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LETTER

When the going gets tough, the tough get going: Effect of extreme climate on an Antarctic seabird's life history

Stéphanie Jenouvrier[1] | Lise Aubry[2] | Silke van Daalen[1] | Christophe Barbraud[3] | Henri Weimerskirch[3] | Hal Caswell[1,4]

[1]Biology Department, MS-50, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA

[2]Fish, Wildlife and Conservation Biology Department, Colorado State University, Fort Collins, Colorado, USA

[3]Centre d'Etudes Biologiques de Chizé, UMR 7372 CNRS/Univ La Rochelle, Villiers en Bois, France

[4]Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands

Correspondence
Stéphanie Jenouvrier, Biology Department, MS-50, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA.
Email: sjenouvrier@whoi.edu

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Abstract

Individuals differ in many ways. Most produce few offspring; a handful produce many. Some die early; others live to old age. It is tempting to attribute these differences in outcomes to differences in individual traits, and thus in the demographic rates experienced. However, there is more to individual variation than meets the eye of the biologist. Even among individuals sharing identical traits, life history outcomes (life expectancy and lifetime reproduction) will vary due to individual stochasticity, that is to chance. Quantifying the contributions of heterogeneity and chance is essential to understand natural variability. Interindividual differences vary across environmental conditions, hence heterogeneity and stochasticity depend on environmental conditions. We show that favourable conditions increase the contributions of individual stochasticity, and reduce the contributions of heterogeneity, to variance in demographic outcomes in a seabird population. The opposite is true under poor conditions. This result has important consequence for understanding the ecology and evolution of life history strategies.

KEYWORDS
fixed heterogeneity, frailty, individual quality, individual stochasticity, unobserved individual heterogeneity, SICs

INTRODUCTION

There exist two sources of variation in life history outcomes (e.g. life expectancy, lifetime reproduction): *individual heterogeneity* and *individual stochasticity*. Individual heterogeneity refers to differences among individuals in life history traits that in turn affect the vital rates. Heterogeneity may be fixed or dynamic (reviewed by Cam et al. (2016); Forsythe et al. (2021); Wilson and Nussey (2010)). Fixed individual heterogeneity may be due to, for example genetic variation, epigenetics, maternal effects. Dynamic individual heterogeneity may be due to time-varying factors such as age, experience, health or dynamic environmental effects (Caswell, 2014). Individual stochasticity is variability in demographic outcomes that is generated by random events in the life cycle of an individual because of chance alone (surviving or not, reproducing or not, etc.). In other words, individuals will differ in their life trajectories and demographic outcomes, even if they are subject to identical vital rates, because of chance alone (Caswell, 2009, 2011a, 2014; Jouvet et al., 2018; Snyder & Ellner, 2016; Steiner et al., 2010; Tuljapurkar et al., 2009, 2020; van Daalen & Caswell, 2017).

The relative importance of these sources of variation in life history outcomes is critically important in improving our understanding of population dynamics and life history evolution, and is currently a topic of intense debate (Bonnet et al., 2016; Cam et al., 2016; Caswell, 2012; Forsythe et al., 2021; Hartemink & Caswell, 2018; Jouvet et al., 2018; Steiner & Tuljapurkar, 2012; van Daalen & Caswell, 2017). Both theoretical models and empirical studies have found that individual stochasticity contributes a large part of the variance in life expectancy and lifetime reproduction, regardless of the variation of life history traits among individuals, and regardless of the life history considered (iteroparous or semelparous) (Snyder & Ellner, 2018; Steiner & Tuljapurkar, 2012).

Some individual differences are readily observable and easily incorporated as state variables (e.g. age, stage, size) in demographic models. Other differences are latent or unobserved, and often referred to as frailty, latent heterogeneity or individual quality (e.g. Cam and Monnat (2000); Vaupel et al. (1979); Wilson and Nussey (2010)). We refer to these as *unobserved heterogeneity*. Unobserved heterogeneity can obscure, or even reverse, patterns of survival and reproduction at the individual level, with consequences for population dynamics and our understanding of life history evolution (Jenouvrier et al., 2018; Kendall et al., 2011; Vaupel & Yashin, 1985; Vindenes & Langangen, 2015).

Environmental conditions affect the expression of heterogeneity. Harsh conditions may remove frail individuals through physiological stress or increased resource competition. Harsh conditions may also inhibit breeding, so that only robust or high-quality individuals survive and breed successfully (Barbraud & Weimerskirch, 2005; Berzins et al., 2020; Chambert et al., 2013; Hamel et al., 2009; Lescroël et al., 2009; Moyes et al., 2009). Under favourable conditions, survival and breeding rates may be high regardless of heterogeneity. Overall, extreme climatic events may act as important filters on demographic rates and on the evolution of life histories (Berzins et al., 2020; Chevin & Hoffmann, 2017; Gutschick & BassiriRad, 2003; Pardo et al., 2017; van de Pol et al., 2017). Very few studies have explored the effect of extreme environmental events on the amount of unobserved heterogeneity in vital rates. But Chambert et al. (2013) have quantified the impact of extreme years, or the unusual disruptive effects of icebergs, on interindividual variability in the reproductive success of Weddell seals (*Leptonychotes weddellii*) in Antarctica. They found little evidence that extreme environmental conditions affect the expression of heterogeneity, because their estimate of interindividual variability was only slightly larger during abnormal iceberg years than in 'normal' years, and they did not partition this variability between heterogeneity and stochasticity. Importantly, the consequences of environmental conditions for life history outcomes such as life expectancy or lifetime reproduction, when unobserved heterogeneity is accounted for, are challenging to calculate and remain virtually unexplored. Our goal here is to partition the variance of several life history outcomes between individual stochasticity and unobserved heterogeneity across different environmental conditions.

