PATTERNS AND DRIVERS OF VARIATION IN WEDDELL SEAL SURVIVAL RATES, AND POPULATION IMPLICATIONS OF UNOBSERVED INDIVIDUAL HETEROGENEITY IN VITAL RATES

by

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ABSTRACT

Variation in vital rates can result from many different factors, have consequences at the individual level, and may alter the structure of populations with implications for population dynamics. Here, different forms of variation in vital rates are investigated and the consequences to population dynamics are assessed using long-term longitudinal data from a population of Weddell seals *(Leptonychotes weddellii)* in Erebus Bay, Antarctica. I assessed how large unobserved individual heterogeneity in the probability of reproduction for female Weddell seals influenced population dynamics using an integral projection model populated with vital rate estimates from this population. I found that changes to the distribution of unobserved individual heterogeneity in reproduction led to small changes in the population growth rate and posit that these results are likely due to the canalization of life history traits. Given that survival is predicted to be an important driver of population dynamics, I evaluated sources of variation in survival for two different periods of life. I assessed patterns of age-specific survival for males and females to assess possible actuarial senescence patterns and to compare patterns between the sexes. To estimate survival rates, I used Cormack-Jolly-Seber models in the Bayesian framework allowing for unobserved heterogeneity with finite mixtures and applied flexible basis splines to model age-specific patterns. I found that males not only exhibited lower survival rates from age three years old to the end of life, but they also exhibited stronger senescence after the age of 12 years old than did females. Results for survival senescence were then used to assess support for different hypotheses for the evolution of sex-differences in survival senescence. Finally, I built upon previous research by evaluating the relationship of different variables to the probability that an individual survives early life and returns to the study area between the ages of two and six years old. I found that pup weaning mass was the most important to a pup’s probability of being recaptured, but that sex differences may also exist. The results from this dissertation highlight the importance of life-history strategies to understanding demographic and population processes and provide avenues for future research.

CHAPTER ONE

INTRODUCTION

The lifetime fitness of an individual is determined by the combined outcomes of individual survival and reproduction. Therefore, variation between individuals and the factors that drive this variation are important to an individual’s lifetime fitness. Scaling up from the individual to the population level this variation in individual vital rates is predicted to lead to different degrees of influence on the structure and growth of a population (Caswell, 2001; Gaillard & Yoccoz, 2003; Vindenes & Langangen, 2015). To fully understand ecological and evolutionary processes knowledge of processes acting at the individual and population levels is necessary (Clutton-Brock & Sheldon, 2010).

At the individual level vital rates may be influenced by many different factors and vary between different stages of life. Sources of variation in vital rates may be fixed throughout life such as the conditions experienced early in life (Lindström, 1999), parental care (Lummaa & Clutton-Brock, 2002) and genetics (Wilson & Nussey, 2010) or change throughout life with an individual’s developmental state (McNamara & Houston, 1996), age (Descamps et al., 2008; Gaillard & Lemaître, 2020; Loison et al., 1999; Pardo et al., 2013; Toïgo et al., 2007) or environmental conditions (Barbraud & Weimerskirch, 2005; Douhard et al., 2014; Fay et al., 2015; Reid et al., 2003). Some of these sources of variation can be measured and used in demographic analyses to account for individual variation but some traits may be less easy to measure but still create between-individual differences in vital rates. When between-individual variation is unobserved because it was not measured or is not measurable and is fixed throughout life it is considered unobserved individual heterogeneity (Cam et al., 2016). The role of unobserved individual heterogeneity in shaping the life histories has been generally recognized and well debated (Cam et al., 2016), but the influence of unobserved individual heterogeneity on population dynamics is less clear although there is reason to suspect it could be important (Clutton-Brock & Sheldon, 2010; Kendall & Fox, 2002; Vindenes & Langangen, 2015).

Another source of variation in vital rates is age. When vital rates decline with age this is considered demographic senescence. It is now widely accepted that survival senescence is pervasive in the wild (Gaillard & Lemaître, 2020), but it remains an open question whether consistent sex-specific patterns in senescence exist and what might be the mechanisms driving recorded sex differences in senescence (Bronikowski et al., 2022; Gaillard & Lemaître, 2020; Lemaître et al., 2020). Additional studies are currently needed to improve our understanding of sex differences in senescence.

I use longitudinal data from long term study of the Weddell seals to better understand individual and population level processes. This population is ideal for studying variation in vital rates and the implications of this variation for population dynamics. Individuals gather in consistent pupping colonies each year, are easily approached and can be marked allowing ages for both sexes and reproductive histories for females to be known. This mark-recapture research has been carried out on this population since 1973 (Cameron & Siniff, 2004) providing high-quality longitudinal data on individuals and across generations. Additionally, the docile nature of this species allows the gathering of morphometric and behavioral data. A great deal of work has already been done that indicates variation in some vital rates exists.

In this dissertation I fill gaps in our knowledge regarding this population while also providing additional evidence for population and evolutionary processes by answering questions regarding variation in survival rates for different portions of the population and how unobserved individual heterogeneity in a vital rate influences population dynamics. In chapter 2, I assess the consequences of previously estimated unobserved individual heterogeneity in vital rates (Chambert et al., 2013; Paterson et al., 2018) for population dynamics. Unobserved individual heterogeneity is thought to be important to different aspects of population dynamics, especially the net reproductive rate, generation time, and demographic and environmental variance (Vindenes & Langangen, 2015), with the few studies on the topic corroborating these predictions (Coulson, 2012; Fung et al., 2022; Lindberg et al., 2013; Plard et al., 2015). Female adult survival rates exhibit little individual and temporal variation (Paterson et al., 2018; Rotella et al., 2012), in contrast substantial unobserved individual heterogeneity in the probability of reproduction has been observed (Paterson et al., 2018) with high-quality females predicted to produce twice as many pups as low-quality individuals (Chambert et al., 2013). I evaluated the consequences of this large unobserved individual heterogeneity in reproduction for population dynamics using an integral projection model and previously estimated vital rate values for this population.

The work in chapter 2 highlights the importance of variation in certain vital rates across life and different developmental stages. The next two chapters of my dissertation investigate how patterns in survival rates across life and potential drivers of survival during a specific stage of life. In chapter 3, I compare patterns of survival across life between the sexes and assess how results fit with proposed explanations for the evolution of sex-specific senescence. I build upon previous research from this population that found that both males (Brusa et al., 2020) and females (Paterson et al., 2018) exhibit actuarial senescence, an increase in mortality with age, but were unable to make comparisons across the entire lifespan. In addition, this research provides a useful data point in in improving our understanding of the evolution of sex differences in senescence. Weddell seals have a unique set of characteristics, specifically that this species shows moderate polygyny and little sexual size dimorphism, that make predictions for patterns of senescence rates difficult and this a useful case study. Cormack-Jolly-Seber models were constructed using a Bayesian framework to independently estimate survival rates for males and females while accounting for unobserved individual heterogeneity with finite mixtures of survival classes and basis splines as a flexible modeling approach to model age-specific survival.

In chapter 4, I evaluated different potential drivers of variation in offspring survival among different individuals, bringing to bear many years of monitoring and measurement data to the question. There is evidence that early life survival of Weddell seals varies with environmental conditions (Stauffer et al., 2013), maternal characteristics (Hadley et al., 2007; Hastings & Testa, 1998), and pup weaning mass (Proffitt et al., 2008). The relative importance of different covariates related to these drivers of early life survival is not known as these covariates have not been assessed together in a single modeling effort. I used Bayesian logistic regression modeling to evaluate the relationship between characteristics of mothers and pups as well as the birth environment and the probability that a pup survives the early life period and is sighted in the study area. This approach assesses the cumulative influence of covariates predicted to be important on an individual's probability of surviving to adulthood.

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CHAPTER TWO

EVALUATING THE IMPORTANCE OF INDIVIDUAL HETEROGENEITY IN REPRODUCTION TO WEDDELL SEAL POPULATION DYNAMICS USING INTEGRAL PROJECTION MODELS

Contribution of Authors and Co-Authors

Manuscript in Chapter 2

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Contributions: Conceived the research idea, managed and coordinated the study, contributed to writing, and approved the final manuscript

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Contributions: Conceived the research idea, assisted in model development, contributed to writing, and approved the final manuscript

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Abstract

1. Identifying and accounting for unobserved individual heterogeneity in vital rates in demographic models is important for estimating population-level vital rates and identifying diverse life-history strategies, but much less is known about how this individual heterogeneity influences population dynamics.

2. We aimed to understand how the distribution of individual heterogeneity in reproductive and survival rates influenced population dynamics using vital rates from a Weddell seal population by altering the distribution of individual heterogeneity in reproduction, which also altered the distribution of individual survival rates through the incorporation of our estimate of the correlation between the two rates and assessing resulting changes in population growth.

3. We constructed an integral projection model (IPM) structured by age and reproductive state using estimates of vital rates for a long-lived mammal that has recently been shown to exhibit large individual heterogeneity in reproduction. Using output from the IPM, we evaluated how population dynamics changed with different underlying distributions of unobserved individual heterogeneity in reproduction.

4. Results indicate that the changes to the underlying distribution of individual heterogeneity in reproduction cause very small changes in the population growth rate and other population metrics. The largest difference in the estimated population growth rate resulting from changes to the underlying distribution of individual heterogeneity was less than 1%.

5. Our work highlights the differing importance of individual heterogeneity at the population level compared to the individual level. Although individual heterogeneity in reproduction may result in large differences in the lifetime fitness of individuals, changing the proportion of above-

or below-average breeders in the population results in much smaller differences in annual population growth rate. For a long-lived mammal with stable and high adult-survival that gives birth to a single offspring, individual heterogeneity in reproduction has a limited effect on population dynamics. We posit that the limited effect of individual heterogeneity on population dynamics may be due to canalization of life-history traits.

Introduction

The structure and dynamics of a population are governed by the vital rates of the individuals that make up the population (Caswell, 2001; Easterling et al., 2000). The way in which vital rates vary between individuals can therefore have consequences for the structure and growth of a population. This variation may arise from sources that are fixed throughout life such as, genetics (Wilson & Nussey, 2010), early life environment (Lindström, 1999), and maternal care (Lummaa & Clutton-Brock, 2002). Differences may also be dynamic throughout life such as body size (Vindenes & Langangen, 2015) or developmental state (Cam et al., 1998; McNamara & Houston, 1996). Often it is possible to observe the heterogeneity among individuals with easily measurable metrics such as, age, mass, or sex, that can capture some of the variation in the vital rates between individuals (Côté & Festa-Bianchet, 2001; Fay et al., 2015; Ozgul et al., 2010; van de Pol et al., 2006). Some heterogeneity among individuals is not as easily measured and can be the result of features such as genetics, maternal care, or resource acquisition (Wilson & Nussey, 2010). In this paper, we consider individual heterogeneity to be the fixed between-individual variation in demographic parameters that is unobserved because it was not measured or because it is intrinsic to the individual and not measurable (Cam et al., 2016). Individual heterogeneity can account for a large amount of variation between individuals and, if so, be important to consider in demographic and population models (Clutton-Brock & Sheldon, 2010; Vindenes & Langangen, 2015).

To obtain accurate estimates of population-level vital rates it is important to account for individual heterogeneity (Cam et al., 2002). An early example from human demography recognized that when individuals within a cohort vary in quality (inherent fitness characteristics), poor-quality individuals will tend to selectively disappear from the population at younger ages such that the average quality of the surviving members of the cohort will increase as the cohort ages (Vaupel et al., 1979). This selective disappearance biases the population-level vital rate estimate obscuring age-specific trends at the individual level if not accounted for in demographic analyses (van de Pol et al., 2006). Multiple statistical approaches have been developed to account for individual heterogeneity when estimating vital rates providing unbiased population-level vital rate estimates (Cam et al., 2002; Hamel, Gaillard, Douhard, et al., 2018). A common method used to account for unobserved individual heterogeneity in a particular vital rate is to include a random effect of individual in a hierarchical regression model (Cam et al., 2002, Cam et al. 2013), thereby quantifying unobserved differences among individuals that might bias the population-level estimate of vital rates.

Population-level vital rates can be used to project the population forward based on the structure of the population, using matrix population models. These population models are useful for understanding under what conditions a population may grow or shrink and what vital rates or states have greater influence on the population trajectories. Matrix population models assign individuals to discrete character states and then project the population forward based on the vital rates associated with these character states (Caswell, 2001). Matrix models have been applied to many ecological questions, informing the optimal management of invasive and endangered species (Govindarajulu et al., 2005; Warchola et al., 2018) and progressing our understanding of the evolution of life history strategies (Pfister, 1998), for example. Integral projection models (IPM) have advanced matrix population models by allowing character states to be continuous attributes such as mass (Plard et al., 2015; Traill et al., 2021) or size (Dahlgren & Ehrlén, 2011), which allows more biologically realistic models to be developed (Easterling et al., 2000; Ellner et al., 2006). The flexibility to include continuous character states in an IPM can also be used to evaluate the influence of unobserved individual heterogeneity on population dynamics, which has received far less attention.

Theoretical investigations suggest that unobserved individual heterogeneity in vital rates can influence the net reproductive rate, generation time, demographic, and environmental variance but that the asymptotic growth rate typically is less sensitive to such heterogeneity unless heritability is strong (Vindenes & Langangen, 2015). Results of the few empirical studies on the topic corroborate predictions for the asymptotic population growth rate (Coulson, 2012; Fung et al., 2022; Lindberg et al., 2013; Plard et al., 2015). Including unobserved individual heterogeneity in recruitment and survival rates in population models for black brant (*Branta bernicla nigricans*) resulted in large changes to reproductive values and smaller changes to population growth rate when compared with results from modeling that ignored individual heterogeneity (Lindberg et al., 2013). Population models parameterized with different underlying distributions of unobserved individual heterogeneity in vital rates resulted in similar estimates of population growth in two different ungulate species (Coulson, 2012; Plard et al., 2015). Given the paucity of empirical research on the effects of unobserved individual heterogeneity on different metrics describing population dynamics, additional studies are needed to understand the effects of unobserved individual heterogeneity across species and different life-histories.

We used vital rates both previously published and estimated using data from a long-term study of the Erebus Bay population of Weddell seals (*Leptonychotes weddelli*) to investigate the importance of unobserved individual heterogeneity to population dynamics. Weddell seals are a long-lived, polygynous marine mammal that is philopatric to breeding site (Stirling, 1969). This southern-most breeding mammal is an intermittent breeder that nearly always gives birth to a single pup at each reproductive event (Chambert et al., 2015). Due to the long-term study of Weddell seals in Erebus Bay, it is possible to estimate age and state specific vital rates and quantify unobserved individual heterogeneity. Recent research for this population of Weddell seals informed our predictions. There is large unobserved individual heterogeneity, hereafter referred to as *ih*, in the probability of reproduction (Paterson et al., 2018), with higher quality individuals potentially producing twice as many pups as lower quality females (Chambert et al., 2013; Paterson et al., 2018). In contrast, adult survival rates tend to be quite high with much less individual and temporal variation (Paterson et al., 2018) than probabilities of reproduction, and survival rates appear to be more strongly buffered than probabilities of reproduction against variation in the environment (Rotella et al., 2012). Given the large amount of individual heterogeneity present in probability of reproduction for the study population, we wanted to know the consequences of *ih* for population dynamics, whether above-average breeders are important to population growth, and how population metrics might change if bias in mortality or temporary emigration shifted the distribution of *ih*. Using an IPM, we evaluated four population scenarios that were associated with differing levels of *ih* and compared the resulting population metrics from each scenario. We predicted that the inclusion of *ih* in population models would affect the population growth rate but were unable to predict the magnitude of resulting changes and expected the scenario that did not include *ih* to result in a greater population growth rate due to the lower variability in vital rates.

Materials and Methods

Study Population

The study area encompasses Erebus Bay, Antarctica, which lies within the western Ross Sea (-77.62° to -77.87° E, 166.3° to 167.0° S) (Cameron & Siniff, 2004). Each austral spring, adult females use perennial cracks that form where fast ice meets land to haul out on the sea ice and give birth (Stirling, 1969). Adult females give birth to a single pup, with twinning occurring very rarely. Mothers are the sole provider of parental care and will nurse their pup for approximately 35-days before weaning the pup (Garrott et al., 2012). Weddell seals are capital breeders, primarily using stored body reserves to meet the energetic demands of lactation (Wheatley et al., 2008). The mean age of first reproduction for females is seven years old (Hadley et al., 2006), with females producing on average five pups during their reproductive lives (Chambert et al., 2013). All animal handling activities were approved by NOAA National Marine Fisheries Service (permit number: 21158 and previous permits) and the Institutional Animal Care and Use committee of Montana State University (protocol number: 2017-11 and previous permits). Weddell seals in this population have been individually marked in the interdigital webbing since 1968, and since 1982 all pups born in the study area have been marked within days of birth. Since 1973, six to eight resight surveys have been conducted approximately every five days from November through mid-December (Cameron & Siniff, 2004). Females are highly philopatric, returning to Erebus Bay prior to first reproduction if they were born to this population (Cameron et al., 2007; Hadley et al., 2007), and on-ice detection of mother-pup pairs is very high (Hadley et al., 2006). Therefore, we assume that females absent from the study area are not reproducing. Due to the extensive mark-resight effort, reproductive histories and ages are known for most adult females.

Population Analysis

The integral projection model (IPM) we constructed modeled the influence of age (a), reproductive state (z), and individual random effects on probability of reproduction (ih_r) and probability of survival (ih_s) on the population dynamics of the Erebus Bay population of Weddell seals. We chose to use an IPM to model population dynamics because of the continuous distribution of individual random effects. Five reproductive states were considered in the IPM which were: pre-breeder, first time breeder, breeding at time *t* with previous experience breeding (experienced breeder), skipping breeding at time *t* and present in the study area ($\text{skip}_{\text{present}}$), or skipping breeding at time t and temporarily emigrating from the study area ($\text{skip}_{\text{absent}}$). Seals could live up to a maximum of 31 years of age beyond which no individuals survive. Four distributions for the random effect of individual on reproduction were considered and are explained in further detail below. The projection kernel projects the population forward through three demographic functions which describe survival, reproductive development (transition between reproductive states), and reproduction. Our study follows a post-reproductive census, where the population is surveyed during and after reproduction; seals are released and surveyed again the next year if they survived and returned to the study area. Thus, the IPM also follows a post-reproductive census. The demographic functions were parameterized using a combination of point estimates from previous modeling efforts and estimates from regression equations (Table 2-1) obtained with a multistate modeling approach (Lebreton & Pradel, 2002) in the Bayesian framework and the resulting posterior (Table A1). Using data for females that recruited to the breeding population and were born between 1982 and 2018, we constructed Bayesian multistate models to model age specific recruitment, survival, and reproduction. Age specific patterns in recruitment, survival, and reproduction were modeled using basis splines. A basis spline can take a non-linear shape which is determined by the data (Hastie & Tibshirani, 1990). The splines used to model survival, recruitment to the breeding population, and reproduction included five knots or pivot points, that connect each segment of the spline (Hastie & Tibshirani, 1990). Further information regarding knot location is presented in the supplementary information. Temporal variation in probability of recruitment, survival, and reproduction was accounted for by including an independent random effect for year. Intercept adjustments for reproductive states were included in models of probability of survival and reproduction. Additionally, the survival and reproduction equations included a random effect of individual. The covariation between the individual random effect of survival and reproduction was modeled given existing evidence for a correlation between the two parameters in our study population (Paterson et al., 2018). Additionally, there is some evidence to suggest ignoring the correlation of random effects has little effect on estimates of population growth but may bias elasticities (Fung et al., 2022). Point estimates were used to parameterize pre-breeder survival probability. The age structure for pre-breeder survival included three age classes (pup, yearling, and 2+ years) (Rotella et al., 2012).

The IPM projects a population forward in time using a function that projects how individuals across one or more character states change from one time step to the next based on survival (Fig. A1), reproduction (Fig. A2), and development (state transition) functions (i.e., a projection kernel) (Fig. A3). The projection kernel is made up of two component kernels, the survival-development kernel and the reproduction kernel. In our IPM the survival-development kernel determines the transition of individuals to reproductive states given survival. The survival function $s(z,\ a,\ \ ih_r)$ calculates the probability of survival from time *t* to *t+1*, based on an individual's reproductive state (*z)*, age (a), and individual random effect on survival (ih_s). An individual's random effect on survival is calculated by multiplying an individual's random effect on reproduction by the correlation between survival and reproduction. The reproductive development function $G(z',\ z,\ a,\ ih_r)$ calculates the probability of transition between reproductive state *z* at time *t* and *z'* at time *t+1*, based on an individual's age (a), current reproductive state (*z*), and individual random effect on reproduction (ih_r). Therefore, the survival-development kernel is defined as:

$$P_a(z',\ z, ih_r) = s(z,\ a, ih_r)G(z',\ z,\ a,\ ih_r)$$

The transition between reproductive state *z*, and *z'* in the development function is governed by a transition matrix that calculates the probability of entering *z'* based on the reproductive state specific probability of reproduction, probability of temporary emigration, and probability of returning from temporary emigration (Table 2-2).

The reproduction kernel determines the number of offspring produced in year *t+1,* based on an individual's current reproductive state *z*, and age a, given survival to *t+1* and is defined by:

$$F_a(z_o,\ z, ih_r) =\ 0.5\ s(z,\ a, ih_r)p_b(z)c_0(z_o, z)$$

In the reproduction kernel $p_b(z)$ specifies the probability of reproducing based on an individual's reproductive state *z* and $c_0(z_o, z)$ specifies the offspring reproductive state (z_o) given the parent reproductive state (*z*). The kernel links the character state distribution at time *t*, $n_a(z, ih_r, t)$ to the next time step *t+1*. The character state distribution at time *t+1* is computed by numerical integration across the values of ih_r and discrete character states (*z)* and then summing the contributions of individuals across all ages at time *t*. Contributions to the character state distribution in time *t+1* by offspring is defined by,

$$n_0(z_o, ih, t+1) = \sum_{a=0}^{M} \iint F_a(z_o, z) n_a(z, ih, t)\, dz\, dih$$

where M=the maximum age. Contributions to the character state distribution in time *t+1* by ages greater than zero is defined by:

$$n_a(z', ih, t+1) = \iint P_{a-1}(z', z, ih) n_{a-1}(z, ih, t)\, dz\, dih$$

We chose to only include females in the analysis because vital rates of females are known for this population and reproductive histories are not available for males. Because the sex ratio of offspring is very close to 1:1, we multiplied reproduction by 0.5 in our females-only model.

