central tenet of life-history theory (Cam et al. 2002, Hamel et al. 2010). Negative correlations between two or more life-history trais may emerge from pleiotropic effects (negative genetic correlation) or physiological constraints that manifest as trade-offs within individuals (Stearns 1992). According to the principle of energy allocation, trade-offs arise because all individuals are constrained by limited resources (e.g., time, energy) and because allocation of limited resources to one life-history trait reduces the amount of resources available to other traits (Williams 1966, van Noordwijk and de Jong 1986). Trade-offs involving phenotypic traits therefore pivot around the question of how limited resources should be divided between fitness components such as reproduction, survival, growth and somatic maintenance, and include life-history problems such as the compromise between offspring quantity and quality, costs of reproduction (the trade-off between current and future reproduction) and senescence (the trade-off between early- and late-life performance) (Stearns 1992).

Individual fitness components may, however, also show positive correlations between traits that are expected to face trade-offs (Cam et al. 2002, Hamel et al. 2010). Positive correlations among individual fitness components such as survival and reproduction indicate that some individuals exhibit both high survival and high reproductive probabilities at the phenotypic level. Positive life-history covariation can emerge from positive pleiotropy (Maklakov et al. 2015), or because physiological trade-offs are masked at the population level by within-cohort selection (Vaupel et al. 1979, Cam et al. 2002) or between-individual variation in resource acquisition and/or utilization (van Noordwijk and de Jong 1986, Hamel et al. 2010). How much resources can be acquired and allocated to life-history traits often differs between individuals because of genetic variation (van Noordwijk and de Jong 1986), physiological variation (Pryke et al. 2012), behavioral differences (e.g., diet, Authier et al. 2012), and variations in past or present environmental conditions experienced (Herfindal et al. 2015). Positive correlations among life-history traits across individuals may thus be common in populations that inhabit environments with heterogeneous resource availability.

Negative or positive life-history correlations occur over a range of time scales. For example, life-history tactics involving the compromise between offspring quantity and quality can occur during the same breeding season. In contrast, the correlation between individual survival and reproduction is frequently studied at annual time scales, where the life-history state in year t + 1 depends on the state at t (Cam et al. 2016). Finally, between-trait correlations can occur over much longer time

scales, such as the lifetime of an individual or even across generations (Reid et al. 2010, Gamelon et al. 2013, Herfindal et al. 2015). Conditions experienced early in life often contribute to positive covariation among early-life and later-life traits (Reid et al. 2003, van de Pol et al. 2006, Cam and Aubry 2011). In this case, individuals with a better start to life (a “silver spoon”, Grafen 1988) perform better on average, leading to persistent fitness differences among individuals (“fixed heterogeneity”, Cam et al. 2016). But, individuals experiencing favorable early life conditions cannot always maintain higher-than-average survival and reproductive rates over their lifetimes; early-late life trait correlations are thus not always positive (Paterson et al. 2018, Spagopoulou et al. 2020). Senescence (age-related declines in fitness components) stems from a weakening in the strength of natural selection with age (Medawar 1952, Hamilton 1966, Maklakov and Chapman 2019) and predicts negative early-late correlations because biological processes are optimized for early but not late life (e.g., rapid development may accelerate the onset of senescence; “developmental theory of ageing”) or because allocation to early life performance comes at a cost in terms of late-life performance (as in the disposable soma theory) (Williams 1957, Hamilton 1966, Kirkwood 1977).

It is important to understand the type of covariation among life-history traits to assess its consequences for life-history evolution and population dynamics. Studies of wild animal populations provide empirical support for both positive and negative early-late life-history correlations (Jones et al. 2014, Lemaître et al. 2015, Rodríguez-Muñoz et al. 2018). However, investigating early-late life correlations is challenging in wild populations, as individual life-histories are often only partially observed. Imperfect detection introduces uncertainty about true life-history trajectories, which may bias inference about life-history evolution if ignored (Gimenez et al. 2008). It thus remains a challenge to extend investigations about early-late life-history correlations to natural populations that are difficult to monitor in great detail. This is an important hurdle to overcome, as covariation among life-history traits may vary with life speed, phylogeny, or environmental influences (Hamel et al. 2010, Jones et al. 2014).

In this paper, we use multievent models to improve inference on early-late life-history correlations in the wild that are based on incomplete observational data. Using more than three decades of capture-recapture data on individual life-histories, we study early-late life-history correlations in female southern elephant seals (Mirounga leonina; hereafter elephant seals) at Marion Island in the Southern Ocean. Specifically, we test whether the onset and rate of actuarial senescence differ between early breeding female elephant seals and those with delayed ages of first reproduction. We formulate testable predictions based on life-history hypotheses proposed to explain negative and positive early-late life covariation in long-lived species. Firstly, under the early-late trade-off hypothesis, we expect that females with an early age of first reproduction should experience an earlier onset of actuarial senescence, or senesce at a faster age-specific rate, than delayed breeders. Age at first reproduction serves as a proxy of rapid development, as individuals with faster growth rates attain adult body sizes earlier, enabling them to reproduce at an earlier age (Laws 1956,

Gaillard and Lemaître 2017). Empirical evidence shows that such trade-offs occur across vertebrate populations (Lemaître et al. 2015). Our alternative hypothesis is that age of first reproduction is a proxy for “fixed heterogeneity” or “individual quality” (i.e., the genetic and environmental challenges that an individual was facing in early life, with favorable conditions potentially leading to “silver spoon” effects). In this case we expect that an early age of first reproduction should correlate positively with late-life survival and estimates of life-time reproductive output (i.e., that females with an early age of first reproduction should have a later onset of actuarial senescence, or senesce at a slower age-specific rate, than delayed breeders).