The southern fulmar (*Fulmarus glacialoides*), an Antarctic seabird, is the first wild species for which the variance in life history outcomes was successfully partitioned into contributions from individual stochasticity and individual heterogeneity (Jenouvrier et al., 2018). The southern fulmar forages near the ice edge, which is an area of high productivity (Jenouvrier et al., 2015). When SICs are extremely low, the distance from the colony to the ice edge is large and foraging trips increase in length. As a result, adults bring less food to their chicks, which then fledge in poor body condition. This leads to reduced probabilities of breeding and breeding success and reductions in population growth rate during those extreme low sea ice years (Jenouvrier et al., 2015). By accounting for unobserved heterogeneity, another study showed that the population is in fact made up of three groups of individuals with distinct sets of life history traits and outcomes (Jenouvrier et al., 2018), but the study did not assess the influence of SICs on these three life history complexes.

These three life history complexes (defined as *sets of life history characteristics that occur together through the lifetime of an individual*, Jenouvrier et al., 2018) are reminiscent of the gradient of life history strategy observed among species (i.e. the slow-fast continuum; in birds: (Saether & Bakke, 2000); in mammals: (Bielby et al., 2007; Gaillard et al., 1998; Gaillard & Yoccoz, 2003; Jones et al., 2008; Oli, 2004)):

1. Group 1 (14% of offspring at fledging) is a slow-paced life history where individuals tend to delay recruitment, recruit successfully and extend their reproductive lifespan.
2. Group 2 (67% of offspring at fledging) consists of individuals that are less likely to recruit, have high adult survival and skip breeding often.
3. Group 3 (19% of offspring at fledging) is a fast-paced life history where individuals recruit early and attempt to breed often, but have a short lifespan.

Individuals in groups 1 and 3 are considered 'high-quality' individuals (Wilson & Nussey, 2010) because they produce, on average, more offspring over their lives than do individuals in group 2. But group 2 is made-up of individuals that experience the highest levels of adult survival.

Differences between these groups, that is individual heterogeneity, only explains a small fraction of variance in life expectancy (5.9%) and lifetime reproduction (22%) when environmental conditions are ordinary. We expect that the environmental context experienced, especially when environmental conditions get extreme, is key to characterising individual heterogeneity and its contribution to life history outcomes. Here, we build on previous studies (Jenouvrier et al., 2015, 2018) to quantify the impact of extreme environmental conditions on the relative contributions of individual heterogeneity and stochasticity to variance in life history outcomes.

METHODS

To quantify the impact of extreme environmental conditions on the relative contributions of individual heterogeneity and stochasticity to variance in life history outcomes, we first define three environmental contexts based on sea ice conditions (SICs) relevant to the southern fulmar's life cycle: low, medium and high concentrations (Jenouvrier et al., 2015). Then, to estimate both unobserved and observed sources of heterogeneity in vital rates for each of those SICs, we use multistate mark–recapture (MSMR) models with finite mixtures which also account for imperfect detection of wild animals. Furthermore, to estimate life history outcomes and their variance (life expectancy and lifetime reproduction) for each level of SICs, we develop absorbing finite-state Markov chains (Caswell, 2009). Finally, we define a stage-classified matrix population model (Jenouvrier et al., 2015, 2018) to compute another integrative demographic outcomes for each group: the population growth rate for each of level of SIC.

The fulmar life cycle and sea ice conditions

The southern fulmar (*F. glacialoides*) breeds during the austral summer in the Southern Hemisphere; a single egg is laid per breeding season. We utilised mark–recapture data from 1964 to 2010 on individuals banded as fledglings ($n = 1165$ individuals) (see Supporting Information A for more details).

The life cycle of the southern fulmar includes four stages based on breeding states defined at the end of the breeding season (Jenouvrier et al., 2015): Pre-breeders, successful breeders, failed breeders and non-breeders. The annual life cycle starts in March of year t, immediately after the fledging period. The vital rates associated with the life cycle transitions among states are: Stage-specific survival, breeding and success probabilities (σ_j, β_j and $\gamma_{j,}$ respectively) (see Supporting Information A for more details). Note that while the vital rates may, in general, vary with stage j and time t we include only the stage subscript in the following notation for clarity, where j corresponds to the life-cycle state ($j = 1, \ldots, s$).

SICs affect the vital rates of southern fulmar (Jenouvrier et al., 2003).We use an index of SIC which combines sea ice cover, and location of the sea ice edge (see Jenouvrier et al. (2015) for more details). We define low and high SIC years as years with an index of SICs lower or higher than the 10th and 90th percentile of the SIC distribution, respectively.

Estimating unobserved heterogeneity in vital rates

To estimate both unobserved and observed sources of heterogeneity in vital rates, we use MSMR models with finite mixtures that account for imperfect detection (Hamel et al., 2017; Pledger et al., 2003). Finite mixture MSMR models define a finite number of groups (hidden states) in the population and provide estimates for vital rates within each group. They also estimate the proportion of the sampled individuals falling into each heterogeneity group. We denote this distribution (the *mixing distribution*) π.