To test how unobserved individual heterogeneity in the probability of reproduction influences population dynamics, we evaluated four scenarios in which the distribution for the random effect of individual for reproduction differed (Fig. 1). The four distributions were chosen to evaluate the influence of including *ih* and the nature of the distribution for ih_r on the population's dynamics. In each scenario, the random effects of individual on the probability of reproduction were normally distributed on the logit scale (Table 2-1). To be consistent with the distribution used to estimate *ih* in the demographic models, the four different scenarios modified the normal distribution (μ, σ) as follows. First, we used the distribution N(0, 0.001) to approximate a scenario with no individual heterogeneity that yields estimates of the population growth rate for a population in which all females have the mean value for the probability of reproduction. This scenario was included to understand how population metrics change if ih_r is not included. In our second scenario, we used the distribution N(0, 0.72) estimated in our demographic model to evaluate dynamics using the observed level of individual heterogeneity for the population. For the observed scenario we only included the range of individual random effects found in our data (Range: -2 to 1). To assess the importance of the mothers with the highest values for *ih* to annual population growth and to evaluate how population dynamics would change if the mothers with the highest values for *ih* were removed through biased mortality or permanent emigration, we right truncated the observed distribution such that approximately the top 15% of *ih* values were eliminated. The right truncation led to a population with a greater proportion of individuals with a low random effect (Low RE scenario) and resulted in a mean of -0.268 and a standard deviation of 0.518. Truncation of the observed distribution was done using accept-reject sampling with the truncnorm package (Mersmann et al., 2018). Lastly, we investigated what would happen to the population dynamics if the mothers with the lowest values for *ih* were removed through biased mortality or permanent emigration by left truncating the observed distribution so that approximately the lowest 20% of observed *ih* values were eliminated. The left truncation resulted in a population with a greater proportion of individuals with a high random effect (High RE scenario) and a mean of 0.268 and standard deviation of 0.518.

For the results presented here, our models assumed that offspring did not inherit their value of *ih* from their mother, i.e., each daughter was assigned a random value from the distribution of *ih* values in the given scenario. However, we did do an exploratory investigation to evaluate the effects of incorporating inheritance of the individual random effect of reproduction by incorporating inheritance using the estimated regression equation from previous work on our study population that linked a daughter's individual random effect to that of her mother and found evidence of a relatively weak but positive relationship between the values (Chambert et al., 2014). For the inheritance function, the distribution of offspring *ih* values depends on the maternal *ih* value and comes from the normal distribution N(-0.02 + 0.05*$ih_{maternal}$, 0.005). We found that including inheritance in *ih* did not alter the patterns of our estimates of population growth rate or dynamics in ways that were notably different from those of models that ignored inheritance (Table A2). Although evidence for weak density dependence in annual population growth rates has been reported in our study population (Rotella et al., 2009), our models were density independent because we do not currently have estimates for the influence of population density on the specific vital rates used in the IPM.

We constructed and evaluated our IPM models using the R statistical computing program (R Core Team, 2021). We constructed component matrices arranged into four-dimensional arrays for both the survival and development kernel and the reproduction kernel that were used in the iteration procedure outlined below (Ellner et al., 2006). The dominant eigenvalue λ (asymptotic growth rate) and eigenvectors *w* and *v* (stable state distribution and reproductive value, respectively) were calculated by iteration of the IPM model one time step, rescaling the population size N_t to a size of one and repeating (Ellner et al., 2006). We determined convergence to a stable distribution by calculating the sum of absolute deviations between N_{t+1} and λN_t. We used a deviation tolerance of 1×10^{-10} as the cutoff for convergence. We calculated elasticities at the level of the kernel components to understand how the kernel components affect λ. Elasticity is the proportional response of λ resulting from a proportional perturbation of an element of the IPM, and so elasticity can be considered a proportional contribution of the kernel component to λ (Caswell, 2001; de Kroon et al., 2000; Easterling et al., 2000). Prospective perturbation analysis was used to calculate elasticities by applying the equations for sensitivity and elasticity to component matrices as outlined in Ellner et al. (2006). We evaluated the IPM using demographic estimates for females that had recruited to the breeding population (recruitment, survival, and reproduction) from the upper and lower bounds of the 95% highest density interval (HDI) and report this range of uncertainty in the population estimates. To determine the influence of *ih* on population dynamics we compared the resulting population structure, λ, net reproductive rate, generation time, and elasticities for each *ih* scenario.

Results

The asymptotic population growth rate was near 1.0 and similar across all four modeled scenarios. The λ resulting from the different scenarios ranged between 0.966 and 0.968 (Table 2-3). We found that including *ih* in reproduction and survival leads to very small differences in λ as reported above. The Low RE scenario that had a greater proportion of individuals that were below-average breeders with slightly higher survival probabilities (due to the negative correlation of -0.334 between individual random effects for survival and reproduction) did have a higher λ compared to what was found for other population scenarios, but the difference was quite small. Similarly, there was little difference in the net reproductive rate (R_0) or the generation time (T_c) between different scenarios (Table 2-3) and all were within rounding error. The wide highest density intervals (Table 2-3) are the result of parameter uncertainty that was fully propagated to population metrics by evaluating the IPM at the upper and lower bounds of the 95% highest density interval.

The stable state distribution showed the same general pattern across all scenarios with pre-breeders being the most abundant followed by experienced breeders. The stable state distribution for the High RE scenario had more pre-breeders and experienced breeders than did distributions from other modeled scenarios. For all scenarios, reproductive values were highest for experienced breeders, followed closely by first-time breeders. For non-reproductive states, $\text{skip}_{\text{present}}$ and $\text{skip}_{\text{absent}}$, reproductive values were relatively higher for the High RE and No IH scenarios compared to others, whereas for pre-breeders, reproductive values were relatively higher for the Low RE and Observed scenarios (Fig. 2-2). In all scenarios, reproductive value increased up to age four before slowly declining out to the oldest ages. Within this age pattern young ages (< 15 years) had slightly higher reproductive values for the High RE and No IH scenarios, whereas reproductive values were slightly higher at older ages for the Low RE and No IH scenarios. In scenarios with *ih*, individuals with random effects slightly below the mean had a higher reproductive value compared to those with a more extreme random effect.

For all four scenarios, λ was more responsive to changes in the survival and development component than to changes in the reproduction component. We found λ's elasticity to changes in values from the survival and development (0.93) and fecundity (0.07) kernels were nearly identical with most of the difference due to rounding error. In all scenarios, λ's elasticity to changes in survival and development of pre-breeders was highest, followed by experienced breeders. Notably, λ's elasticity to changes in the survival and development of experienced breeders was slightly greater for the High RE scenario ($e_{\text{exp}} = 0.21$) compared to the Low RE scenario ($e_{\mathrm{exp}} = 0.20$), but this pattern was reversed for skips$_{\mathrm{present}}$ ($e_{skip\text{-}p} = 0.08$ for Low RE vs. $e_{skip\text{-}\mathrm{p}} = 0.06$ for High RE), indicating the relative importance of experienced breeders and skips$_{\mathrm{present}}$ for the two scenarios. For all scenarios, λ's elasticity to changes in survival and development was much higher for young individuals than older individuals as evidenced by large declines in elasticities that occur near the age of first reproduction (Fig. 3), with little difference between scenarios. In all three scenarios with *ih*, λ's elasticity to changes in both the survival and development kernel and the reproduction kernel, was highest for individuals with a random effect slightly below the mean.

In all scenarios, λ's elasticity to change in the reproduction kernel was greater for experienced breeders compared to first time breeders. When comparisons were made across scenarios, the elasticity value associated with experienced breeders was slightly higher in results for the High RE scenario than for other scenarios. For all scenarios, λ's elasticity to changes in the reproduction kernel was greatest for 12-year olds and lower for both younger and older individuals (Fig 2-3). When comparing scenarios, elasticity values for females <17-years old were slightly higher in the High RE scenario than in the Low RE scenario, whereas at older ages elasticities were slightly higher for the Low RE scenario relative to the High RE scenario.

Discussion

Individual heterogeneity in vital rates can be quite important to evaluations of life history patterns (Aubry et al., 2009; Cam et al., 2002; van de Pol et al., 2006; Vaupel & Yashin, 1985) and can lead to substantial differences in the fitness of individuals (Bergeron et al., 2011; Wilson & Nussey, 2010). Previous research has revealed a large degree of individual heterogeneity in the reproductive rate for this long-lived species, the Weddell seal. For our study species, the inclusion of individual heterogeneity in models of reproduction clearly identified a cost of reproduction to future reproduction which is not detected if individual heterogeneity is not included (Chambert et al., 2013). Additionally, above-average individuals are predicted to potentially produce twice as many pups as a below-average mother (Chambert et al., 2013; Paterson et al., 2018). Our work adds to the accumulating literature on the roles of individual heterogeneity in population dynamics and provides evidence that individual heterogeneity in reproduction is less important at the population level than at the individual level for a long-lived species with low annual reproductive output and low offspring survival. In particular, we found that adjustments to the distribution of *ih* in reproduction and through its correlation with survival, *ih* in survival, led to very small changes in λ and other population metrics even when the underlying distribution was weighted more heavily towards individuals with an above- or below-average random effect for the probability of reproduction. Our results reinforce previous findings (Rotella et al., 2012) that elements of the survival and growth component contribute more to population change and add the novel finding that individual heterogeneity in reproduction, which has important effects on lifetime reproductive output and helps detect reproductive senescence (Chambert et al., 2013; Paterson et al., 2018), does not strongly affect population dynamics even when the correlation between reproduction and survival is included.

Our evaluation of four very different scenarios of *ih* with an age- and state-structured IPM demonstrated that λ is quite similar across the different scenarios. These results show that removing a substantial portion of either above- or below-average breeders does not result in large changes to population dynamics and agree with previous findings from theoretical and empirical work. A previous evaluation of the effect of *ih* in reproduction and inheritance on population dynamics in another long-lived mammal, roe deer (*Capreolus capreolus*), found that populations characterized by above- and below-average individuals resulted in little change to population dynamics (Plard et al., 2015). In Soay sheep (*Ovis aries*) incorporation of *ih* in growth, reproduction, and survival into population models led to small changes in population dynamics (Coulson, 2012). Theoretical research has found that ignoring *ih* in traits that influence vital rates will generally have a greater effect on population measures other than λ (Vindenes & Langangen, 2015) and that *ih* in reproduction will have little influence on λ unless heritability is strong (Kendall et al., 2011). It is possible that results would differ for short-lived species or for a long-lived species with the potential to produce many offspring per reproductive event. For example, *ih* in a phenotypic trait, size, had a greater influence on λ when results from IPMs for a theoretical short-lived species were compared to those of a long-lived species (Plard et al., 2016). Plard et al. (2016) state that population dynamics are most sensitive to the curvature of the relationship between the phenotypic trait and demographic rates, and this curvature likely drives differences in response of lambda to phenotypic variation for short and long-lived species.

Asymptotic growth rates estimated for each of the four scenarios evaluated in this study are all quite similar to the growth rate of 0.98 obtained in earlier work (Rotella et al., 2012) despite the fact that our IPM incorporated *ih* in probability of reproduction and survival, used a more complex structure, more highly detailed age-specific vital rates, and data from a slightly different (though largely overlapping) set of years. The similarity of estimated growth rates from the two efforts may occur because adult survival rates, which are theoretically key drivers of population growth, are so stable across years and ages. The similarity also provides additional evidence that although individual heterogeneity in reproduction may be quite relevant to the study of life histories (Cam et al., 2013) and evolution (Bergeron et al., 2011), it appears less important to population growth, which is the integrated result of animals with diverse vital rates; at least for a large, long-lived vertebrate that produces a single offspring per year.

Although there were small differences among estimated elasticities across the different scenarios, the primary result remained the same. The elasticity analysis suggests that survival and development of young individuals and reproduction of 11- to 13 year olds are most important to population growth (Fig. 2-3). The higher elasticities observed for average and near average individuals are likely due to the high proportion of these individuals in the population and the relative rarity of individuals with very high individual random effects. Additionally, we found the highest elasticities observed were for individuals with random effects just below average, which can be explained by the negative correlation between reproduction and survival, where individuals that are slightly below average probabilities of reproducing, have slightly above average probabilities of survival. The importance of young individuals in the survival and development kernel reflects the large number of young individuals in the stable-age distribution and the poor survival of these age classes. The high elasticity of λ to changes in the fecundity kernel for 11- to 13-year-olds is interesting because these ages do not make up a large portion of the stable age distribution and reproductive values peak at 4-years old. Instead, most females have recruited to the population by 10-years-old and so the greatest number of breeders is observed for ages between 11- and 13-years and explains the high elasticity among these ages. There were a few notable differences between the scenarios. We found that as the proportion of below-average individuals increased in the population, the elasticity values for $\text{skips}_{\text{present}}$ in the survival and development kernel increased. This seems to reflect the fact that below-average individuals spend less time in the experienced breeder state, therefore making the skip breeder state more important to λ. Although the few differences in population metrics between scenarios reflect individual variation in reproduction and survival, these differences did not lead to substantial changes in λ.

Our finding that the distribution used for individual heterogeneity in reproduction had little consequence for λ differs from results of previous research at the individual level that identified a difference in the number of potential pups produced by above-average and below-average mothers. Above-average female Weddell seals are predicted to produce approximately twice as many pups when compared to below-average females (Chambert et al., 2013; Paterson et al., 2018). However, the numbers of pups are quite modest with an estimated difference of approximately four pups of which half are daughters. Therefore, above average mothers only produce a few extra offspring which can matter when evaluating lifetime reproductive output and for individual fitness, but there are very few individuals with a high random effect for reproduction in the population and those individuals are limited to producing a single offspring each year. Further, only about 20% of those pups will survive to adulthood and eventually recruit to the breeding population (Garrott et al., 2012). Given the energetic trade-off between survival and reproduction for a long-lived mammal that incurs large energetic costs when raising offspring, it is likely few mothers can maintain high survival and reproduction throughout life (Hamel et al., 2010). Therefore, *ih* in reproduction is also limited by the need of mothers to protect their own survival. Our results quantify the influence of *ih* in probability of reproduction on λ and add to the limited empirical evidence on the topic.

The results from this study may be explained by the canalization hypothesis that states that those life-history traits most important to individual fitness and population growth are buffered against environmental (Gaillard & Yoccoz, 2003) and genetic perturbations (Stearns & Kawecki, 1994). Previous work from this population has found evidence for environmental canalization (Rotella et al., 2012). Specifically, survival rates of adults were strongly buffered against temporal variability and probability of reproduction was least buffered against temporal variability. This previous work aligns with our finding that the survival and development kernel had a much higher elasticity compared to the reproduction kernel and appears to be much more important to population growth. The canalization hypothesis also helps to explain why we did not see much change in the population growth rate when including different distributions for individual heterogeneity in the probability of reproduction. We posit that in populations where canalization occurs, changing the distribution for the trait that shows large unobserved individual heterogeneity will not lead to a substantial shift in λ, because it is less important to population growth and therefore more variable. Following this thought pattern, the vital rates that exhibit more individual heterogeneity should be linked to the life-history of the species. Recent work that found that *ih* in survival was lower in species with a long generation time compared to species with a short generation time (Péron et al., 2016) provides evidence for a relationship between life-history strategy and individual heterogeneity. Our results and those for other long-lived mammals (Coulson, 2012; Plard et al., 2015) provide support for the idea that canalization is related to influence of the observed *ih* on population dynamics in many species. This would suggest that the inclusion of *ih* in population models may not result in large changes to population dynamics, even if this *ih* is important at the individual level.

This study advances our understanding of population dynamics of the Weddell seal and adds to the limited literature regarding the influence of *ih* on population dynamics. As our understanding of this population grows there are multiple avenues through which future work can build upon this research. This population has remained at a consistent size for much of the study duration, but recent increases in pup production (J. Rotella, unpublished data) provide a future opportunity to investigate any differences between the estimated asymptotic population growth rate and current population trends. Our estimate of λ that suggests a shrinking population was based on vital rates for local females, therefore both the historical stability of the population and more recent increases in pup production may be partially driven by immigration. Changes to population structure either through direct disturbances or through perturbations to vital rates can also create unstable short-term adjustments to the population growth rate resulting in a difference in the long-term population size compared to that resulting from a population at a stable state, which is considered population inertia (Koons et al., 2007; Stott et al., 2011). Large birth cohorts in the late 1990's and high recruitment to the breeding population of these cohorts (Garrott et al., 2012) may have provided the perturbation for population inertia away from the stable population size (Koons et al., 2007). Using transient life table response experiments, a recent study of a Cuvier's beaked whale (*Ziphius cavirostris*) population found that temporal variation of realized population growth rates was largely due to changes in immigration and population structure (Tenan et al., 2023). In the future transient life table response experiments may be useful for understanding the contribution of vital rates and population structure to observed population dynamics (Koons et al., 2016).

Our IPM was density-independent but recent increases in pup production may present the opportunity to investigate which vital rates might be density dependent. For long-lived vertebrates, juvenile survival and reproductive rates are predicted to change more readily as populations reach high densities (Eberhardt, 2002), but in Soay sheep there is evidence that population responses to density can interact with weather and the population structure (Coulson et al., 2001) indicating potentially more complex patterns of density dependence in long-lived vertebrates. Therefore, understanding the relationship between density dependence, population structure and environmental variables will be important to incorporating density in future IPMs. Theoretical work suggests that including density dependence in reproduction for our models would not have changed our findings because heritability (when included) was weak and *ih* in survival rates is quite small (Stover et al., 2012). Additionally, research regarding environmental canalization in ungulates has demonstrated that selection associated with population density and selection associated with environmental variation result in similar patterns of demographic variation (Gaillard & Yoccoz, 2003). Therefore, density dependence can be treated as a type of environmental variation (Gaillard et al., 2000; Gaillard & Yoccoz, 2003).

In the future, the role of individual heterogeneity to population dynamics for this population may need to be reexamined. As this study continues to accumulate information regarding reproductive output of daughters it may be worthwhile to update estimates of heritability in reproductive rates. If heritability is found to be different from prior estimates it would be worthwhile to re-evaluate the current study as greater heritability might increase the effect of individual heterogeneity on the population growth rate (Kendall et al., 2011). Although recent work found little *ih* in survival rates (Paterson et al., 2018), variation in survival could increase in the future as a result of environmental shifts due to a reduction in land-fast sea ice (Fraser et al., 2021) and sea ice extent (Parkinson, 2019) in the Ross Sea region or increased population density. The influence of *ih* in survival on population dynamics should be re-evaluated in future work if evidence for increased variation in survival rates is found. Although opportunities exist to re-evaluate the current study in the future, the population model used reflects the most important processes known to act on the population and adds to our understanding of the consequences of *ih* to population dynamics.

Although the presence of individual heterogeneity in demographic rates remains important to many questions in ecology (Hamel, Gaillard, & Yoccoz, 2018; Jenouvrier et al., 2018), our results suggest *ih* is less important to population growth, for a long-lived species, and are in agreement with previous work (Plard et al., 2015; Vindenes & Langangen, 2015). Our work adds to previous research (Coulson, 2012; Plard et al., 2015) that *ih* in reproduction and survival has little influence on population dynamics for long-lived mammals that generally produce few offspring in a reproductive event and exhibit low levels of *ih* in survival. Given the differing effects of individual heterogeneity in survival (Péron et al., 2016), and *ih* in a phenotypic trait (Plard et al., 2016) on λ along the fast-slow life history continuum, we speculate that the effects of *ih* in vital rates on population dynamics may differ according to life-history. It may also be the case that, due to canalization, in nature the observed *ih* in vital rates may not be important to population growth because higher levels of *ih* occur in the vital rate that λ is least sensitive. The current research focusing on the influence of observed *ih* in vital rates on population dynamics is dominated by long-lived species. Additional empirical studies that assess the influence of observed *ih* on population dynamics across the spectrum of slow-fast life histories is needed to determine if the influence of *ih* on population dynamics varies across the slow-fast life history continuum. It will be especially important that future work assess the influence of observed *ih* on population dynamics as it will clarify whether canalization reduces the influence of *ih* on population dynamics.

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Table 2-1. Regression equations used to calculate the probability of recruitment, reproduction, and survival for females that had previously recruited to the breeding population. Basis splines were used as the functional form for age specific changes in vital rates.

Vital rate	Model
Survival	$logit(s) = state\ intercept.phi + f(age) + \varepsilon_{ih}^{\varphi} + \varepsilon_{year}^{\varphi}$
Recruitment	$logit(rec) = f(age) + \varepsilon_{year}^{\psi_{PB}}$
Reproduction	$logit(r) = state\ intercept.psi + f(age) + \varepsilon_{ih}^{\psi} + \varepsilon_{year}^{\psi}$

Table 2-2 Reproductive state at time t+1 (columns) given reproductive state at time t (rows). Ψ is the reproduction probability, γ is the probability of temporarily emigration, and ρ is the probability of returning from the temporary emigration state.

	Pre-Breeder (PB)	First-Breeder (FB)	Experienced Breeder (EB)	Skip-present (SP)	Skip-absent (SA)
PB	$\mathbf{1-\Psi^{FB}}$	$\mathbf{\Psi^{FB}}$	0	0	0
FB	0	0	$(\mathbf{1-\gamma^{FB}})\mathbf{\Psi^{FB}}$	$(\mathbf{1-\gamma^{FB}})(\mathbf{1-\Psi^{FB}})$	$\mathbf{\gamma^{FB}}$
EB	0	0	$(\mathbf{1-\gamma^{EB}})\mathbf{\Psi^{EB}}$	$(\mathbf{1-\gamma^{EB}})(\mathbf{1-\Psi^{EB}})$	$\mathbf{\gamma^{EB}}$
SP	0	0	$(\mathbf{1-\gamma^{SP}})\mathbf{\Psi^{SP}}$	$(\mathbf{1-\gamma^{SP}})(\mathbf{1-\Psi^{SP}})$	$\mathbf{\gamma^{SP}}$
SA	0	0	$(\boldsymbol{\rho})\mathbf{\Psi^{SA}}$	$(\boldsymbol{\rho})(\mathbf{1-\Psi^{SA}})$	$\mathbf{1}-\boldsymbol{\rho}$

Table 2-3 The resulting population metrics from each distribution scenario evaluated in the IPM for the random effect of individual on reproduction: no individual heterogeneity (No IH), observed individual heterogeneity (Observed), a population skewed below average (Low RE), and a population skewed above average (High RE). Shown is the IPM run with the mean parameter estimates from the breeder demographic model with the upper and lower bounds of the 95% highest density interval shown in parentheses.