Methods

Study species and data collection

Southern elephant seals are large, capital breeding marine predators inhabiting the Southern Ocean. They have a synchronous annual breeding season in the austral spring (Appendix S1). Pregnant females haul out at Subantarctic breeding sites from mid‐September to late October, giving birth to a single pup soon after arrival at the colony. Females return to breeding colonies from the age of 3 years to give birth, but most first give birth at age 4 or later. The age of first reproduction correlates with early life conditions experienced by females, with favorable early life conditions (measured as body mass at weaning) enabling earlier reproduction (Oosthuizen et al. 2018). Breeding females remain ashore for the entire lactation period. They rely on catabolism of blubber lipids for metabolic energy, and lose around 8 kg per day during 23 days of lactation (Postma et al. 2013). The females are often noticeably emaciated when they return to sea, 28 days after first coming ashore. All breeding females have returned to sea by mid‐November. After breeding, females forage at sea for approximately 10 weeks, then return to land for a month or more to molt (Kirkman et al. 2003). After the molt, which is a compulsory annual event for all seals, adult seals typically return to and remain at sea until the next breeding season. Juvenile females do not attend breeding aggregations. Instead, they frequently return to land for short periods during the austral winter, in addition to the annual molt (Appendix S1).

We analyzed long-term capture-recapture data on female elephant seals collected at Marion Island in the southern Indian Ocean (Bester et al. 2011, Pistorius et al. 2011). From 1983 to 2013, nearly all elephant seal pups born here and alive at weaning were marked with two hind-flipper tags. We

analyzed data from 7,420 marked females encountered 71,287 times throughout the course of each year from 1983 to 2019 (Appendix S2). The flipper tags that give every individual a unique identity are sometimes lost as seals age (Oosthuizen et al. 2010). The loss of two tags presents a problem to estimating survival, as it mimics death because we then have no way to identify the individual anymore. We therefore incorporated tag loss parameters within the analysis (see below) to provide estimates of survival that are corrected for flipper tag loss.

Multievent model

Multievent models or hidden Markov chain capture-recapture models are a generalization of multistate capture-recapture models that deal not only with imperfect detection of individuals, but also with uncertain state assignment upon detection (Pradel 2005). Such models have been widely applied to analyze individual-based datasets to deal with, for example, breeding state uncertainty (Lorentzen et al. 2012, Barbraud and Weimerskirch 2012, Desprez et al. 2018). In our study, we used the states of multievent models to encode the age of first reproduction within the state process of the model. Thus, rather than using a group covariate to represent the age of first reproduction, we used the states of the model to distinguish between age 3 first-time breeders, age 4 first-time breeders, and all the individuals that started to breed at 5 year-old or later. We refer to the age of first reproduction as the age when a female elephant seal first gives birth (conception occurs approximately one year earlier).

The model featured 14 states plus the “dead” state and included the following main reproductive classes: pre-breeders (females that have not yet started to breed), first-time breeders, and experienced breeders (females that have reproduced at an earlier time). The model states were: pre-breeder (PB); age 3 first-time breeder (FTB3); age 4 first-time breeder (FTB4); age ≥5 first-time breeder (FTB5); age 3 first-time breeder as an experienced breeder (EB3), age 4 first-time breeder as an experienced breeder (EB4); and age ≥5 first-time breeder as an experienced breeder (EB5) (Fig. 1). The age of first reproduction is therefore encoded in the state that an individual occupies, irrespective of whether it is a first-time breeder or an experienced breeder. Each of these seven states (Fig. 1) : firstly coding for seals marked with two flipper tags, and secondly representing seals marked with one remaining flipper tag. Individuals that died, emigrated from the study area, or lost both flipper tags permanently entered the final (fifteenth) “dead” state (†) (Fig. 2).

All individuals entered the study population as weaned pups (i.e., age 0 in the pre-breeder state) and nearly all (> 98%) were marked with two tags at the first encounter. Subsequently, individuals moved between states according to a first-order Markov chain. The state process was described by transition matrices for tag loss, survival and breeding probability, with departure states in rows and arrival states in columns (Fig. 2). In practice, individuals were not assigned a priori to a particular state. Instead, the states were assigned by fitting the model to the data via an observation process. The observation process considered a probabilistic relationship between the states of the model and the field observations that were summarized in an encounter history matrix (Gimenez et al. 2012). The model fitting procedure therefore estimated the most likely age of first reproduction for each individual based on the individual's capture-recapture history (Péron et al. 2010a). In this study the observation process combined sighting data collected within each breeding season with auxiliary observations that were made outside of breeding seasons (Oosthuizen et al. 2019a, Appendix S3). We fitted the model to the data in a frequentist framework using the software E-SURGE 2.1.2 (Choquet et al. 2009). Matrices of state transitions and the observation process are given in Appendix S4; detailed model fitting instructions in Appendix S5.