We build on previous studies that identified three groups of individuals (i.e. life history complexes, Jenouvrier et al., 2018) based on unobserved heterogeneity in vital rates ($g = 3$) (see Supporting Information B). The observed states are the four breeding states described in the section *The fulmar life cycle* ($s = 4$). We perform model selection to test for the effect of sea ice conditions on all vital rates of interest, once unobserved heterogeneity is accounted for. The best-performing models selected (as measured by ΔAIC) comprised 90% of the overall AIC weight among the set of candidate models tested. All analyses were conducted in the E-surge software (Choquet et al., 2009).

Our umbrella (i.e. most general) model was based on results from Jenouvrier et al., 2018 (see Supporting Information B). Based on the structure of the umbrella model, we included effects of extreme SICs on vital rates following the approach of Jenouvrier et al. (2015) using covariates which define 'extremely low years' ($\text{ECE}_t = -1$), 'extremely high years' ($\text{ECE}_t = 1$) and average SIC years ($\text{MED}_t = 0$) on all vital rates. We expect extreme SICs during chick rearing (January) in year ECE_t to have a *direct effect* on breeding success in year t. Seabirds may also skip breeding in year t as a consequence of ECE_t, if they are able to rely on proximal cues that are indicative of sea ice habitat, and are aware of a high likelihood of poor foraging and reproductive success that year. In that case, they may skip reproduction in an effort to preserve their own survival. ECE_t may also have *indirect and lagged effects* on breeder survival and breeding probabilities from year t to $t + 1$ if reproduction in ECE_t influence subsequent survival and breeding probability (i.e. cost of reproduction). Reproductive costs may be expressed *only in extremely poor environmental years*, when resources are scarce. Because the model selection process supported six different models with various parameterisations of unobserved heterogeneity in vital rates equally well (Jenouvrier et al. (2018), Supporting Information B, Table B2), we use model averaging to generate a set of vital rate estimates from all six models. Supporting Information C describes estimates and their confidence intervals. Finally, to formally quantify differences among group of unobserved heterogeneity, we compute the coefficient of variation in vital rates (Supporting Information D).

Life history outcomes and their variance

We first estimate life history outcomes (life expectancy and lifetime reproduction) using absorbing finite-state Markov chains (Caswell, 2009) for the three environments characterised, respectively, by low, medium and high SICs. Then we decompose the variance in life history outcomes into two components—individual heterogeneity and individual stochasticity.

An absorbing finite-state Markov chain

The life cycle graph of the southern fulmar defines the transition structure of an absorbing finite-state Markov chain with death as an absorbing state (Caswell, 2001, 2009). For each for heterogeneity group k ($k = 1, \ldots, g$), in each environmental conditions E, the transition matrix for the absorbing Markov chain is:

$$\mathbf{P_{kE}} = \left(\begin{array}{c|c} \mathbf{U}_{kE} & 0 \\ \hline \mathbf{M}_{kE} & 1 \end{array}\right) \tag{1}$$

where $\mathbf{U}_{kE}$ contains probabilities of transitions and survival for living individuals and $\mathbf{M}_{kE}$ includes the probabilities m_{ij} that an individual in transient state j enters absorbing state i. For the southern fulmar, life cycle $\mathbf{U}_{kE}$ is given by Jenouvrier et al. (2018):

$$\mathbf{U}_{kE} = \begin{pmatrix} (1-\beta_1)\sigma_1 & 0 & 0 & 0 \\ \sigma_1\beta_1\gamma_1 & \sigma_2\beta_2\gamma_2 & \sigma_3\beta_3\gamma_3 & \sigma_4\beta_4\gamma_4 \\ \sigma_1\beta_1(1-\gamma_1) & \sigma_2\beta_2(1-\gamma_2) & \sigma_3\beta_3(1-\gamma_3) & \sigma_4\beta_4(1-\gamma_4) \\ 0 & \sigma_2(1-\beta_2) & \sigma_3(1-\beta_3) & \sigma_4(1-\beta_4) \end{pmatrix} \tag{2}$$

Note that while the vital rates may, in general, vary with heterogeneity group k and environmental conditions E, we include only the stage subscript in the following notation for clarity, where j corresponds to the life-cycle state ($j = 1, \ldots, s$).

Life expectancy and lifetime reproduction

To calculate life expectancy, we use a single-absorbing state: death, thus $\mathbf{M}_{kE}$ is a vector of dimension $1 \times s$ whose entries are the probabilities of dying for each breeding state. The mean and variance of life expectancy (the time required to reach the absorbing state of death) and the mean and variance of lifetime reproduction are calculated from the fundamental matrix (Supporting Information D). The fundamental matrix gives the mean ($\mathbf{N}_{kE}$) of the time spent in state i, conditional on starting in state j.

Variance decomposition: Stochasticity versus heterogeneity

Decomposition of variance into components due to individual stochasticity and unobserved heterogeneity proceeds following Caswell (2009, eqn. 90). For any variable ξ, the interindividual variance $V(\xi)$ can be written as follows:

$$V(\xi) = E_\pi\left[V\left(\xi_k\right)\right] + V_\pi\left[E\left(\xi_k\right)\right] \tag{3}$$

where E_π and V_π denote the expectation and variance calculated over the mixing distribution π and ξ_k is the outcome variable within group k. That is, the variance in ξ is equal to the weighted mean of the variances in each group plus the weighted variance of the group means.