Scenario	λ	R_0	T_c
Low RE	0.968 (0.684, 1.056)	0.610 (0.004, 2.864)	14.10 (13.8, 18.4)
Observed	0.967 (0.682, 1.056)	0.605 (0.003, 2.886)	14.0 (13.9, 18.4)
No IH	0.968 (0.681, 1.056)	0.611 (0.003, 2.789)	13.9 (13.9, 17.97)
High RE	0.966 (0.678, 1.057)	0.598 (0.003, 2.95)	13.8 (13.9, 19.3)

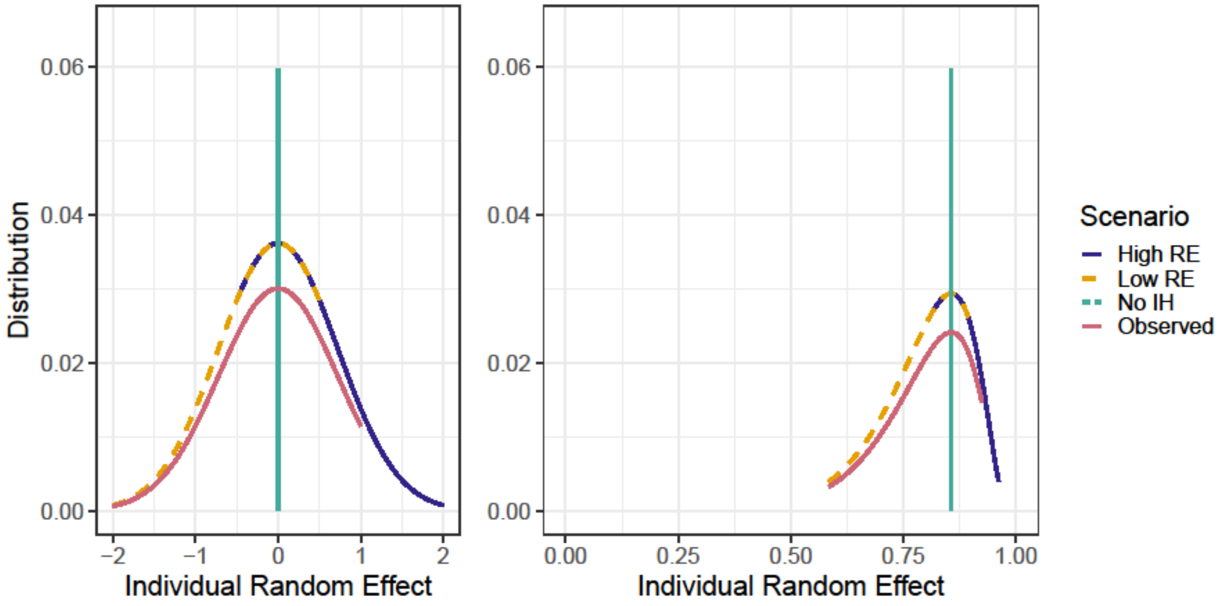

Figure 2-1 Distributions evaluated in the IPM for the random effect of individual on reproduction include: no individual heterogeneity (No IH), observed individual heterogeneity (Observed), a population skewed below average (Low RE), and a population skewed above average (High RE). The distribution of individual random effects is shown on the logit scale (left) and the probability scale (right) centered on the mean breeding probability.

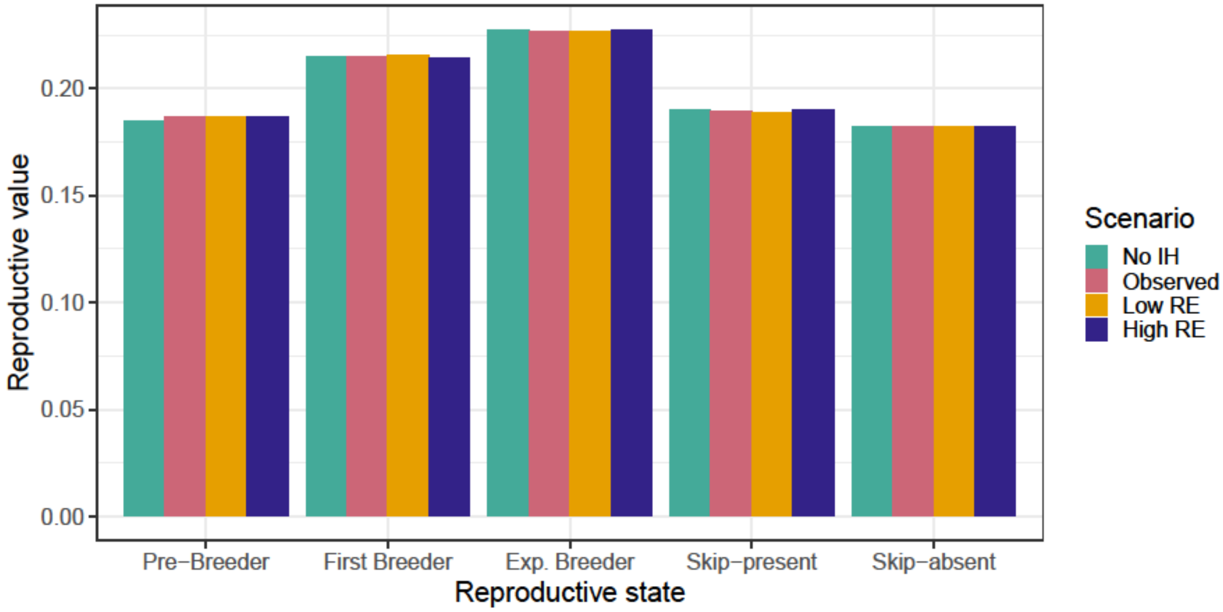

Figure 2-2 Estimated reproductive value partitioned by scenario and reproductive state. The distribution scenarios evaluated in the IPM for the random effect of individual on reproduction include: no individual heterogeneity (No IH), observed individual heterogeneity (Observed), a population skewed below average (Low RE), and a population skewed above average (High RE).

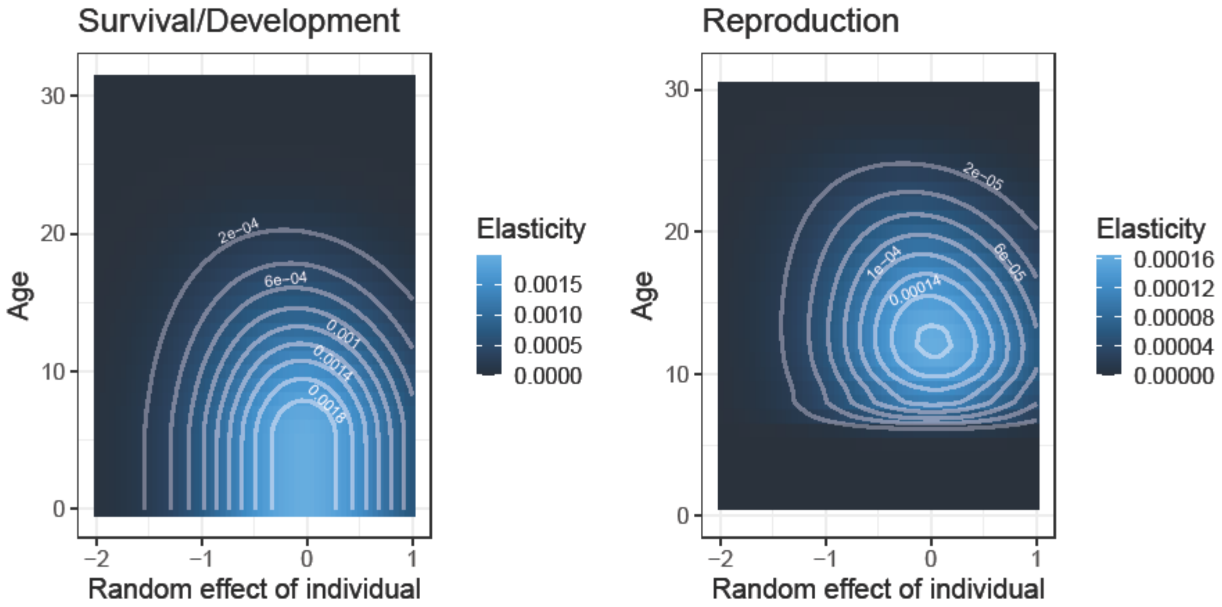

Figure 2-3. Estimated elasticities for the Observed scenario partitioned by age and individual heterogeneity for (left) the survival and development kernel and (right) the reproduction kernel.

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CHAPTER THREE

A COMPARISON OF SEX-SPECIFIC SENESCENCE PATTERNS IN A LONG-LIVED MARINE MAMMAL

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

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Contributions: Contributed to the development of research, managed and coordinated the study, and contributed to writing

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Contributions: Contributed to the data analysis

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Abstract

The lifetime fitness of an individual is determined by the integrated results of survival and reproduction. Improving our understanding of variation in survival senescence within and between species will therefore provide greater insight into the evolution of different life history strategies. Survival is influenced by multiple factors, consequently, variation in patterns of senescence is expected between individuals and sexes and across mating systems and the continuum of life histories strategies. To date there is little consensus regarding the mechanisms driving the evolution of sex differences in actuarial senescence, necessitating the need for studies of sex-specific senescence for species across a wide range of life histories. Here we used 37 years of data for 1,879 female and 1,474 male Weddell seals from Erebus Bay, Antarctica, to estimate and compare sex-specific patterns of survival rates using basis splines which allow flexible modeling of age-specific patterns. The Weddell seal is a species of long-lived mammal that displays moderate polygyny and little sexual size dimorphism, which makes it an unusual species compared to other long-lived mammals that share the polygynous mating system. We found that males had lower rates of survival throughout life and higher rates of actuarial senescence after early adulthood compared to females. These results add to our understanding of sex-specific survival rates in the species and contribute information for a long-lived, polygynous species that should aid in achieving a broader understanding of aging between sexes and across the tree of life.

Introduction

Patterns of senescence, the progressive deterioration of an organism that leads to a decline of fitness components with increasing age, may be driven by the optimization of energy allocation, reproductive schedules, background mortality rates, or a combination of these mechanisms (Monaghan et al., 2008; Lemaître et al., 2015). A large body of research has accumulated that suggests actuarial senescence, an increase in mortality with age (Ricklefs, 2010; Gaillard and Lemaître, 2017; Ronget and Gaillard, 2020) is common among many species (Promislow, 1991; Nussey et al., 2013; Jones et al., 2014). Patterns of senescence have been shown to vary interspecifically across the slow-fast continuum of life history strategies in birds and mammals (Jones et al., 2008). Intraspecific variation in patterns of senescence may occur across populations (Lemaître et al., 2013; Cayuela et al., 2020), different environments (Garratt et al., 2015) and sexes (Clutton-Brock and Isvaran, 2007). Of particular interest is the origin and evolution of sex differences in senescence. Although, there is evidence for a sex-bias in lifespan, there is less consensus regarding sex-differences in the onset and rate of actuarial senescence among mammals and more broadly vertebrates (Lemaître et al., 2020). Several hypotheses have been presented to explain the evolution of sex-bias in senescence stemming from evolutionary theories of senescence, but a dearth of studies and consistent evidence of sex-bias in senescence make this an open topic of research (Lemaître et al., 2015).

Three dominant theories have been put forth to explain the evolution of senescence. The mutation accumulation theory suggests that deleterious mutations accumulate at older ages due to increased baseline mortality as individuals age, which leads to weak selection against mutations arising at older ages (Medawar 1952). In an extension of the mutation accumulation theory, antagonistic pleiotropic genes that are deleterious in old age but contribute positively to survival and reproduction at young ages were posited to explain senescence (Williams, 1957). The disposable soma theory hypothesizes that irreparable damage accumulates to the soma due to the trade-off between allocating limited resources to self-maintenance, reproduction, and other activities and that optimal allocation of resources to these activities is based on the expected lifespan of an individual (Kirkwood, 1977; Kirkwood and Austad, 2000). More recently the disposable soma theory has been broadened beyond the cellular level and reinterpreted within the context of life history evolution suggesting that trade-offs in energy allocation throughout life may explain patterns of senescence (Baudisch and Vaupel, 2012; Lemaître et al., 2015; Gaillard and Lemaître, 2020). There is now an increasing understanding that the process of senescence can be explained by the latter three theories presented above (Lemaître and Gaillard, 2017; Gaillard and Lemaître, 2020).

Common among the evolutionary theories to explain senescence is the idea that reproductive effort early in life leads to greater declines in fitness traits at older ages. Based on this theory it is predicted that the rate and onset of senescence among individuals and species will be driven by patterns of reproduction, with the onset of actuarial senescence predicted to occur at the age of first reproduction (Williams, 1957; Hamilton, 1966). Reproduction schedules are shaped by resource demands of reproduction (gamete production and parental care), and sexual selection that drives mating strategies is therefore likely to account for variation in senescence patterns among species and drive observed differences between males and females within a species (Bonduriansky et al., 2008; Brooks and Garratt, 2017). Intense male combat for mating opportunities, a reproductive strategy in many species, is predicted to result in an accumulation of damage to the soma or increased energetic allocation and increased mortality earlier in life compared to females that do not engage in combat (Bonduriansky et al., 2008). Therefore, in species where males exhibit strong competition for mating opportunities or territoriality it is expected that males will experience an earlier onset or greater rate of actuarial senescence compared to females (Bonduriansky et al., 2008; Brooks and Garratt, 2017). Alternatively, it could be argued that in species where one sex provides a greater amount of energy towards parental care, often females in mammals (Gittleman and Thompson, 1988), that sex will show stronger senescence due to the greater resource demands of reproduction. There is some evidence for this hypothesis in monogamous bird species for which males provide more parental care (Pardo et al., 2013). Sexual size dimorphism is often associated with mating strategies and has also been offered as an explanation for sex-bias in senescence (Promislow, 1992; Loison et al., 1999). The larger sex must achieve a greater size through either more rapid development or a longer growth period, which likely comes at a physiological cost either in terms of an energetic trade-off or damage to the soma, and may lead to an earlier onset and/or higher rate of senescence (Marais et al., 2018; Lemaître et al., 2020). The sex hormones that mediate sex-specific differences in reproduction may also contribute to sex differences in actuarial senescence (Brooks and Garratt, 2017). Testosterone has been assumed to lower survival of males through physiological costs such as reduced immunocompetence (Foo et al., 2017) or the behavioral changes it induces such as increased aggression and risk taking (Bonduriansky et al., 2008). In this regard the role of sex hormones in senescence can be linked to the antagonistic pleiotropy theory, although evidence suggests the role of testosterone in senescence may be more complicated (Metcalf et al., 2020). There are many explanations for how sex differences in senescence may arise, with predictions for a given species being strongly tied to the life history of the species and the relative energetic expenditures of each sex towards reproduction and somatic maintenance.

There is now an abundance of evidence for a sex-difference in lifespan in wild animals with many males exhibiting shorter lives compared to females in polygynous species (Lemaître and Gaillard, 2013), while males have similar or longer lives compared to females in monogamous species (Clutton-Brock and Isvaran, 2007). Evidence for a relationship between senescence and mating system is accumulating with results showing a stronger rate of actuarial senescence (Clutton-Brock and Isvaran, 2007) or earlier onset of senescence (Tidière et al., 2015) for males of polygynous compared to monogamous species although there is conflicting evidence for these predicted patterns (Lemaître et al., 2020). For example in polygynous, large herbivores, male wild boars (*Sus scrofa*) exhibit an earlier onset, but similar rate of actuarial senescence to females (Gamelon et al., 2014), whereas male red deer (*Cervus elaphus*) exhibit an increased rate but similar onset of actuarial senescence compared to females (Catchpole et al., 2004). A comparative study of large herbivores found that males exhibit shorter lifespans and a greater intensity of senescence but that different measures of male allocation to sexual competition were unrelated to patterns across species (Lemaître and Gaillard, 2013). A similar study of captive ruminants found that males in polygynous species experienced shorter lives and earlier onset of senescence compared to monogamous species and that the difference between sexes in rate of senescence was higher in tending species compared to harem holding and territorial species but unrelated to mating system (Tidière et al., 2015). There is also contrasting evidence for the relationship between mating system and sex-specific senescence among monogamous species. Male wandering albatross (*Diomedea exulans)* (Pardo et al., 2013) exhibit a higher rate of senescence compared to females. In contrast, in meerkats (*Suricata suricatta*) (Thorley et al., 2020) and Atlantic puffins (*Fratercula arctica)* (Landsem et al., 2023) there is no sex difference in senescence patterns following predictions laid out earlier. Based on the conflicting results regarding the origins of sex-differences in actuarial senescence, it seems likely that these differences might not be so easily explained by single measure such as mating system but may reflect the complex array of mechanisms that govern life histories and reproductive schedules.

Early work estimating and comparing sex-specific senescence patterns has relied on cross sectional data (Clutton-Brock and Isvaran, 2007), but cross sectional data can lead to misleading estimates of age-specific patterns in vital rates and longitudinal data is now considered ideal for estimating senescence patterns (Nussey et al., 2008, 2013). An accurate estimation of age-specific vital rates should not only be based upon longitudinal data but should also account for other sources of variation that might bias estimates. Individual heterogeneity is a potential source of variation that may bias the age-specific patterns in vital rates at the population level if not accounted for in models (Cam et al., 2002). An example of this bias has been shown to occur when the quality of individuals within a cohort varies and below average individuals disappear from the population earlier in life, resulting in an increase of the average quality of the population as the cohort ages (Vaupel and Yashin, 1985). This progressive disappearance can mask age-specific patterns in vital rates at the individual level (Forslund and Pärt, 1995; Péron et al., 2010). Empirical studies that use longitudinal data and can account for bias created by individual heterogeneity are needed to progress our understanding of the evolution of senescence.

Here we use long-term data from a population of Weddell seals (*Leptonychotes weddelli)* in Erebus Bay, Antarctica to estimate and compare sex-specific actuarial senescence. Weddell seals are a long-lived marine mammal that aggregate in breeding colonies during the austral spring to give birth and breed. Weddell seals are easily approached by humans and have high site fidelity, which allows individuals to be monitored throughout life. We estimate and compare the age-specific survival patterns of males and females from early life to death using multi-decadal data on large samples of animals individually marked at birth and monitored annually to better understand sex differences in patterns of actuarial senescence in this long-lived species that exhibits modest polygyny. We employ a modeling approach that provides greater flexibility in the shape of the relationship between age and survival than previous research from this population. Using longitudinal data on individuals we account for individual heterogeneity in vital rates using mixture classes, which results in estimation of within-individual patterns of aging. This modeling approach allows for accurate estimation of actuarial senescence that can be compared between sexes.

Weddell seals provide an interesting case study for investigating sex-specific actuarial senescence as they don’t strictly follow the general patterns of highly polygynous species. Weddell seals show modest polygyny with males defending underwater breeding territories (Harcourt et al., 2007a). Males use aggressive competition to retain positions under the ice, which is associated with large energetic demands and physical costs. Males lose up to 24% of their initial body mass over the breeding season (Harcourt et al., 2007b) and males are often found hauled out on the ice with lacerations to their body (Harcourt et al., 2007a). The reproductive strategies of male Weddell seals lead to moderate variance in successful siring of pups in any given year (Gelatt, 2001; Harcourt et al., 2007a). Given the polygynous mating system of Weddell seals and the male-male combat for mating opportunities one prediction is that male Weddell seals exhibit a higher rate of senescence compared to females. This higher rate could be due to greater energy allocation to reproduction through combat and territory guarding, continued damage to the soma from competition in accordance with the disposable soma theory, the physiological costs of testosterone in accordance with antagonistic pleiotropy or a combination of all three. The onset of senescence has been reported to occur at three years old in male Weddell seals (Brusa et al., 2020), and we predict that we will observe a similar onset in this study.

Weddell seals are a particularly interesting species in that attributes of the mating system and sexual size dimorphism do not clearly predict whether males or females will senesce more strongly. Contrary to the commonly observed male-biased, sexual-size dimorphism of polygynous species, Weddell seals do not exhibit strong sexual-size dimorphism (Hill, 1987; Harcourt et al., 2007b) with some early research suggesting that females may be slightly larger (Stirling, 1975). As capital breeders, reproduction is energetically intensive for females with mothers nursing pups for ~30-45 days while primarily fasting, resulting in ~34% of body mass loss over the course of lactation (Macdonald et al., 2020). Therefore, females are not only subject to the extreme energetic demands of gestation and lactation but also the energetic requirements of a similar body size to males. Given the large energetic requirements of females, an alternative prediction under the energy allocation theory of senescence is that females are subject to greater energetic demands and will exhibit a higher rate of actuarial senescence compared to males. Previous research estimating age-specific survival of females started modeling from the average age of first reproduction at age seven and found immediate declines in survival probability (Paterson et al., 2018). Therefore, the onset of actuarial senescence in females will likely occur between ages three and seven and we predict that it will occur later in this age range given very few females in this population give birth to a pup prior to age six.

Methods

Study Area and Population

This study focuses on a population of Weddell seals located in Erebus Bay, Antarctica (-77.62° to -77.87°S, 166.3° to 167.0°E) that has been monitored annually since 1969 (Siniff et al., 1977). Seals form pupping and breeding colonies each austral spring, from October-December, on the land-fast ice using perennial cracks that form from tidal movement to access the ice surface (Cameron and Siniff, 2004). Females give birth to pups starting in mid-October through November (Rotella et al., 2016) and remain with their pups for approximately five to six weeks to nurse (Stirling, 1969a). Males join the pupping colonies shortly after the pupping season begins to establish underwater territories and breed with females (Stirling, 1969a). Male and female Weddell seals in this population can become sexually mature at 3 years of age (Gelatt, 2001). Males have been recorded siring offspring as early as four years old (Harcourt et al., 2007a). The mean age of first reproduction for females is 7-8 years-old (Hadley et al., 2006), giving birth at five years of age is rare, and just a few females have given birth at four years of age.

Data Collection

Since 1968 Weddell seals have been individually marked in the hind flipper and resighted (Siniff et al., 1977). Since 1982 each pup born in the study area has been marked and most pups are marked within 1-2 days of birth (Garrott et al., 2012). Individuals with broken, worn, or missing tags have been retagged when encountered to preserve the annual live-encounter histories for known individuals. Six to eight study area wide resighting surveys have been conducted each year approximately 3-5 days apart starting in early November since 1973 (Cameron and Siniff, 2004). All animal handling activities were approved by NOAA National Marine Fisheries Service (permit number: 21158 and previous permits) and the Institutional Animal Care and Use committee of Montana State University (protocol number: 2017-11 and previous permits). The extensive mark-resight efforts allow ages to be known for virtually every individual born in the study area. Weddell seals exhibit strong adult philopatry to Erebus Bay if they were born to this population (Cameron and Siniff, 2004; Hadley et al., 2007). Pre-breeding females, mothers with pups, females on sabbatical from reproduction, as well as males are all detected at high rates in the study area over the course of multiple surveys (Cameron and Siniff, 2004; Rotella et al., 2009; Brusa et al., 2020).