Testing early-late correlations in elephant seals

Although evolutionary theory predicts that senescence begins at first reproduction, analyses of the demographic trajectories of a wide range of organisms indicate that the onset of senescence often only becomes apparent later in life (Péron et al. 2010b). To estimate this age at the onset of senescence, we modelled survival as a function of age using regression spline functions with two knots (Crainiceanu et al. 2005, Appendix S6). Our use of regression splines is equivalent to that of Jones et al. (2008) and Lemaître et al. (2013) who used generalized additive models to estimate the age at onset of senescence in terrestrial vertebrates. However, our framework also deals with imperfect detection, whereas these authors relied on longevity datasets that did not feature missing observations. Importantly, regression splines were only used to estimate the age at the onset of senescence; their nonlinear slopes were not used to make inference about senescence rate. The age at which survival started to decrease was delineated in two ways. First, we took the age following the peak value of survival as estimated by the penalized spline model as the onset of senescence (Jones et al. 2008, Lemaître et al. 2013). Second, we accommodated the fact that the decrease in survival after the peak is typically negligible for several years, i.e., during a "prime-age stage" during which survival does not decrease decidedly with increasing age (Péron et al. 2019). To identify the upper-limit of prime-age survival we fitted piecewise-regression models to capture-recapture survival estimates to test for the existence of breakpoints in the survival data. Breakpoints represent the threshold value where two linear regressions with different slopes meet. The age at onset of senescence was then defined as the breakpoint age after which survival started to decline. Piecewise-regression models were fitted using the segmented package (Muggeo 2008) in R 3.6.1 (R

Core Team 2019). To estimate the rate of actuarial senescence after the onset, we used the logit-linear slope of the regression of survival against age. This model of senescence is empirically very close to the classical Gompertz model of ageing (Gaillard et al. 2004). We chose this metric of the rate of senescence instead of the rate computed by the spline regression models to facilitate comparisons between the different states of our model, and with other senescence estimates from the literature.

We always estimated the survival probability of first-time breeders separately from that of experienced breeders. First-time breeders are especially vulnerable to short-term reproductive costs (Desprez et al. 2014) and are thus expected to have a lower survival probability than experienced breeders of the same age. For the survival probabilities of experienced breeders, the most general model ("umbrella model") included the interaction between the current age x and the age of first reproduction A. Thereby we estimated age-specific survival probability as a function of the age of first reproduction. Because of the sparseness of data at old ages (nine individuals were observed at age ≥ 21, four at age ≥ 22 and none was seen after age 25) we specified a terminal age-class for all seals aged 22 years and older. We used results previously obtained from the same population to guide model specification of tag loss, breeding and capture probabilities (Appendix S7). We compared the fit of the umbrella model against the fit of simpler, nested models using the quasi-likelihood Akaike's Information Criterion (QAICc), which ranks models based on parsimony (Burnham and Anderson 2002). QAICc, rather than AICc, was used for model selection to appropriately reflect a minor degree of overdispersion (= 1.29) in the observational data (Appendix S8). We estimated the probability of each model (), given the data and the model set, as a measure of strength of evidence. The ratios of any two model probabilities represent an "evidence ratio" as a measure of the relative empirical support for each model (Burnham and Anderson 2002).

When individuals vary in their baseline survival probability, the proportion of individuals with high survival probabilities increases with age within each cohort. This effect may counteract the influence of actuarial senescence, given that age-specific survival is averaged over the remaining individuals in the population ("heterogeneity's ruse"; Vaupel and Yashin 1985). We used finite mixture models (Pledger et al. 2003) to determine whether hidden individual heterogeneity had marked influence on our estimates of actuarial senescence (Péron et al. 2010a). We applied the heterogeneity model structure onto the best supported survival models from every section of the analysis (Appendix S10).

Age-specific net reproductive rates

To assess the relative contribution of individuals with different life-history trajectories to population growth, we calculated net reproductive rates () for each age of first reproduction as an integrated measure of fitness. For each age of first reproduction A, we calculated age-specific net reproductive rates, i.e., the mean number of offspring which an individual of age is expected to produce from age until death (Caswell 2001). We used mean survival probabilities from the best supported multievent model to calculate age-specific from matrix population models fitted using the popbio R package (v 2.4.4, Stubben and Milligan 2007) and assuming annual breeding after the age of first reproduction. Parametric bootstrap methods (10,000 iterations with random survival probabilities drawn from a normal distribution with mean and variance equal to the observed values) were used to calculate 95% confidence intervals (CI) for. The fitness cost of actuarial senescence was estimated for each age of first reproduction as, where is the observed mean at the onset of senescence and is the hypothetical mean given the absence of actuarial senescence. To calculate we assumed that the survival probability remained constant throughout the experienced breeder state (Bouwhuis et al. 2012, Zhang et al. 2015).

Results

The mean recruitment probability (probability of first reproduction) of female elephant seals was 0.34 (95% CI: 0.32 - 0.37) at age 3, 0.73 (0.70 - 0.76) at age 4, and 0.48 (0.42 - 0.54) at age ≥5. The probability of first reproduction at age 3 and 4 varied over time, generally being lower during the initial years of the study (Appendix S11).

Onset of senescence

Spline regression models indicated that the age at onset of senescence was delayed past the age of first reproduction (Table 1). According to these models survival peaked at age 12 for females in the EB3 state (“early recruits”; 3 years old at first reproduction) and at age 9 for those in the EB4 and EB5 states (“delayed recruits”; 4 years and older at first reproduction) (Appendix S12). Piecewise-

regression models indicated that the prime-age stage of survival lasted until age 17 (95% CI: age 16 – 17) for early recruits (EB3) and age 18 (95% CI: age 17 – 18) for delayed recruits (EB4 and EB5) (Fig. 3). Therefore, piecewise-regression results indicated that the onset of senescence was one year earlier in females with an early age of first reproduction than in those that delayed breeding.

The rate of actuarial senescence

The model with the lowest QAICc score treated age-variation in pre-breeder and first-time breeder survival as fixed effects, and the survival of experienced breeding females as a continuous function with a breakpoint allowing for senescence in survival probability (Fig. 3). Competing models with similar support from the data assumed that survival did not vary by recruitment age (ΔQAICc = 1.54) or assumed no age effects among experienced breeders in the presence of recruitment age affects (ΔQAICc = 1.16) (full details in Appendix S13). Though no single model was clearly supported by the data, the joint empirical support for a significant correlation between the age of first reproduction and long-term survival was more than three times that that of the null model of state-constant experienced breeder survival (evidence ratio: 0.78/0.22). The joint model support for the occurrence of actuarial senescence was twice that of the null hypothesis of age-independent experienced breeder survival (evidence ratio: 0.63/0.29). Incorporating individual heterogeneity did not improve model parsimony (ΔQAICc > 6.60, Table 1; Appendix S14), indicating that "heterogeneity's ruse" was unlikely to have flawed our results.

