Title: The impact of boldness on demographic rates and life-history outcomes in the wandering albatross

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Abstract

1. Differences among individuals within a population are ubiquitous. Those differences are known to affect the entire life cycle with important consequences for all demographic rates and outcomes. One source of among-individual phenotypic variation that has received little attention from a demographic perspective is animal personality, which is defined as consistent and heritable behavioral differences between individuals. While many studies have shown that individual variation in individual personality can generate individual differences in survival and reproductive rates, the impact of personality on all demographic rates and outcomes remains to be assessed empirically.

2. Here, we used a unique, long-term, dataset coupling demography and personality of wandering albatross (*Diomedea exulans*) in the Crozet Archipelago and a comprehensive analysis based on a suite of approaches (capture-mark-recapture statistical models, Markov chains models and structured matrix population models). We assessed the effect of boldness on annual demographic rates (survival, breeding probability, breeding success), life-history outcomes (life expectancy, lifetime reproductive outcome, occupancy times), and an integrative demographic outcome (population growth rate).

3. We found that boldness had little impact on female demographic rates, but was very likely associated with lower breeding probabilities in males. By integrating the effects of boldness over the entire life cycle, we found that bolder males had slightly lower lifetime reproductive success compared to shyer males. Indeed, bolder males spent a greater proportion of their lifetime as non-breeders, which suggests longer inter-breeding intervals due to higher reproductive allocation.

4. Our results reveal that the link between boldness and demography is more complex than anticipated by the pace-of-life literature and highlight the importance of considering the entire life cycle with a comprehensive approach when assessing the role of personality on

individual performance and demography.

Keywords: demography, fitness, life history, pace-of-life, personality, population growth rate

Introduction

Demographic rates are not equal between individuals and this variation is typically brought about by phenotypic differences (Hamel et al., 2018). The recognition that different individuals contribute differently to population growth motivated the development of, for example, age- (Leslie, 1945; Lotka, 1939), stage- (Caswell, 2001; Lefkovitch, 1965) and size- (Easterling et al., 2018) structured population models. One source of among-individual phenotypic variation that has received little attention from a demographic perspective is animal personality, which is defined as consistent and heritable behavioral differences between individuals (Sih et al., 2004). Some individuals are, for example, consistently more aggressive, more explorative, and bolder than others. Those personality differences, because they may dictate how individuals respond towards risks and allocate resources, are expected to correlate with survival rates, reproductive performance, and life-history strategies (Stamps, 2007; Wolf et al., 2007). Many empirical studies have shown behaviourally or personality-associated differential survival and reproductive performance (Ellis et al., 2017; Niemelä et al., 2015; Réale et al., 2009; Santicchia et al., 2018; Smith & Blumstein, 2008).

Comprehensive assessments of the effect of among-individual differences over the entire life cycle (i.e., over survival and reproductive parameters simultaneously) and on multiple facets of individual performance are critical to understand the role of personality in shaping demography, but also to assess the selective pressures at play (Santicchia et al., 2018). This is because individual fitness is multidimensional, integrating both performance in survival and reproduction (Mcgraw & Caswell, 1996). Consequently, antagonistic effects (or trade-offs) between demographic rates can arise (Jenouvrier et al., 2018; Sebens et al., 2018), and the expression of a given phenotype can increase one aspect of individual performance while decreasing another (e.g. Van de Walle et al., 2018). In the case of personality, its consistent nature across contexts and situations may lead to trade-offs, for example between survival and reproduction, making the cumulative effect hard to predict. This is because expressing one behaviour can be rewarding in one context or situation, but costly in another (Sih et al., 2004). Those trade-offs are thought to play an important role in the maintenance of among-individual variation in personality at the population level (Sih et al., 2004; Stamps, 2007; Wolf et al., 2007).

The shy-bold continuum (Wilson et al., 1994) is among the most studied axes of animal personalities and is expected to have implications for individual life histories. Those expectations are theoretically grounded in the pace-of-life syndrome framework, which stipulates that the shy-bold axis of individual variation should correlate with a slow-fast continuum of life-history strategies, with bolder individuals showing faster life cycles (e.g. shorter lifespan, higher reproductive rates) compared to shyer individuals (Dammhahn et al., 2018; Réale et al., 2010). This is because the risk-proneness of bolder individuals is thought to facilitate resource acquisition and, consequently, body condition and reproductive success at the cost of higher vulnerability to mortality factors (Biro & Stamps, 2008; Réale et al., 2010; Stamps, 2007). In a meta-analysis of published empirical studies, Smith and Blumstein (2008) reported clear evidence of relationships between personality and fitness and concluded that, in general, bolder individuals, and especially bolder males, have higher reproductive success, but suffer a higher survival cost. However, these relationships only held in captive populations and not in wild populations. More recently, a meta-analysis by Moiron et al. (2020) focusing on the correlation between among-individual variation in personality and survival found that across species, risky behavioural types, including boldness, did not lead to lower survival rates. In fact, in wild populations, individuals expressing riskier behaviours had higher survival rates, with no sex-specific differences. Therefore, the link between personality and survival may be more complex than we would expect and vary across species, contexts and systems (Dhellemmes et al., 2021; Dingemanse, 2021; Laskowski et al., 2021). More empirical studies are needed to better understand the relationship between personality and individual performance in wild populations.