The first term in (3) is the within-group variance, and is due to individual stochasticity. It captures the variance among individuals each of which experiences exactly the same stage-specific probabilities. These variances are calculated from the Markov chain formulation of the life cycle model, as described above. The second term in (3) is the between-group variance; it is due to the differences in vital rates among the UH groups. In the absence of unobserved heterogeneity, this component is zero.

Growth rate

We estimate the growth rate of a group of individuals with the same realised life history using a structured population model based on the life cycle of the southern fulmar, as described above. We construct a population matrix for each heterogeneity group k and each set of environmental conditions E, and calculate the deterministic growth rate λ_{kE} as the maximum eigenvalue of the population matrix $\mathbf{A}_{kE} = \mathbf{U}_{kE} + \mathbf{F}_{kE}$ (Caswell, 2001), with $\mathbf{U}_{kE}$ containing the probabilities of transitions and survival for living individuals and $\mathbf{F}_{kE}$ including the fertilities.

RESULTS

Environmental effects on life history complexes

Individual differences and vital rates across sea ice conditions (SICs)

To compare vital rates θ across environmental conditions, we weighted the average vital rates by π, noted $E_\pi(\theta)$. We found that for all three life history complexes, breeding and success probabilities all decrease when SICs are low, but adult survival remains unchanged (Figure 1; Table 1). The impact of SICs on vital rates depends on the group individuals belong to (Figure 1). For example, the breeding probability of previously successful breeders (β_2) decreases by ~17% between medium and low SICs for group 1 and 3 individuals, while it decreases by 45% for group 2.

As a consequence, individual differences in vital rates depend on SICs. The coefficient of variation over the mixing distribution of heterogeneity groups, π, measures these individual differences in vital rates. We found that the difference in breeding and success probabilities among groups increases when SICs are low (Figure 2). Differences between groups are more pronounced for the recruitment probabilities of pre-breeders, followed by the breeding probabilities of successful breeders, the breeding success of pre-breeders, and that of successful breeders.

Individual differences and demographic outcomes across SICs

We examine three integrative demographic outcomes for each of the three groups: lifetime reproductive output, life expectancy and population growth rate λ. These quantities are calculated for each environment, *as if* the population was living in such an environment permanently. This counterfactual calculation is typical of population projections being used to characterise the environment of a population by asking what would happen if that environment was maintained permanently (Caswell, 2001). State transitions defined by the vital rates (Figure 1) and the time spent in each state (Figure 4) interact to define life history outcomes (Figure 3). For example, life expectancy varies across environmental conditions even if adult survival remains unchanged across SICs because adult survival differs among breeding states and the transitions among breeding states depend on SICs. The average life expectancy for groups 1 and 3 are larger for low SICs than for high SICs (Figure 3) because individuals within this group spend most of their life as pre-breeder (i.e. 85% and 79% of their lifetime, respectively; Figure 4), a state that achieves higher levels of survival when compared to adults (Table 1).

Overall, mean demographic outcomes across group vary among SICs. The average life expectancy for the mixture of groups are larger for low SICs than for high SICs (red bars on Figure 3). However, the average lifetime reproduction is larger when SICs are high and smaller when SICs are low.

The impact of SICs on life history outcomes depends on the group individuals belong to. Individuals of group 1 have the largest life expectancy, while individuals of group 2 experience the shortest for an environment characterised by medium or low SICs (Figures 3). In contrast, for high SICs, individuals of group 2 achieve the highest life expectancy, while individuals of group 3 experience the shortest. In such high SICs, individuals spend most of their life as adult breeders, and individuals of group 2 have higher survival during adulthood than during the pre-breeding stage, while individuals that belong to life history group 3 have the lowest adult survival.