Delayed recruits (EB4 and EB5) grouped together in the model with the lowest QAICc (E3; 0.31). This means that the effect of the age of first reproduction on experienced breeder survival was restricted to the difference between the earliest breeders and all the individuals that did not breed at age 3. Delayed recruits had lower mean survival probability immediately after their first breeding attempt (first-time breeder survival) and in the long-term (experienced breeder survival). Early recruits (EB3) had a prime-age survival of 0.81 (0.79 - 0.83) between the ages of 4 and 17, compared to 0.78 (0.76 - 0.80) for delayed recruits. Early recruits had a lower senescence rate (slope: −0.22 [−0.57 - 0.14]) than delayed recruits (slope: −0.41 [−0.86 - 0.05]).

Age-specific net reproductive rates

Age-specific net reproductive rates were highest in early recruits (females that started breeding at age 3) and lowest for females aged ≥5 at first reproduction (Fig. 4). The higher prime-age survival and slower rate of senescence of early recruits thus compensated for the one year earlier onset of senescence in that state. Among early recruits, was highest at age 4, at 5.16 offspring per female; thereafter declined with age to 3.77 at age 17, the age at the onset of senescence. Net reproductive rates for age ≥5 recruits were initially lower than those of age 4 recruits, reflecting their later age at first reproduction and lower survival probability as first-time breeders. From age 6, was the same for EB4 and EB5 females as their estimated survival probabilities were equal. Excluding actuarial senescence from the survival trajectory of early recruits increased at age 17 from 3.77 to 5.20, a 27.6 % increase. The net reproductive rate of delayed recruits increased by 35.6 %, from 2.89 to 4.48 at age 17, in the absence of actuarial senescence.

Discussion

We used capture-recapture data of several thousand individuals collected over more than three decades to test for negative or positive early-late life-history covariation in elephant seals. Specifically, we tested whether the onset and rate of actuarial senescence correlated with the age of first reproduction. Our analysis made use of multievent models specifically designed to test hypotheses about correlations between the age of first reproduction and late-life survival in partially monitored populations. By integrating the age of first reproduction in the state process of a multievent model, our approach overcame problems associated with assigning individuals to a specific covariate group based on the first observed breeding encounter. Our approach makes it possible to study early-late life-history covariation in wild animal populations even when some breeding attempts go undetected. Our results showed that early reproduction correlated positively with survival in both the short- and the long-term. Females with an early age of first reproduction had lower rates of senescence and higher age-specific net reproductive rates than those that delayed breeding. Our results provide the first evidence of actuarial senescence in female southern elephant seals, and show that “fixed heterogeneity” (i.e., the genetic and environmental conditions that an individual was facing in early life) may lead to “silver spoon” effects, contributing to heterogeneity in ageing rates observed at the population level.

Early-late life correlations in elephant seals

Our results provide support for individual heterogeneity in the survival probabilities of experienced breeders, and that part of this variation is explained by age at first reproduction. The age at first reproduction better explained variation in experienced breeder survival compared to models that incorporated frailty (mixture models specifying hidden individual heterogeneity) (Appendix S14). Individuals with an early age of first reproduction survived better in both the short- and the long-term than those that delayed breeding. The data supported distinct prime-age and senescent phases of survival. Péron et al. (2010b) predicted an onset of actuarial senescence in elephant seals from age 11.6 years using a fast-slow continuum life-history model, but our results show that the prime-age survival phase lasted until age 17 (95% CI: age 16 – 17) in early breeders and age 18 (95% CI: age 17 – 18) in average and late breeders. The differences in estimated survival between early breeders and average to late breeders were relatively small (Fig. 3); nonetheless, we consider these differences biologically important given that adult survivorship strongly impacts individual fitness in long-lived species (Crone 2001). Higher estimates of net reproductive rate for females with an earlier age of first reproduction (Fig. 4) showed the influence that small differences in age-specific survival can have on the expected number of offspring produced per female over its lifetime.

Because of their smaller body size, energy resources are on average more limiting for younger than for older breeding female elephant seals. Yet, our results showed that female elephant seals which entered the breeding population at Marion Island at an early age (age 3) had the highest survival probability as first-time breeders and as experienced breeders. Though the onset of senescence was predicted to occur one year earlier in age 3 recruits, these individuals had a lower rate of senescence than average and later breeders. Therefore, the trade-off hypothesis prediction that early reproduction should lead to an earlier onset of actuarial senescence was supported, but the slower rate of senescence among early breeders contradicts our expectation of early-late life trade-offs. Overall, the higher prime-age and senescent survival probabilities and increased number of offspring expected to be produced per female with an early age of first reproduction (A = 3) provide support for the hypothesis that age of first reproduction is a proxy for “fixed heterogeneity”, and that genetic and environmental conditions that an individual was facing in early life may lead to “silver spoon” effects. Positive correlations between life-history traits measured at the population level make sense if individual differences in resource acquisition exists (Van Noordwijk and de Jong 1986, Cam et al. 2002). Vriation in resource availability during the natal period may lead to between-individual heterogeneity in senescence (Nussey et al. 2007) as individuals born under favorable developmental conditions need not employ compensatory strategies such as catch-up growth that may increase rates of senescence (Lee et al. 2013). Prior to reproducing for the first time, female elephant seals have to invest a lot of energy into growth to increase from an average weaning mass of 114 kg to over 300 kg, the breeding threshold body mass (Laws 1956). Female southern elephant seals that are heavier as pups have improved survival (McMahon et al. 2000), start breeding at an early age

(Oosthuizen et al. 2018) and may also be able to allocate more resources to somatic maintenance. By contrast, individuals that were smaller during early development may face a bigger trade-off between allocating limited resources to maintenance or growth. In the Marion Island elephant seal population an early age of first reproduction thus appears to correlate with favorable early developmental conditions (Oosthuizen et al. 2018, 2019a), a lower rate of actuarial senescence and a higher expected fitness.