The wandering albatross (*Diomedea exulans*) is a long-lived seabird species in which personality has been linked to many aspects of its biology. In this species, boldness has been shown to be repeatable and heritable (Patrick et al., 2013), and to correlate with pair-bond maintenance (Sun, Van de Walle, et al., 2022), parental care behaviours (Mccully et al., 2022), and foraging behaviours (Patrick et al., 2017; Weimerskirch et al., 2023). Foraging behaviours, by reflecting an individual's ability to acquire resources, should have cascading effects on reproduction and survival. As for pair-bond dynamics and parental care, they play a central role in reproduction in monogamous species, such as the wandering albatross (Sun, Barbraud, et al., 2022). A link between boldness and reproductive success has been established in the wandering albatross, with bolder males having greater reproductive success compared to shyer males in late life (Patrick & Weimerskirch, 2015). However, whether boldness also affects other demographic rates remains unknown and antagonistic effects can be expected. For instance, fishery bycatch is an important source of mortality in albatrosses (Barbraud et al., 2012) and boldness may increase the vulnerability of birds to this type of mortality. We know that passive harvest can unintentionally claim more deaths of individuals of a certain personality type, with bolder individuals being typically more vulnerable compared to shyer individuals (reviewed in Leclerc et al., 2017). Assessing the demographic role of personality and whether it is under selection thus requires the simultaneous incorporation of the multiple pathways through which boldness can influence demographic rates, individual performance and population dynamics.

Here, based on a unique long-term demographic and personality dataset, we investigated the demographic impact of boldness in the wandering albatross. We used a comprehensive approach, investigating the effect of boldness over different time scales and levels of organization. At the individual level, we explored 1) short-term consequences with annual demographic rates: survival, breeding probability, and breeding success probability. We also explored 2) long-term consequences over the lifetime of individuals through life expectancy and lifetime reproductive outcomes and 3) the relative proportion of lifetime spent in the different reproductive states and the time between breeding events. Finally, at the population level, we computed the effect of boldness on an integrative demographic outcome, namely the population growth rate. We relied on several demographic approaches, including multi-event capture-mark-recapture models, absorbing Markov chains, and structured matrix population models. Following predictions from the pace-of-life syndrome literature, the previously established links between boldness and reproductive success (Patrick & Weimerskirch, 2015), and expected higher vulnerability to bycatch for bolder individuals, we predicted that bolder wandering albatrosses would have lower survival rates, but higher breeding probabilities and breeding success. However, it is difficult to make general predictions as to the role of personality on more integrative measures of fitness, (e.g. lifetime reproductive success, population growth rate), as antagonistic effects between parameters over the life cycle (e.g. a trade-off between survival and reproduction) could arise and generate unexpected consequences (Jenouvrier, 2013).

Materials and Methods

We investigated the demographic role of boldness in four steps. First, we estimated the effect of boldness on three annual adult demographic rates (survival, breeding probability, and breeding success probability) using Bayesian multi-event capture-mark-recapture models (MECMR). Second, relying on absorbing Markov chains (AMC) and boldness-specific demographic rates calculated from the MECMR, we assessed the role of personality on life-history outcomes (expected life expectancy and lifetime reproductive success). Third, to further understand how boldness affects individual life histories, we explored transient state transitions (i.e., how individuals transit between the different breeding states within the life cycle during their lifetime) of bold vs shy individuals again within an AMC framework. Specifically, for shy vs bold individuals, we estimated the relative proportion of their lifetime spent in the different reproductive states (e.g. breeder vs non-breeder), as well as their average interval of time between breeding events. Fourth, as another integrative demographic outcome, we assessed the overall performance of different boldness scores by calculating the population growth rate (λ) for theoretical populations composed of only individuals of a given boldness value.

Study system and species monitoring

We studied the entire breeding population of wandering albatrosses from Possession Island (46°24'S, 52°46'E), in the Crozet Archipelago, south-western Indian Ocean. The breeding season, from egg laying to chick fledging, lasts almost a year (Weimerskirch, 2018) and most breeders take a sabbatical year at sea after a successful breeding event (Tickell, 1968). However, a small proportion of successful breeders can breed the next year, and thus the wandering albatross is considered a quasi-biennial breeder (Barbraud & Weimerskirch, 2012).

At Possession Island, a capture-mark-recapture program has been undertaken since 1966 (Weimerskirch, 2018). Fledglings and adults are banded annually using individually-coded stainless-steel leg rings. Birds are monitored, and their reproductive status determined, during the breeding season. Between January and February, i.e., right after egg-laying, nests are visited three to four times to determine the identities of breeding birds. Chicks are ringed in September and October prior to fledging in November-December. Breeding success is determined based on chick survival until fledging. Each year, unmarked individuals found at the colony are also ringed. Sex is based on morphology and genetic assessment (Weimerskirch et al., 2005). We relied on data collected from 1966 to 2020 on 11,591 individuals (8,697 males and 2,894 females). Licences and permissions for capture and handling of animals were granted by the Ethic Committee of Institut Polaire Francais (IPEV) and by the Préfet of Terres australes et antarctiques francaises (TAAF) after advice from the Comité de l'Environnement Polaire (CEP).