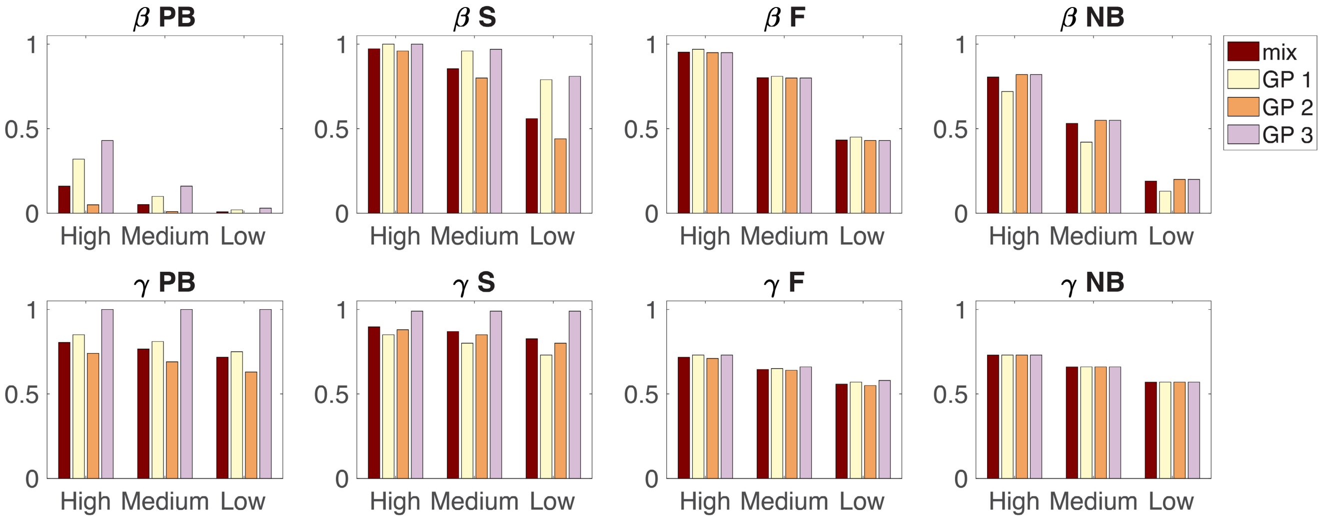

FIGURE 1 Vital rates of the southern fulmar for each reproductive state and sea ice conditions (SICs). Vital rates are averaged for environments characterised by: *High SICs* (1979, 1998, 2001), *low SICs* (1986, 1987, 2000) and *medium SICs* (all other years), as defined by Jenouvrier et al. (2015). Colour bars refer to the 3 groups of unobserved heterogeneity (yellow: complex 1; orange: complex 2; and purple: complex 3), as well as the weighted average over the mixing distribution $\pi = [0.14\ 0.67\ 0.19]$ (maroon). The panels are ordered by reproductive state at the previous breeding season (column 1: pre-breeders (PB); column 2: successful breeders (S); column 3: failed breeders (F); and column 4: non-breeders) and vital rates (first line: breeding probabilities β; and second line: success probabilities given breeding γ). Note that survival probabilities do not vary with time nor sea ice conditions, and thus are not shown here but in electronic Supplementary Material.

TABLE 1 Estimates of vital rates across environmental conditions for the southern fulmar. Pre-breeders are denoted: PB, successful breeders: S, failed breeders: F and NB: non-breeders. The groups stand for the three different life history *complexes* (sets of life history traits that persist throughout the lifetime of an individual, Jenouvrier et al., 2018) exist within the studied population of Southern fulmar

		High			**Medium**			**Low**		
		Group 1	**Group 2**	**Group 3**	**Group 1**	**Group 2**	**Group 3**	**Group 1**	**Group 2**	**Group 3**
Survival	PB	1.00	0.92	1.00	1.00	0.92	1.00	1.00	0.92	1.00
	S	0.93	0.99	0.89	0.93	0.99	0.89	0.93	0.99	0.89
	F	0.94	0.93	0.93	0.94	0.93	0.93	0.94	0.93	0.93
	NB	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88
Breeding	PB	0.32	0.05	0.43	0.10	0.01	0.16	0.02	0.00	0.03
	S	1.00	0.96	1.00	0.96	0.80	0.97	0.79	0.44	0.81
	F	0.97	0.95	0.95	0.81	0.80	0.80	0.45	0.43	0.43
	NB	0.72	0.82	0.82	0.42	0.55	0.55	0.13	0.20	0.20
Success	PB	0.85	0.74	1.00	0.81	0.69	1.00	0.75	0.63	1.00
	S	0.85	0.88	0.99	0.80	0.85	0.99	0.73	0.80	0.99
	F	0.73	0.71	0.73	0.65	0.64	0.66	0.57	0.55	0.58
	NB	0.73	0.73	0.73	0.66	0.66	0.66	0.57	0.57	0.57

Note: All parameters θ are identifiable. These estimates and their standard deviations are available USAP-DC repository.

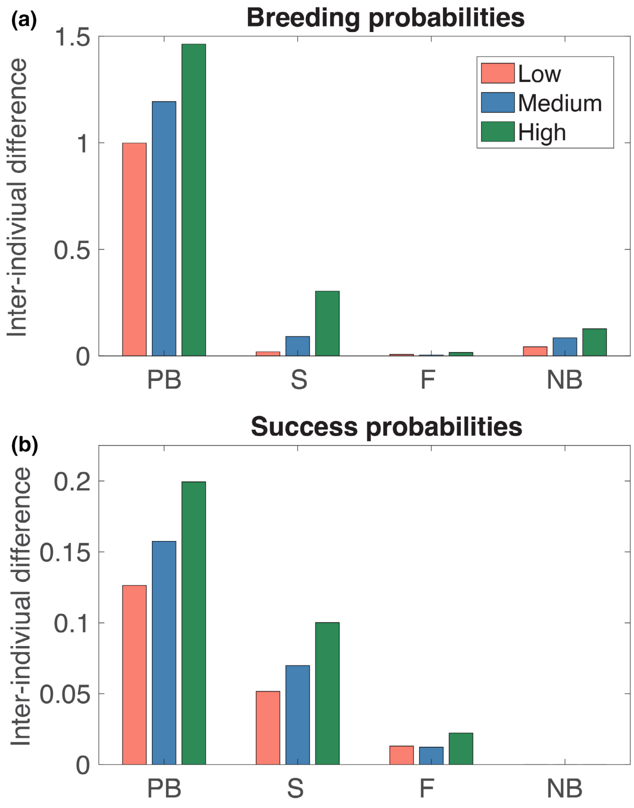

FIGURE 2 Individual differences in (a) breeding probabilities and (b) success probabilities given breeding across life history complexes for each set of sea ice conditions (SICs). Interindividual differences are measured by the coefficient of variation over the mixing distribution. The x-axis indicates the reproductive state (see Figure 1 for legends) and the bar colours refer to SICs (low: Red, medium: Blue and high: Green).

