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Research Article

Linking differences in personality to demography in the wandering albatross

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Population dynamics are shaped by individual differences. With a good understanding of the relationships between individual differences and vital rates, population models can be improved to yield more realistic and detailed demographic projections. Personality is expected to shape individual differences in performance. Yet, an empirical quantification of its impact on population dynamics is currently lacking. Here, we developed and analyzed a three-dimensional hyperstate population model that accounts for three sources of individual differences simultaneously in its structure: age, breeding state and boldness as a measure of personality. We parameterized our model using empirical demographic and boldness data on the wandering albatross *Diomedea exulans* population from Crozet. We quantified the relative importance of boldness through sensitivity analyses and simulations of increased strength of relationship between boldness and three vital rates (survival, breeding probability and breeding success). We showed that sensitivity of population growth rate to changes in vital rates followed the normal distribution of boldness within the population with population growth rate being less sensitive to changes in the vital rates of extreme shy or bold individuals. Our simulations showed that increasing the strength of the relationship between boldness and survival would yield the greatest shift in boldness distribution over time compared to breeding probability and breeding success. However, shifts in boldness distribution appeared constrained by the low heritability (< 0.2) value and the large variance in boldness in this population. Our study provides an important contribution to our understanding of the role of personality in shaping the population dynamics of wild species. In the face of global change, our approach offers a promising avenue to predict the potential for behavioral adaptation. More generally, our approach may help to unravel the complex interplay between individual variations in any (or many) traits and population dynamics.

Keywords: boldness, demography, matrix population model, personality, population dynamics, sensitivity

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Introduction

Personality – defined as consistent, heritable individual differences in behaviour (Sih et al. 2004) – is ubiquitous in wild animal populations. Considerable effort has been directed towards understanding individual differences in single or multiple behavioural traits and their ecological (Smith and Blumstein 2008, Sih et al. 2012), evolutionary (Wolf and Weissing 2012) and, more recently, conservation implications (MacKinlay and Shaw 2023). Theoretical and empirical work suggests that demographers should be concerned with personality. Individuals with different personalities can differ in detectability, potentially causing sampling bias (e.g. the increased trappability of bolder individuals; Biro and Dingemanse 2008). Personality is also linked to migratory propensity and dispersal decisions (Clobert et al. 2009, Chapman et al. 2011, Beukeboom et al. 2023). Moreover, individuals expressing different personalities can exhibit different survival and reproductive patterns (Sih et al. 2004, 2012, Biro and Stamps 2008, Smith and Blumstein 2008, Moiron et al. 2020), thereby yielding consequences for individual lifetime performances. Another consequence is that, as individuals within a population do not contribute equally to population growth rate, the distribution of personality at the population level could affect population dynamics. In a theoretical study, Kendall et al. (2018) demonstrated that personality-mediated differences in survival and reproduction can alter the equilibrium density of the population. Given that behavioural adaptation has the potential to shape population responses to anthropogenic change (Bro-Jørgensen et al. 2019, Buchholz et al. 2019, Maspons et al. 2019), quantifying the demographic consequences of personality in natural populations is therefore imperative.

Surprisingly, the influence of behavioral traits or personality on population dynamics remains under-explored empirically. This may be explained by the fact that incorporating behavioral stages, like personality, into population models poses a particular challenge because of the requirement for detailed longitudinal long-term data, and because the connections between personality and all demographic rates throughout the life cycle are rarely understood in most systems (Van de Walle et al. 2024). Yet, accounting for behavioural ecology in the construction of population models is expected to improve the accuracy of population size projections (Sæther and Engen 2019).

Identifying and quantifying the importance of sources of individual variation is challenging, but crucial to adequately understand and predict population dynamics. Structured population models directly account for individual variation in their construction. Ever since the publication of Leslie (1945)'s work, the predominant structuring element in structured projection models has remained age. This is because there has been a longstanding recognition that mortality and fertility patterns often vary as individuals progress in age. However, in many systems, e.g. in invertebrates, plants and fishes, development stage often better captures the differences between individuals than age, justifying the use of stage-structured population models (Lefkovitch 1965, Caswell 2001). Morphological traits, e.g. size, also constitute a major structuring element in plant populations and have also been increasingly incorporated into animal population models (reviewed by Doak et al. 2021). For instance, size is central to integral projection models (Easterling et al. 2000). More generally, individuals can be classified by any attribute, to build models tailored to our understanding of what best accounts for individual differences in a given population. For example, the consideration of breeding states in seabirds is essential, as survival and breeding probabilities differ among breeders and non-breeders (Jenouvrier et al. 2008).

As long-term data accumulates and our understanding of what shapes individual differences deepens, we will be facing the challenge of having to incorporate multiple sources of individual differences (e.g. age, state, size, etc.) into matrix population models. One common practice is to aggregate information into combined classes, for example having classes defined by a combination of age classes and stages (Jenouvrier et al. 2018, Van de Walle et al. 2021). However, this approach can lead to very large matrices that are harder to manipulate and are error prone. Another approach is to use multistate models, i.e. models in which individuals are simultaneously classified by two attributes. Such models were introduced by Rogers (1967) and their construction and analysis were later expanded by Hunter and Caswell (2005) through the use of the vec-permutation technique. Multistate models have been used in many systems for diverse combinations of individual attributes (Ozgul et al. 2009, Metcalf et al. 2012, Caswell and Salguero-Gómez 2013). Megamatrices and multitrait population models are other alternative matrix construction approaches that use the vec-permutation approach to analyze models in more than one dimension (Pascarella and Horvitz 1998, Coste and Pavard 2020).

A substantial development in matrix population models came from Roth and Caswell (2016)'s work which extended the vec-permutation approach to models with virtually any number of attributes (hereafter referred to as 'dimensions'). They called such models 'hyperstate matrix models'. This recent development now makes possible the integration of multiple known, or expected, sources of individual differences into a single, comprehensive, matrix population model. Those models allow to track current and future changes in the proportion of individuals within several categories (e.g. age, sex, breeding states, phenotypic class) simultaneously, which can be of great interest in ecological and evolutionary studies. In addition, this model formulation facilitates the implementation of classical analytical sensitivity analyses using matrix algebra. Sensitivity analyses allow the assessment of the impact of a perturbation in each vital rate on population properties, such as population growth rate (Caswell 2019), and answer questions such as: what would happen to population growth rate if survival within or across dimensions was to change Yet, hyperstate models have remained largely underused in natural populations. Obstacles to their general use do not lie in running and analyzing such models, but in parametrizing them because they require detailed empirical estimates of vital rates across all dimensions (Roth and Caswell 2016). In this study, we had access to a remarkable dataset that allowed us to rigorously investigate the impact of personality on population growth.

Here, we quantitatively assessed the role of personality in shaping the population dynamics of a long-lived seabird, the wandering albatross *Diomedea exulans* from Crozet Archipelago. In this population, survival and breeding performance vary across age classes and breeding states. In addition, in this population individuals differ in their personality, with personality being heritable (Patrick et al. 2013), and a previous study empirically estimated the effects of boldness on vital rates (Van de Walle et al. 2024). This study showed that the effects of boldness on vital rates were of low magnitude in this population but added up over the entire life cycle could nevertheless affect individual lifetime reproductive success, especially in males. Therefore, there is a need to incorporate three interactive dimensions – personality, age and breeding state – into the matrix population model. An hyperstate model allows us to achieve this by capturing these interactions and their influence on population dynamics.

Our main objective was to use the vital rates and relationships with boldness previously estimated in Van de Walle et al. (2024) to assess how changes in boldness influence overall population growth rate and structure through a series of sensitivity analyses. With rapid global change, individuals will be faced with novel environments, such as altered wind patterns (Sun et al. 2025). Individual vulnerability or success under those new conditions may depend on their behavioral type (Buchholz et al. 2019). For example, individuals expressing different personality trait values might be differentially susceptible to mortality factors, such as predation or exploitation, or could be more or less efficient at exploiting resources under more challenging environmental conditions. Sensitivity analysis can help predict how population growth rate would change if the survival or breeding performance of individuals with specific personality traits were perturbed.