Personality assessment

Since 2008, boldness of breeding wandering albatrosses has been assessed for 1,746 individuals (931 males and 815 females) through personality tests. During incubation, breeding individuals were approached on foot and their reaction towards human approaches was evaluated on a scale from 0 to 4 (0 = no response, 1 = lifts the head, 2 = stands on tarsus, 3 = vocalizes, and 4 = stands up). The higher the score, the bolder the individual (Patrick et al., 2013). Those scores were then adjusted to control for differences between observers and observation number, and were standardized (mean = 0, sd = 1) prior to analyses. For adult wandering albatrosses, boldness in reaction to human approaches is correlated to that in reaction to a novel object. Boldness is also highly repeatable (Patrick et al., 2013) and assumed as fixed over an individual's life as a previous study did not find evidence of change in boldness with age (Patrick & Weimerskirch, 2015). More information on personality assessment can be found in Patrick et al. (2013).

Life cycle of the wandering albatross

All the demographic analyses were based on the wandering albatross life cycle (Fig. 1). In a species life cycle, individuals move between a specific set of stages over the course of a time step (here a year), conditional on transition probabilities. The wandering albatross life cycle includes age classes and breeding states. Annual transitions are from year t to t +1 and depend on survival (α) and changes in individual breeding status, which are determined by breeding probability (β), and breeding success probability (γ). Breeding probability is the probability that an individual at time t returns to the colony to breed at time $t+1$, whereas breeding success probability represents the probability that an individual breeding at time $t+1$ raises successfully a chick until fledging. In each year t, individuals of any age a were classified into six breeding states s:

1. Pre-breeder (**PB**): individuals that have not yet started to breed. Pre-breeders are of age classes one and over.

2. Successful breeder (**SB**): adults that have bred and successfully fledged a chick in year t. As wandering albatrosses can start to breed (i.e., lay an egg for the first time) at six years-old (Fay et al., 2016), individuals can only reach this state upon age six years-old and older

3. Failed breeder (**FB**): adults that have bred, but failed to successfully fledge a chick in year t. As for **SB**, individuals can only reach this state at the age of six years old and older.

4. Post-successful breeder (**PSB**): adults during their sabbatical year after having successfully

fledged a chick at year $t-1$. Individuals can only reach this state at the age of seven years old and older.

5. Post-failed breeder (**PFB**): adults during their sabbatical year after having failed to successfully fledge a chick at year $t-1$. As for **PSB**, individuals can only reach this state at the age of seven years old and older.

6. Non-breeder (**NB**): adults that are still not breeding after a sabbatical year, i.e., after states **PSB** or **PFB**. Individuals in this state are adults of age eight years-old and older.

A capture-mark-recapture model to estimate demographic rates

Demographic rates, i.e., survival (α), breeding probability (β) and breeding success probability (γ) were estimated using Bayesian multi-event capture-mark-recapture models (MECMR). Survival and breeding probabilities vary with age in the wandering albatross, but the pattern of age variation differs between survival and breeding probabilities (Fay et al., 2015, 2016; Patrick & Weimerskirch, 2015). Therefore, we estimated survival, breeding probabilities, and breeding success probabilities for different age classes based on those previous studies. For pre-breeders, we used the same age classes as in Fay et al. (2015): four age classes for survival (age classes 1-2, 3-8, 9-13, and 14+), and five age classes for breeding parameters (age classes 6, 7, 8, 9 and 10+). For pre-breeders of age classes 1 through 5 (i.e., juveniles) we set breeding probabilities and breeding success probabilities at 0 due to immaturity (Fay et al., 2016). For adults, we considered three age classes. Wandering albatrosses show signs of survival senescence after age 30 (Pardo et al., 2013). Thus, for survival, we followed (Fay et al., 2015; Pardo et al., 2013) and used the following age classes: 7-8, 9-30 and 31+, with the age class 31+ consisting of senescent individuals. Breeding senescence occurs at age 22 (Patrick & Weimerskirch, 2015), thus for breeding probability and breeding success probability we considered age classes 7-10, 11-21, and 22+.

Survival and breeding probabilities can vary depending on the breeding states of the birds. Therefore, we estimated survival, breeding probabilities, and breeding success for each of the five adult breeding states separately. Due to the computational demands and extended runtime of Bayesian models, we performed an initial model selection using a frequentist approach in E-Surge Version 2.0 (Choquet et al., 2009) to identify constraints in demographic rates between the different breeding states (Figure 1). A step-down model selection was performed using quasi-Akaike Information Criterion (QAIC) as a criterion for model selection. Results from model selection are shown in Supplementary Materials S1. From the best-supported model (i.e., lowest QAIC value), survival rates were found to be similar between breeding states SB and FB, and between PSB and PFB, whereas they were different for PB and NB individuals. Breeding probabilities were different for each breeding state. Breeding success probabilities were similar between PSB and PFB, but were different for all other reproductive states (PB, SB, FB and NB). For each demographic rate, the respective constraints identified from the model selection were then used in the Bayesian MECMR framework in a second step. For example, survival rate for SB and FB were constrained to be equal in the Bayesian model.