Our results provide the first evidence of actuarial senescence in female southern elephant seals. As in many other long-lived iteroparous species, the onset of actuarial senescence in female elephant seals was delayed (by more than ten years) beyond the age of first reproduction. In northern elephant seal (Mirounga angustirostris) females, survival appears to decline abruptly after age 16 (Condit et al. 2014), though these estimates hinge on a small sample (n = 15) of individuals observed at age 10 or older. By contrast, actuarial senescence in female Weddell seals (Paterson et al. 2018) and male elephant seals (Lloyd et al. 2020) starts at the age of first reproduction, i.e., from ages 6 to 8 where female elephant seals have stable (prime age) survival. Earlier actuarial senescence in male elephant seals agrees with the higher reproductive effort among males of this highly polygynous species. Our results contrast that of Pistorius and Bester (2002) and Pistorius et al. (2004), who found no evidence of senescence and no influence of recruitment age on subsequent survival. While their results stem from the same population, their analysis was limited to a much shorter time-series, which they later identified as a shortcoming (Pistorius et al. 2011). Our opposing conclusion is likely attributed to an increase in statistical poer, an improved analytical approach, or both.

Advantages of our multievent approach

Studies of free-ranging animal populations are important to identity the mechanisms that underpin age-related risks of mortality in the wild. However, few studies can follow individuals with great precision, and imperfect detection of breeders is a very common situation in natural populations. Observational studies should therefore account for imperfect detection, as failure to do so may lead to flawed inference (Gimenez et al. 2008). Imperfect detection of breeding females means that a female may have started to breed at a time prior to its first observation as a breeder, yielding partial state uncertainty. Yet, standard approaches that use the age of first observed breeding as an explanatory variable in capture-recapture modelling assumes it to be known without error (e.g., Tavecchia et al. 2001, Pistorius et al. 2004, Bowen et al. 2015). This approach not only leads to misclassification, but the apparent confidence in the data leads to underestimates of the variance. This may increase the rate of Type I errors, i.e., detecting a difference in survival rates among

individuals with different ages of first reproduction that does not exist. Instead of omitting individuals with incomplete life-histories (i.e., those individuals with missing breeding attempts; e.g., Nakagawa and Freckleton 2008, Bouwhuis et al. 2010) or using the first observed breeder encounter of an individual as a proxy of the age of first reproduction, we treat the age of first reproduction as a latent individual-specific state, without state transition. Consequently, the multievent model correctly accounts for the uncertainty associated with the age of first reproduction as a result of imperfect detection, and propagates this uncertainty in the model to appropriately estimate parameter variances. This means that correlations between early-late life-history traits are corrected for the biasing effect of imperfect detection.

Age at first reproduction is the most common metric used to describe early development and allocation to reproduction during early-life across vertebrate populations (Lemaître et al. 2015). We used a multievent model that incorporated the observational uncertainty associated with the age of first reproduction in the state process to assess the correlation between age of first reproduction and actuarial senescence in long-lived female elephant seals. The modelling approach we used can be applied to all capture-recapture data, but we specifically recommend it for studies where offspring are marked, breeder detection is incomplete, and interest lies in testing hypotheses about early-late life-history trait covariation. The models we fitted can also be extended to consider the association between age of first reproduction and reproductive senescence. For such analysis the state process would be expanded to allow transitions between “experienced breeders” (pupped in the current year) and “non-breeders” (pupped previously, but not in this year), until death. Increased reproductive skipping due to senescence can then be quantified by estimating the frequency of transitions to the non-breeder state.

Conclusion

Age-specific changes and covariation among demographic traits are important features of population dynamics. Using data from a long-term study of elephant seals, we showed that female actuarial senescence (a proxy for late-life performance) varied with age at first reproduction (a proxy for early-life performance). Females with an early age of first reproduction survived better during prime-age and had lower rates of senescence, leading to higher age-specific net reproductive rates (i.e., fitness prospects) than those that delayed breeding. Our results support previous work (e.g., Fay et al. 2016, Paterson et al. 2018) that age at first reproduction is a measurable trait of among-individual demographic heterogeneity. Although age of first reproduction may be difficult to pinpoint in wild animal populations, recent advances in hierarchical modelling can overcome problems associated

with imperfect detection and state uncertainty to facilitate studies of the patterns of covariation between age of first reproduction, survival and other life-history traits.