To address this, we conducted three types of sensitivity analyses:

1) Local sensitivity analysis. We performed a classic sensitivity analysis (i.e. the impact of a local change in a given vital rate on population growth rate, λ, holding all other parameters constant; Caswell 2001) based on empirical values of vital rates for every combination of age class, breeding state and boldness class (Supporting information). Local sensitivity analysis can be used to calculate the relative contribution of any age class, breeding state and/or boldness class to the observed population growth rate. This approach also answers the following questions: 'Through which pathway (e.g. survival of bolder individuals) boldness has the greatest impact on population dynamics?' and 'What would happen to population growth rate if bolder individuals experienced a reduced survival rate due to e.g. higher vulnerability to human-induced mortality?'
2) Sensitivity to the shape of boldness distribution. We examined whether population growth rate is influenced by changes in the overall shape of the boldness distribution at the population level. This approach answers the following question: 'are some boldness classes contributing relatively more to population growth rate compared to others?'.
3) Scenario-based global sensitivity analysis. We explored more substantial changes in the relationship between boldness and vital rates and varied the magnitude of heritability to assess how larger shifts in boldness could affect the population growth rate. This simulation approach answers the following question: 'which conditions would be required to result in a shift in boldness distribution at the population level and a change in population growth rate?'.

This comprehensive set of analyses, based on both empirical analysis and simulations, allowed us to understand the role of boldness in the wandering albatross population dynamics and predict future changes resulting from any specified alterations in vital rates based on individual differences in boldness.

Material and methods

Study population and parameters

Our study is based on the long-term (1966–2022) monitoring of wandering albatrosses breeding on Possession Island (46°24′S, 52°46′E), in the Crozet Archipelago, south-western Indian Ocean. There, a capture–mark–recapture program allows the empirical estimation of vital rates (σ: survival, β: breeding probability and γ: breeding success probability). Here, those vital rates were estimated from multi-state capture–mark–recapture models applied to juveniles and adults. Personality tests were conducted on breeding adults from 2008 to 2020, which allowed the estimation of the impact of boldness on vital rates in adults (i.e. individuals that have bred at least once). Briefly, boldness was measured as the response of incubating individuals to human approach from 5 m, and took the form of an ordinal scale: (0 = no response, 1 = lifts the head, 2 = stands on tarsus, 3 = vocalizes, 4 = stands up). The higher the score, the bolder the individual (Patrick et al. 2013). Then, boldness scores were adjusted to control for differences between observers and observation number, and were standardized (mean = 0, SD = 1). Boldness was added as a covariate in the multi-state capture–mark–recapture models to estimate its influence on survival, breeding probability and breeding success. Further, we measured the heritability of boldness by analyzing an animal model based on the pedigree of the population. Detailed methodology for the estimation of vital rates and the impact of boldness can be found in Van de Walle et al. (2024) and in the Supporting information, with demographic rates in the Supporting information. Also, see the Supporting information and Patrick et al. (2013) for full description of how boldness was measured on wandering albatrosses at Crozet and for pedigree description and results from the animal model for the estimation of boldness heritability.

Model description

Our model is female-based as are most demographic models, based on the fact that population growth is typically limited by female reproduction and survival (Caswell 2001). In the wandering albatross, the vital rates vary according to age and breeding state (Van de Walle et al. 2024) and our population model included these two sources of individual variation. In addition, we included a third dimension, i.e. personality, to evaluate its importance as a structuring characteristic. To account for these three sources of individual variation simultaneously, we built an hyperstate matrix population model following Roth and Caswell (2016) to characterize individuals along three distinct dimensions, or stages: age class (i), breeding state (j) and boldness class (k);

Stage 1, $i, \in \{1, \ldots, w\}$
Stage 2, $j, \in \{1, \ldots, b\}$
Stage 3, $k, \in \{1, \ldots, g\}$

We considered transitions on an annual basis, from year t to year $t+1$. We used 31 age classes ($w = 31$), with age class 1 corresponding to individuals of age 0 (fledglings). All other age classes corresponded to a year, with the exception of the last age class, for individuals aged 30+, which was left open-ended, following Fay et al. (2018).

We classified individuals into six breeding states ($b = 6$): pre-breeders (PB), successful breeders (SB), failed breeders (FB), post-successful breeders (PSB), post-failed breeders (PFB) and non-breeders (NB). The life cycle illustrating breeding state transitions and fertilities is presented in Van de Walle et al. (2024) and in the Supporting information. Transitions between breeding states are conditional on survival probability σ, breeding probability β and breeding success probability γ. The state PB includes individuals that have not yet bred. These individuals are of age class 1 and over. Wandering albatrosses can start to breed (lay an egg for the first time) at six years-old (Fay et al. 2016) and transition to the SB or FB states, conditional on whether they have successfully raised a chick or not. Although some wandering albatrosses can breed two years in a row (Barbraud and Weimerskirch 2012), most individuals skip breeding and take a sabbatical year in-between breeding events away from the colony (Tickell 1968). The states PSB and PFB include those individuals during their sabbatical year after having successfully raised a chick or not, respectively. Individuals can thus only reach the PSB and PFB states after having first reached the SB or FB states. After a sabbatical year, an individual skipping breeding again will transition to the NB state. Individuals within all breeding states at time t can produce a chick the following year at time $t+1$, conditional on transiting to the SB state.

We classified individuals into 6 boldness classes ($g = 6$) of equal width, ranging from −3 to 3 (class 1: −3 to −2, class 2: −2 to −1, class 3: −1 to 0, class 4: 0 to +1, class 5: +1 to +2 and class 6: +2 to +3), with higher values corresponding to bolder classes. We chose to model six boldness classes to have a matching number of classes across dimensions (here $b = g = 6$). This allowed us to directly compare the relative importance of breeding state with the boldness structure for population growth rate. We could not test the scenario of an equal number of classes for boldness and age stages (i.e. $g = w = 31$) because of computational limitations. A model with this many classes would run, but the analytical calculation of sensitivities becomes too cumbersome.

Matrix construction

Here, we briefly present the main constituents of the hyperstate matrix, which are also presented in Fig. 1. More detailed information on hyperstate matrix construction and notation can be found in the Supporting information. Fig. 2–5

The hyperstate matrix $\tilde{\mathbf{A}}$ projects the hyperstate population vector $\tilde{\mathbf{n}}$ forward in time, from time t to time $t+1$,

$$\tilde{\mathbf{n}}(t+1) = \tilde{\mathbf{A}}\tilde{\mathbf{n}}(t), \text{ where} \tag{1}$$

$$\tilde{\mathbf{A}} = \tilde{\mathbf{U}} + \tilde{\mathbf{F}}. \tag{2}$$

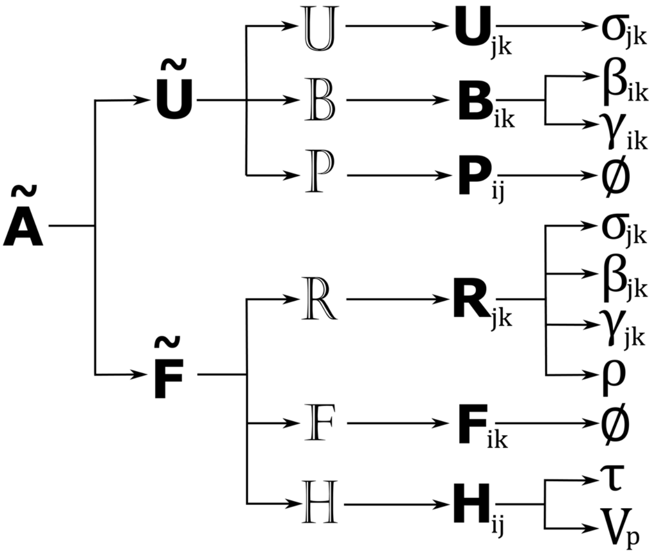

Figure 1. Schematic representation of the $\tilde{\mathbf{A}}$ matrix and its constituents. The projection matrix $\tilde{\mathbf{A}}$ is of dimensions $w \times b \times g$ and can be decomposed into transitions of live individuals (within $\tilde{\mathbf{U}}$) and production of new individuals (within $\tilde{\mathbf{F}}$), which are also of dimensions $w \times b \times g$. $\tilde{\mathbf{U}}$ and $\tilde{\mathbf{F}}$ are each further decomposed into three subprocesses, captured by block-diagonal matrices containing parameters linked to transition probabilities between the different classes within each dimension. The block matrices are also of dimensions $w \times b \times g$, but are arranged differently, depending on whether transitions occur along age classes, breeding states or boldness classes. For example, in $\mathbf{U}_{jk}$ are transitions between age classes and are given by survival rates, σ. The $\mathbf{U}_{jk}$ matrices are of dimensions $w \times w$. There is one $\mathbf{U}_{jk}$ matrix for each breeding state and each boldness class and as a result, survival rates, σ, between age classes are specific for each breeding state (j) and boldness class (k). All the $\mathbf{U}_{jk}$ matrices are assembled together along the diagonal of the $\mathbb{U}$ matrix. Note that Ø stands for empty set. Other parameters are: breeding probability (β), breeding success (γ), sex ratio at birth (ρ), and heritability value (τ).

