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RESEARCH ARTICLE

Evaluating the importance of individual heterogeneity in reproduction to Weddell seal population dynamics using integral projection models

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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.

KEYWORDS
age-and state-structured population model, integral projection model, population dynamics, unobserved individual heterogeneity, Weddell seal

1 | 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, Gaillard, Coulson, Hewison, 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, Gaillard, Coulson, Delorme, 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 modelling 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;P lard, Gaillard, Coulson, Delorme, 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.

2 | MATERIALS AND METHODS

2.1 | 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 7 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 5 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.

2.2 | Population analysis

The integral projection model (IPM) we constructed modelled 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 modelling efforts and estimates from regression equations (Table 1) obtained with a multistate modelling approach (Lebreton & Pradel, 2002) in the Bayesian framework and the resulting posterior (Table S1). 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 modelled 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 Supporting 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 modelled 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 (Figure S1), reproduction (Figure S2) and development (state transition) functions (i.e. a projection kernel; Figure S3). 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 $G(z\prime, z, a, ih_r)$ 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:

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

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).

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:

$$n_a(z\prime, ih, t+1) = \iint P_{a-1}(z\prime, z, ih)n_{a-1}(z, ih, t)dz\,dih.$$

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.

TABLE 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	$\text{logit}(s) = \text{state intercept. phi} + f(\text{age}) + \varepsilon_{ih}^{\varphi} + \varepsilon_{year}^{\varphi}$
Recruitment	$\text{logit}(rec) = f(\text{age}) + \varepsilon_{year}^{\psi_{rec}}$
Reproduction	$\text{logit}(r) = \text{state intercept. psi} + f(\text{age}) + \varepsilon_{ih}^{\psi} + \varepsilon_{year}^{\psi}$

TABLE 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	$1-\Psi^{FB}$	Ψ^{FB}	0	0	0
FB	0	0	$(1-\gamma^{FB})\Psi^{FB}$	$(1-\gamma^{FB})(1-\Psi^{FB})$	γ^{FB}
EB	0	0	$(1-\gamma^{EB})\Psi^{EB}$	$(1-\gamma^{EB})(1-\Psi^{EB})$	γ^{EB}
SP	0	0	$(1-\gamma^{SP})\Psi^{SP}$	$(1-\gamma^{SP})(1-\Psi^{SP})$	γ^{SP}
SA	0	0	$(\rho)\Psi^{SA}$	$(\rho)(1-\Psi^{SA})$	$1-\rho$

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 (Figure 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 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_r to annual population growth and to evaluate how population dynamics would change if the mothers with the highest values for ih_r 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_r were removed through biased mortality or permanent emigration by left truncating the observed distribution so that approximately the lowest 20% of observed ih_r 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_r from their mother, that is each daughter was assigned a random value from the distribution of ih_r 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 $N(-0.02+0.05{*}ih_{\text{maternal}}, 0.005)$. 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 S2). 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, 2022). 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 cut-off 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.

3 | RESULTS

The asymptotic population growth rate was near 1.0 and similar across all four modelled scenarios. The λ resulting from the different scenarios ranged between 0.966 and 0.968 (Table 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 3) and all were within rounding error. The wide highest density intervals (Table 3) are the result of parameter uncertainty that was fully

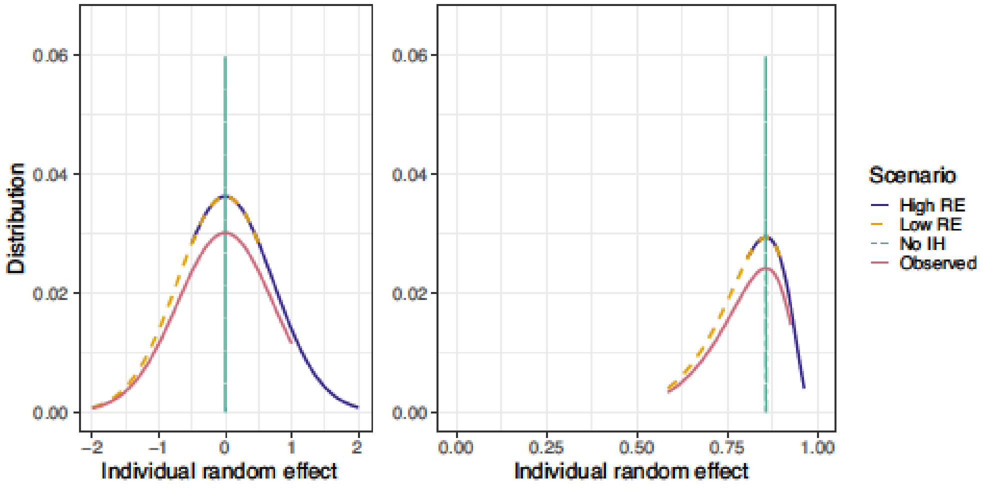

FIGURE 1 Distributions evaluated in the IPM for the random effect of individual on reproduction include: no individual heterogeneity (No IH), observed individual heterogeneity (observed), a population skewed below average (low RE), and a population skewed above average (high RE). The distribution of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

TABLE 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)