For an environment characterised by medium or low SICs, individuals in groups 1 and 3 produce, on average, more offspring over their lives than do individuals in group 2 (Figure 3). When SICs are low, individuals in group 2 are unlikely to recruit and their lifetime reproduction is null. However, for high SICs, individuals in group 2 produce, on average, more offspring over their lives than do individuals in groups 1 and 3, because they experience a longer lifespan.

Finally, we calculated the population growth rate λ to integrate all the rates into a measure that shows how successful a set of vital rates in one environment would be. Individuals of group 3 have, on average, the highest λ regardless of environmental conditions (Figure 3).

SIC impacts on variance in demographic outcomes

The total variance in life history outcomes also varies across environmental conditions (Table 2). The total variance of life expectancy is larger when SICs are extremely low. On the other hand, the total variance of lifetime reproduction is much larger when SICs are extremely high.

Both individual stochasticity and unobserved heterogeneity among individuals generate variability in life history outcomes (Caswell, 2011a; Steiner & Tuljapurkar, 2012), in response to changes in both within-group (stochasticity) and between-group (heterogeneity) variances. For example, both the between-group and within-group variances of life expectancy increase when SICs are extreme. However, for an environment characterised by high SICs, the increase in between-group variance is smaller than that in the within-group variance, resulting in a smaller proportion of individual heterogeneity to the total variance.

In spite of these complex patterns, the proportion of variance in life expectancy and lifetime reproduction

FIGURE 3 Demographic outcomes of southern fulmar for each complex for each set of sea ice conditions, as if the population was permanently living in such an environment. Colour bars refer to the three groups of unobserved heterogeneity (yellow: complex 1; orange: complex 2; and purple: complex 3), as well as the weighted average over the mixing distribution π (maroon).

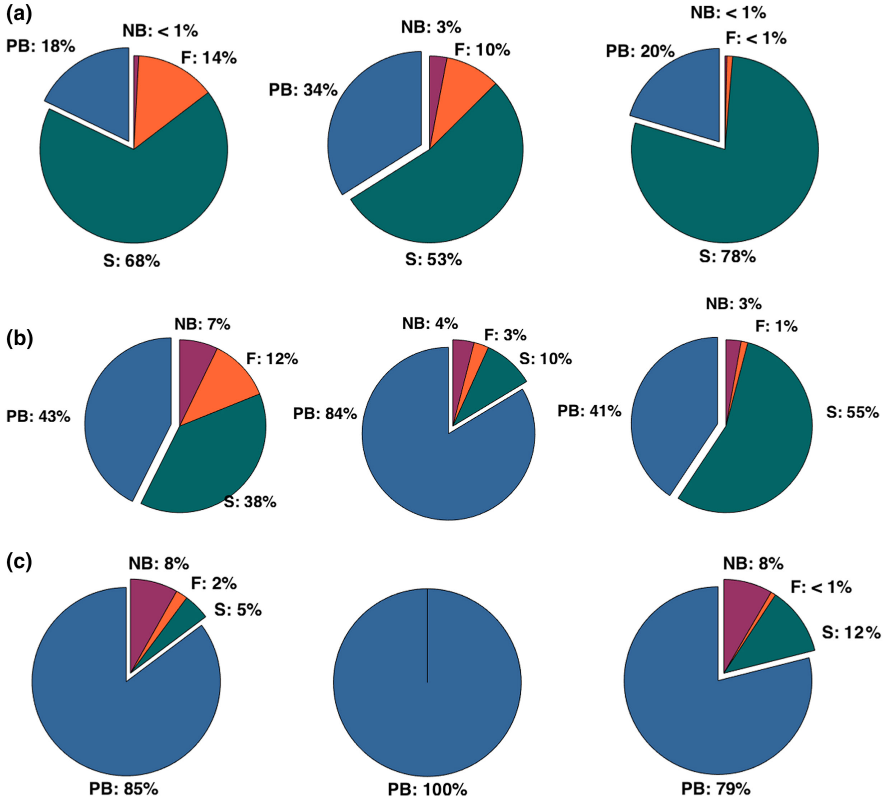

FIGURE 4 Percentages of time spent in each state for individuals in each complex for each set of sea ice conditions, as if the population was permanently living in such an environment: (a) high, (b) medium or (c) low. Complex 1 is shown by the left pie chart, while complex 3 is the right pie chart for each panel. Pre-breeders are denoted: PB, successful breeders: S, failed breeders: F, and NB: non-breeders.

due to heterogeneity are smaller when SICs are high and larger when SICs are low. Indeed, partitioning the variance in life expectancy and lifetime reproduction reveals that only 2.7% of the variance in life expectancy and 0.4% of the variance in lifetime reproduction are due to individual heterogeneity when SICs are high, while 35.3% of

TABLE 2 Life expectancy and lifetime reproduction for the southern fulmar in three environments and their variance partitioning

	Total variance	Within-group	Between-group	% heterogeneity
High				
Life expectancy	807.4	785.4	22	2.7
Lifetime reproduction	510.1	508.2	1.8	0.4
Medium				
Life expectancy	200.4	188.7	11.7	5.9
Lifetime reproduction	55.7	43.5	12.3	22
Low				
Life expectancy	1254.6	821.8	432.7	35.3
Lifetime reproduction	9.3	5.2	4.1	44.3

Note: The three environments are characterised by high, medium or low sea ice conditions. The variance partitioning of demographic outcomes shows the between individual stochasticity and unobserved heterogeneity with % H being the percentage explained by unobserved heterogeneity.

the variance in life expectancy and 45.1% of the variance in lifetime reproduction are attributable to heterogeneity when SICs are low (Table 2).