All demographic rates were modeled following Bernouilli distributions. Survival was modeled as:

$$(\text{Alive}_{k,t} \mid \text{Alive}_{k,t-1} = 1) \sim \text{Bernoulli}(logit^{-1}(\mu_{\alpha,a,s})) \tag{1}$$

where $Alive_{k,t}$ indicates whether an individual k survived (1) or died (0) from year $t-1$ to year t conditional on its previous survival ($\text{Alive}_{k,t-1} = 1$) and $\mu_{\alpha,a,s}$ is the logit transform mean survival rate of individuals of age a and state s. Conditional on being alive, individual k may breed following an additional Bernoulli process:

$$(\text{Breed}_{k,t} \mid \text{Alive}_{k,t} = 1) \sim \text{Bernoulli}(logit^{-1}(\mu_{\beta,a,s})) \tag{2}$$

where $\text{Breed}_{k,t}$ indicates whether an individual k has breed (1) or not (0) in year t and $\mu_{\beta,a,s}$ is the logit transform mean breeding probability of individuals of age a and state s. Following the same logic, conditional on breeding, individual i may be successful at fledging a chick following a third Bernoulli process:

$$(\text{Success}_{k,t} \mid \text{Breed}_{k,t} = 1) \sim \text{Bernoulli}(logit^{-1}(\mu_{\gamma,a,s})) \tag{3}$$

where $\text{Success}_{k,t}$ indicates whether an individual k has successfully fledged a chick (1) or not (0) in year t and $\mu_{\gamma,a,s}$ is the logit transform mean breeding success probability of individuals of age a and state s.

For recruited individuals, we investigated the linear effect of boldness on each demographic rate (θ), i.e., α, β or γ, by including boldness (B) as an additive individual covariate:

$$\theta_{k,t} \sim \text{ Bernoulli}(logit^{-1}(\mu_{\theta,a,s} + \rho_\theta \times B_k)) \tag{4}$$

where $\mu_{\theta,a,s}$ is the mean demographic rate of individuals of age a and state s, ρ_θ is the linear effect of boldness on the vital rate, and B_k is the boldness score of individual k. The parameter ρ_θ was assumed constant across breeding states and age classes. We verified whether the effect of boldness on demographic rates differed among age classes by adding an interaction term between boldness and age in the models and found little statistical support for the inclusion of such interaction (Supplementary Materials S2). Therefore, to limit model complexity, we kept a constant impact of boldness across all age classes.

Along with the vital rates, we also estimated detection probability, p_k, which is the probability of observing an individual depending on its reproductive state s. For pre-breeders, we considered 6 age classes (1-5, 6, 7, 8, 9, 10+) for detection probability. For recruited individuals, detection probability was assumed fixed for all age classes. We also assumed detection to be equal between SB and FB (set to 1), and between PSB and PFB (set to 0).

To maintain the statistical independence among female and male life histories, we built and separately ran one model per sex. Because personality has only been measured on breeding adults since 2008, our analysis focused on testing the impact of personality on demographic rates exclusively in the adult phase of the life cycle. Therefore, we split the juvenile and adult components of the population and estimated their respective demographic rates into separate models. This allowed us to consider the whole life-history dataset during the entire study period (1965-2020) to estimate juvenile demographic rates. Individuals born after 2016 were not considered for the estimation of juvenile demographic rates because their low detection rates between age classes 1 through 5 can lead to underestimated survival rates. For adults, we restricted the analyses to the 2008-2020 period using the life histories of individuals with a personality score. To further simplify model complexity and reduce runtime, we examined the influence of personality on each demographic adult rates separately. Thus, a total of eight models were built: three models to test the effect of boldness on survival, breeding probability, and breeding success probability for adults of each sex, and two models for juveniles (one for each sex).

MECMR analyses were conducted in JAGS (Plummer, 2003) from R (R Core Team, 2021) using the R package “jagsUI” (Kellner, 2021). MECMR models assume a closed population, i.e., there is no emigration or immigration. This is a reasonable assumption in the wandering albatross from Crozet as a previous study have found high philopatry in adults at this colony (Gauthier et al., 2010). By computing male and female models separately, we also assumed that their demographic rates are independent of each other. Further, with such models, survival estimates represent apparent survival due to imperfect detection. We used Markov chain Monte Carlo (MCMC) methods for posterior sampling. For each model, we ran 3 parallel chains with 20,000 iterations, a burn-in phase of 4,000, and a thinning interval of 2 for a total of 24,000 iterations. Convergence was confirmed by visual examination of the posterior distributions and the Gelman-Rubin statistic, with a R-hat lower than 1.1 indicating that convergence was reached (Brooks & Gelman, 1998). Evidence for covariate effects was gauged by the proportion of the posterior distribution that had the same sign as the posterior mean (referred to as the F-statistics). We followed the Intergovernmental Panel on Climate Change (IPCC) terminology (IPCC, 2021) to determine the likelihood of an effect and considered 66-100% as likely, 90-100% as very likely, 95–100% as extremely likely, and 99- 100% as virtually certain.

Predictions of boldness-specific demographic rates

Further investigation of the role of personality in demographic outcomes relied on a set of boldness-specific demographic rates. We used the parameters estimated from the MECMR model to predict adult demographic rates over a range of boldness scores. We randomly drew values from the posterior distributions for intercept and boldness effect (on the logit scale) in adults. Then, for each age- (a) and state- (s) we predicted demographic rates for each boldness score B as follows:

$$\alpha_{a,s,B} = logit^{-1}(\mu_{\alpha,s,b} + \rho_{\alpha} \times B) \tag{5}$$

$$\beta_{a,s,B} = logit^{-1}(\mu_{\beta,s,b} + \rho_{\beta} \times B) \tag{6}$$

$$\gamma_{a,s,B} = logit^{-1}(\mu_{\pi,s,b} + \rho_{\gamma} \times B) \tag{7}$$

For life-history outcomes (life expectancy and lifetime reproductive success) and population growth rate, we predicted 1,000 boldness-specific demographic rates for each of 100 values of boldness ranging from -3 to 3. For state transitions analyses, we contrasted extreme shy (B = -3) and extreme bold (B = 3) individuals and results were averaged across 1,000 model-based predictions.