Data Analysis

We constructed extensions of Cormack-Jolly-Seber (CJS) models using a Bayesian framework to estimate age- and year-specific apparent survival and detection rates independently for males and females. CJS modeling cannot distinguish between death and permanent emigration so estimates of survival from populations where permanent emigration occurs will be biased low and the resulting survival estimates are considered apparent survival (Lebreton et al., 1992). Although the population is open to temporary emigration and possibly to low levels of permanent emigration (Cameron and Siniff, 2004; Chambert et al., 2015), Weddell seals display high philopatry to the Erebus Bay study area such that apparent survival estimates are expected to be quite close to estimates of true survival. We evaluated two competing model structures (see below) and estimates from the best-supported models were used for comparison between male and female Weddell seals. We compared patterns of estimated annual survival rates and rates of actuarial senescence, measured as the slope of change in survival rate with age (Ronget and Gaillard, 2020).

Due to low survival and detection rates of seals during the first few years of life the inclusion of an individual in the data set was conditioned on recapture of the individual at age 3 or older. With regards to age-specific variation in survival, we modeled survival with a spline function starting at age 3 years. To model age-specific patterns of survival and detection we used basis splines, which provide a flexible modeling approach that allows for a covariate to have a nonlinear relationship with the response variable and does not require any prior assumption about the shape of the relationship (Hastie and Tibshirani, 1990). The shape of the spline is determined by the data and is made up of segments that are connected by knots, or pivot points (Hastie and Tibshirani, 1990). The spline for age-specific survival included eight internal knots, placed at evenly spaced sample quantiles. The number of knots was chosen to allow a smooth flexible function without overfitting the relationship. Temporal variation in survival was accounted for by including a random effect for year (see below for specific model details).

Additionally, we evaluated whether there was support for heterogeneity in survival by adding a finite mixture of two survival classes to the basic survival model. Finite mixture models allow individuals with similar vital rates to be clustered together in a finite number of heterogeneity classes (Pledger et al., 2003). Random effects have previously been used to model individual heterogeneity in survival for this population (Paterson et al., 2018; Brusa et al., 2020), but this method assumes that individual intercepts are normally distributed, which can be violated if there is any clustering for the trait being assessed (Hamel et al., 2016), therefore we chose to use a finite mixture model to account for individual heterogeneity in survival. In the survival model individuals in the same heterogeneity class share an intercept.

We evaluated a base model for age-related variation in detection rates that included a basis spline identical to that used to model survival. We chose a spline to allow greater flexibility in age -related patterns of detection compared to the logarithmic functional form of age or age bin models previously used to model detection for males (Brusa et al., 2020) and females (Hadley et al., 2007; Rotella et al., 2012) in this population. We also evaluated a model that included heterogeneity in detection by adding a finite mixture of three detection classes to the base detection model. In both models a random effect for year was included to account for temporal variation in detection.

Model convergence was assessed using visual inspection of trace plots, the potential scale-reduction factor (Gelman and Rubin, 1992), and the Geweke diagnostic with the R package ggmcmc (Fernández-i-Marín, 2016). Model selection was carried out using the Watanabe-Akaike Information Criterion (WAIC) a fully Bayesian information criterion, based on the posterior predictive distribution (Watanabe, 2010; Hooten and Hobbs, 2015). Additionally, WAIC is appropriate for model selection when evaluating hierarchical and mixture models (Watanabe, 2013; Hooten and Hobbs, 2015). We fit all models in the R computing environment (R Core

Team, 2023) using the package NIMBLE (de Valpine et al., 2017, 2023). All regression coefficients on age for survival and detection, along with the survival intercept were assigned weakly informative priors. The prior for proportion of individuals in each heterogeneity class was assumed to come from a uniform Dirichlet distribution. Random effects of year were assumed to be normally distributed around a mean of zero with unique standard deviations. Standard deviations for random effects of year were assigned weakly informative priors $N(0, 2)$, truncated above zero to be positive values. Three chains were run for 240,000 iterations each with every fifth sample saved for posterior predictions resulting in 48,000 samples from each chain. The first 12,000 iterations of each chain were removed as burn-in. Due to the large number of dependent nodes in the model that are used to calculate a WAIC score, every 20th sample was saved to the posterior distribution and subsequently used to calculate a WAIC score resulting in a posterior of 9,000 samples per chain after a burn-in of 3,000 for a total of 27,000 samples.

Goodness of fit was evaluated for the most supported model using posterior predictive checks (Gelman et al., 2013; Conn et al., 2018). For each of the 6,000 iterations from the posterior distribution used to calculate WAIC, we calculated survival and detection probabilities for each individual in each year using the estimated parameters. Binomial trials were conducted for each individual in each year using the predicted probabilities to simulate whether an individual survived from one season to the next and was detected if alive. These 6,000 simulated data sets were then summarized by age class, and the number of individuals seen at each age was then compared to the corresponding number in the actual field data. The four age classes used for posterior checks corresponded to four biologically relevant periods of life. Early life (3-6 years), recruitment ages (7-12 years), prime reproductive ages (13-20 years), and late life (21 years and older). We calculated the Bayesian P-value as the proportion of simulated data sets for which the number of detected individuals in an age class was equal or greater than that observed in the data providing a measure of how well the most supported model predicted observed encounter histories. Bayesian P-values were above 0.90 for females during the early life period, but within an acceptable range for all other periods of life for males and females (0.33-0.80), which included the ages of interest for making inferences regarding senescent patterns. The overestimate of females seen during early life could be a result of overestimating detection or survival probabilities, but it occurs during a time when survival is quite high and senescence is quite weak.

Results

We used capture-mark-recapture encounter histories from 1,474 male and 1,879 female Weddell seals tagged as pups between 1982 and 2018 to model vital rates. Seals were monitored through 2019 at which point our data included 6,159 observations for males and 12,191 observations for females after birth. The maximum age recorded was 28 years for males and 31 years for females. Encounter histories for individual males ranged from one observation (n=386) to 17 observations (n=4), and females ranged from one observation (n=336) to 27 observations (n=2).

Parameter estimates are represented by the mean of the posterior distribution and are presented on the probability scale unless otherwise noted. Results are presented with 89% highest density intervals (Meredith and Kruschke, 2020). Survival rates can be biased low if marks are lost throughout the study period (Arnason and Mills, 1981). Estimated tag-retention rates ($\hat{\theta}$) for the study population are quite high with the probability of retaining at least one tag being 0.989 for adult females and 0.982 for adult males (Cameron, 2001; Cameron and Siniff, 2004). Survival rate estimates presented below are corrected for tag loss using the adjustment equation $\hat{\varphi}_{adj} = \frac{\hat{\varphi}}{\hat{\theta}}$ (Arnason and Mills, 1981).

The model that received the most support for both males and females included splines to model age- specific survival and detection as well as a mixture of two survival classes and three detection classes (Table 3-1). A large proportion of individuals were estimated to be in the high survival class, 0.75 (0.58, 0.98) of females and 0.88 (0.75, 1.0) of males.

Table 3-1 Model selection results for male and female survival and detection models.

Female	WAIC	ΔWAIC	Male	WAIC	ΔWAIC
$\boldsymbol{\varphi_{spline,2-mix}; p_{\mathrm{spline},3-mix}}$	**15111.09**	**0**	$\boldsymbol{\varphi_{spline,2-mix}; p_{\mathrm{spline},3-mix}}$	**13726**	**0**
$\varphi_{spline}; p_{\mathrm{spline}}$	16745.51	1634.42	$\varphi_{spline}; p_{\mathrm{spline}}$	14366.05	640.05

Patterns of age-specific survival were similar between male and female Weddell seals early in life before diverging and provided clear evidence of senescence. Annual apparent survival for females was estimated to be highest at three years old with survival estimated to be 0.98 (89% HDI: 0.96, 1.0) for individuals in the high survival class and 0.72 (0.47, 0.85) for the low survival class. Estimates of male survival are lower than females for all ages although the highest density intervals for each sex moderately overlap from ages 3-14 years (Fig. 3-1). Apparent survival of males is estimated to be highest at 6 years old, 0.96 (0.94, 0.97) for the high survival class and 0.55 (0.17, 0.90) for the low survival class. This indicates onset of senescence for females is at 3 years old and males at 6 years old, although the highest density intervals widely overlap point estimates at younger ages so it's possible the age of onset of senescence may be earlier or later. Earlier in life senescence was stronger in females, but after 12 years of age, senescence in males becomes stronger whereas the rate of decline for females was slight from age 12 to 19 (apparent survival at 12 years ($\hat{\varphi}_{12yo}$)= 0.94 [0.92,0.97]; $\hat{\varphi}_{19yo}$ = 0.88 [0.87, 0.91]). Female senescence in survival rates accelerated with rates declining steadily from age 20 years through the oldest age of 31 years old. In contrast, survival rates for males continued to decline in steady fashion from ages 12 to 19 ($\hat{\varphi}_{12yo}$ = 0.92 [0.90, 0.94]; $\hat{\varphi}_{19yo}$ = 0.82 [0.78, 0.86]). Males experience an acceleration in senescence after age 19 years old as well with apparent survival declining more rapidly to the oldest observed age of 28 years.

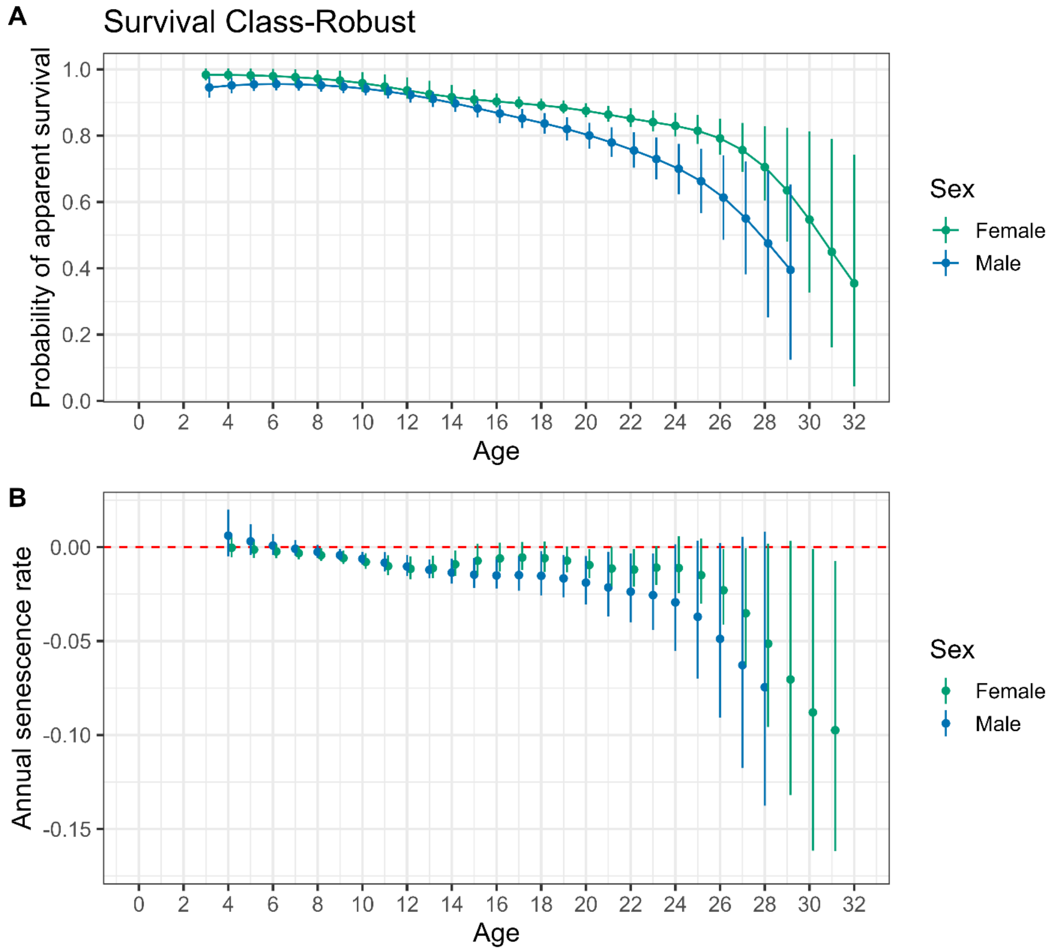

Figure 3-1 Comparisons of male and female A) probability of apparent survival for ages observed and B) calculated rate of senescence between each age, with the dashed red line representing no change in probability of survival. Error bars represent 89% highest density intervals.

Detection of males and females increases steadily from age three years to 12 years before stabilizing and declining at the oldest ages (Supplementary Information). Male detection was estimated to be lower than females with larger uncertainty surrounding estimates of detection probability at young and old ages. There was support for individual heterogeneity in probability of detection with most females being assigned to the high detection class and most males being assigned to the average detection class (Supplementary Information). There was much greater annual variation in probability of detection compared to survival. Annual variation in probability of survival was low and ranged from 0.94 (0.91, 0.97) to 0.91 (0.82, 0.95) for a 12-year-old female and between 0.94 (0.91, 0.97) and 0.79 (0.69, 0.91) for a 12-year-old male (Fig. 3-2). Annual variation in detection was greater than survival with probability of detection ranging from 0.99 (0.99, 1.0) to 0.67 (0.62, 0.72) for a 12-year-old female and 0.94 (0.90, 0.98) to 0.43 (0.35, 0.52) for a 12-year-old male.

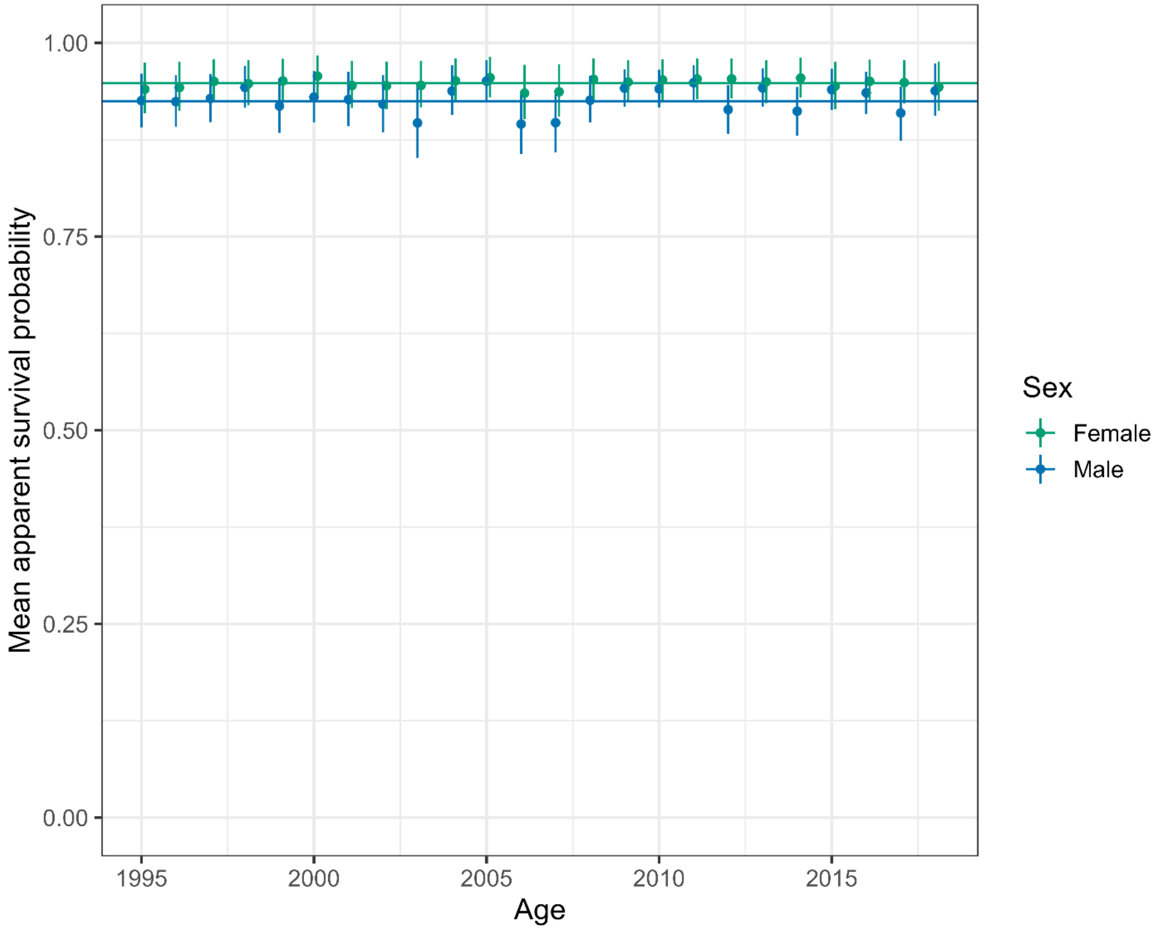

Figure 3-2 Annual variation in probability of apparent survival for a 12-year old male (blue) and female (green). Horizontal lines represent survival probability with a random effect of year equal to zero. Only years for which the survival probability of a 12-year old individual could be estimated are included. Error bars represent 89% highest density intervals.

Discussion

Using data from a long-term mark recapture study of Weddell seals, we confirmed predictions of sex-specific patterns of actuarial senescence for a moderately polygynous species. Our research built upon previous work from this population that estimated actuarial senescence in males (Brusa et al., 2020) and compared senescence patterns to those estimated for females after age of first reproduction (Paterson et al., 2018). We calculated age-specific survival probabilities of individuals recaptured at age three years or older for males and females separately and used basis splines, a more flexible modeling approach that does not force age specific survival to take a certain shape. These methods allowed us to make a full comparison of male and female senescence patterns and place the results within the context of evolutionary theories for senescence.

Our findings broadly align with previous work from this population. We found that male and female Weddell seal survival probabilities peak around the age of sexual maturity and that there are some differences in the rate and pattern of senescence between the sexes, similar to previous work from this population (Brusa et al., 2020). Our estimate of peak male apparent survival is 0.96 (0.94, 0.97) at six years old for an individual in the high survival class which is a slightly higher probability of survival and later age of onset of senescence compared to the previously reported estimate of 0.94 (95% CI: 0.92, 0.96) at two years old (Brusa et al., 2020). We found that females exhibited a decline in probability of survival from ages 3-6 years old compared to the estimated increase in probability of survival for males adding to our understanding of survival patterns for females prior to the average age of first reproduction, although the highest density intervals are wide enough for the potential of different patterns to those shown by point estimates. We found a near plateau in probability of survival for females between the ages of 12 to 19 years old, which is different from results of previous work that found more rapid declines in survival during these ages (Paterson et al., 2018). It is important to note that previous estimates of age specific survival for females only included females that reproduced at least once in their lives and also accounted for breeding state and temporary emigration (Paterson et al., 2018). To make estimates for females and males as comparable as possible, we did not account for breeding state or temporary emigration in the female model and it's possible that not accounting for these state transitions may have resulted in a plateau. If a greater proportion of females skipped reproduction between the ages of 12 to 19 years old and therefore avoided survival costs of reproduction this might result in the plateau of survival probabilities, we observed. However, the explanation that the absence of state transitions accounts for the plateau in survival probabilities seems unlikely given that females exhibit a peak in probability of reproduction during these ages (Paterson et al., 2018).

The onset of senescence is estimated to be slightly earlier for females occurring between ages of three and four years old, compared to ages between six and seven years old for males. The onset of senescence for females occurs at the age of first ovulation recorded in the literature (Gelatt, 2001) although our records indicate it is very rare for individuals in our study population to begin reproduction at this age. For females the age of onset occurs several years earlier than the mean age of first reproduction which is estimated to be approximately seven years old for females (Hadley et al., 2006; Paterson et al., 2018). The estimated onset of senescence for males does coincide with the approximate age when males have been recorded competing for territories (Gelatt, 2001). Interestingly, males as young as four years are known to have sired pups

(Harcourt et al., 2007a), so the average age that onset of senescence occurs is after the age of sexual maturity, perhaps because a small proportion of young males actually attempt to sire pups at such ages. It is notable that while males and females can become sexually mature at the same age, there is a difference in the onset of senescence. There is now evidence that predictions for the onset of senescence at reproductive maturation do not hold in all species (Gaillard and Lemaître, 2017), and others have found the onset of senescence to be plastic (Hammers et al., 2013). Given that Weddell seal females exhibit a large range in the age of first reproduction (Hadley et al., 2006), our findings suggest that the onset of reproduction may be related to age at first breeding and not to the age at which individuals become reproductively mature. Changes in the probability of survival from ages three to ten years are quite small for both males and females so although there is a small difference in onset of senescence between sexes the pattern of senescence appears to be quite similar during this early life period. Our findings suggest that onset of senescence may be related to the age of first reproduction but that the costs to survival of sexual maturity and first reproduction are likely low given the small declines in survival rates during the early reproductive years.

We found that the senescence rate of males and females diverge around 12 years old (Fig. 1). Male survival probabilities continue to decline at an increasing rate, but females show a diminished rate of senescence with a near plateau in survival probabilities from ages 12-19 years. This pattern of a decline in mortality rate during prime ages after age of first reproduction has been exhibited in other large mammals, and it’s hypothesized that this is due to risk avoidance by females whereby they modify reproductive effort in response to environmental conditions (Gaillard et al., 2003). Our findings are in agreement with this hypothesis as Weddell seal females will often skip reproduction every few years or during environmentally challenging conditions, which may allow them to avoid energetic costs of reproduction and provide the chance to focus energy on somatic maintenance (Chambert et al., 2013, 2015). The population of individual females greater than 11 years old will be made up of nearly all experienced breeders (Hadley et al., 2006) therefore, it may be that females are able to slow the rate of senescence during prime age due to reproductive experience and improved energetic efficiency during lactation (Macdonald et al., 2020), freeing up resources for somatic maintenance. Additionally, there is evidence that non-reproductive adult female Weddell seals carry higher blood oxygen stores compared to males, which translates to a slight increase in the calculated aerobic dive limit (Hindle et al., 2011). The aerobic dive limit can constrain the time and efficiency of foraging for animals that forage underwater (Hindle et al., 2011), and it is possible this difference in oxygen stores may contribute to the observed differences in survival rates of males and females at these prime ages.