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 modelled 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 (Figure 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 ($e_{exp} = 0.21$) compared to the low RE scenario ($e_{exp} = 0.20$), but this pattern was reversed for $\text{skips}_{\text{present}}$ ($e_{skip\text{-}p} = 0.08$ for low RE vs. $e_{skip\text{-}p} = 0.06$ for high RE), indicating the relative importance of experienced breeders and $\text{skips}_{\text{present}}$ 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 (Figure 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 (Figure 3). When comparing scenarios, elasticity values for females <17-years old were slightly higher in the high RE scenario than in

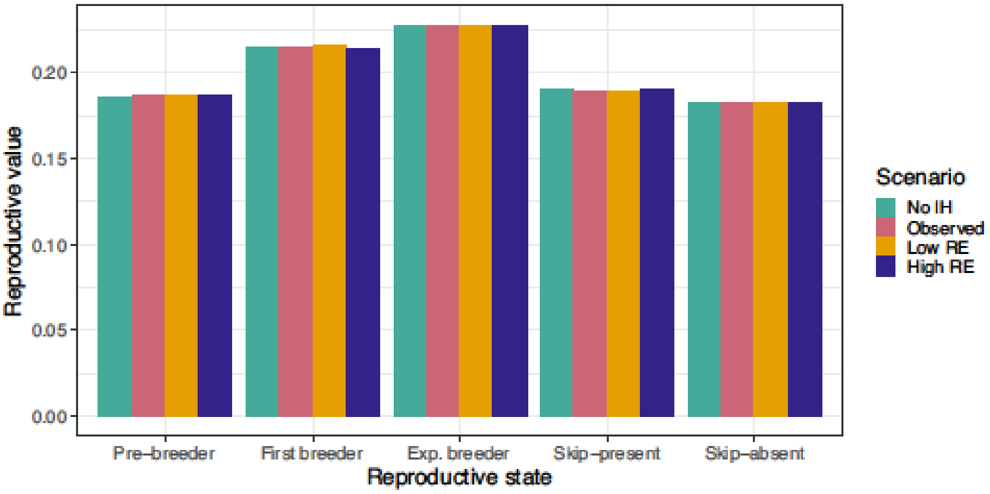

FIGURE 2 Estimated reproductive value partitioned by scenario and reproductive state. The distribution scenarios evaluated in the IPM for the random effect of individual on reproduction include: no individual heterogeneity (No IH), observed individual heterogeneity (observed), a population skewed below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

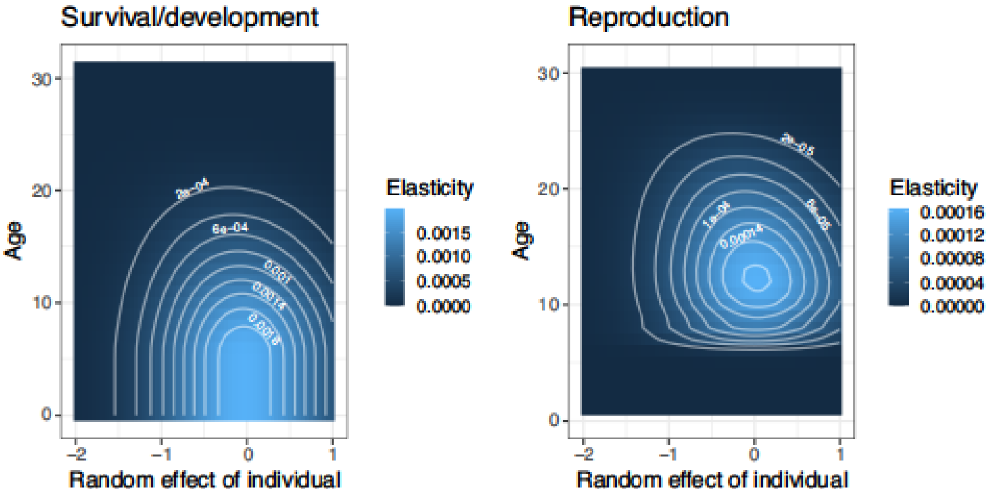

FIGURE 3 Estimated elasticities for the Observed scenario partitioned by age and individual heterogeneity for (left) the survival and development kernel and (right) the reproduction kernel.

the low RE scenario, whereas at older ages elasticities were slightly higher for the low RE scenario relative to the high RE scenario.

4 | 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, Gaillard, Coulson, Delorme, 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 (Figure 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, Gaillard, Coulson, Delorme, et al., 2015) provide support for the idea that canalization is related to the 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, unpubli. 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 1990s 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, Gaillard, Coulson, Delorme, et al., 2015; Vindenes & Langangen, 2015). Our work adds to previous research (Coulson, 2012; Plard, Gaillard, Coulson, Delorme, 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.

AUTHOR CONTRIBUTIONS

Jay J. Rotellaa and J. Terrill Paterson. conceived the research ideas, and Kaitlin R. Macdonald contributed to the development of research; J. Terrill Paterson assisted in model development and Kaitlin R. Macdonald performed the analysis and drafted the manuscript. All authors contributed critically to the final draft and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.wh70rxwt3 (Macdonald et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. 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 S2. 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 S3. 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).

Figure S4. 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 S5. 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 S6. 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.

Table S1. 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.

Table S2. Results for the four different individual heterogeneity scenarios with and without inheritance included in the IPM.

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