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Supporting Information

Additional supporting information may be found in the online version of this article

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 in female southern elephant seal survival, breeding, and recapture probabilities. Model H1 is the most parsimonious model without heterogeneity (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**

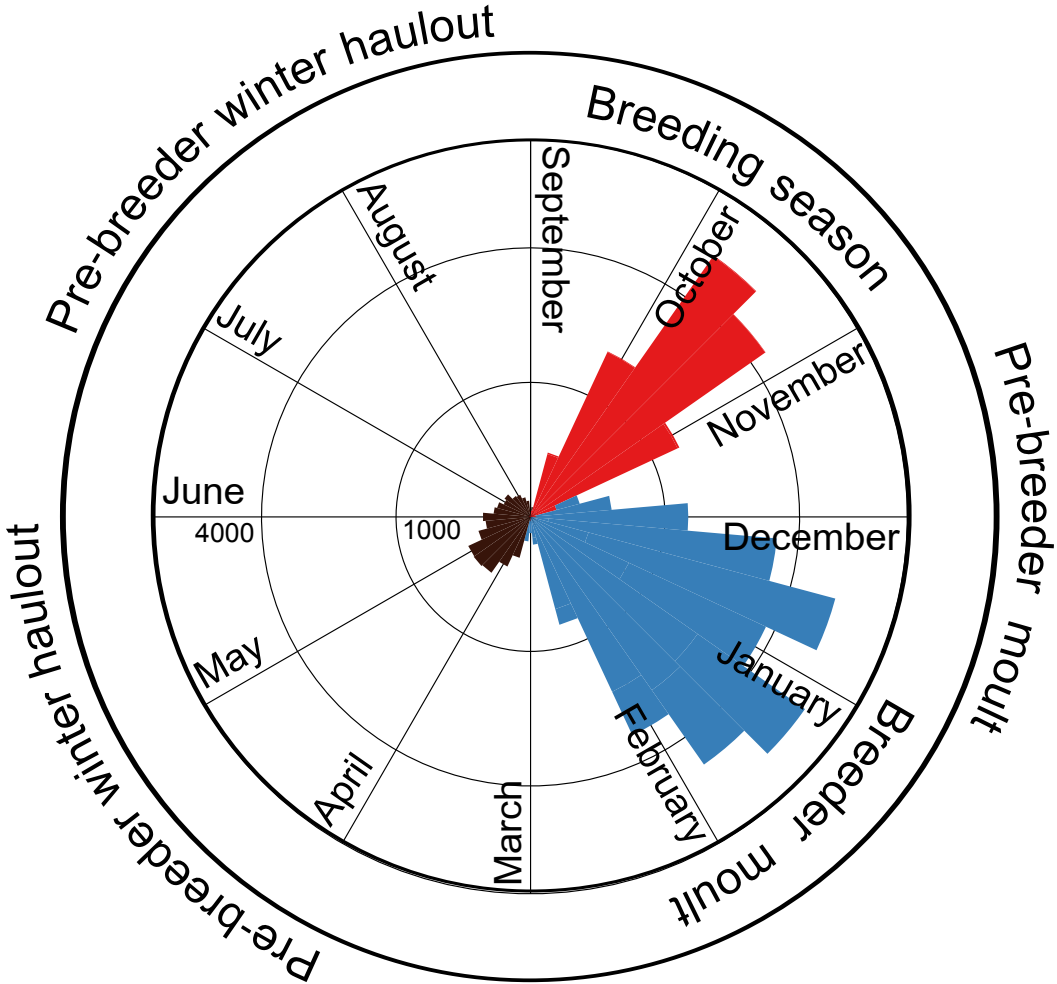
Figure legends

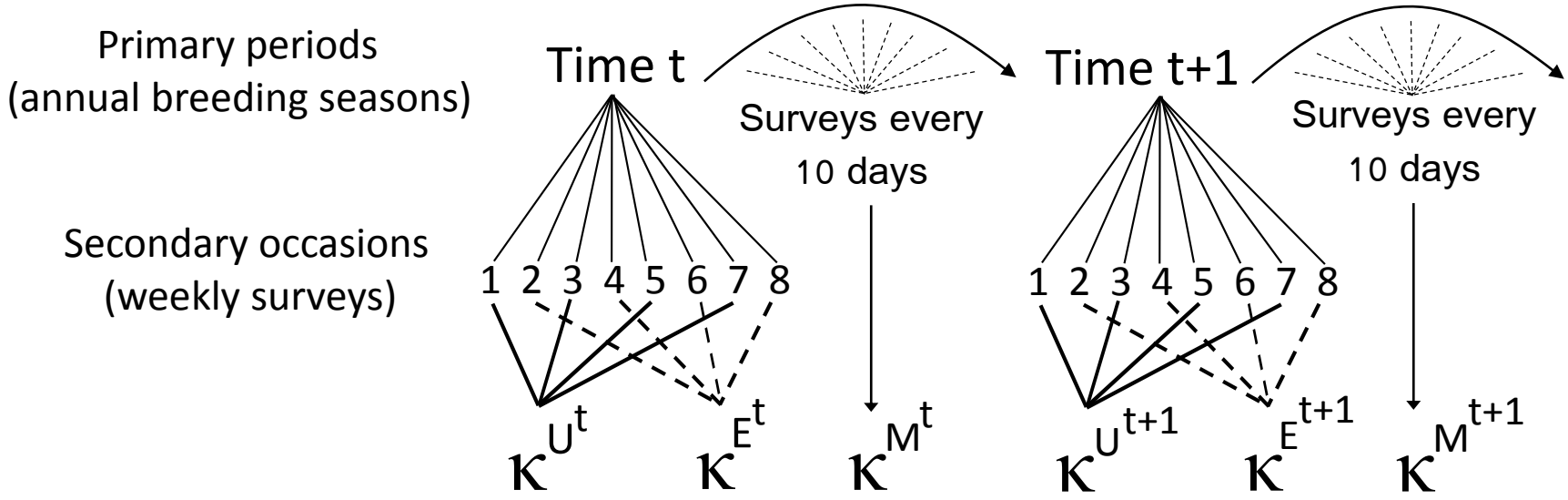
Fig. 1. Diagram representing the model structure. The arrows represent state transitions from one year to the next, conditional on survival (the “dead” state is not depicted for clarity). All individuals enter the model in the pre-breeder state (PB) and remain there until reproducing for the first time, when they become first-time breeders (FTB). The ψ parameters are recruitment probabilities (i.e., the age-specific probability to transition from the pre-breeder to breeder state). At age 3 there is a probability ψ3 that a pre-breeder will breed and thus transition to the FTB3 state. In the transition matrix of the model, parameter ψ3 is fixed to zero for all instances except for age 3 pre-breeders, for which it is estimated from the data. The transition ψ4 is only possible for 4-year olds and represents the probability to start breeding at age 4. Only individuals age 5 and older transition to the FTB5 state upon first reproduction (with a probability ψ5). First-time breeders always become experienced breeders in the following year. These seven statesoccurred twice in the model structure: first to code for seals marked with two flipper tags, and second to represent seals marked with one remaining flipper tag (Fig. 2).