Unlike females, males exhibit intense competition for access to mating opportunities, with competition often resulting in deep lacerations to the body (Harcourt et al., 2007a). During the mating season males can lose almost a quarter of their body mass (Harcourt et al., 2007b) likely because they are allocating more energy to competition and foregoing opportunities to forage in order to spend more time defending mating territories. Therefore, an explanation for increased rate of senescence of prime age males may be in line with the energetic allocation hypothesis (Bonduriansky et al., 2008). It seems that while energetic allocation towards mating and not somatic maintenance may play a part in the rate of senescence for males during this period the mass loss of males is much lower to that of females and so energetic allocation alone likely does not fully explain the increased rate of senescence compared to females in the prime and old ages. Another mechanism that might explain the increased senescence of males compared to females during prime ages may be that of reduced immune response of males due to increased testosterone production of sexually mature males (Metcalf et al., 2020; Tidière et al., 2020). As males accumulate mating seasons, they accumulate damage from successive years of competition with other males. Therefore the increased rate of senescence for males, especially at older ages, may be due to the accumulating deterioration of the soma from the damage of competition, and reduced energetic allocation towards somatic repair combined with reduced immune response (Bonduriansky et al., 2008).These explanations would be in line with the disposable soma theory of senescence but also implicate antagonistic pleiotropy if reduced immune response of males contributes to their stronger rate of senescence during this period.

We found evidence that senescence rates of males and females increase after 19 years of age. Males show strong increases in senescence rates after 19 years old whereas for females the increase in senescence rate is more moderate out to 25 years old at which point the rate of senescence occurs more rapidly. The increase in rate of senescence for both males and females is not surprising as damage to the soma and accumulation of mutations at older ages is expected based on evolutionary theory (Williams, 1957; Kirkwood, 1977; Kirkwood and Austad, 2000; Baudisch and Vaupel, 2012). Results from a physiology study suggests a potential mechanism behind the faster rate of senescence exhibited by older males. While older female and male Weddell seals (ages 19+ years) both show muscular senescence, males also exhibit lower densities of myofiber compared to females, which was hypothesized to be the result of elevated muscle stress due to competition for mating territories (Hindle et al., 2009). Evidence for muscular senescence (Hindle et al., 2009) and advanced tooth wear (Stirling, 1969b) at older ages suggest physical wear and tear may reduce foraging efficiency and the ability to maintain breathing holes at old ages, which could potentially reduce survival rates of both sexes.

Our finding that male survival was lower than females throughout life and that the maximum observed male lifespan was three years shorter than for females aligns with results from the literature for a species that displays a polygynous mating system (Lemaître and Gaillard, 2013; Tidière et al., 2015; Gaillard and Lemaître, 2020). This result also aligns with life history theory that predicts in species where the burden of sexual reproduction is greater or variance in reproductive success is lower for females, males are expected to sacrifice longer lifespans for greater mating success, while females adopt more low-risk strategies that allow greater reproductive success over a longer time (Bonduriansky et al., 2008). Sexual selection is not only predicted to be a driver of observed lifespan but also contribute to sex differences in senescence patterns.

We generally found support for the hypothesis that sex differences in senescence rates of Weddell seals could be explained by sexual selection. We found that males had lower probabilities of survival throughout life and a higher rate of senescence compared to females after the age of 12 years old. As part of sexual selection, sexual size dimorphism is considered a potential driver behind sex differences in senescence rates but we found no evidence to support this hypothesis given there is little difference in size between the sexes (Stirling, 1975; Hill, 1987; Harcourt et al., 2007b), and still found that males exhibited stronger actuarial senescence after early adulthood. Instead our results match predictions that for a species with high sexual competition the competing sex will experience increased senescence and mortality due to maintenance of sexual traits (Bonduriansky et al., 2008). It also seems possible that the optimal energetic trade-off between somatic maintenance and reproduction as described by the disposable soma theory may drive some of the sex differences in senescence found here. For example, female Weddell seals loose a larger proportion of their mass over the course of lactation mobilizing a great energetic investment into reproduction (Macdonald et al., 2020) but females also display a flexible, risk averse reproductive tactic, skipping reproduction to regain body reserves (Chambert et al., 2013, 2015). Males appear to lose less mass over the course of the breeding season compared to females, but males may also show less flexibility in competition for mating opportunities, putting forth energy towards competition and reproduction on an annual basis accumulating damage to the soma. It is not currently known if males show a more flexible pattern of reproduction, skipping mating and the necessary competition in some years, but a better understanding of the relative amount and timing of reproductive effort expressed by each sex should shed some light on this question.

Although our results generally follow predictions for a moderately polygynous species, some interspecific comparative studies have not found that this theory explains variation across species (Tidière et al., 2015; Lemaître et al., 2020). Instead, authors suggest that sex differences in aging rates may be due to a complex interaction between environment and sex-specific reproductive costs (Lemaître et al., 2020). This interaction between environment and sex-specific reproductive costs may be at play in Weddell seals as males adopt the risky behavior of fighting for mating territories accumulating wounds and within the potentially pathogen rich environment of a seal colony this may lead to a greater rate of senescence. Sex specific differences in senescence have been hypothesized to be driven by sex differences in response to pathogens

(Tidière et al., 2020). Blood samples from this population during the breeding season show evidence of increased indicators of stress and lower levels of nourishment in males (Mellish et al., 2011). Additionally, tooth wear increases with age in this species and infections from tooth abscesses have the potential to be fatal especially in conjunction with pre-existing conditions and may affect a seals ability to maintain breathing holes (Stirling, 1969b). This evidence in conjunction with some evidence for reduced immune response of males linked to testosterone levels (Metcalf et al., 2020; Tidière et al., 2020) could also explain the increased rates of senescence we found for male Weddell seals.

Although our study cannot distinguish the mechanisms leading to sex differences in both longevity and strength of senescence of Weddell seals our results generally align with predictions that life history strategies, specifically sexual selection leads to greater senescence in the sex that competes for opportunities to mate and has less investment in offspring (Bonduriansky et al., 2008; Brooks and Garratt, 2017; Bronikowski et al., 2022) and with more recent suggestions that differences may arise from an interaction between sex-specific physiological pathways and environmental conditions (Lemaître et al., 2020). To further understand the mechanisms behind sex differences in senescence patterns of Weddell seals it would be useful to improve our knowledge regarding patterns of reproductive effort and understanding of the relationship between reproductive effort and survival for male Weddell seals. Currently, we cannot measure either reproductive effort or reproductive success of males because mating occurs in the water. Should this information become more easily measured in this species, perhaps through genomic methods, it would be useful to investigate survival costs of reproduction for males. Additionally, longitudinal physiology studies provide an opportunity to better understand physiologic pathways of senescence in the Weddell seal.

Our work adds to a growing number of studies that explore sex differences in survival senescence within a species (Pardo et al., 2013; Gamelon et al., 2014; Tompkins and Anderson, 2019; Fay et al., 2020; Thorley et al., 2020; Reichard et al., 2022) and can be used in the future to add to studies across species (Gaillard et al., 2003; Clutton-Brock and Isvaran, 2007; Lemaître and Gaillard, 2013; Tidière et al., 2015; Lemaître et al., 2020). These results suggest that for a long-lived, moderately polygynous mammal, differences in actuarial senescence between the sexes may be driven primarily by sexual selection, but that environmental conditions may also be involved. Given that explanations for patterns of sex-specific senescence across species lack consistent evidence there is a need for additional studies that include species across a wide range of different life-history strategies. It seems that within mating systems the sex differences in amount and timing of energetic allocation towards reproduction may be quite different across species and may explain why sex-specific senescence rates cannot be fully explained by the mating system itself. Clearly more work is needed to elucidate the mechanisms driving patterns in sex-specific senescence and our results provide a useful data point towards that end.

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CHAPTER FOUR

OFFSRPING CHARACTERISTICS DRIVE EARLY SURVIVAL IN A LONG-LIVED MARINE MAMMAL

Abstract

The survival of juveniles is important both for individual fitness and potentially for population dynamics, particularly in a long-lived species. Juvenile survival can be influenced by both endogenous and exogenous forces, which may act directly or indirectly on the probability of survival. Here we use encounter histories and diverse covariates related to pups and their birth environment from a long-term study of Weddell seals to build upon previous work that has related juvenile survival to specific covariates. We evaluated the relationship between characteristics of mothers and pups as well as the birth environment and the probability that a pup survives the early life period and is sighted in the study area as an adult using logistic regression within the Bayesian framework. There was large support for a relationship between probability of recapture and pup weaning mass with heavy pups exhibiting a 33% increase in probability of survival over a light pup. There was also some evidence to suggest that male pups have a lower probability of surviving the juvenile period and returning to the study area as an adult compared to females. Although juvenile survival is primarily and directly related to pup weaning mass, we posit that some covariates likely drive juvenile survival indirectly through weaning mass. Given this likely indirect relationship it is possible that shifts in maternal characteristics and environmental conditions could influence pup survival and have consequences for population dynamics.

Introduction

Individual fitness and population growth may both be influenced by juvenile survival. Juvenile survival is critically important to an individual’s ability to survive to reproduction and pass traits on to the next generation. Survival rates of juveniles are not only important to individual offspring fitness but can also be important to population dynamics. In long-lived species, population growth is sensitive to adult survival, which is buffered against temporal variation (Gaillard and Yoccoz 2003). In contrast, variation in juvenile survival can be much greater, which can allow juvenile survival to be an important driver of population dynamics (Gaillard et al. 2000, Sæther et al. 2013).

The probability that an individual lives to a certain age can be driven by luck, observable traits that improve their probability of survival, and unobservable features of the individual that is often considered to be quality of the individual (Cam et al. 2016, Jenouvrier et al. 2018, Snyder and Ellner 2022). Random variation in outcomes (did you live or die) among individuals with identical traits, observed and unobserved, in a vital rate such as juvenile survival can be considered luck (Snyder et al. 2021, Snyder and Ellner 2022), alternatively called individual stochasticity (Caswell 2009, Cam et al. 2016, Jenouvrier et al. 2018, Steiner et al. 2021). Recent research found the role of luck in individual fitness is highest soon after birth, with survival luck being more important, for the studied species that exhibit slow, steady growth (Snyder and Ellner 2022). There is also evidence that conditions experienced in early life create individual trait variation that can influence fitness early and later in life (Lindström 1999, Van De Pol et al. 2006, Tung et al. 2016). The effects of early life conditions can be transient or more persistent on offspring fitness components. Transient effects will act as a filter for the population (Gaillard et al. 1997, Douhard et al. 2014), whereas persistent effects will create heterogeneity among individuals within the population later in life (Metcalfe and Monaghan 2001, Lummaa and Clutton-Brock 2002, Douhard et al. 2016).

Conditions experienced early in life that have consequences for offspring fitness may be driven by exogenous and endogenous forces. Exogenous forces can be considered the environmental conditions experienced by the mother prior to birth (Lummaa and Clutton-Brock 2002, Douhard et al. 2016) and conditions after birth (Van De Pol et al. 2006, Monaghan 2008, Cam and Aubry 2011, Fay et al. 2015). Environmental conditions can be specific to the individual or be shared by an entire cohort (Gaillard et al. 2000, Reid et al. 2003, Jones et al. 2005, Descamps et al. 2008). The characteristics of parents and the offspring are considered endogenous to the offspring and may lead to variation in survival. The influence of parental phenotype on the offspring phenotype beyond genetic inheritance can be considered parental effects (Bernardo 1996, Mousseau and Fox 1998, Benton et al. 2008). Because parental effects were first recognized in mammals for which mothers gestate young and often provide the majority of post-natal care for offspring, maternal effects are more often considered in studies of mammals than paternal effects are. However, in birds (Fay et al. 2016) and other taxa, paternal effects are often evaluated and may be more important (Bernardo 1996). Maternal effects have consequences beyond the fitness of offspring as evidence suggests that changes to population dynamics can stem from maternal effects on offspring that influence offspring survival or reproduction (Benton et al. 2008, Plard et al. 2015a, Hernández et al. 2020).

Maternal effects may influence the fitness of offspring either positively or negatively because mothers may adjust allocation of resources to maximize maternal fitness not offspring fitness

(Stearns 1992, Wilson et al. 2005). Often maternal effects are driven by the allocation of resources from mother to offspring (Gittleman and Thompson 1988, Martin et al. 2010, Lecomte et al. 2010, Hamel et al. 2012, Oosthuizen et al. 2015). Parental age may influence variation in offspring survival (Monaghan et al. 2020), especially in the sex that does the majority of offspring care (Fay et al. 2016, Reichert et al. 2020). Offspring survival may increase with parental age due to an increase in experience of care or resource acquisition (Travers et al. 2021), but there may also be a negative relationship with parental age (Descamps et al. 2007) due to senescent declines in physiological functions (Karniski et al. 2018), gamete quality (Monaghan and Metcalfe 2019), or ability to provision young (Fay et al. 2016). A quadratic relationship between maternal age and offspring fitness has also been observed in many species with offspring fitness initially increasing with maternal age before declining at older maternal ages (Ivimey-Cook and Moorad 2020). The number of previous offspring produced by a mother, parity, may also influence offspring survival if maternal care or provisioning improves with experience (Curio 1983, Cameron et al. 2000, Robbins et al. 2006, Aubry et al. 2009, Pardo et al. 2013). The age of a mother when she first reproduces, age of primiparity, has been associated with individual quality in some (Cam et al. 2002) but not all (Moore and Harris 2003), species and can be related to survival probabilities for a mother’s offspring. A mother’s reproductive status in the previous year can influence survival of offspring born in the current year with survival being lower for young born to mothers that reproduced in the previous year (Hamel et al. 2009). Additionally, offspring born to mothers reproducing for the first time generally experience lower survival rates early in life (Jones et al. 2005, Robbins et al. 2006, Ruiz-López et al. 2010).

Individual variation in offspring characteristics may also lead to variation in offspring survival. Consistent behavioral variation has been detected across a number of species (Réale et al. 2007) and may be important as offspring prepare for independence and navigate life on their own (Boon et al. 2007). Additionally, there is evidence for maternal effects on offspring behavior (Mateo 2014), especially in species that exhibit extended maternal care (Maestripieri 1995, Maestripieri and Mateo 2009). For example, there is evidence that specific foraging behaviors can be passed from mother to offspring in bottlenose dolphins *(Tursiops sp.)* (Sargeant and Mann 2009). Differences in behavioral development and experience, whether a result of maternal effects or not, may lead to differences in fitness outcomes for offspring. Physical differences among individuals may also contribute to differences in early life survival. The mass of offspring at weaning or independence has been positively linked to offspring survival in birds and mammals (Bowen et al. 2015, Oosthuizen et al. 2018, Weimerskirch 2018, Ronget et al. 2018). Higher offspring mass at independence may buffer offspring from starvation and be especially important in populations where juvenile mortality is driven by starvation more than predation (Monteith et al. 2014). Survival rates can be sex dependent throughout life (Descamps et al. 2007) or early in life (Lunn et al. 1994). In animals that display sexual size dimorphism, the larger sex often displays lower survival rates due to the additional energetic requirements of growing larger (Clutton-Brock et al. 1985). For some species this difference in energetic requirements of one sex can result in an interactive effect between offspring sex and mass (Beauplet et al. 2005). For example, in mountain goats (*Oreamnos americanus)* heavier female offspring have a higher survival rate but for male offspring survival is not influenced by mass (Côté and Festa-Bianchet 2001). In many species, particularly those that rely on pulsed resources, that face high predation risk, or harsh seasonal conditions, birth date is associated with probability of survival early in life (Estes 1976, Guinness et al. 1978, Wilson et al. 2005, Kerr Tricia D et al. 2007, Feder et al. 2008). Birth date can also influence survival through improved growth and mass gain of young (Feder et al. 2008, Plard et al. 2015b).

We use data from a long-term study of a long-lived marine mammal, the Weddell seal (*Leptonychotes weddellii)*, to evaluate how maternal and pup characteristics as well as environmental conditions influence offspring probability of surviving to adulthood and being recaptured. For our response variable, we used the binary outcome for whether an individual was sighted alive or not when it was two to six years old, which indicates that an individual had survived the early life stages when most mortality occurs (Cameron and Siniff 2004, Rotella et al. 2012), to evaluate the cumulative influence of multiple covariates on an individual's probability of surviving to adulthood. For our study population, there is evidence for maternal and environmental effects on offspring traits (Paterson et al. 2016b, Macdonald et al. 2020, Petch et al. 2023) as well as probability of survival early in life and recruitment to the breeding population (Hastings and Testa 1998, Hadley et al. 2007a, Garrott et al. 2012, Stauffer et al. 2013). Here, we build upon previous work that has demonstrated effects of pup weaning mass on offspring survival in the first two years of life (Proffitt et al. 2008), by considering the many factors that have been suggested to influence offspring survival in a single analysis. Past analyses of cohort strength have relied on monitoring what proportion of a cohort is seen again by key ages and been productive for population-level analyses (Garrott et al. 2012). Thus, to learn about how diverse covariates might affect the cumulative probability of surviving across multiple early ages when most early-life mortality occurs, we took a similar approach here. This allows us a broad understanding of what shapes an individual's ability to survive early in life and return to their natal population.

Methods

Study Area and Population

The study population inhabits Erebus Bay, Antarctica along the western coast of Ross Island (Siniff et al. 1977). Each austral spring pupping colonies are formed around cracks in the sea ice where the ice meets land. Females arrive at pupping colonies around late-September to give birth to pups (Stirling 1969) and remain with the pups for the next 30-45 day lactation period before weaning pups (Tedman and Bryden 1979). Males arrive in late-October to compete for underwater breeding territories and mate with females (Stirling 1969). Adult Weddel seals exhibit philopatry to the study area if they were born in the Erebus Bay population (Cameron and Siniff 2004, Hadley et al. 2007b). Sexual maturity occurs as early as three years of age in both sexes (Gelatt 2001), with an average age of first reproduction of 7.62 years for females (Hadley et al. 2006). Females will typically give birth to a single pup and will provide all postnatal care for that pup.

Data Collection

Every year pups are marked with identifiable livestock tags in the interdigital webbing of the rear flipper (Siniff et al. 1977) and since 1982 every pup born in the study area has been marked each year (Garrott et al. 2012). This marking effort allows the ages of individuals born in the study area to be known. Each year from early November to mid-December two to eight study area wide resight surveys are conducted (Cameron and Siniff 2004). Attempts are made to visit each colony every 24-48 hours to record newborn pup birthdates and the association between mothers and pups. Since 2002, a subset of pups is weighed at or near birth and again in late lactation (30-40 days after birth), using custom made weighing bags and hanging spring scales. The amount of time pups spend in the water prior to weaning has also been monitored since 2009 for a subset of pups each year. To monitor time spent in water, sheep livestock tags with attached temperature data loggers iButton (DS1922L/T) are attached to the hind flipper of pups at birth and removed between 30-40 days after birth (Petch et al. 2023). The sea water in the area is approximately -1.8°C, so when records of ambient temperature approximate the sea water temperature pups are reliably known to be in the water. Data from the removed temperature data loggers were extracted and processed using the methods described in Petch et al. (2023). Swim time records are for ages 11-30 days old to ensure consistency in the monitoring period across individuals.

Data Analysis

We used Bayesian logistic regression modeling to evaluate the relationship between the probability an individual would be sighted in the study area between the ages of two- and six-years old and characteristics of mothers and pups as well as the birth environment. We chose this response variable because it is a measure of the cumulative effects of maternal, offspring, and environmental variables on an individual's ability to survive the juvenile period and return to the study area as an adult. The ages by which recapture occurred for the response variable were strategically chosen to provide a measure of the probability an individual had survived the multi-year juvenile period. Previous research has shown that survival (Cameron and Siniff 2004, Hadley et al. 2006, Rotella et al. 2012, Brusa et al. 2020) and detection (mean estimate < 0.082

for males and females) (Cameron 2001) probabilities for Weddell seals during the first two years of life are quite low, which makes it difficult to incorporate covariates in traditional capture-mark-recapture models for analyses focused at those ages. After age two, age-specific survival and detection rates improve dramatically (Cameron 2001, Hadley et al. 2006, Rotella et al. 2012), and rates of colony attendance increase as well (Stauffer et al. 2014). Therefore, we chose to impose a floor of age two years on recaptures considered in this analysis. If an individual is resighted as a yearling the probability it survives to age two or older is much lower than if it is resighted as a two-year-old or older (Hadley et al. 2006, Stauffer et al. 2013, Brusa et al. 2020). This means that only individuals that were recaptured between the ages of two to six years old were considered. We restricted our recapture histories to ages six years or younger so that as many cohorts as possible had the opportunity to survive to age six and be included in the analysis, while maximizing the cumulative probability of being recaptured. If individuals in this population are recaptured, they have an 78% probability of being recaptured by age six. Additionally, previous research has shown that birth year conditions influenced subsequent survival of pups out to six years old (Stauffer et al. 2013), so this window of recapture should allow us to identify the influence of birth year conditions if they show a relationship with probability of recapture.

We included maternal attributes as covariates in our models to assess the influence of maternal effects on probability of recapture. We included maternal age as there is evidence of higher offspring survival (Hastings and Testa 1998, Hadley et al. 2007a) and pup weaning mass with maternal age (Macdonald et al. 2020). A quadratic functional form of maternal age was evaluated as pup birth mass and maternal mass has been shown to be quadratically related to maternal age (Proffitt et al. 2007b, Paterson et al. 2016b), and both are considered measures of energetic reserves available to a female for lactation (Wheatley et al. 2006). We also included age at first reproduction for the mother because this attribute has been linked to individual quality in the Weddell seal (Hadley et al. 2007a). Parity or the number of pups previously born to a mother was included as a measure of reproductive experience that has some evidence of being linked to offspring survival in this population (Hastings and Testa 1998) and is moderately related to pup birth mass (Paterson et al. 2016b). Parity was highly correlated with maternal age therefore relative parity was calculated to measure an individual's parity relative to other individuals of the same age. Relative parity was calculated by subtracting the mean and dividing by the standard deviation for the number of pups produced by mothers of the same age. Lastly the reproductive status of mothers in the year prior to giving birth to the offspring was included as a dummy variable because costs of reproduction have been identified in this species (Chambert et al. 2013, Paterson et al. 2018) and influence allocation of resources to offspring and pup weaning mass (Paterson et al. 2016b, Macdonald et al. 2020). The reproductive status of the mother in the year prior was described by four categories: pre-breeder, first time breeder, skipping reproduction with previous experience breeding, or reproducing with previous experience breeding. Some mothers had multiple pups in the dataset therefore maternal identity was included as a random effect in the models to account for lack of independence of pups from the same mother.