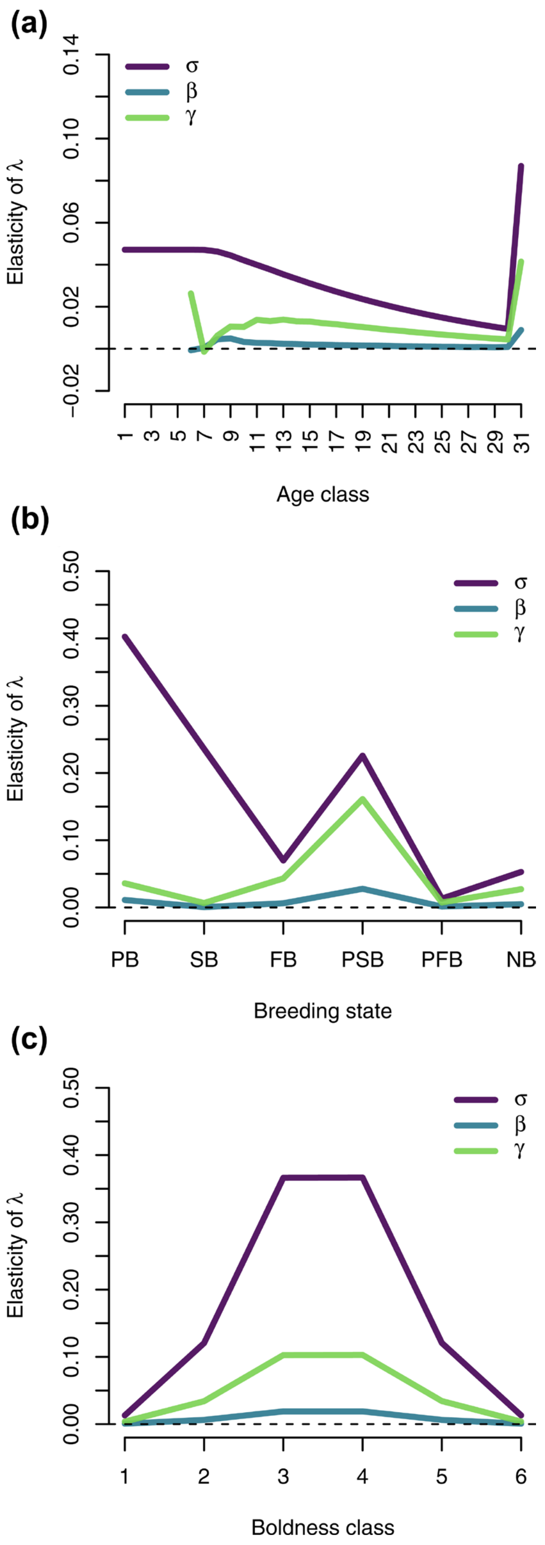

Figure 2. Elasticities (relative sensitivities) of population growth rate, λ to vital rates (survival σ, breeding probability β and breeding success probability γ) along the three dimensions included in the hyperstate model: age class, breeding state and boldness class in female wandering albatrosses at Possession Island. Note that the age class 31 includes all individuals of age 30 years-old and over, hence the drastic increase in elasticities for this age class.

The matrix $\tilde{\mathbf{U}}$ contains transition probabilities for living individuals and consists of three sub-processes: 1) transitions between age classes included in the block-diagonal matrix $\mathbb{U}$, 2) transition between breeding states included in the block-diagonal matrix $\mathbb{B}$, and 3) transitions between boldness classes included in the block-diagonal matrix $\mathbb{P}$. In the wandering albatross, annual transitions between boldness classes are not expected. This is based on a previous study showing that boldness is a repeatable trait, i.e. individuals show consistency in their boldness over time (Patrick et al. 2013). Alternative scenarios, such as plastic changes in boldness, could be explored.

The matrix $\tilde{\mathbf{U}}$ is obtained by sequentially multiplying the three sub-processes:

$$\tilde{\mathbf{U}} = \left(\mathbf{K}_3\mathbf{K}_2\right)^{\mathrm{T}} \mathbb{P}\mathbf{K}_3\mathbb{B}\mathbf{K}_2\mathbb{U}. \tag{3}$$

The $\mathbf{K}$ matrices are vec permutation matrices that allow rearrangement of the vector $\tilde{\mathbf{n}}$ prior to matrix multiplication in the next dimension (Roth and Caswell 2016). In the block-diagonal matrix $\mathbb{U}$, entries are the matrices $\mathbf{U}_{jk}$. The $\mathbf{U}_{jk}$ matrices are of dimension $w \times w$ and move individuals between age classes i according to their age-, state- and personality-specific survival rates σ_{ijk}:

$$\mathbf{U}_{jk} = \begin{pmatrix} 0 & \dots & 0 & 0 & 0 \\ \sigma_{1jk} & \dots & 0 & 0 & 0 \\ \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & \dots & \sigma_{w-2jk} & 0 & 0 \\ 0 & \dots & 0 & \sigma_{w-1jk} & \sigma_{wjk} \end{pmatrix} \tag{4}$$

The matrices $\mathbb{B}$ and $\mathbb{P}$ have matrices $\mathbf{B}_{ik}$ and $\mathbf{P}_{ij}$ on the diagonal, respectively. The $\mathbf{B}_{ik}$ matrices are of dimension $b \times b$ and move individuals between the six breeding states (PB, SB, FB, PSB, PFB, NB) for each combination of age class (i) and boldness class (k). They have the following structure, where β_{ijk} and γ_{ijk} represent age-, state- and personality-specific breeding probabilities and breeding success probabilities, respectively:

$$\mathbf{B}_{ik} = \begin{pmatrix} 1-\beta_{i1k} & 0 & 0 & 0 & 0 & 0 \\ \beta_{i1k}\gamma_{i1k} & \beta_{i2k}\gamma_{i2k} & \beta_{i3k}\gamma_{i3k} & \beta_{i4k}\gamma_{i4k} & \beta_{i5k}\gamma_{i5k} & \beta_{i6k}\gamma_{i6k} \\ \beta_{i1k}\left(1-\gamma_{i1k}\right) & \beta_{i2k}\left(1-\gamma_{i2k}\right) & \beta_{i3k}\left(1-\gamma_{i3k}\right) & \beta_{i4k}\left(1-\gamma_{i4k}\right) & \beta_{i5k}\left(1-\gamma_{i5k}\right) & \beta_{i6k}\left(1-\gamma_{i6k}\right) \\ 0 & 1-\beta_{i2k} & 0 & 0 & 0 & 0 \\ 0 & 0 & 1-\beta_{i3k} & 0 & 0 & 0 \\ 0 & 0 & 0 & 1-\beta_{i4k} & 1-\beta_{i5k} & 1-\beta_{i6k} \end{pmatrix} \tag{5}$$