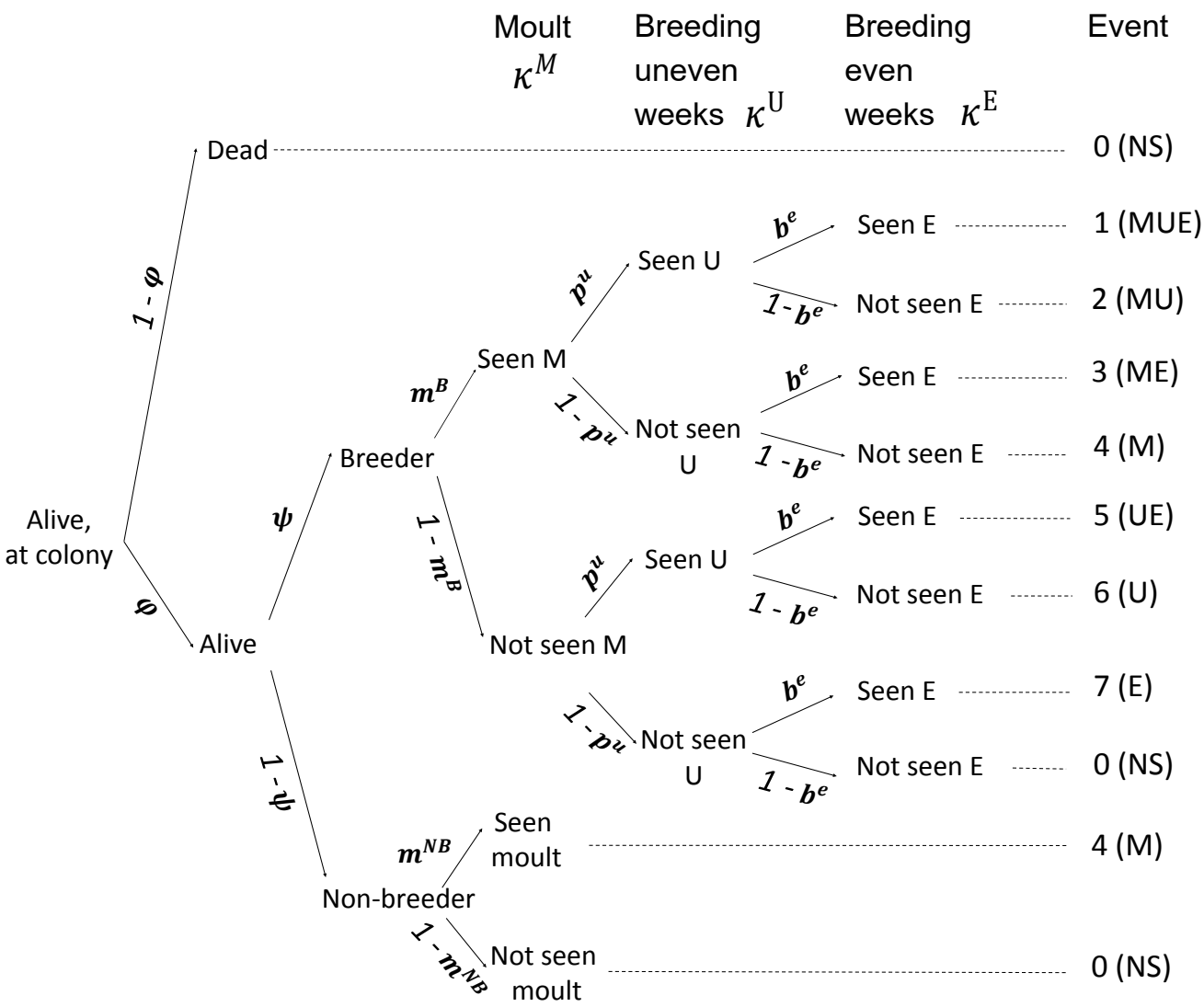
Fig. 2. The transition matrices representing the stochastic transitions (tag loss (), survival () and breeding probability ())) between states of the multievent model. The states code for the breeding status, age at first breeding, and number of flipper tags with which an individual is marked. PB, pre-breeder; FTB3/FTB4/FTB5, first-time breeders breeding for the first time at ages 3/4/≥5; EB3/EB4/EB5, experienced breeders that were first-time breeders at ages 3/4/≥5; †, dead. Superscripts (in parentheses) indicate the number (1 or 2) of flipper tags. In each matrix, the value of cell () corresponds to the probability to go from state (in rows) to state (in columns) from one breeding occasion to the next. For clarity, matrix zeroes are given as points. is the probability to lose one tag if marked with two tags, and the probability to transition from one to zero tags. In the survival and recruitment matrix we use the indicator function to show which is set to zero by the GEMACO model formula (Supplement 5) depending on the age. if age , and if age . For example, the first row of the matrix becomes for individuals of age 4 (as 3 and 5 are set to 0 when = 4).