DISCUSSION

The impact of environmental conditions on unobserved heterogeneity in all fitness components of a species has virtually never been studied for wild species (but see, e.g. Steiner et al. (2021) for an experimental population of common ribwort plantain *Plantago lanceolata*). Three different life history *complexes* (sets of life history traits that persist throughout the lifetime of an individual, Jenouvrier et al., 2018) exist within a population of southern fulmar. Here, we show that the differences in vital rates and demographic outcomes among complexes depend on the environmental conditions individuals experience. Importantly, differences across life history complexes are amplified when SICs get extremely low. Sea ice conditions did not only affect patterns of life history traits, but also the variance of life history outcomes and the relative proportion of individual unobserved heterogeneity to the total variance. These new results advance the current debate on the relative importance heterogeneity (i.e. potentially adaptive) and stochasticity (i.e. enhances genetic drift) in shaping potentially neutral vs. adaptive changes in life histories (Bonnet et al., 2016; Cam et al., 2016; Caswell, 2012; Hartemink & Caswell, 2018; Jouvet et al., 2018; Steiner & Tuljapurkar, 2012; van Daalen & Caswell, 2017).

Our results indicate that extreme SICs affect vital rates, and the difference in vital rates among groups (life history complexes) depends on the SICs fulmars experience (Figures 1 and 2). In years when SICs were low, fulmars travelled greater distances to forage and adults found less food to provision their chicks, ultimately affecting chick body condition and fledging success (Jenouvrier et al., 2015). Fulmars feed mainly on krill (*Euphausia superba*) and other crustaceans, as well as on small fish (*Pleuragramma antarctica*) and squid. During years with lower SICs, the abundance of preys such as krill may be considerably reduced (Loeb et al., 1997). As a result, the breeding and success probabilities decline regardless of the group individuals belong to, and differences in vital rates among life history complexes are larger when SICs are extremely low. Low SICs could intensify intra-competition for uneven resources and reveal differences among individuals of different 'quality' (Bergeron et al., 2011; Chambert et al., 2013; Hamel et al., 2009; Lomnicki, 1978; Weladji et al., 2006; Wilson & Nussey, 2010).

Differences among life history complexes in vital rates vary among reproductive states. Individual differences in breeding and success probabilities are larger for first-time breeders than experienced breeding adults (Figure 2), probably because of pre-breeders' limited experience with foraging in their ability to acquire, store, and conserve energetic resources (Chambert et al., 2013). Individual differences in breeding and success probabilities are smaller for individuals which previously failed or skipped breeding when compared to individuals that previously succeeded. Raising an offspring successfully may impose an important energetic constraint on the probability of breeding (successfully) the following year and may intensify differences among groups.

We also demonstrate that groups differ in their demographic outcomes (life expectancy, lifetime reproduction, population growth rate λ), which further depend on the environmental conditions experienced (Figure 3). Group 1 individuals (slow-paced life histories, with a delayed but high probability of recruitment and extended reproductive lifespan) have higher life expectancy and lifetime reproduction than any other group when SICs are medium. Group 2 individuals (low and delayed recruitment, skip breeding often, but with highest adult survival rate) have higher life expectancy and lifetime reproduction than any other group when SICs are high, but a null lifetime reproduction and shortest life expectancy when SICs are low. Group

3 individuals (fast-paced life histories), have higher lifetime reproduction than any other life history group when SICs are low, and do achieve the lowest life expectancy in any environment.

Group 3 individuals have the highest λ regardless of environmental conditions because they breed at younger ages than any other group across all SICs. For southern fulmars, recruitment probability is a key vital rate that has great potential in influencing population growth rate (Jenouvrier et al., 2015). Extreme low SICs select for robust and high-quality individuals (i.e. groups 1 and 3 with $\lambda > 1$ Figure 3), because the competition for food resources increases. Thus '*when the going gets tough, only the tough get going*'. On the other hand, when SICs are extreme high, all individuals are more likely to access food resources, hence survive and breed successfully, achieving a high fitness regardless of the group they belong to.

Finally, our results indicate that the variance of life history outcomes also depends on SICs. The total variance in life expectancy is larger when SICs are extremely low, while the total variance in lifetime reproduction is larger when SICs are high (Table 2). The mean lifetime reproduction is much larger in extreme high than low SICs for group 2, which may contribute substantially to the increasing total variance in lifetime reproduction when SICs are high. However, the mean life expectancies of group 1 and 3 are much larger when SICs are high, while we observe an increased total variance in life expectancy when SICs are low.