The $\mathbf{P}_{ij}$ matrices are of dimension $g \times g$ and move individuals from their boldness class at time t to a boldness class at time $t+1$. Assuming individuals keep their boldness score over their lifetime, the $\mathbf{P}_{ij}$ matrices are then identity matrices as follows:

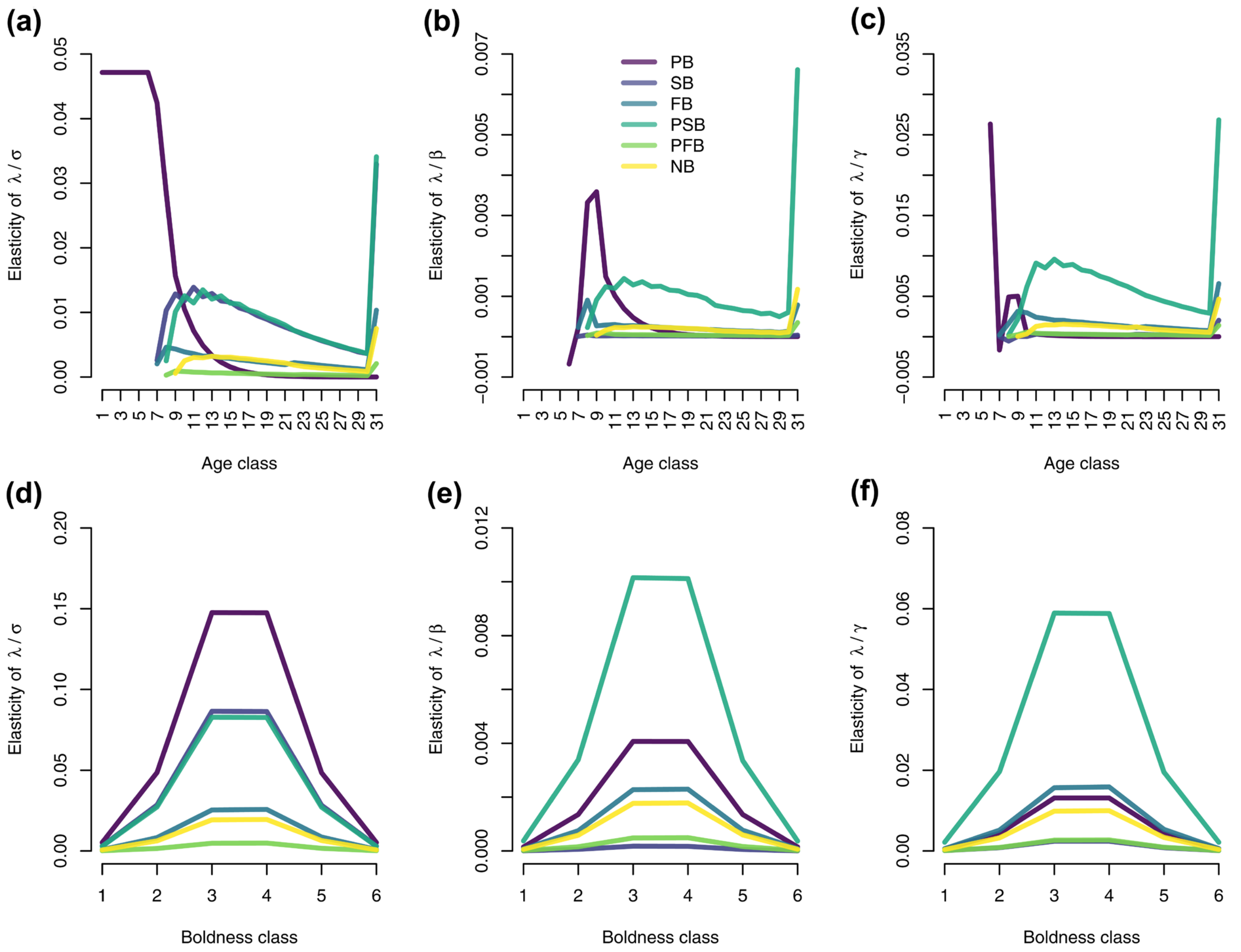

Figure 3. Elasticities (relative sensitivities) of population growth rate, λ to vital rates: survival σ (left column), breeding probability β (middle column) and breeding success probability γ (right column) for female wandering albatrosses at Possession Island.

$$\mathbf{P}_{ij} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \tag{6}$$

The hyperstate matrix $\tilde{\mathbf{F}}$ characterizes the production of new individuals by mature individuals and consists in three sub-processes: 1) production of individuals of age class 1 through $\mathbb{R}$, 2) classification of age class 1 individuals within the first breeding state PB through $\mathbb{F}$, and 3) personality class assignation through $\mathbb{H}$.

The hyperstate matrix $\tilde{\mathbf{F}}$ is obtained as follows:

$$\tilde{\mathbf{F}} = \left(\mathbf{K}_3\mathbf{K}_2\right)^{\mathrm{T}} \mathbb{H}\mathbf{K}_3\mathbb{F}\mathbf{K}_2\mathbb{R}, \tag{7}$$

In $\mathbb{R}$, entries in the block-diagonal matrices are the matrices $\mathbf{R}_{jk}$, which capture the production of offspring (all in the first age class or first row) from mothers within each of the adult age classes (columns). Offspring production is dependent upon age-, state- and boldness-specific maternal survival σ_{ijk}, breeding probability β_{ijk}, breeding success probability γ_{ijk} and the offspring sex-ratio ρ, which we fixed at 0.5. The $\mathbf{R}_{ik}$ matrices have the following structure:

$$\mathbf{R}_{jk} = \begin{pmatrix} \sigma_{1jk}\beta_{1jk}\gamma_{1jk}\rho & \sigma_{2jk}\beta_{2jk}\gamma_{2jk}\rho & \cdots & \sigma_{wjk}\beta_{wjk}\gamma_{wjk}\rho \\ 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & 0 \end{pmatrix} \tag{8}$$

The matrix $\mathbb{F}$ then reclassifies all newly produced offspring within the pre-breeder (PB) state. The $\mathbf{F}_{ik}$ matrices, which are on the diagonal of the $\mathbb{F}$ matrix, put back within the PB state the offspring produced by mothers in each breeding state :

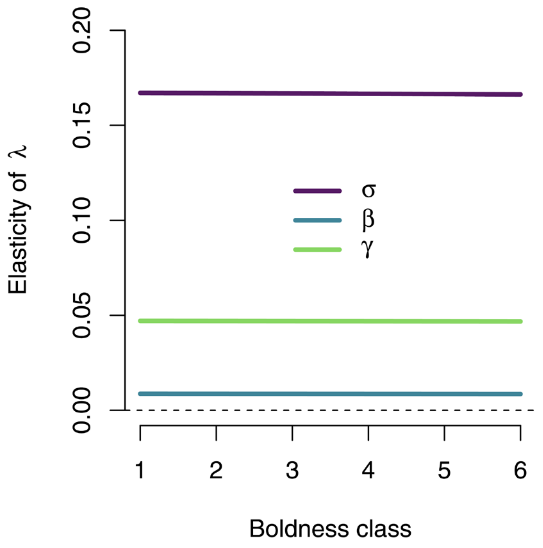

Figure 4. Elasticities (relative sensitivities) of population growth rate, λ to vital rates: survival σ, breeding probability β and breeding success probability γ for female wandering albatrosses at Possession Island of different boldness classes, assuming a uniform distribution of boldness.

$$\mathbf{F}_{ik} = \begin{pmatrix} 1 & \dots & 1 \\ 0 & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & 0 \end{pmatrix} \tag{9}$$