An absorbing Markov Chain to estimate life-history outcomes

To assess the impact of boldness on life-history outcomes and state occupancy times, we used an Absorbing Markov chain framework, following Caswell (2009) and Roth and Caswell (2018). Specifically, we calculated life expectancy, mean lifetime reproductive success, expected proportion of time spent in each reproductive state in an individual's lifetime and breeding return times (i.e., expected time required for a breeder to return to breeding) for individuals expressing different boldness scores B.

The life cycle can be formulated as a Markov chain to extract life-history outcomes (Caswell, 2009). A Markov chain model tracks the trajectory of a particle (here, an individual) as it transits among a predefined set of states. In this stochastic process, future movements are solely determined by the current state and are independent from past movements. The transient matrix $\mathbf{U}$ contains live annual transitions between the states and can be extracted directly from the life cycle. In an absorbing Markov chain, an absorbing state (here a death state) is added to the life cycle and individuals reaching such state remain there indefinitely (they become "absorbed"). We built a separate Markov chain models for each boldness score, assuming that all individuals within a given boldness score share the same vital rates. Let $\mathbf{U}_B$ be the transient matrix for individuals of boldness score B. The transient matrix includes all the demographic rates predicted for the given boldness score B (see Section *Predictions of boldness-specific demographic rates*), except for pre-breeders who were assigned average parameter values estimated in the juvenile models given the absence of boldness measurements for this category of individuals. The transition matrix for the absorbing Markov chain can be calculated from $\mathbf{U}_B$ as follows:

$$\mathbf{P}_B = \left(\begin{array}{c|c} \mathbf{U}_B & 0 \\ \hline \boldsymbol{m}_B & 1 \end{array}\right) \tag{8}$$

where $\boldsymbol{m}_B$ is a mortality vector whose entries are the probabilities of mortality for individuals of personality B within each stage.

Based on the concept of absorbing Markov chains, we can examine several meaningful life-history characteristics. For instance, using the personality-specific demographic rates estimated above, we can examine for individuals of different personalities B how long it takes before death and the dynamics of transitions between the different states prior to death. As individuals progress in time (e.g. age), they randomly move between the different stages following the probability distributions associated with each stage transition. Individuals can ”visit” some stages multiple times over their lifetime. The fundamental matrix $\mathbf{N}_B$ gives occupancy times, i.e., the average number of occasions (years) an individual of personality B is expected to visit one (or several) stages over its lifetime given it starts at a specific initial stage. The matrix $\mathbf{N}_B$ can be obtained from the matrix $\mathbf{U}_B$ as follows:

$$\mathbf{N}_B = (\mathbf{I} - \mathbf{U}_B^{-1}) \tag{9}$$

Summing over all i for any given initial stage j in the matrix $\mathbf{N}_B$ gives the number of years individuals of personality B are expected to live from the moment they reach stage j. Here, we estimated life expectancy by summing occupancy times over all stages starting from the stage PB1 (fledglings). The wandering albatross life cycle explicitly includes a successful breeding state (SB), which means that the fundamental matrix $\mathbf{N}_B$ also gives information about the total number of years individuals are expected to successfully produce fledglings (Jenouvrier et al., 2018). Since wandering albatrosses only produce one chick per year, expected lifetime reproductive success can be calculated by summing occupancy times across all SB stages (SB of age classes 7 through 31+).

To better understand individual lifetime allocation to reproduction and how this is affected by boldness, we contrasted for extreme bold vs shy individuals the proportion of their adult lifetime spent in each reproductive state. Starting from each of successful or failed breeder stages (i.e, SB7 to SB31+ and FB7 to FB31+), we divided the total time spent in each adult state (SB, FB, PSB, PFB and NB) by the adult life expectancy (sum of time spent in all adult stages). Then, those proportions were averaged across the initial stages to produce an average occupancy time in each reproductive state for extreme bold and shy individuals.

Also, to further understand the role of boldness in breeding, we calculated the time it takes for extreme shy vs bold individuals to breed again after either failing or succeeding at fledging a chick.

This calculation relied on the estimation of return times, i.e., the time between two visits in a target set of stages, which is described in detail in Roth and Caswell (2018). Briefly, within the absorbing Markov chain framework, we defined a new set of stages as absorbing, i.e., once an individual reached one of those stages, the iterative process stopped and the individual could no longer move between stages in the next time step (it was "absorbed", as for the death state). Individuals can reach those stages through many different paths. For example, some individuals can reach an absorbing stage after one year, and others after multiple years, depending on the stage transition probabilities. Here, we set breeding stages (SB7 to SB 31+ and FB7 to FB31+) as absorbing and estimated the average time it took before reaching any of those absorbing stages along all possible paths for extreme bold and shy individuals starting as either 1) successful breeders or 2) failed breeders.