Variation in offspring characteristics may be associated with differences in probability of recapture and those suspected to be important were included in models of probability of recapture. Pup sex was included in the probability of recapture model as there is some evidence for sex differences in survival to adulthood in Weddell seals (Proffitt et al. 2008). The pup mass at the end of lactation was included as a predictor of probability of recapture, as there is evidence that pup weaning mass is associated with pup survival during the first two years of life (Proffitt et al. 2008). Individual mother pup pairs were not monitored to determine the actual date of weaning so pup mass at the end of lactation is an approximate measure of weaning mass, because weaning is known to occur between 30-45 days after birth (Stirling 1969, Tedman and Bryden 1979). Although this mass measurement is not true weaning mass, we refer to it here as “pup weaning mass” for ease of reading. Pup weaning mass was measured between 30-40 days after birth, and to account for the difference in days between measurements a simple linear regression was performed to estimate the mass gained each day during this period. The coefficient for day of mass measurement was used to adjust mass based on the number of days from the target date of 35 days after birth. The total time pups spent in the water during the monitoring period was assessed as a predictor of the probability of recapture. We refer to time spent in the water as pup swim time because observations of pups suggest that much of the time spent in water before weaning is spent swimming with mothers (Sato et al. 2003), but we acknowledge that we did not monitor the activity of pups and do not know how much time was spent swimming or resting in the water. There is evidence that the total swim time of pups during the lactation period varies considerably among individuals and is related to maternal age and pup birth mass (Petch et al. 2023). There are alternate predictions for how this considerable behavioral variation could influence the probability of recapture. Total swim time could either be positively related to probability of surviving to adulthood if learning and experience are gained by pups that spend more time in the water as has been suggested (Sato et al. 2003). Alternatively there could be a negative relationship if pups lose more mass by spending more time swimming, which has been demonstrated in grey seal *(Halichoerus grypus)* pups (Jenssen et al. 2010), and decrease their energy reserves at weaning. The birthdate of a pup has been associated with maternal quality (Rotella et al. 2016) and was included in models because it is predicted pups born late in the season may not have enough time to build up mass and experience. Pup sex was included in models because previous work has indicated that survival both early (Cameron and Siniff 2004, Proffitt et al. 2008) and later in life (Brusa et al. 2020) may vary between the sexes. Pup sex was also important to include in models because there is some reason to suspect detection rates may differ between the sexes (Cameron and Siniff 2004). Males may spend more time in the water defending underwater territories after age 4 when they generally start breeding (Gelatt 2001, Harcourt et al. 2007a), frequent peripheral areas prior to breeding ages (Brusa et al. 2021), and potentially exhibit different attendance patterns than females, which may all influence detection rates of males.

Lastly, different measures of the natal environment were included in models to evaluate the influence of environmental factors early in life on the probability of recapture. Birth cohort size was included as an integrated measure of favorable conditions for mothers producing pups and has been linked to the combined probability of early life survival and recruitment to the breeding population for female Weddell seals (Garrott et al. 2012). The average sea ice extent in September of the birth year, obtained from NASA NSIDC (Stroeve and Meier 2024), was included as a measurement of the environmental conditions experienced by a mother during gestation, which has been linked to offspring survival to adulthood (Stauffer et al. 2013) and probability of recruitment to the breeding population (Garrott et al. 2012). Additionally, birth year was included as a random effect to account for annual environmental variation not included in the measured variables.

Logistic regression within the Bayesian framework was used to model the binary response variable. Variable selection was done using reversible jump Markov chain Monte Carlo (RJMCMC) to determine which variables held the most support for model inclusion. RJMCMC executes model selection by attaching an indicator variable to coefficients in the model and jumping between different sets of parameters in each iteration of sampling (Green 1995) with covariates that explain variation in the response being included in models more often.

Models were fit in the R computing environment (R Core Team 2023) using the package NIMBLE (de Valpine et al. 2017, 2023) to construct Bayesian RJMCMC models. All continuous regression coefficients were centered and scaled by one standard deviation. Analyses were carried out to determine which functional form of pup weaning mass to carry forward to the final models. Logistic regression of recapture with all variables besides random effects was performed and Watanabe-Akaike Information Criterion (WAIC) (Watanabe 2010) was used for model selection. In the final models of probability of recapture regression coefficients were assigned weakly informative priors N(0, 0.001) and inclusion probabilities were assigned U(0, 1). Random effects of year and maternal id were assumed to be normally distributed with U(0, 20) as the prior on the standard deviations for random effects. Constraints were added to the model so that indicators on the quadratic terms or interactions could only be included in the model if the indicators on the fixed effects were also included. Three chains were run for 200,000 iterations with a burn-in of 10,000 iterations saving every other sample resulting in a posterior of 285,000 samples for each model. Model convergence was assessed using visual inspection of trace plots and the potential scale-reduction factor (Gelman and Rubin 1992) where applicable with the package MCMCvis (Youngflesh 2018).

Results

Using encounter histories from pups born in the Erebus Bay population of Weddell seals we evaluated probability of being recaptured by six years old for two data sets. To evaluate whether the amount of time a pup spends in the water influences probability of being recaptured, we used a data set of 609 individuals that had measurements for time spent in the water, and all other offspring, maternal, and environmental variables. In the swim-time data set, 476 individuals were never recaptured by age six years, and 133 were recaptured. The monitoring for recapture was carried out through 2023, and the swim time data set included individuals born between 2009 and 2017, with the exception of 2013 when logistical constraints precluded deployment of temperature loggers on pups. Additionally, we evaluated a much larger data set (n=1,339) that did not include time spent in the water by pups but did include all other covariates to achieve a greater power of detecting relationships between response and explanatory variables. This larger weaning-mass data set included 1,015 individuals who were never recaptured and 324 that were recaptured by age six years. Again, monitoring for recapture was carried out through 2023, and the weaning mass data set included individuals born between 2002 and 2017. Covariates included in the model represent a large range of values typical of this population and are summarized below (Table 4-1). Pups varied greatly in the covariates considered, and raw plots of continuous covariates suggest that there is a great deal of overlap in values for pups that were recaptured as adults compared to those that were not (Fig. 4-1). All coefficient estimates are presented as the mean of the posterior distribution. The modeling effort to determine the functional form on pup weaning mass indicated that the log functional form (WAIC=1431.48) was better supported over the linear form of weaning mass (WAIC=1436.853). All models were subsequently run using a logarithmic functional form on weaning mass.

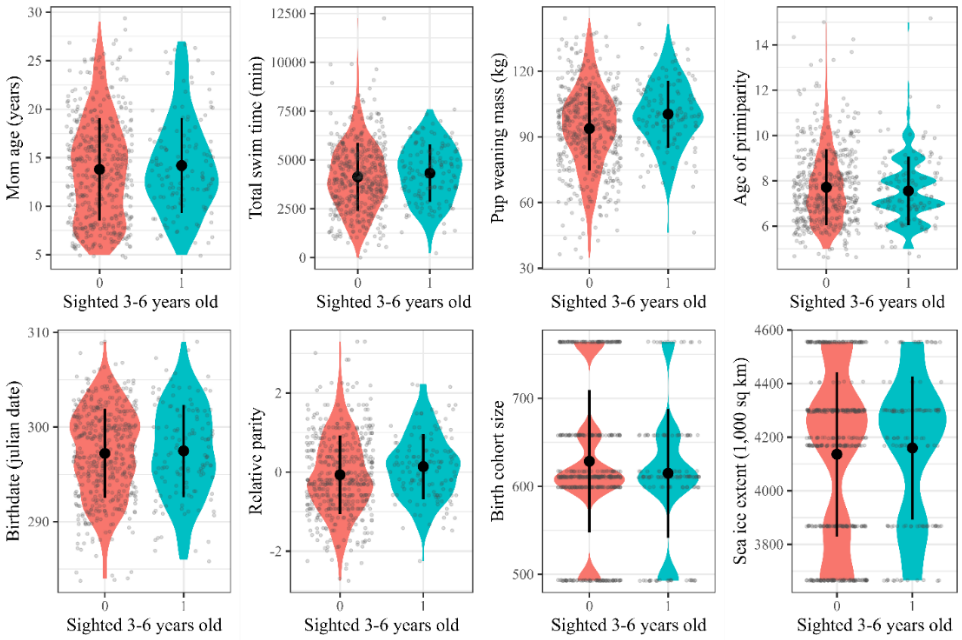

Figure 4-1 Violin plots of covariate values in the swim time data set for pups sighted (1) and not sighted (0) (n=609). The mean is shown as a point with one standard deviation shown with a black line. Open circles represent observations from the data.

Table 4-1 Summary statistics for covariates included in models of probability of recapture by six years old.

	Swim time model (n=609)		Weaning mass model (n=1339)	
Covariate	Mean (SD)	Range	Mean (SD)	Range
Mom age (years)	13.9 (5.2)	(5, 29)	14.9 (5.0)	(5, 31)
Julian birthdate	297 (4.8)	(284, 309)	298.6 (5.11)	(282, 317)
Weaning mass (kg)	95.3 (18.6)	(34.9, 144.2)	96.8 (18.7)	(31, 149.4)
Total swim time (min)	4174 (1688.6)	(0, 12252)	------------	----------
Relative parity	-0.02 (0.97)	(-2.8, 3.3)	-0.04 (0.99)	(-3.1, 3.3)
Primiparity age (years)	7.7 (1.6)	(5, 15)	7.6 (1.6)	(5, 15)
Cohort size	625.5 (79.5)	(493, 764)	562 (128.7)	(199, 764)
Winter SIE (100 km^2)	41,413.2 (2,981.2)	(36,658, 45,546)	42020 (2,849.8)	(36,658, 48,286)

Table 4-2 Proportion of models selected that include each covariate and mean coefficient estimates from the posterior for the probability of recapture analysis. Means, standard error, and 90% highest density intervals are for model averaged estimates. Estimates are reported on the log odds scale.

	Swim time model (n=609)			Weaning mass model (n=1339)		
	Proportion selected	Mean (SE)	90% HDI	Proportion selected	Mean (SE)	90% HDI
Intercept	----------	-1.338 (0.124)	(-1.541, -1.135)	-----------	-1.073 (0.154)	(-1.295, -0.822)
Mom age	0.000	0.000 (0.001)	(0.000, 0.000)	0.000	0.000 (0.000)	(0.000, 0.000)
Mom age^2	0.000	0 .000 (0.000)	(0.000,0.000)	0.000	0.000 (0.000)	(0.000, 0.000)
Birthdate	0.000	0.000 (0.001)	(0.000, 0.000)	0.000	0.000 (0.000)	(0.000, 0.000)
Birthdate^2	0.000	0.000 (0.000)	(0.000, 0.000)	0.000	0.000 (0.000)	(0.000, 0.000)
ln(Wean mass)	0.020	0.010 (0.070)	(0.000, 0.000)	**0.999**	**0.513 (0.085)**	**(0.372, 0.651)**
Pup sex (male)	0.000	0.000 (0.004)	(0.000, 0.000)	**0.455**	**-0.281 (0.321)**	**(-0.723, 0.000)**
Swim time	0.000	0.000 (0.000)	(0.000, 0.000)	----------	-----------	----------
Mass*sex (male)	0.000	0.000	(0.000, 0.0000)	0.000	0.000 (0.000)	(0.000, 0.0000)
Relative parity	0.000	0.000 (0.002)	(0.000, 0.0000)	0.000	0.000 (0.000)	(0.000, 0.0000)
Primiparity age	0.000	0.000 (0.001)	(0.000, 0.0000)	0.000	0.000 (0.000)	(0.000, 0.0000)
Cohort size	0.000	0.000 (0.001)	(0.000, 0.0000)	0.000	0.000 (0.000)	(0.000, 0.0000)
Winter SIE	0.000	0.000 (0.001)	(0.000, 0.0000)	0.000	0.000 (0.001)	(0.000, 0.0000)
FirstBreeder (t-1)	0.000	0.000 (0.004)	(0.000, 0.0000)	0.000	0.000 (0.002)	(0.000, 0.0000)
PreBreeder (t-1)	0.015	-0.015 (0.141)	(0.000, 0.0000)	0.000	0.000 (0.011)	(0.000, 0.0000)
SkipBreeder (t-1)	0.000	0.000 (0.002)	(0.000, 0.0000)	0.000	0.000 (0.001)	(0.000, 0.0000)
σ_{mother}	------------	0.062 (0.044)	(0.003, 0.128)	------------	0.040 (0.036)	(0.004, 0.075)
σ_{year}	------------	0.089 (0.077)	(0.000, 0.168)	------------	0.044 (0.042)	(0.002, 0.077)

Notes: The reference level for the intercept is for a female pup and a mother that was an experienced breeder that pupped the previous season. Winter SIE is the mean sea ice extent for September (the end of austral winter) in the birth year of the pup.

The mean probability of recapture was estimated as 0.2108 (90% HDI: 0.208, 0.243) for an individual with average values for all covariates based on the model averaged coefficient estimates for the RJMCMC model for the smaller swim-time dataset. Two variables, weaning mass and reproductive status of mother as a pre-breeder in the previous year had inclusion probabilities above zero, although below 0.05 and coefficient estimates were poorly estimated (Table 4-2). Annual variation in this model was estimated to be low with high uncertainty around the estimates. To better assess whether the lack of support for total swim time was due to lack of power from a smaller data set or a lack of relationship between the covariate and probability of recapture we ran an additional logistic regression model with this data set. When a model was run with all covariates and random effects but without variable selection from RJMCMC the relationship between total swim time and probability of recapture was estimated to be quite weak with a mean coefficient estimate of -0.011 (SE: 0.123).

The mean probability of recapture was estimated as 0.255 (0.215, 0.305) for an individual with average values for all covariates based on the model averaged coefficient estimates for the RJMCMC model for the larger weaning-mass dataset. When probability of recapture was evaluated with the larger dataset two variables, weaning mass and pup sex, had inclusion probabilities greater than zero (Table 4-2). There was less certainty around selection for pup sex in the model with only approximately half of models including it. The probability of recapture for male pups conditional on pup sex being included in the model was 0.175 (SE: 0.528). Weaning mass was heavily supported to be in the model with a positive relationship between probability of recapture and log weaning mass. The estimated coefficient on log weaning mass conditional on its inclusion in the model was 0.513 (SE: 0.08) on the log odds scale. A 95 kg female pup with average covariate values and an experienced mother that pupped the previous year is predicted to have a 0.256 (0.213, 0.302) probability of recapture, whereas female pups whose weaning mass was 35 kg or 145 kg had recapture probabilities of 0.208 (0.167, 0.252) and 0.278 (0.233, 0.327), respectively (Fig. 4-2). For male pups with those same weaning mass values (95, 35, 145 kg), the predicted probabilities of subsequent recapture were 0.207 (0.156, 0.252), 0.166 (0.123, 0.207), and 0.227 (0.171, 0.275), respectively (Fig. 4-2). The annual variation in probability of recapture was estimated to be quite low with large uncertainty around the estimates (Fig. 4-3).

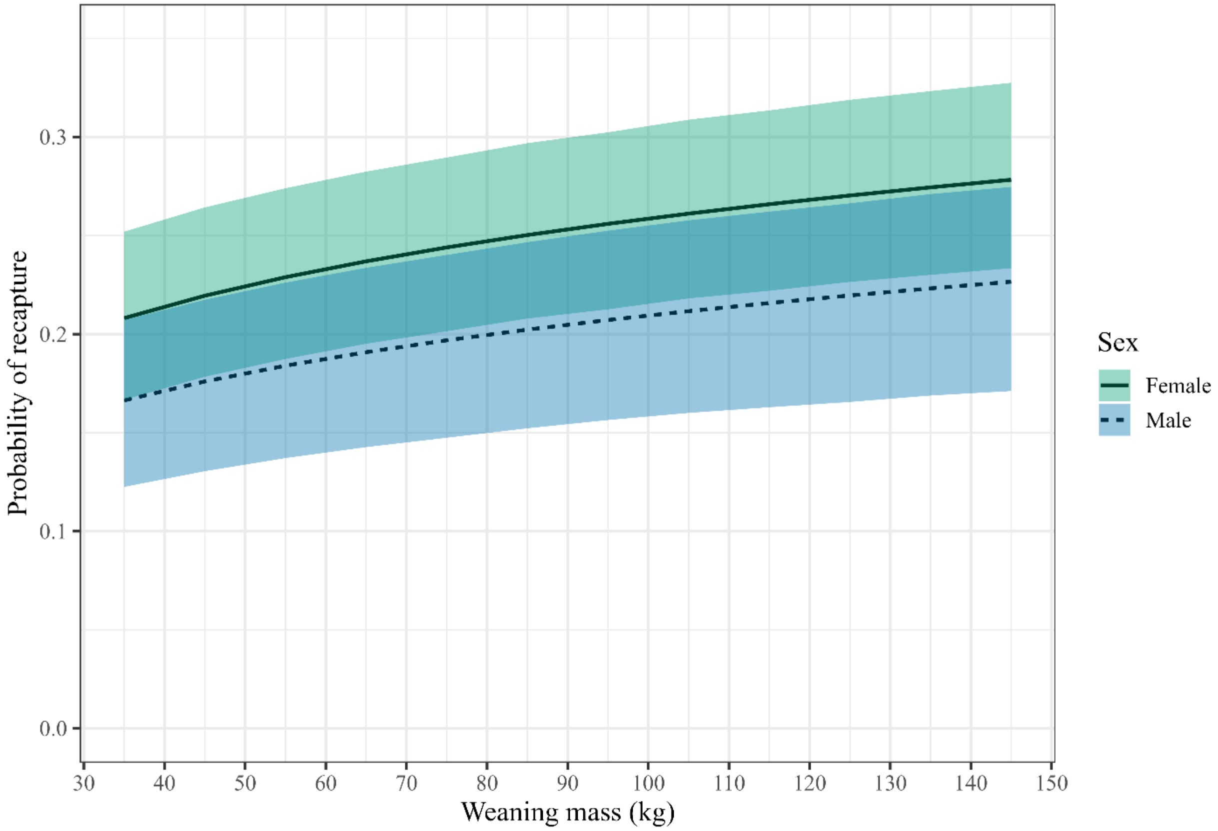

Figure 4-2 Estimated probability of recapture by six years old of male and female pups for masses observed in the data set. Colored bands represent 90% highest density intervals.

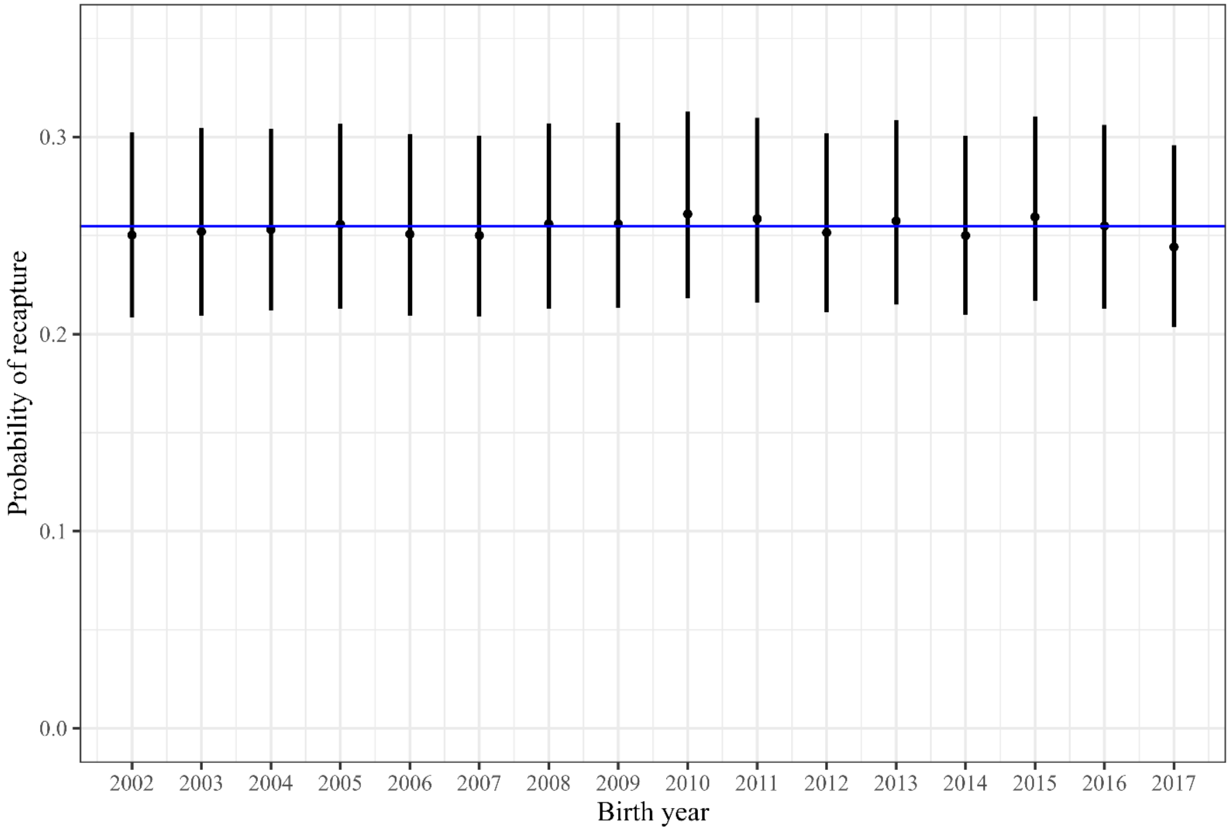

Figure 4-3 Estimated probability of recapture by six years old for an average pup across different years represented in the dataset. 90% highest density intervals are shown in gray.

Discussion

We found that offspring characteristics, mass at weaning and pup sex, were important to the probability of recapture by six years old. Our evaluation of a smaller dataset that included the total swim time of pups during lactation indicated that total swim time was not associated with probability of recapture. When we evaluated a model without variable selection for the smaller swim time dataset, we found that although there was evidence for an effect of pup weaning mass and whether a mother was a prebreeder in the previous year, total swim time was estimated to have very little effect on the probability of recapture. This suggests that the lack of relationship found between total swim time and probability of recapture was not due to a lack of power from the smaller dataset, but simply due to a lack of relationship between total swim time and probability of recapture. These findings suggest that both pup characteristics and likely maternal characteristics mediated through resource allocation have cumulative effects on offspring survival to adulthood in this long-lived mammal.