Then, the matrix $\mathbb{H}$ classifies the newly produced offspring within a phenotypic class. The matrix $\mathbb{H}$ contains the matrices $\mathbf{H}_{ij}$ on its diagonal. Matrices $\mathbf{H}_{ij}$ capture the phenotypic transmission process, which is based on a resemblance factor, r, corresponding to half of the heritability, τ ($r=\tau/2$). Heritability of boldness was estimated at 0.196 in female wandering albatrosses from Crozet (Supporting information). Given a starting maternal phenotype, daughter phenotype was approximated using the following relationship:

$$\text{Pheno}_{\text{daughter}} = r\text{Pheno}_{\text{mother}} + \epsilon, \tag{10}$$

with

$$\epsilon \sim \text{N}\left(0, \sqrt{Vp}\right) \tag{11}$$

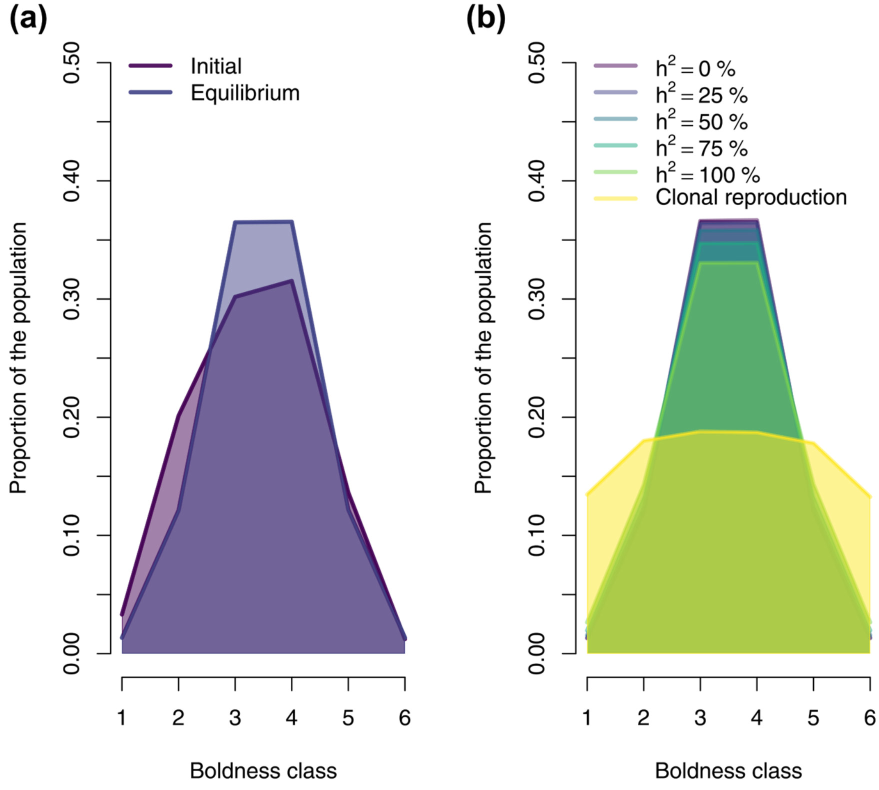

Figure 5. (a) Proportion of the female wandering albatross population within each boldness class observed (initial distribution) and at equilibrium using empirical parameters, and (b) proportion of the population within each boldness class using different scenarios of heritability values. Under the scenario of clonal reproduction, we assumed perfect correlation between mother and daughter phenotype, but accounted for environmental variance in daughter phenotypes.

where the term ϵ corresponds to environmental noise and Vp corresponds to the observed variance in boldness score distribution at the population level, which corresponded in our case to 0.89. The distribution of observed boldness score in female wandering albatrosses is presented in Fig. 5a. Each column of $\mathbf{H}_{ij}$ (or starting maternal phenotype k) consisted in a probability distribution of obtaining a given offspring phenotype (row).

Model analysis

Age-, state- and boldness-specific vital rates were estimated empirically for the wandering albatross in Crozet (Supporting information, Van de Walle et al. 2024). Those vital rates were used to parameterize the population matrix $\tilde{\mathbf{A}}$. We calculated the asymptotic population growth rate (λ) as the dominant eigenvalue associated with the dominant right eigenvector, $\tilde{\mathbf{w}}$ (i.e. the stable stage structure) of the population matrix $\tilde{\mathbf{A}}$ (Caswell 2001). Here, we presented and analyzed a female-based model, but a similar model based on males only was also analyzed and results are presented in the Supporting information.

Local sensitivity analysis

We performed sensitivity analyses to explore the relative importance of age-, state- and boldness-specific vital rates for population growth rate, λ. Briefly, using the population matrix $\tilde{\mathbf{A}}$ parameterized using empirical estimates of age-, state- and boldness-specific vital rates and matrix calculus, we calculated by how much population growth rate (λ) would be affected by a local (derivative) change in a vital rate, let's say survival (σ), while all other parameters remained set at their empirical value. We calculated this for the survival rate (or breeding probability or breeding success) of every age class (i), breeding state (j) and boldness class (k). Larger values of sensitivities would signify that population growth rate is mostly affected by what happens in terms of survival and breeding rates to individuals of a specific age class, or breeding state or boldness class. As described in Roth and Caswell (2016), in hyperstate population models, the dynamics of the population depend on the matrix $\tilde{\mathbf{A}}$, which in turn depends on the block-diagonal matrices (e.g. $\mathbb{A}$). The block-diagonal matrices depend on the dimension-specific matrices (e.g. $\mathbf{A}$), which in turn depend on the vector of parameters of interest $\boldsymbol{\theta}$. In our case such a vector contains the age-, state- and boldness-specific vital rates, and we can trace the dependency of $\tilde{\mathbf{A}}$ to such vectors through $\tilde{\mathbf{U}}$ and $\tilde{\mathbf{F}}$ and their components (Fig. 1). Following Roth and Caswell (2016) and matrix calculus rules (Magnus and Neudecker 1985), we calculated the sensitivity of λ with respect to, for example, $\boldsymbol{\sigma}_{jk}$ as follows:

$$\frac{d\lambda}{d\boldsymbol{\sigma}_{jk}^{\mathrm{T}}} = \frac{d\lambda}{d\mathrm{vec}^{\mathrm{T}}\tilde{\mathbf{A}}} \left[\frac{d\mathrm{vec}^{\mathrm{T}}\tilde{\mathbf{U}}}{d\mathrm{vec}^{\mathrm{T}}\mathbb{U}} \frac{d\mathrm{vec}^{\mathrm{T}}\mathbb{U}}{d\mathrm{vec}^{\mathrm{T}}\mathbf{U}_{jk}} \frac{d\mathrm{vec}^{\mathrm{T}}\mathbf{U}_{jk}}{d\tilde{\mathbf{A}}_{jk}^{\mathrm{T}}} + \frac{d\mathrm{vec}^{\mathrm{T}}\tilde{\mathbf{F}}}{d\mathrm{vec}^{\mathrm{T}}\mathbb{R}} \frac{d\mathrm{vec}^{\mathrm{T}}\mathbb{R}}{d\mathrm{vec}^{\mathrm{T}}\mathbf{R}_{jk}} \frac{d\mathrm{vec}^{\mathrm{T}}\mathbf{R}_{jk}}{d\boldsymbol{\sigma}_{jk}^{\mathrm{T}}} \right] \qquad (12)$$

which gives:

$$\frac{d\lambda}{d\boldsymbol{\sigma}_{jk}^{\mathrm{T}}} = \frac{\tilde{\mathbf{w}}^{\mathrm{T}} \otimes \tilde{\mathbf{v}}^{\mathrm{T}}}{\tilde{\mathbf{v}}^{\mathrm{T}}\tilde{\mathbf{w}}} \left[\sum_{d=1}^{m} \left(\mathbf{R}_d^{\mathrm{T}} \otimes \mathbf{L}_d \right) \left(\sum_{a=1}^{s/s_d} \left(\mathbf{I}_{s/s_{sd}} \otimes \mathbf{K}_{s_d, s/s_d} \otimes \mathbf{I}_{s_d} \right) \left(\mathrm{vec}\,\mathbf{E}_{aa} \otimes \mathbf{I}_{s_d^2} \right) \frac{d\mathrm{vec}\mathbf{A}_a^d}{d\boldsymbol{\theta}^{\mathrm{T}}} \right) \right] \qquad (13)$$

where $\tilde{\mathbf{w}}$ and $\tilde{\mathbf{v}}$ correspond to left and right eigenvectors of to the maximum eigenvalue λ. $\mathbf{R}_d$ and $\mathbf{L}_d$ correspond to the segment on the right- or left-end side of the block-diagonal matrix corresponding to the sub-process (or dimension) of interest in Eq. 4 or 10 (depending on the process in which the parameter is implied), respectively. For example, when focusing on the age dimension ($d=1$), $s_d=\omega=31$ and the term $s/s_d=60$. This means that within dimension 1, there are a total of 60 $\mathbf{A}$ matrices (one for each combination of state j and boldness score k). More details on the derivation of parameters within the dimension-specific matrices $\mathbf{A}$, as well as the equations for breeding probabilities (β) and breeding success (γ), can be found in the Supporting information. We present results in terms of elasticities, i.e. relative sensitivities, which were calculated by dividing sensitivities by parameter values.