A matrix population model to estimate population growth rate

To assess the role of boldness on the overall performance of individuals expressing different boldness scores, we used structured matrix population models. For each of 100 simulated boldness scores (B) within the interval -3 and 3, we built one population matrix model $\mathbf{A}_B$. The population matrix $\mathbf{A}_B$ projects the vector of population size $\mathbf{n}_B$ from year t to year $t+1$ and is a function of the vector of parameters $\boldsymbol{\theta}_B$, so that:

$$\mathbf{n}_{B,t+1} = \mathbf{A}_B \mathbf{n}_{B,t} \tag{10}$$

where

$$\mathbf{A}_B = \mathbf{U}_B + \mathbf{F}_B \tag{11}$$

with the matrices $\mathbf{U}_B$ representing the annual transitions of live individuals and $\mathbf{F}_B$ representing fertilities (i.e., the production of new individuals) for boldness score B. The full population matrix can be found in Supplementary Materials S3. In each population matrix $\mathbf{A}_B$, we included 16 age classes for the PB stage, leaving the 16th age class open-ended to account for late recruitment. For adults, we included 25 age classes for each of SB, FB, PSB, PFB and NB stages, starting at age class 7 (pre-breeders can only become breeders between age class 6 at time t and age class 7 at time $t+1$), and leaving the last age class 31+ open-ended. This resulted in 125 age/stage combinations for adults and a $\mathbf{A}_B$ age and stage matrix of total dimension 141 by 141. Population growth rate was calculated at equilibrium as the dominant eigenvalue of the matrix $\mathbf{A}_B$. We used Matlab (The MathWorks Inc, 2022) for demographic analyses and relied on occupancy time codes provided in Roth and Caswell (2018). Figures were made in R (R Core Team, 2021).

Results

Demographic rates estimation

Estimates of average vital rates are provided in Supplementary Materials S4, Table S5 for juveniles and Table S6 for adults. In females, boldness was not likely to affect survival or breeding probability (Fig. 2a,c) as the posterior distribution of ρ was largely centered on zero for both parameters (all F <60%). Boldness in females was likely associated with lower breeding success (F = 66.0%; Fig. 2e), however the effect was weak. The mean effect of boldness (ρ) on female breeding success was (on the logit scale) -0.019 (95% Credible Interval = [-0.108, 0.072]), which corresponds to a 1.8% reduction in the odds of breeding with success for every unit of increase in boldness score. In males, boldness was not likely to affect survival (F = 49.3%; Fig. 2b) or breeding success (F = 52.2%; Fig. 2f). Boldness in males was extremely likely (F = 98.8%) associated with lower breeding probabilities (Fig. 2d). The mean effect of boldness (ρ) on breeding probability was (on the logit scale) -0.078 (95% Credible Interval = [-0.147, -0009]), which corresponds to a 7.5% reduction in the odds of breeding for every unit of increase in boldness score. Posterior distributions of ρ for each vital rate and sex can be found in Supplementary Materials S4 Fig. S2.

Life history outcomes, population growth rate and occupancy times

Boldness had no discernible effect on life expectancy in males and females (Fig. 3a). Lifetime reproductive success was unaffected by boldness score in females (Fig. 3b). In males, lifetime reproductive success decreased from a median of 5.8 (95% Confidence Interval = [4.1, 7.9]) fledglings in shy males to a median of 4.9 (95% Confidence Interval = [3.6, 7.5]) fledglings in bold males. In females, there was no detectable decline in population growth rate with increasing boldness score. In males, population growth rates declined with increasing boldness score, from a median of 1.038 (95% Confidence Interval = [1.028, 1.045]) for shy to a median of 1.031 (95% Confidence Interval = [1.021, 1.041] for bold individuals (Fig. 3c).

For males, time spent in the different reproductive states varied between extreme shy and bold individuals (Fig. 4a). Bold males spent 5.8% and 1.8% less time as successful and failed breeders, respectively, compared to shy males. Bold males also spent 11.8% more time in the non-breeder state. Overall, shy males spent 47.4% of their adult life breeding (52.6% non-breeding) and bold males spent 39.8% of their adult life breeding (60.1% non-breeding). In contrast, for females the time spent in the different reproductive states was similar between shy and bold individuals (Fig. 4b).

We found that return times to breeding varied according to the age of the individuals at their previous reproductive state (Fig. 5). Overall, return times were longer after a breeding success. Return times to breeding states were on average greater in males compared to females (Fig. 5). In males, return times to breeding states were longer in older compared to younger individuals regardless of previous reproductive state. Further, in males, return times were longer for bold vs shy individuals, and this difference increased over adult life (Fig. 5a,b). Specifically, it took 0.59 years more to return to breeding for a bold male of age class 31+ compared to a bold male of age class 7 after a reproductive failure. This difference was 0.24 years when previous reproductive outcome was success. For shy males, the difference in return time to breeding between age class 31+ and age class 7 was 0.11 and 0.31 years when previous reproductive outcome was success or failure, respectively. This means that bolder males take disproportionately longer to breed again as they get older compared to shy males. After age 21, breeding probabilities for males decreased (Supplementary Materials S4; Table S6). This caused return times to increase abruptly up to 21 years old as more and more of the state transitions included in the calculation of return times implied breeding probabilities after age 21. For females, the time taken to breed again after a successful reproductive event declined over adult life, which means that older, but successful, females returned to breeding quicker compared to younger females (Fig. 5a). Such a decline with age was not observed for females having failed their previous reproduction (Fig. 5b). A similar pattern was observed in both bold and shy females.