Partitioning the total variance in demographic outcomes reveals that 35.3% and 45.1% of the variance in life expectancy and lifetime reproduction, respectively, is due to differences among groups when SICs are low, while only 5.9% and 22% of the variance is due to individual heterogeneity when the SIC is average. This supports the hypothesis that more variability in life history outcomes is attributable to persistent intrinsic differences between individuals when competition intensifies for uneven resources (Hamel et al., 2009; Lomnicki, 1978). Indeed, differences across individuals in their ability to secure limited food resources may be exacerbated when SICs are low (Jenouvrier et al., 2015), leading to the observed increased contribution of individual heterogeneity to variance in life history outcomes.

When SICs are high, 2.7% and 0.4% of the variance in life expectancy and lifetime reproduction, respectively, is due to differences among groups. Under such conditions, foraging trips are shorter (sea-ice edge is closer to the colony) and food resources likely more abundant (Jenouvrier et al., 2015). Hence, more variability in life expectancy and lifetime reproduction is attributable to stochasticity under 'favourable' conditions probably because all individuals survive and breed successfully regardless of the life history complex they belong to.

To quantify the relative importance of potentially adaptive versus selectively neutral heterogeneity in a varying environment requires an experimental system that tracks many individuals with known genotypes over their lives, with the environment perfectly known, and no measurement or processing errors (Jouvet et al., 2018; Steiner et al., 2021). Using a unique experimental study of the common ribwort plantain, Steiner et al. (2021) partitioned the variance in life expectancy and lifetime reproduction among the joint effect of the environment (non-selective environmental variations), the genes, and their interactions. They found that despite large year-to-year variations in survival and reproduction, non-selective environmental variability among years explained little variance (2.5%–4.6%) in lifetime reproduction but substantial variance in life expectancy (~25%). Only a small fraction (~0.5%–1%) is explained by additive genetic and genotype-by-environment interactions (4.6% to 6.7%) suggesting that selective changes will be slow with a large genetic drift. Although, genotypes of the various complex are unavailable in our study system, given the low estimates of heritabilities for fitness components in natural populations (Merilä & Sheldon, 1999; Teplitsky et al., 2009), and that southern fulmars are long-lived species with complex life cycle, we similarly expect a small genetic variance.

To further partition the variance of life history outcomes across life history complexes and environmental conditions, a stochastic model is required. Although our results are based on a deterministic analysis within each environment, this analysis places bounds on the degree to which individual heterogeneity can contribute to the variance of life history outcomes. Using our data and a new 'megamatrix' models for individuals in a Markovian time-varying environment, Snyder and Ellner (2022) partitioned the variance of lifetime reproduction into a contribution from fixed trait variation plus age-specific contributions from different kinds of individual stochasticity and environmental stochasticity. They found that the variance in lifetime reproduction is minimally inflated by ongoing environmental variation (Snyder & Ellner, 2022), probably because extreme conditions are rare events (10% and 90% percentiles of the range of historical measurements, Jenouvrier et al., 2015). However, whether environmental variability among years may explain a larger variance in life expectancy of southern fulmars, like in the ribwort plantain (Steiner et al., 2021), remains an open question.

It is extremely difficult to estimate unobserved individual heterogeneity in natural populations (Fay et al., 2022) and to compare those estimates across studies because they depend on the statistical methods used (Authier et al., 2017; Cam et al., 2016). These challenges hamper a comparative analysis that draws general conclusions on the role environmental conditions and individual heterogeneity play in shaping life histories. The other study which has explored the effect of environmental variations did not find strong support that environmental conditions affected the expression of heterogeneity but the authors used a different methodological framework (Chambert et al., 2013). In Chambert et al. (2013), the individual deviation from the population mean value of reproductive rate can change within the life of the individual according to environmental conditions. Thus, they studied whether environmental conditions affected the variance of individual deviations in reproductive rates from the mean, while this study characterised whether environmental conditions affected the mean demographic parameter of the life history complex.

Furthermore, individuals may belong to various life history complexes during their lifetime (i.e. dynamic individual heterogeneity). Unfortunately, a model that estimates transitions among unobservable states contains model parameters that are not identifiable (Jenouvrier et al., 2018). Further work entails exploring the consequences of such dynamic heterogeneity on life history complexes within a theoretical framework.

CONCLUSION

Based on our findings in a long-lived vertebrate species, individual stochasticity makes a substantial contribution to variance in demographic outcomes when environmental conditions are favourable, but individual heterogeneity contributes substantially to these outcomes when environmental conditions are poor. Because the strength of selection on fitness components often varies considerably from 1 year to the next in wild populations (Siepielski et al., 2009), we expect phenotypic selection on life history traits to intensify when conditions are poor. These results advance the debate on how neutral versus potentially adaptive processes shape variance of life history outcomes, and we further observe that the environmental context is key to moulding the relative contribution of these process to the evolution of life histories. Our findings support the hypothesis that both observed and unobserved differences across individuals can be tempered by environmental conditions, and ultimately define the diversity of life history strategies within a species.

AUTHOR CONTRIBUTIONS

SJ and HC conceived the ideas, designed methodology and obtained funding for the analyses; CB and HW collected the data and obtained funding for field-work; SJ and SVD performed preliminary analyses; SJ analysed the data; SJ led the writing of the manuscript with LA and HC. All authors interpreted the data, contributed critically to the intellectual content and gave final approval for publication.

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ORCID

Stéphanie Jenouvrier https://orcid.org/0000-0003-3324-2383

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