Sensitivity to the shape of boldness distribution

We evaluated the impact of the distribution of boldness scores observed within the population on the pattern of elasticities. This was achieved by modifying the stable-stage distribution $\tilde{\mathbf{w}}$ vector, which represents the expected proportion of individuals that should be observed within each combination of age class, breeding state and boldness class at equilibrium (i.e. once stabilized) under empirical values of parameters. We modified this vector simulating a scenario where the distribution of boldness at equilibrium would be uniform (equal proportions of individuals across all boldness classes). We then recalculated the sensitivities of λ with respect to survival (σ), breeding probability (β) and breeding success (γ) using the modified vector $\tilde{\mathbf{w}}$ in Eq. 13.

Scenario-based global sensitivity analyses

Our global sensitivity analysis was performed by simulating scenarios of differing heritability values for boldness and differing strengths of selection on boldness. We evaluated the impact of heritability (h^2 or τ) – i.e. the strength of the relationship between mother and daughter phenotypes – by comparing the initial distribution of boldness with that obtained at equilibrium under observed value of heritability in this population (i.e. 0.196). This corresponds to the outcome that would be expected based on empirical data only. Then, we simulated different values of heritability ranging from 0 to 1 with increments of 0.25. A heritability value of 0 means that the boldness score of daughters is independent of that of the mothers (i.e. it is randomly drawn within the observed distribution of boldness scores in the population). In contrast, a heritability value of 1 means that the boldness score of daughters is half that of their mother, the other half

– i.e. male's contribution – is randomly drawn. In addition, because we wanted to test the sensitivity of our results to our parametrization of heritability in the matrix model, as an extreme case we also considered a scenario of clonal reproduction where mothers transmit exactly their phenotype to their daughters. For each scenario, we verified whether the simulated conditions could lead to shifts in the trait distribution (i.e. adaptation) by comparing the resulting boldness distribution at equilibrium. The distribution of boldness was obtained by summing the proportions of individuals within each boldness class across the other two dimensions given in the vector $\tilde{\mathbf{w}}$, with the one obtained based on empirical data only. In all simulations, we kept the effect of environmental noise in daughter phenotype attribution.

Lastly, we simulated scenarios of different magnitudes of the functional relationship between boldness and vital rates (i.e. strength of selection) to further explore conditions under which shifts in boldness distribution could be observed and have demographic consequences. We considered scenarios where boldness would have a positive impact on vital rates in our explorations. Opposite scenarios would yield similar conclusions as to relative magnitude of boldness impacts on population dynamics. We simulated six scenarios with slopes between vital rates and boldness varying from 0 to 0.5 (logit scale) with increments of 0.1. For each scenario, we tested five heritability values ranging from 0 to 1 with increments of 0.25. For each simulation, we calculated asymptotic population growth rate (λ) and mean boldness value at equilibrium.

Results

Local sensitivity analysis

Using empirical values for parameters in the $\tilde{\mathbf{A}}$ projection matrix, population growth rate λ was 1.018. When summed across all age classes, breeding states and boldness classes, survival (σ) has the largest impact on λ (i.e. largest associated elasticity value), followed by breeding success (γ) and then breeding probability (β; Fig. 2). Age class 31 had a large impact on λ, and this, for all vital rates (Fig. 2a) because this last age class consists of individuals of age 30 and over and thus includes more individuals relative to the other single age classes. Elasticity of λ was also greatest for survival of pre-breeders (PB), who are the sole representative of age classes < 6. Changes in the survival and breeding parameters for post-successful breeders PSB would affect population growth rate more strongly than any other adult breeding state (Fig. 2b).

Elasticities of λ to all three vital rates showed a bell shape along boldness classes (Fig. 2c), with higher values around intermediate boldness classes, which comprises a greater proportion of the population. Perturbing survival and breeding parameters of individuals of average boldness scores had the greatest impact on population growth. Overall, the relative impact of boldness and breeding state on λ was similar; the magnitude of differences in elasticity values (Fig. 2c) was similar across boldness classes (range: 0.00–0.367) to what was found across breeding states (range: 0.00–0.402; Fig. 2b).

When analyzing patterns of elasticities at a finer resolution, i.e. when sensitivities are decomposed along two dimensions, such as per age class and breeding state, or per boldness class and breeding state, we found that λ was most sensitive to perturbations in survival rates of pre-breeders, but only for age classes < 8 (Fig. 3a). For age classes 8 and over, changing survival of successful breeders and post-successful breeders would yield the greatest impact on λ. Increasing breeding probabilities β of pre-breeders of age class 6 would have a negative impact on population growth (Fig. 3b). Individuals starting to breed at age class 6 will become either SB or FB at age class 7 and then either PSB or PFB at age class 8, where survival rate is the lowest across all adult age classes and breeding states (0.68; Supporting information). Increasing breeding probabilities of PB would have the greatest positive impact on population growth in age classes 7 and 8 (Fig. 3b), after this the benefit for population growth rate of increasing breeding probability for pre-breeders declines with age. Higher breeding probabilities and breeding success for PSB would also have strong impacts on population growth rate, especially at prime ages (ages 10–20; Fig. 3b–c). Interestingly, despite a negative impact on population growth rate of increasing breeding probabilities of age class 6 individuals, an increase in breeding success in that age class would have a strong positive impact. However, increasing breeding success of pre-breeders of age class 7 would have a negative impact on population growth rate because it means more individuals will reach the state successful breeder early, where breeding success is low (average breeding success of successful breeders in age class 7–10 = 0.50; Supporting information).

For each breeding state taken separately, the pattern of elasticities of λ to vital rates was also bell-shaped with greater values at intermediate boldness scores (Fig. 3d–f). However, results varied between survival and breeding parameters. The greatest elasticities were found for pre-breeders of intermediate boldness classes for survival (Fig. 3d) and for post-successful breeders of intermediate boldness classes for breeding probability (Fig. 3e) and breeding success (Fig. 3f).

Sensitivity to the shape of boldness distribution

Changing the boldness distribution to a uniform distribution and recalculating the elasticities of λ to vital rates resulted in an absence of variation in elasticity between boldness classes (Fig. 4). Patterns of elasticities observed at Fig. 2c, 3d–f, 4 all reflect the distribution of boldness in the population.

Scenario-based global sensitivity analyses

Using the empirical estimate of heritability, the initial distribution of boldness and that observed at equilibrium are similar (Fig. 5a). Changing the value of heritability would only slightly change the distribution of boldness at equilibrium by mostly reducing the proportion of individuals within the intermediate boldness classes (Fig. 5b). Only under an extreme scenario assuming clonal reproduction would we observe a marked change in the boldness distribution towards a increased proportion of shyer and bolder individuals.

Further, for different values of heritability, here we tested six hypothetical scenarios of variations in the strength of the relationship between boldness and vital rates (Fig. 6a, d, g). For each scenario, we inspected population growth rate (Fig. 6b, e, h) and the mean boldness score at equilibrium (Fig. 6c, f, i). Across all simulations, the resulting changes in average boldness score and population growth was minimal for survival (boldness score: 0.066; population growth: 0.004) and were even smaller for breeding probabilities (boldness score: 0.017; population growth: 0.0007) and breeding success (boldness score: 0.012; population growth: 0.0005). For example, when the slope of the relationship between boldness and survival is increased from 0.0 to 0.5, population growth rate increases from 1.018 to 1.021 (corresponding to an ~ 8% increase in total population abundance over one generation, i.e. 30 years) and mean boldness at equilibrium increased from 0.00 to 0.05 (Fig. 6a–c). Increasing heritability value had a lower impact on population growth rate and mean boldness score compared to increasing the slope of the relationship between boldness and vital rates. However, population growth rate and mean boldness score increased more rapidly with increasing heritability when the slope of the relationship was higher.