Discussion

Using a unique long-term series of coupled data on individual life histories and personality in wandering albatrosses, we conducted a comprehensive analysis of the role of boldness on demographic rates, life-history outcomes, and population growth rate. We showed that the impact of boldness was sex-specific. Contrary to our expectations, boldness did not affect survival rates in either sex. However, our results showed differential impact of personality on reproductive rates in females and males, with an influence of personality on breeding probabilities in males and little effects in females. Bolder males bred less frequently and spent a relatively greater proportion of their adult lifetime not breeding, compared to shyer males because they took longer to breed again after a reproductive attempt. As a result, bolder males had slightly lower lifetime reproductive outcomes and overall population growth rates compared to shyer males, whereas female life history outcomes seemed invariable across the shy-bold spectrum.

Traditionally, the impact of personality is assessed by measuring the impact of a personality trait on one or (sometimes) multiple fitness-related traits (reviewed in Smith and Blumstein, 2008). However, there is a limited focus on assessing its impact throughout the life cycle, including survival, breeding, and success probabilities. This could explain why inconsistent results about the role of personality in individual performance are found across studies, especially in the pace-of-life literature (Moiron et al., 2020; Royauté et al., 2018). Here, our holistic approach, combining multiple statistical and mathematical tools and considering all aspects of the life cycle simultaneously, offers great potential to unveil the actual pattern of personality-mediated impacts in wild populations. Our approach provides many advantages. First, capture-mark-recapture (CMR) models account for detection issues, which often hinder the proper estimation of survival and breeding probabilities in natural systems. In using CMR models, we were able to directly measure the impact of boldness on all demographic rates of the wandering albatross adult life cycle. Secondly, Markov chain modeling and matrix models enable the integration of the complex, sometimes opposing, effects of personality on demographic rates to calculate its impact on life history outcomes (e.g. lifetime reproductive success and life expectancy), occupancy times (time spent as non-breeder during lifetime and return time to breeding), and population growth rates.

We found that boldness had no discernible impact on survival and breeding success, but led to reduced reproductive probabilities in male wandering albatrosses. Overall, our results suggest slightly lower lifetime reproductive success and population growth rates for bolder males, due to reduced breeding probabilities. Most studies assessing the role of personality on reproductive rates focus on breeding success, ignoring reproductive probability. Many species breed every year, with little inter-individual differences in breeding frequencies. Also, tracking individuals between reproductive events poses an important logistical challenge. This may explain why personality impacts on breeding probabilities are less commonly investigated. Yet, long-lived species typically have a conservative strategy characterised by a prioritization of maintenance over reproduction (Gaillard et al., 1998), and breeding can be skipped if it may impair future reproductive prospects (Hamel et al., 2010). In those species, breeding probability can represent an important life-history trait affecting individual fitness and population dynamics (Jenouvrier et al., 2005; Van de Walle et al., 2021).

Our results deviate from the pace-of-life syndrome (POLS) hypothesis (Réale et al., 2010), which suggests that the trade-off between survival and reproduction (Stearns, 1989) should be mediated by individual differences in boldness. The POLS hypothesis suggests that due to their expected shorter lifespan, bolder individuals should invest more heavily in reproduction (Réale et al., 2010; Wolf et al., 2007). Instead, we observed no influence of boldness on survival, indicating the absence of antagonistic effects of boldness on survival and reproduction in wandering albatrosses. Expectations from the POLS hypothesis are grounded in the assumption that a slow-fast continuum of life histories exists at the individual level. However, the existence of such a continuum is currently being questioned (Royauté et al., 2018), with poor evidence within bird and mammal populations, including the wandering albatross (Van de Walle et al., 2023). Our study thus aligns with Moiron et al. (2020)'s statement that boldness in the wild is generally not associated with lower survival rates and that the shy-bold axis of variation does not correlate with a slow-fast continuum. Laskowski et al. (2021) suggested that the theory on POLS could nevertheless be reconciled if we considered the possibility that boldness can mediate resource acquisition by individuals, and in turn, resource allocation to survival and reproduction. For example, if bolder individuals could acquire more resources, they would be able to allocate more resources to their current reproduction and their maintenance, which would mask the expression of the trade-off. In the wandering albatross, bolder individuals are at the explorative end of the exploitation-exploration continuum, making shorter foraging trips within smaller, but more, foraging patches (Patrick et al., 2017), but it remains unknown whether bold vs shy individuals differ in their foraging success. Answering how boldness affects foraging effort and success would improve our understanding of the mechanistic linkages between personality, resource acquisition and allocation, and ultimately individual fitness.