Our findings align well with those for this species and other long-lived mammals. We estimated that a female pup with average covariate values whose mother was an experienced breeder and pupped the previous year had a 0.255 (90% HDI: 0.210, 0.312) probability of being sighted again as an adult, a result that aligns well with previous work that found on average the proportion of a cohort that survived to adulthood and recruited to the breeding population by 10 years old was 0.20 (SD = 0.07) (Garrott et al. 2012). Additionally, the average proportion of a female cohort that survives to six years old is estimated to be 0.25 (SE = 0.02), which is consistent with our findings (Stauffer et al. 2013). Mass of offspring at birth or independence has been positively linked to early life survival in many mammals (Ronget et al. 2018), including other phocid species (Bowen et al. 2015, Oosthuizen et al. 2018). Similar to our results, weaning mass was associated positively with offspring survival only for the first two years of life, in another study of this population and the mass relationship was estimated to be stronger for males but with uncertainty around these estimates (Proffitt et al. 2008). Our study differs in that we focus on the cumulative effects of weaning mass to probability of recapture to age six. If weaning mass is only important during the first two years of life its relationship to probability of recapture by six years old will potentially be diminished. To that end it does appear the relationship between weaning mass and juvenile survival estimated by Proffitt et al. (2008) is slightly stronger than estimated in this study, so it may be that this relationship is stronger for survival early in life and less so as individuals reach maturity. Future analyses of annual survival rates will address this and complement the work presented here. Additionally, we found evidence that a pseudo threshold relationship was better supported for weaning mass, which contrasts with results of previous work on the study population (Proffitt et al. 2008) but similar to results for other phocid species (Bowen et al. 2015, Oosthuizen et al. 2018). Previous work has shown evidence for an effect of sex on offspring survival that interacts with measures of maternal allocation with one study of survival to age six years finding an interaction between offspring sex and maternal body size (Hastings and Testa 1998) and a more uncertain relationship between offspring sex and weaning mass on survival to two years old (Proffitt et al. 2008). We did not find any evidence of an interaction between offspring sex and weaning mass but instead found some support for reduced probability of recapture of male offspring compared to females. It is important to note that our response variable is not apparent survival but instead probability of recapture. Thus, possible sex-specific variation in detection rates may be affecting our results. If for example, males have a lower probability of detection, we will find that male pups have a lower probability of being recaptured but that this is not a reflection of their survival probability but instead their detection probability. In chapter 3 we estimated that males have lower age-specific probabilities of detection than do females and male rates increase more slowly with age in males than in females in early life, which is similar to what others have found (Cameron and Siniff 2004). Notably though, previous research from this population found males had slightly lower survival rates compared to females throughout life (Cameron and Siniff 2004), which is consistent with results from chapter 3 and with our findings here. When combined together these results suggest that the effect of sex that we found here is likely representative of true differences in survival processes but that the magnitude of the difference may be slightly overestimated due to differences in detection between the sexes.

The mass of offspring at independence can be critically important to the survival of offspring (Ronget et al. 2018). For many organisms the period directly after independence is quite difficult as offspring navigate foraging on their own and avoid predation and starvation (Marchetti and Price 1989, Gaillard et al. 2000, Naef-Daenzer et al. 2001). This is also true of Weddell seal pups as the period directly after independence requires exploration of new environments, foraging on their own, and evasion of predators (Siniff et al. 1977, Burns et al. 1999). This period of time also occurs when pups are still developing and physiologically may be disadvantaged in terms of diving and foraging ability due to high rates of growth during the lactation period (Burns et al. 1999, Burns 1999). There is some evidence that larger weaned seal pups may be capable of a longer diving duration and higher foraging efficiency (Burns 1999), which helps to explain the importance of weaning mass to probability of recapture. It is likely that starvation is a large source of mortality for Weddell seal pups during their first few years of life. Our findings back this up as it has been suggested that offspring mass at independence is more important to offspring survival in populations where starvation is a greater risk of mortality than predation (Monteith et al. 2014).

Our finding that there was some support for an effect of pup sex on probability of recapture is not surprising given results from chapter 3 that males ages 3-6 years old have a lower annual probability of survival compared to females (Macdonald, 2024). Indeed in many mammals males often have a lower probability of survival throughout life and a shorter lifespan (Clutton-Brock and Isvaran 2007, Lemaître and Gaillard 2013, Lemaître et al. 2020). Sex differences in early survival have often been attributed to the additional growth required of males when males are the larger sex in sexually dimorphic species (Clutton-Brock et al. 1985). Interestingly, Weddell seals display minimal sexual dimorphism in size (Stirling 1975, Harcourt et al. 2007b) and so this explanation is not consistent with our findings. Sex differences in the foraging and diving behaviors of recently weaned pups, as has been found for grey seals (Carter et al. 2017) may explain the sex differences in probability of recapture, if the behavior of males is less successful. It may also be that there are different energetic requirements of Weddell seals due to hormonal differences between the sexes as has been exhibited in northern elephant seals *(Mirounga angustirostris)* (Kelso et al. 2012) that make the risk of starvation more acute for males. Although Weddell seals exhibit strong philopatry it is possible that males are permanently emigrating at higher rates than females, or that males have much lower detection rates than females, two things our analysis could not account for.

We added to previous work from this population by assessing the importance of maternal and pup characteristics along with environmental variables to probability of recapture by six years old. Notably, we did not find that variables beyond weaning mass and pup sex influenced the probability of recapture by six years old. Our failure to detect a relationship between most variables and probability of recapture is important in two different ways. First, probability of recapture is a proxy of survival but doesn’t estimate survival because we do not account for probability of detection, so it is possible this approach may have limited our ability to detect some relationships. However, given previous work on the study population, it seems unlikely that our approach could have limited our ability to detect certain relationships. First we know that detection of a prebreeder female given it is present in the study area is quite high >0.90

(SE<0.01) with at least 5 or more surveys per year (Stauffer 2012) and that for adult males the average probability of sighting is 0.84 which is slightly lower than the rate for females but still quite high (Cameron 2001). Additionally, for these data the cumulative probability of being recaptured by six years old is 78%, which is similar to what has been estimated previously for the study population with mark-recapture modeling (Cameron 2001). Thus, the period of two to six years that we used in building our response variable as a measure of whether an individual survived the juvenile phase of life likely covered a sufficiently large window of time that most individuals that survived and would eventually be recaptured in the study would have been seen during the period used such that the response variable should approximate juvenile survival reasonably well. Although it is possible that some relationships between some covariates and survival were obscured because we did not use formal mark-recapture methods to account for detection rates and did not model annual survival rates, detailed knowledge of demographic processes in the study population and the fact that results of previous research are consistent with our results suggest that our results reflect the factors important to a pup surviving the juvenile period and returning as an adult. Additionally, we are primarily interested in investigating the cumulative effects of different factors on an individual’s ability to survive the juvenile period and return to the study area as an adult, and the approach used here allowed for estimating cumulative effects rather than annual effects. Second, many factors influence offspring weaning mass and may play a role in the probability of recapture through offspring weaning mass.

Weaning mass is not simply an offspring characteristic but can also be mediated by maternal effects, such as maternal mass at birth of the offspring, birthdate, and reproductive status of the mother and the environment (McMahon Clive R and Burton Harry R 2005, Rödel et al. 2008, Postma et al. 2013, Plard et al. 2015a, Michel et al. 2019). Weddell seal pups with heavier mothers at birth, later birthdates, and mothers that were not first time mothers wean at a larger mass (Macdonald et al. 2020). Additionally, offspring weaning mass shows moderate individual variation among mothers (Macdonald et al. 2020) and maternal mass at birth of the pup a predictor of offspring weaning mass is related to maternal age (Proffitt et al. 2007b, Paterson et al. 2016a). This suggests that the weaning mass of a pup is heavily influenced by the allocation of resources by mothers to pups and therefore the probability of recapture is likely influenced by maternal characteristics mediated through offspring mass. There is also evidence that pup weaning mass is related to environmental variables with years of low sea ice extent during the summer directly prior to birth and strong positive southern oscillation resulting in higher average weaning masses (Proffitt et al. 2007a). It is likely that much of the environmental variation in offspring survival previously demonstrated in this population (Garrott et al. 2012, Stauffer et al. 2013) is explained through pup weaning mass.

Although the effect of weaning mass, the variable with the most support, on probability of recapture is clear, it is possible that beyond weaning mass, chance may drive much of the differences in survival outcomes of young Weddell seals. A potential explanation for the lack of relationship between most variables in the model and probability of recapture is that most or some of this period is when variance in lifetime success is most influenced by luck in survival and not trait variation (Snyder and Ellner 2022). There is evidence that luck (individual stochasticity) accounts for a large portion of variance in survival outcomes of identical individuals in different species (Jenouvrier et al. 2018, Hartemink and Caswell 2018). Alternatively, it is possible the models used did not include other, unmeasured variables that are important to the probability of recapture in young Weddell seals. Additionally, the influence of mass or sex or other variables may be transient only influencing survival during the first year or two of life and that the cumulative effect of these variables on probability of recapture by age six is much lower.

The work presented here could be extended in useful ways to understand the origination of differences in weaning mass that contribute to offspring survival and the consequences of variation in weaning mass and offspring survival for population dynamics. Parsing out the direct effects on offspring survival and the indirect effects that are mediated through weaning mass using path analysis as others have done (Plard et al. 2015a) would help inform the mechanistic pathways between different variables and offspring survival. Future work could also estimate age-specific survival of offspring to better understand which variables are important at different stages and use the results in an integral projection model to understand the importance of variation in offspring survival and the traits that influence this vital rate on population dynamics (Ozgul et al. 2010, Plard et al. 2015c, Hernández-Pacheco et al. 2021). Further analyses that aim to partition how much of the variation in probability of recapture is due to observed and unobserved traits and how much is due to luck, could also be informative.

This research adds to previous work that demonstrated pup survival during the first two years of life varies with pup weaning mass and pup sex (Proffitt et al. 2008), maternal characteristics (Hastings and Testa 1998, Hadley et al. 2007a), and environmental conditions (Garrott et al. 2012, Stauffer et al. 2013), by combining all potential drivers and analyzing the influence on probability of surviving and being recaptured by age six years. Our work suggests that a Weddell seal pup's cumulative probability of surviving and being recaptured as an adult two to six years after birth is primarily driven by its weaning mass. A female pup's probability of recapture, i.e., surviving the juvenile period, increases from approximately 0.208 to 0.278 when going from a light to heavy mass, which is an increase of 33%. Given that weaning mass is influenced by maternal characteristics and environmental conditions, these factors may be influencing probability of recapture indirectly through offspring weaning mass. Based on these relationships it is possible shifts in the variation of maternal quality, maternal age structure, and environmental conditions may have consequences for population dynamics via their effects on pup weaning mass and offspring survival.

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CHAPTER FIVE

CONCLUSION

Vital rates may be influenced by many different factors causing inter-individual variation that is important to individual fitness and can often be reflected in the evolution of life histories. A species life history and the pattern of vital-rate variation will also determine which groups of individuals are most important to population growth and how variation in vital rates influences population dynamics. The research presented in this dissertation aims to answer questions related to these topics for a long-lived marine mammal, the Weddell seal. Variation in survival rates of males and females are explored across the life of this species and the influence on population dynamics of large individual heterogeneity in the probability of reproduction for females is assessed.

Starting at the population level, I found in chapter 2 that changes to the distribution of unobserved individual heterogeneity in reproduction and therefore survival via the correlation between the two rates does not lead to an appreciable impact on population growth and other population metrics. Although individual heterogeneity in the probability of reproduction predicts that an above-average female will produce twice as many pups as a below-average female (Chambert et al., 2013), the consequences of this individual heterogeneity do not scale up from the individual to the population level. I speculate that the life history strategy used by female Weddell seals explains these results. Females are constrained in the number of pups they produce, as they give birth to, at most, a single offspring each year and face high energetic costs to reproduction. Furthermore, as a long-lived species adult survival is prioritized (Gaillard & Yoccoz, 2003) and is therefore buffered against temporal variability while reproduction is not

(Rotella et al., 2012). Due to canalization of the vital rate most important to population growth, I expect the traits with large individual heterogeneity will have minimal influence on population growth rates because there is more variability in the vital rate to which population growth is least sensitive.

In chapter 3, I assessed sex differences in survival rates from age 3 years old using a different modeling approach than that used in previous research: I included a finite mixture of survival and detection classes and I used flexible basis splines to model age-related variation in survival. Age-specific estimates of male survival were lower than those for females throughout life which is consistent with results from many mammal species (Lemaître et al., 2020). Males also exhibited stronger actuarial senescence after the age of 12 years old than did females, which is consistent with predictions if sex-specific patterns of senescence are shaped by mating system (Bonduriansky et al., 2008; Bronikowski et al., 2022). I suggest that sex differences in senescence patterns in this species are likely influenced by the mating system and the environment, and that fully understanding the evolution of these differences for this, and other species may require better knowledge and accounting of the amount and timing of energetic allocation towards reproduction for each sex.

Finally, in chapter 4, I conducted a thorough analysis of diverse factors hypothesized to influence the probability a pup survives the juvenile period and returns to the study area as an adult. I found that a pup’s weaning mass is a primary factor influencing the probability a pup is recaptured between two to six years old. I also found some evidence to suggest that male pups have a lower probability of being recaptured compared to females, which is consistent with results of previous research on the study population (Cameron & Siniff, 2004) and results from chapter 3. I suggest other factors such as maternal characteristics and the environment may be indirectly influencing the probability of recapture through weaning mass given previously established relationships between these variables and weaning mass.

There are several directions for future research based off the work presented in this dissertation. Estimates of the asymptotic population growth rate suggest this population should be shrinking slightly, but recent observed increases in pup production suggest the population may be growing. Transient life table response experiments may be a useful avenue for investigating how our predictions differ from observations and what factors contribute to observed population dynamics. In chapter 3, I found that our ability to understand the drivers of differences in actuarial senescence between the sexes is somewhat hindered due to our lack of knowledge regarding male reproductive effort. As our ability to measure male reproductive effort or even just the number of pups sired by males on a larger scale improves, it would be useful to revisit this work and interpret the results in light of this information. Collaboration with physiologists working with this population of seals to carry out longitudinal physiological studies would be useful for understanding some of the physiological mechanisms behind actuarial senescence observed. The work presented in chapter 4 highlights a few avenues for future research. Future work might compare findings on the cumulative effects of many variables on the probability of surviving to adulthood to results of age-specific mark-recapture analyses that partition out relationships between offspring survival and maternal and offspring characteristics and annual environmental conditions. It might also be interesting to understand the importance of variation in survival rates during the juvenile period to the population dynamics using methods similar to those presented in chapter 2. Finally, now that we have a better understanding of how measured covariates relate to the probability of survival to adulthood, it may be informative to partition how much of the variation in probability of survival during the juvenile period is due to measured traits, unobserved heterogeneity, and luck.

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APPENDICES

APPENDIX A

SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Graphs of Functions Used in the IPM

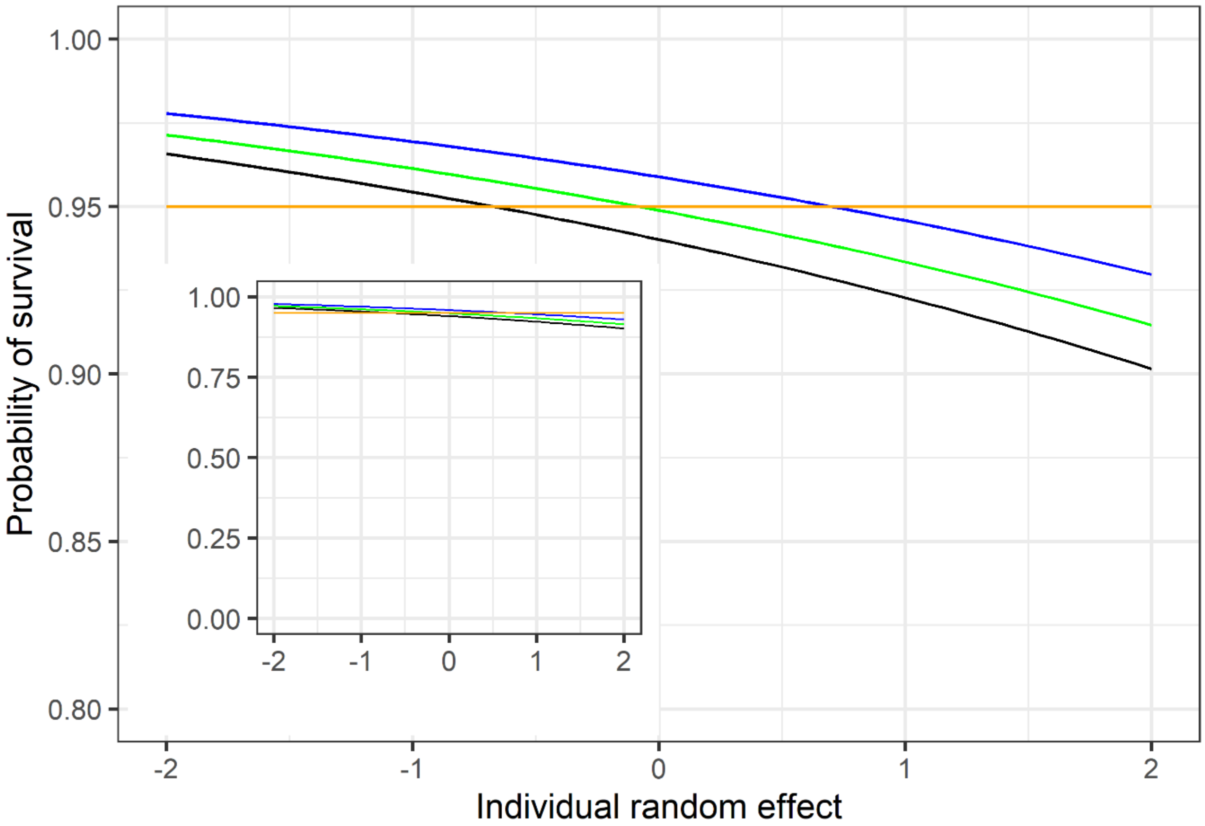

Figure A-1 Graph of change in probability of survival across different individual random effects of reproduction for an 8 year old that was a pre-breeder (orange), first-time breeder (green), experienced breeder (black), and skip breeder seen and away (blue) the year previously. The larger graph is shown with unequal axes to visualize the differences more easily among reproductive states and the inset graph shows the graph with equal axes.

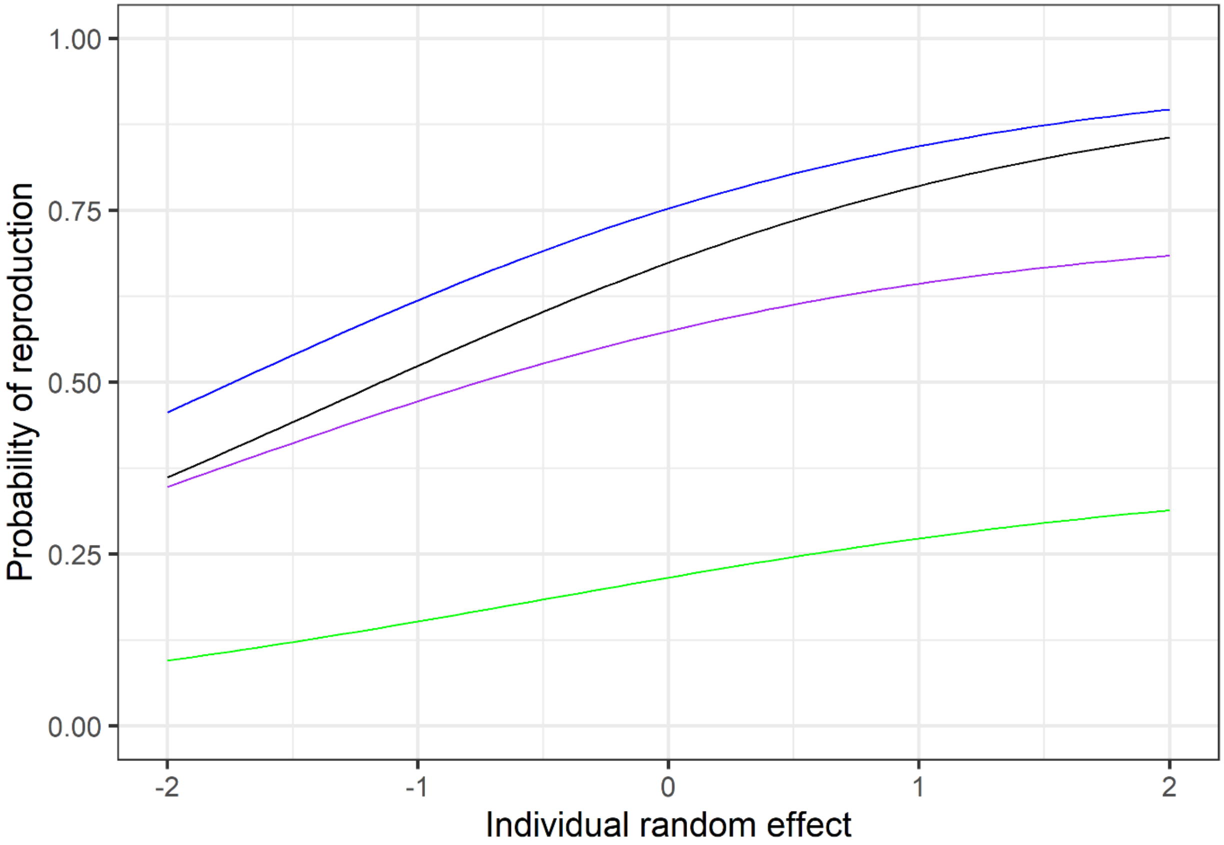

Figure A-2 Graph of change in probability of reproduction across different individual random effects of reproduction for an 8 year old that was a first-time breeder (green), experienced breeder (black), and skip breeder seen (blue) and skip breeder away (purple) the year previously.

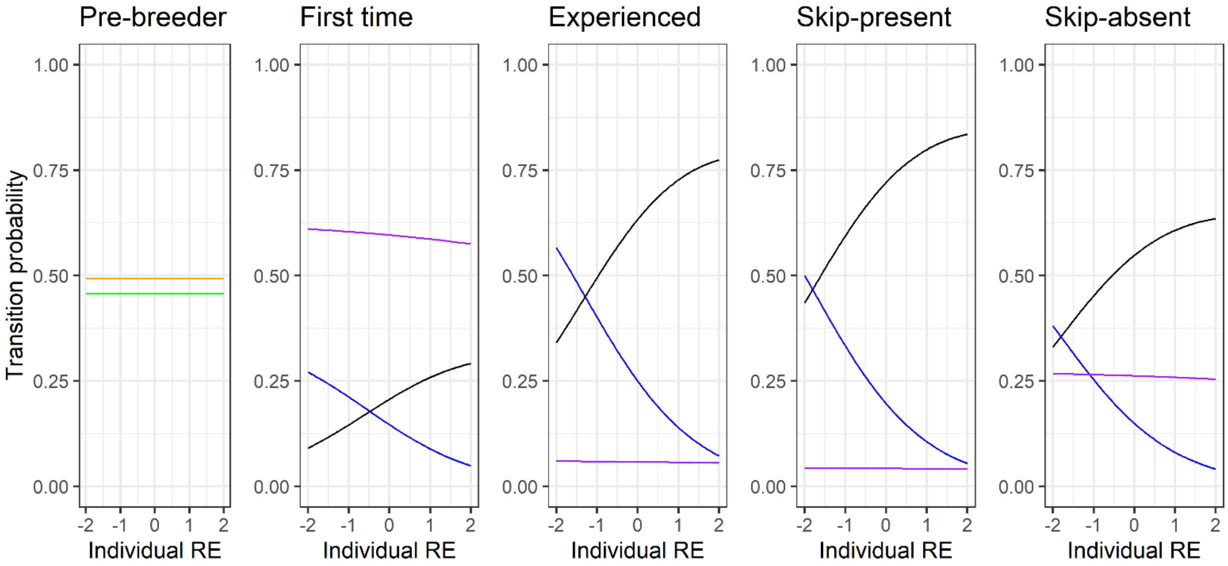

Figure A-3 Graphs of probability of transition from each state (shown in graph title) to other states across different individual random effects for an 8 year old. Pre-breeder (orange), first-time breeder (green), experienced breeder (black), skip breeder-present (blue), and skip breeder-absent (purple).