Discussion

Our main objective was to evaluate whether individual differences in personality can affect population dynamics. We used the hyperstate matrix formulation (Roth and Caswell 2016) to develop a three-dimensional population model structured by three attributes: age, breeding state and personality. We applied this model to empirical data from the long-term demographic monitoring of the wandering albatross from Crozet and used boldness as a measure of personality. We tested for the relative sensitivity of population growth rate to vital rates of individuals across the shy–bold axis of variations and, using simulations, made projections of population growth rate and average boldness score under various pathways of selection. Our work provides a demonstration that sensitivity of population growth to vital rates perturbations is conditional on personality structure within a population. We show that perturbations of individual vital rates may have more impact when directed towards the most common phenotype classes, which in our case was intermediate boldness. We applied the model to boldness, but our approach would be suitable for any phenotypic trait.

In a simulation study, Kendall et al. (2018) assumed that boldness mediated aggressiveness and a trade-off between survival and reproduction, following expectations from the pace-of-life hypothesis (Réale et al. 2010, Dammhahn et al. 2018). They then theoretically explored the impact of boldness on population dynamics using a population model with two morphs: bold (aggressive) and shy (nonaggressive) individuals. They predicted that accounting for individual differences in boldness could have an impact on morph frequencies and population abundance at equilibrium, but they advocated the necessity of using empirical data to verify their predictions. In our study, we directly incorporated individual differences in boldness into a population model parameterized using empirical data and found a limited impact of boldness-mediated differences in vital rates on equilibrium distribution. This may be explained by the absence of evidence that boldness correlates with a tradeoff between survival and reproduction in the wandering albatross (Van de Walle et al. 2024), which is in accordance with limited support for the pace-of-life syndrome in empirical studies in wild animal species (Moiron et al. 2020).

Our results show that the equilibrium distribution of boldness, which is bell-shaped, plays a key role in population dynamics by determining which boldness classes most influence population growth. When boldness offers little fitness benefit – as seen in the wandering albatross – changes in vital rates of average boldness classes have the greatest effect on population growth. In contrast, if bolder individuals gain higher fitness and boldness is heritable, the distribution and sensitivity would shift toward bolder classes (Supporting information). However, such large shifts are unlikely in this population. Both the heritability of behavioural traits and the strength of selection appear limited, implying that the Crozet wandering albatross is not expected to evolve markedly toward either end of the shy–bold continuum. In particular, selection against boldness through reduced survival – often assumed in other systems (Réale et al. 2010, Kendall et al. 2018) – seems too weak here to generate substantial evolutionary change.

Our findings emphasize that changes in the equilibrium distribution of Gaussian-distributed traits become noticeable primarily under significant selective pressures. This observation becomes particularly significant when strong relationships between maternal and daughter phenotypes come into play. It's worth noting, however, that these shifts have a limited influence on the overall population growth rate. It is possible that the limited impact of personality on population dynamics in our study stems from the little influence of boldness on female vital rates. To delve deeper into these dynamics, we conducted simulations using an extreme scenario characterized by high heritability and a much stronger link between survival and boldness. This could represent an hypothetical scenario where bolder wandering albatrosses would have better access to food resources. The inverse relationship could represent a scenario of increased vulnerability to mortality factors, such as fishery bycatch, for bolder individuals. These simulations unveiled an amplified sensitivity of population growth rate to variations in survival rates of bolder individuals in females and males.

In males, boldness was found to have a more decisive impact on vital rates; bolder males reproduced less frequently (Van de Walle et al. 2024). Overall, because they skipped reproduction more, bolder males had lower lifetime reproductive success compared to their shyer counterparts. However, our sensitivity analyses and simulations applied to males yielded very similar patterns to females (Supporting information). Considering the lower relative sensitivity of

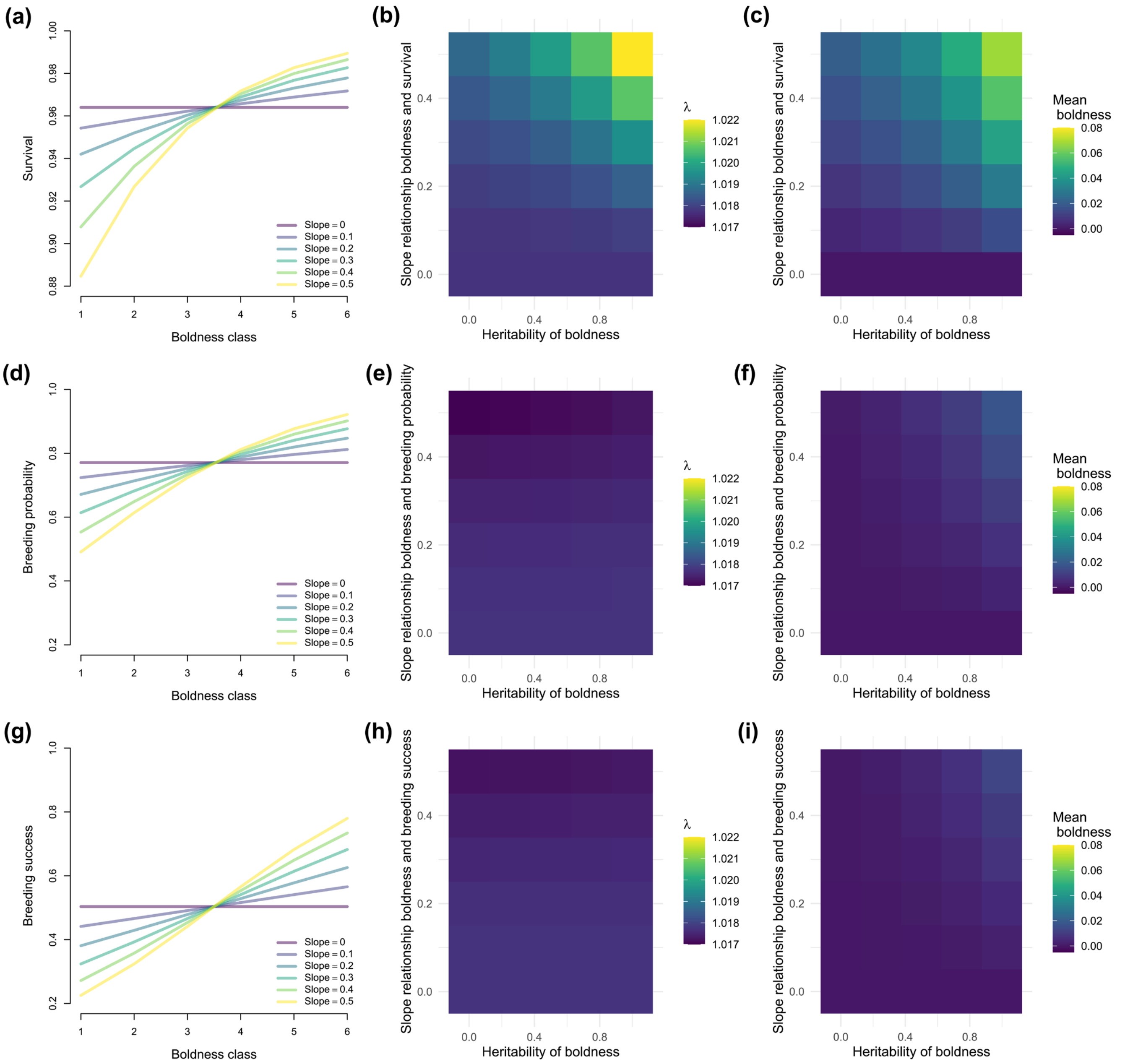

Figure 6. Interactive effects of heritability value and slope of the regression between boldness and survival on population growth rate in the wandering albatross at Possession Island. (a, d and g) show the six functional relationships between boldness and the three vital rates (survival, breeding probability and breeding success) tested. (b, e, and h) and (c, f, i) show the impact of the different slopes (y-axis) and heritability values (x-axis) combinations on population growth rate (λ) and mean boldness value at equilibrium, respectively. Boldness values were calculated by multiplying the number of individuals within each boldness class at equilibrium with the mid value of each boldness class. For reference, using only empirical values for the relationships between boldness and vital rates and for heritability in the wandering albatross, population growth rate and mean boldness value at equilibrium are estimated at 1.018 and 0.001, respectively.

population growth rate to reproductive rates compared to survival in long-lived species (Gaillard and Yoccoz 2003), a stronger impact of boldness on breeding probably has no noticeable impact on population growth rate overall.