Fig. 3. Age- and state-dependent variation in the survival probability of female southern elephant seals at Marion Island. (A) Survival trajectory of females recruiting at age 3. (B) Survival trajectory of females recruiting at ages 4 or later. Solid circles correspond to the annual survival probability of experienced breeders (model A3, Table 1). The regression line indicates the logit-linear relationship between age and survival of experienced breeders (model E3). Vertical lines and shaded areas are 95% confidence intervals. The age at the onset of senescence is indicated with a dotted line.

Fig. 4. Age-specific net reproductive rates () for each age of first reproduction A (first-time breeder (FTB) = 3, 4, ≥5) of female southern elephant seals at Marion Island. The minimum age of first breeding (A = 3) is indicated with a dotted line. Vertical lines are 95% confidence intervals.


Pre-breeder winter haulout
Breeding season
Pre-breeder moult
Breeder moult
Pre-breeder winter haulout
September
October
November
December
January
February
March
April
May
June
July
August
4000
1000


Primary periods
(annual breeding seasons)
Time t
Surveys every
10 days
Time t+1
Surveys every
10 days
Secondary occasions
(weekly surveys)
1 2 3 4 5 6 7 8
1 2 3 4 5 6 7 8
κ^{U^t}
κ^{E^t}
κ^{M^t}
$\kappa^{U^{t+1}}$
$\kappa^{E^{t+1}}$
$\kappa^{M^{t+1}}$


Moult
κ^M
Breeding uneven weeks κ^U
Breeding even weeks κ^E
Event
Dead
0 (NS)
Seen E
1 (MUE)
Seen U
Not seen E
2 (MU)
Seen M
Seen E
3 (ME)
Not seen U
Not seen E
4 (M)
Breeder
Seen E
5 (UE)
Seen U
Not seen E
6 (U)
Alive, at colony
Alive
Not seen M
Seen E
7 (E)
Not seen U
Not seen E
0 (NS)
Seen moult
4 (M)
Non-breeder
Not seen moult
0 (NS)
$1 - \varphi$
φ
ψ
$1 - \psi$
m^B
$1 - m^B$
p^u
$1 - p^u$
p^u
$1 - p^u$
b^e
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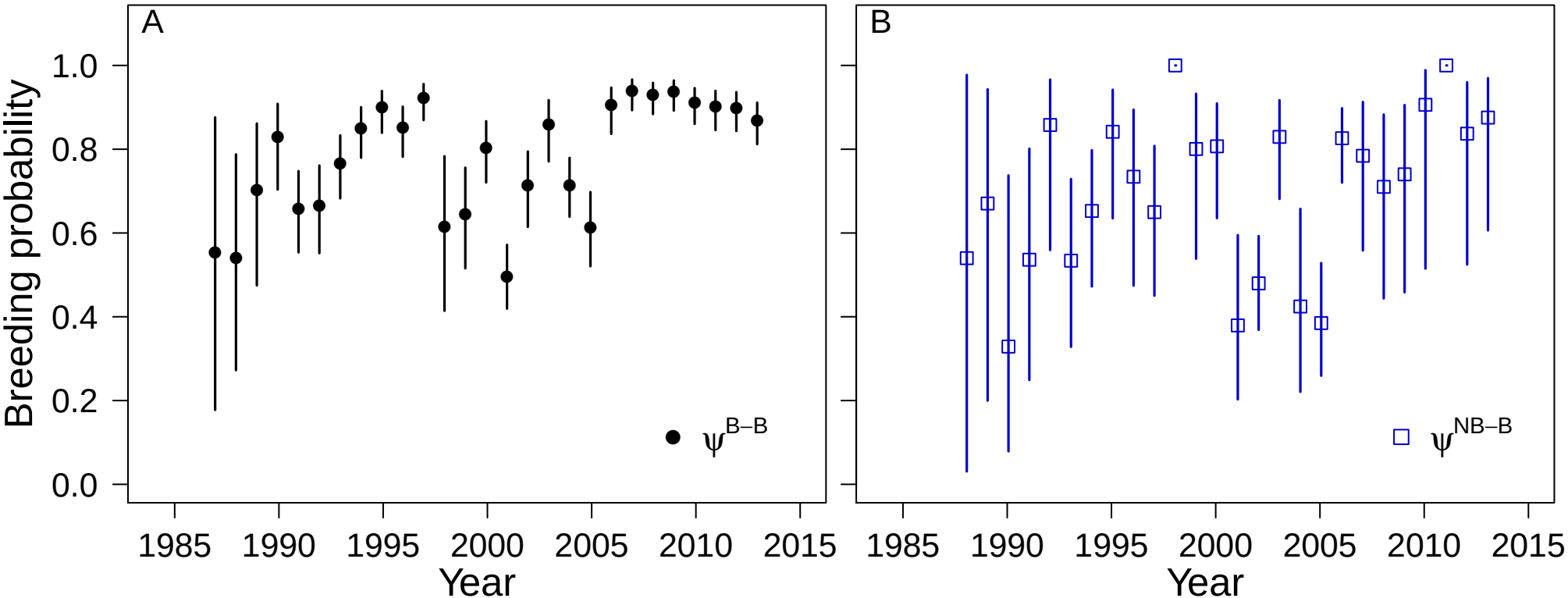
m^{NB}
$1 - m^{NB}$


A
B
Breeding probability
1.0
0.8
0.6
0.4
0.2
0.0
1985
1990
1995
2000
2005
2010
2015
Year
ψ^{B-B}
ψ^{NB-B}