Bayesian Multi-state Modeling Effort

Splines were used to model survival, recruitment to the breeding population, and reproduction. We chose biologically relevant locations of knots for the spline on recruitment placing the knots at ages 4, 6, 8, 10, and 12. Knots for the survival and reproduction models were placed at evenly spaced sample quantiles. Knots for these models were placed at ages 6.17, 12.33, 18.5, 24.67, and 30.83.

Below are results from the Bayesian multi-state modeling of recruitment, reproduction, survival, and temporary emigration for females that have recruited to the breeding population. We checked convergence of posteriors using visual inspection of trace plots and the potential scale-reduction factor (Gelman & Rubin, 1992) with the R package ggmcmc (Fernández-i-Marín, 2016). We fit all models in the R computing environment (R Core Team, 2022) using the package NIMBLE (de Valpine et al., 2017, 2022).

Table A-4 Coefficient values used in the survival regression equation for females that have recruited to the breeding population. Coefficients reported on the log odds scale, betas are coefficients for the spline.

Parameter	Mean (95% HDI)
Survival (φ)	
α_{ϕ}	8.492 (6.697, 10.434)
First Breeder adjustment	-7.066 (-9.543, -5.431)
Experienced breeder adjustment	-7.209 (-9.780, -5.504)
Skip-present adjustment	-6.878 (-9.439, -5.168)
Skip-away adjustment	-6.878 (-9.439, -5.168)
$\beta_{\phi 1}$	-0.005 (-0.01, -0.001)

$\beta_{\phi 2}$	-0.001 (-0.01, 0.01)
$\beta_{\phi 3}$	0.002 (-0.017, 0.02)
$\beta_{\phi 4}$	-0.003 (-0.017, 0.01)
$\beta_{\phi 5}$	-0.011 (-0.022, -0.0004)
Reproduction (ψ)	
α_{ψ}	1.78 (1.18, 2.46)
First Breeder adjustment	-0.942 (-1.159, -0.729)
Experienced breeder adjustment	-0.368 (-0.509, -0.226)
$\beta_{\psi 1}$	-0.005 (-0.01, -0.001)
$\beta_{\psi 2}$	-0.001 (-0.01, 0.01)
$\beta_{\psi 3}$	0.002 (-0.017, 0.02)
$\beta_{\psi 4}$	-0.003 (-0.017, 0.01)
$\beta_{\psi 5}$	-0.011 (-0.022, -0.0004)
Temporarily Emigrate (γ), Return (ρ)	
$\gamma_{First-time\ Breeder}$	-0.5244 (-0.888, -0.169)
$\gamma_{Experienced\ Breeder}$	-1.725 (-2.073, -1.367)
$\gamma_{Skip-present}$	-2.079 (-2.477, -1.691)
ρ	0.979 (0.603, 1.354)
Recruitment ($\psi_{Pre-breeder}$)	
$\alpha_{\psi PB1}$	2.542 (1.702, 3.363)

$\beta_{\psi PB1}$	-0.337 (-0.383, -0.294)
$\beta_{\psi PB2}$	-0.082 (-0.124, -0.043)
$\beta_{\psi PB3}$	-0.370 (-0.539, -0.204)
$\beta_{\psi PB4}$	-0.169 (-0.203, -0.133)
$\beta_{\psi PB5}$	-0.056 (-0.082, -0.029)

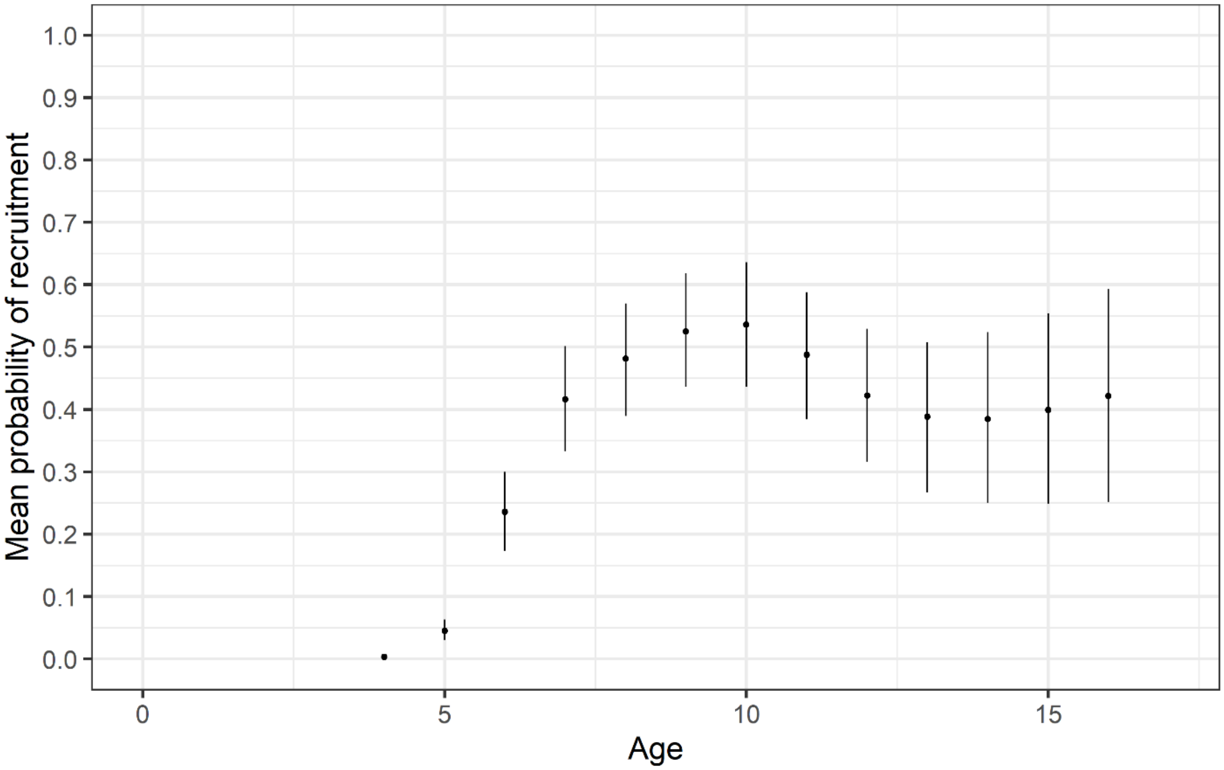

Figure A-4 Age-specific mean probability of recruitment to the breeding population for ages observed in our data in an average year. Error bars display 95% highest density intervals.

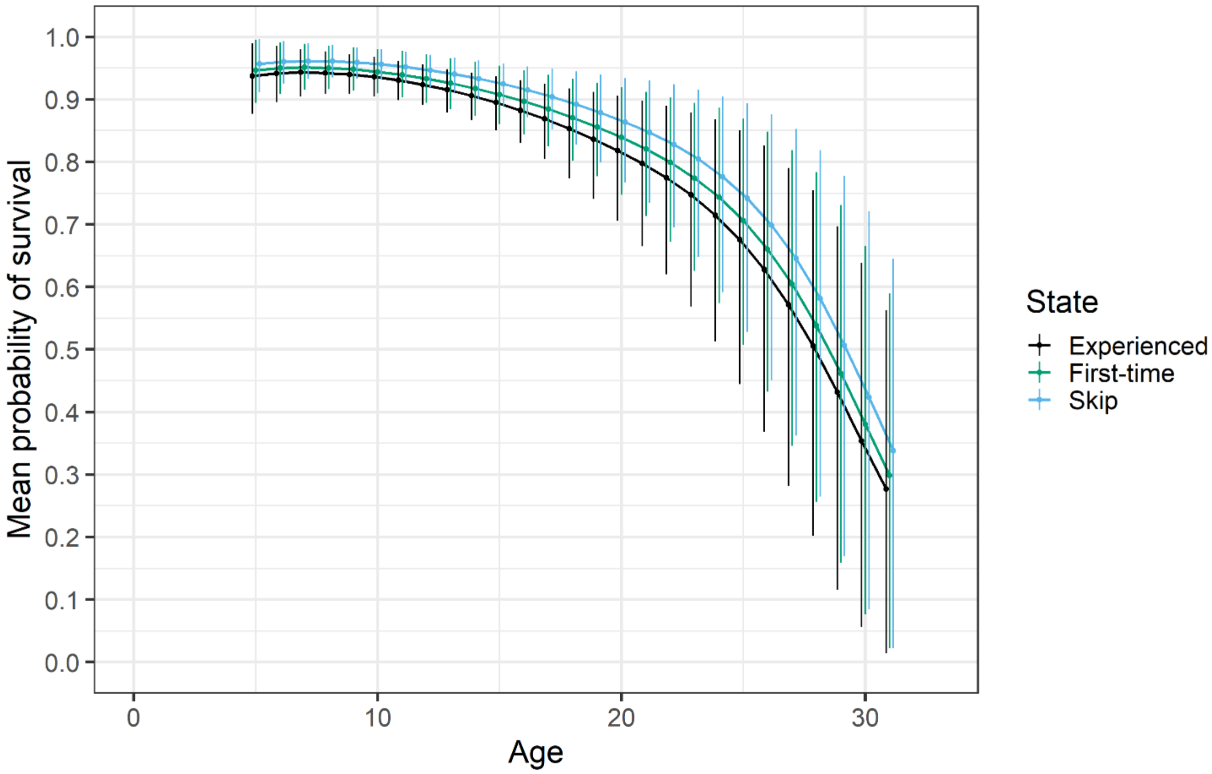

Figure A5 Age-specific probability of survival for females that have recruited to the breeding population for ages observed in our data in an average year. Probability of survival is shown for individuals in different reproductive states at t-1. Error bars display 95% highest density intervals.

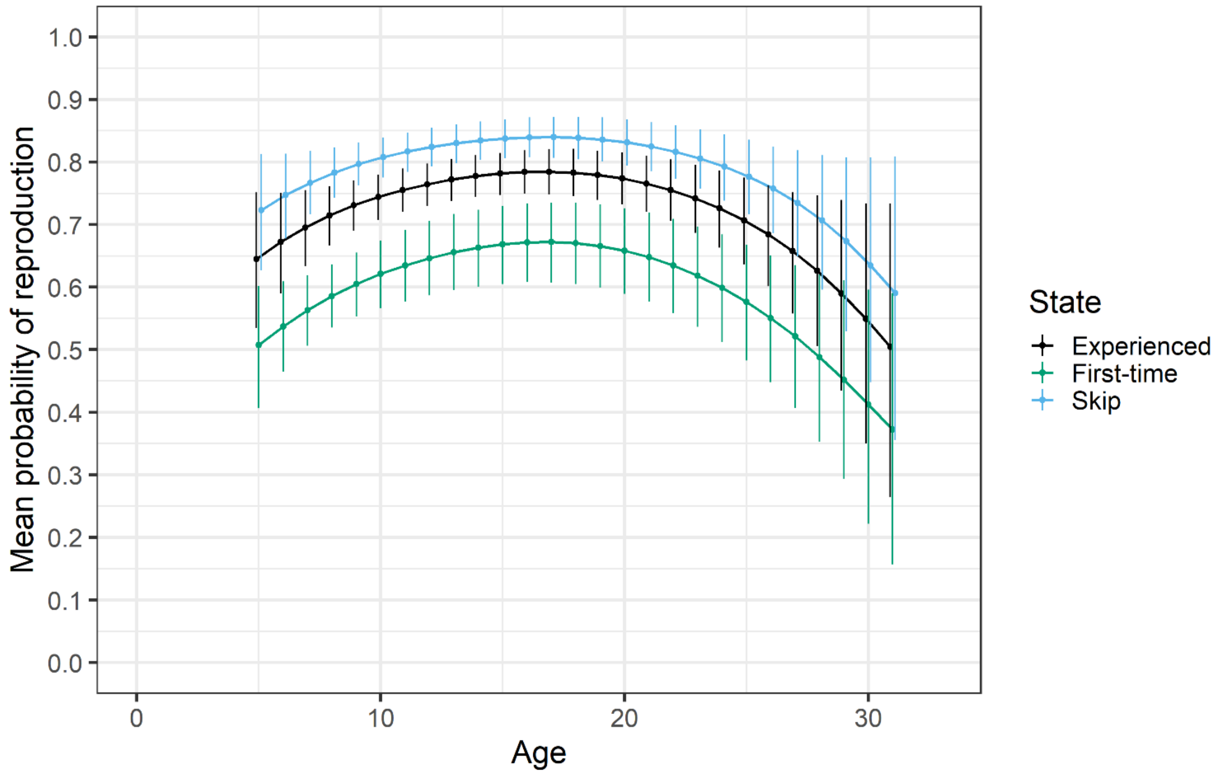

Figure A6 Age-specific probability of reproduction for ages observed in our data in an average year. Shown is the probability of reproduction for individuals in different reproductive states at t-1. Error bars display 95% highest density intervals.

Results of Inheritance IPM

Table A5 Results for the four different individual heterogeneity scenarios with and without inheritance included in the IPM

Scenario	λ with inheritance	λ without inheritance
Observed	0.963	0.967
No IH	0.963	0.968
High RE	0.963	0.966
Low RE	0.963	0.968

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APPENDIX B

SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Variation in Probability of Detection

There was support for three mixture classes on probability of detection for both males and females. A large proportion of females were estimated to be in the high detection class 0.71 (89% HDI: 0.65, 0.77), with lower proportions 0.23 (0.18, 0.29) and 0.06 (0.04, 0.07) estimated to be in the average and low detection classes, respectively. Males were more equally distributed between the high 0.39 (0.29, 0.49) and average 0.46 (0.36, 0.55) detection classes with a low proportion of individuals in the low detection class 0.15 (0.06, 0.24).

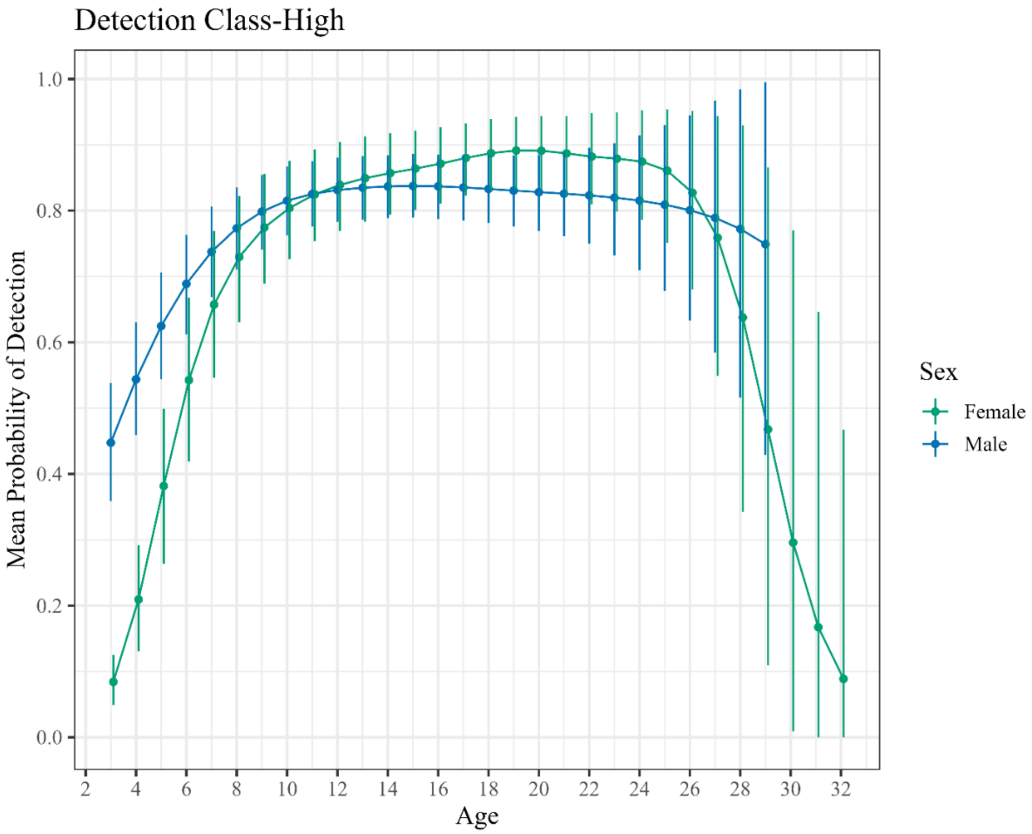

Figure B-4 Estimated mean probability of detection for males and females in the high detection class across ages represented in these data. Error bars represent 89% highest density intervals.

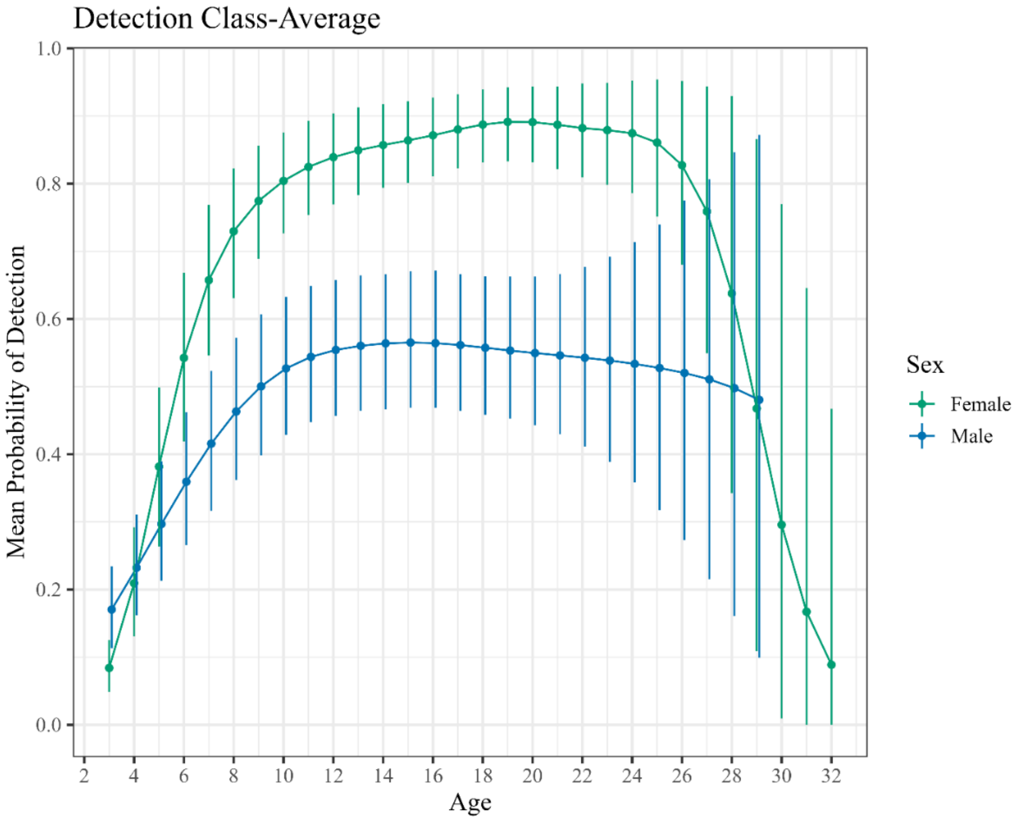

Figure B-5 Estimated mean probability of detection for males and females in the average detection class across ages represented in these data. Error bars represent 89% highest density intervals.

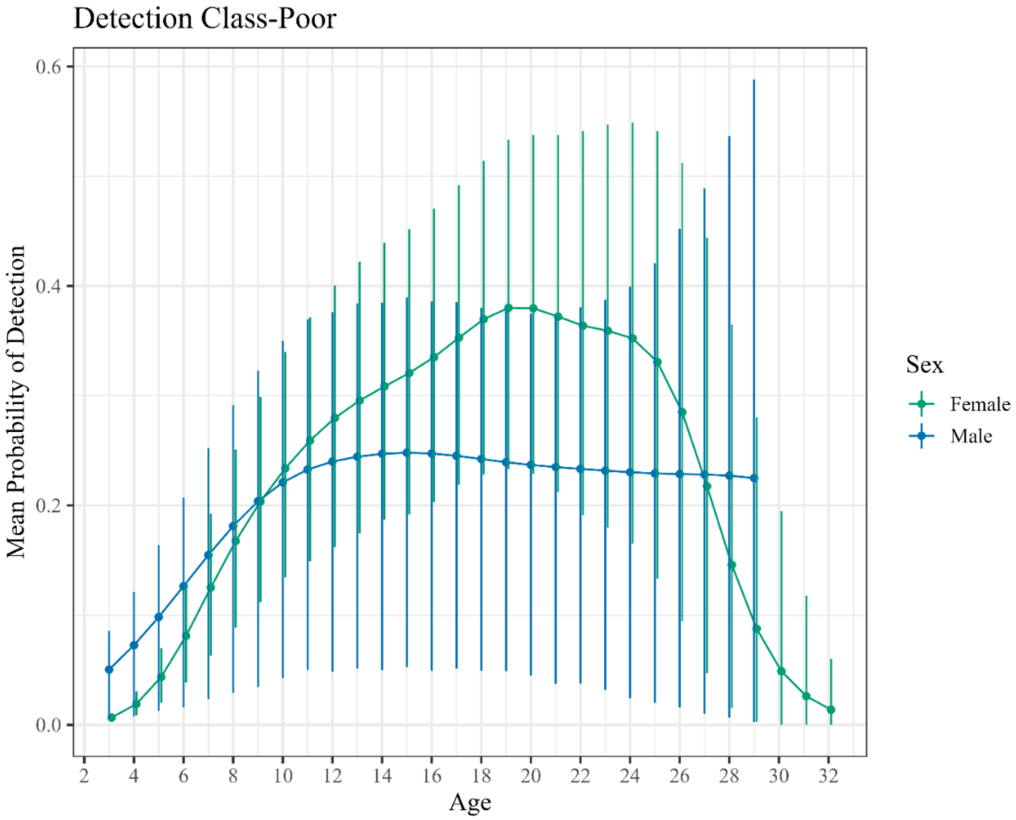

Figure B-6 Estimated mean probability of detection for males and females in the poor detection class across ages represented in these data. Error bars represent 89% highest density intervals.

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