By using hyperstate models and conducting sensitivity analyses at a fine scale, our study also reveals other interesting results. First, we found that within and across dimensions, population growth rate was very sensitive to perturbations in pre-breeder survival, especially for age classes 7 and below, after which sensitivities declined rapidly. All individuals of younger age classes are pre-breeders, and only upon age class 7 can individuals be in other breeding states. Thus, a large proportion of the population is within the pre-breeder state, which may explain the large elasticities for this breeding state. Also, juveniles can only contribute to the population if they survive to recruitment, hence reducing their survival would greatly reduce population growth rate. The combined elasticities of population growth rate to survival across all adult breeding states nevertheless outpaces those of pre-breeders (juveniles). This result is in line with the expectation and empirical evidence showing that for long-lived species population growth rate is more sensitive to changes in survival in adults compared to juveniles (Gaillard and Yoccoz 2003). Second, our analysis revealed that early reproduction might have a negative impact on population growth rate. Allowing more pre-breeders to breed for the first time at age class 6, i.e. the earliest age for first reproduction in our population (Fay et al. 2015), leads to a reduced future survival probability. This might appear contradictory to results from (Fay et al. 2016) showing that individuals recruiting earlier had a greater probability to become higher quality (sensu Nussey et al. 2008) adults, i.e. have higher breeding probabilities, breeding success and survival. However, individuals recruiting as six years old had lower success compared to individuals recruiting later (Fay et al. 2016). Our demographic analysis shows that in fact, an increase in recruitment rate at age class six would be detrimental when considered at the population level. In wandering albatrosses, breeding is conditional on reaching a threshold body mass (Weimerskirch 2018). Even though some individuals may attain this threshold at six years old (2% of the birds; Fay et al. 2015), this seems to come at the cost of a short-term reduction in breeding success and survival. Considering that body mass has increased in this population over the last decades (Weimerskirch et al. 2012), we can expect a shift towards earlier reproduction. Our results thus highlight the fact that such a change is likely to impact the population dynamics of the wandering albatross. Third, we showed that population growth was highly sensitive to perturbations in the vital rates of post-successful breeders. Individuals in this state are in their sabbatical year and have a great reproductive potential; their survival and return to the breeding grounds to produce a fledgling brings a disproportionate contribution to population growth.

Our model facilitated the examination of potential shifts in boldness distribution under varying conditions of heritability and selection strength. Our findings indicate that, based on our empirical data, mean boldness value is unlikely to change in the wandering albatross from Crozet. This phenomenon could stem from the way we parametrized the transmission of phenotypes from mothers to daughters. We acknowledge that incorporating principles of quantitative genetics would improve model realism and predictions of evolutionary response. Introducing an additional dimension into the hyperstate model formulation could enable tracking changes in both breeding values and phenotypes (Van de Walle et al. 2025a). However, the focus of the present study revolved around demography rather than evolution, and extending our already complex model to a four-dimensional model would pose a significant computational challenge. But we can speculate that given the species' extended generation time, the low heritability of boldness and the large environmental variance in offspring boldness attribution, the potential for evolution of boldness over short time scales is likely limited in the wandering albatross. Indeed, for species with long generation times, the rate of genetic adaptation per year is expected to be low (Fig. 3 in Van de Walle et al. 2025a). Another mechanism that could maintain behavioural diversity and limit directional shifts in phenotypes is frequency-dependent selection, whereby the advantage of a particular behavioural type changes with environmental conditions, allowing one type to replace another as conditions shift. A notable example is provided by the 'rock–paper–scissors' dynamics in side-blotched lizards *Uta standburiana*, where the abundance of three morphs differing in morphology and aggressiveness levels follows cyclic dynamics in response to frequency-dependent selection (Sinervo and Lively 1996). Whether frequency-dependent selection of boldness operates in the wandering albatross population from Crozet remains a possibility, but remains to be explored.

In this study, we conducted a quantitative examination of the impact of boldness on the population dynamics of wandering albatrosses in Crozet. Boldness is assumed fixed over an individual life in this population, hence we included no dynamic progression in this trait in the model. Using an hyperstate model formulation in this case could be perceived as an unnecessary complication. But, several gains can be obtained from using an hyperstate model. For instance, sensitivity analyses are simplified by the use of already published analytical solutions for hyperstate models (Roth and Caswell 2016). The hyperstate model formulation also allows much flexibility in how sensitivities are summarized, i.e., they can be looked at along one, or multiple, dimensions either separately or together, as we have presented here. This allows for a greater understanding of the interplay between multiple facets of individual differences in shaping population dynamics. Importantly, the hyperstate matrix formulation holds broader applicability, extending beyond this specific species and trait. This inclusive approach opens avenues for addressing various ecological and evolutionary questions. For instance, while our study assumed a fixed phenotype (boldness) throughout an individual's life and across varying environmental conditions, this does not need to be the case. In fact, the flexible model construction permits the incorporation of environment-dependent transitions between phenotypic classes, a valuable feature when investigating situations involving phenotypic plasticity (Childs et al. 2016). The primary prerequisite and potential constraint lies in the quantification of the relationships between phenotypic traits and vital rates over the entire life cycle of a species to construct the dimension-specific transition matrices.

In conclusion, we empirically investigated the influence of personality on the population dynamics of a wild species. While our investigation delved deeply, we observed limited effects, even when simulating more pronounced impacts of personality on vital rates. The extent to which these results can be extrapolated to other species remains an open question that requires further exploration. The potential for phenotypic change and impact on population growth rate may depend on the strength of selection, the species life history and also through which pathway selection acts. For instance, greater impacts on population growth rate would be expected when selection acts through survival in species with longer generations times as the wandering albatross, whereas we may expect the greatest impact to occur when selection acts through breeding parameters in species with shorter generation times (Vedder et al. 2013, Van de Walle et al. 2025a). The intricate interplay between behaviors and demography is an active, but still underexplored research area. Consequently, more studies are needed to unravel the complexity and subtlety of behavioral effects on population dynamics, especially as populations will have to adapt to novel environmental conditions (Maspons et al. 2019).

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Author contributions

Joanie Van de Walle: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Silke van Daalen**: Formal analysis (supporting); Methodology (supporting); Validation (supporting); Writing – review and editing (supporting). **Samantha C. Patrick**: Data curation (supporting); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Validation (supporting); Writing – review and editing (supporting). **Christophe Barbraud**: Data curation (lead); Funding acquisition (supporting); Project administration (lead); Resources (supporting); Validation (supporting); Writing – review and editing (supporting). **Karine Delord**: Data curation (lead); Funding acquisition (supporting); Project administration (lead); Resources (supporting); Validation (supporting); Writing – review and editing (supporting). **Henri Weimerskirch**: Data curation (supporting); Funding acquisition (supporting); Project administration (supporting); Resources (supporting); Validation (supporting); Writing – review and editing (supporting). **Jack Thorley**: Data curation (supporting); Formal analysis (supporting). **Stéphanie Jenouvrier**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (lead); Software (supporting); Supervision (lead); Validation (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.d51c5b0hw (Van de Walle et al. 2025b).

Supporting information

The Supporting information associated with this article is available with the online version.

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