An alternative possibility is that high resource allocation in reproduction by bold males may come at a cost in terms of future reproduction, rather than in survival. Reproduction is costly in the wandering albatross. After a successful breeding attempt, most individuals will take a sabbatical year to replenish body reserves, whereas unsuccessful individuals are more likely to breed again the following year (Barbraud & Weimerskirch, 2012; Tickell, 1968). Therefore, there is an implicit trade-off between breeding success and breeding frequency in this species and bolder males may face a stronger trade-off. In addition, boldness being linked with risk-proneness (Réale et al., 2010), it should also dictate the amount of risk individuals are willing to support with regard to reproduction, such as protecting and continuing their reproductive allocation. For example, in a wild population of great tits, shyer individuals were more likely to abandon their nest under risky situations (Cole & Quinn, 2014). Bolder wandering albatross males are also expected to have a higher threshold for nest abandonment (Patrick & Weimerskirch, 2015). Bolder birds in late adulthood also make longer foraging trips and gain more mass per foraging trip during the breeding season compared to shyer birds (Patrick & Weimerskirch, 2015). Furthermore, breeding success of bolder males declines less rapidly with age than that of shyer males (Patrick & Weimerskirch, 2015), suggesting they continue to allocate more to reproduction throughout their life. For those bold males, higher allocation to current reproduction may mean that the sabbatical year is insufficient to replenish body condition, forcing them to spend longer periods of time away from the colony not breeding. Our results support this view as bolder males take more time to come back to breeding after a breeding event and have a stronger increase in inter-breeding intervals with age (i.e., reproductive senescence) compared to shyer males.

With the rationale that boldness should correlate with vulnerability to fishery bycatch and higher mortality rates, we expected to find a negative impact of boldness on survival. However, starting in the late 1990s, several mitigation measures were implemented in the French Exclusive Economic Zones (EEZ) of Crozet and Kerguelen Islands to reduce fishery bycatch, such as night settings (albatrosses are diurnal foragers; Bentley et al., 2021), closing period, and the use of scaring line spreading. This probably contributed to lessening the fishery-induced mortality pressure on the population, which could have led to an absence of differential mortality along the shy-bold continuum for male and female wandering albatrosses. This is also coherent with model-based predictions from Barbraud et al. (2012) and Tuck et al. (2015) suggesting that the most vulnerable birds to fishery bycatch were removed from the population around 1990.

It is possible that boldness affects juvenile survival and the probability of returning to the population, but this is something our study system does not allow to evaluate. Personality tests are designed to be performed on incubating birds only. Pre-breeders are not tied to a nest and thus wander off if approached, preventing personality to be tested. Overall, about 60% of individuals die before recruitment (Fay et al., 2015), constituting an invisible fraction for this study. Juveniles are more vulnerable to mortality risks, including bycatch (Gianuca et al., 2017) and density dependence (Fay et al., 2015), and boldness may modulate these risks. Boldness in pre-breeders could affect their competitive ability, and thus influence their sensitivity to density dependence and exposure to bycatch (bolder individuals could be more exposed to bycatch). Boldness could also affect pre-breeders capacity to acquire resources and gain mass. Since body mass determines age at first reproduction in this species (Weimerskirch, 2018), it could have implications for lifetime reproductive success of both males and females. Measurements of personality on this invisible fraction combined with a better understanding of pre-breeders mortality causes would be useful to assess whether differential selective pressures act on juveniles and adults and what maintains boldness variation in wild populations.

Our results showed that adult personality has relatively little impact on individual performance (life expectancy, lifetime reproductive outcomes) and population growth rate, suggesting either no or only slight selection against boldness in males. The mechanisms that would maintain boldness variation in males despite lower associated reproductive performance are not clear in the wandering albatross. Fluctuating selection on personality according to annual variations in environmental pressure is expected in avian populations and can represent a mechanism maintaining genetic variation in personalities (Dingemanse et al., 2004). It is also possible that personality is under selection with opposite selective pressure on adults and juveniles. Indeed, measuring selective pressures at different stages can lead to different conclusions about selective pressures (Grafen, 1988), and future research priorities include developing methods to measure personality in juveniles. We also acknowledge that boldness represents one dimension of animal personality. Thus, continued efforts to monitor boldness, and the consideration of other personality traits, such as e.g. foraging tactics, would help clarify the role of personality in shaping individual fitness in the wild.

Drawing definitive conclusions about the selective pressures at play is challenging due to methodological limitations that may have constrained our ability to detect ongoing selective pressures. Here, we were limited to the period of personality measurements from 2008 to 2020 to assess the role of boldness on adult demographic rates. Despite this representing a very long-term study on personality, it is still relatively short (12 years) in comparison to the wandering albatross lifespan ($>$ 60 years; Weimerskirch, 2018). This has likely limited our statistical power to detect impacts on survival as relatively few individuals have died during the period 2008-2020. As a result, uncertainties around demographic rates were large, which resulted in even larger uncertainties when used in combination to compute life-history outcomes. Further, it is possible that cohort effects might have masked the impact of boldness on individual performance. However, whereas earlier studies have shown an impact of early life condition on juvenile survival (reviewed in Weimerskirch, 2018) and cohort differences in age at first breeding (Weimerskirch & Jouventin, 1987), so far cohort effects on adult performance has not been reported for this population making such interference effects unlikely.

Our comprehensive approach, combining an evaluation of the effect of boldness at different temporal scales (annual demographic rates and lifetime outcomes) and on all adult demographic rates, revealed that the link between boldness and demography is not as straightforward as would be expected from the pace-of-life literature. It may be sex-specific and play a more important role in one sex compared to the other. The wandering albatross population at Crozet has a male-biased adult sex ratio (Weimerskirch et al., 2005), which might affect the relative impact of boldness for males and females there (Sun, Barbraud, et al., 2022; Sun, Van de Walle, et al., 2022). Further investigations could address the role of the operational sex ratio in mediating the demographic impact of personality in wild populations. Finally, despite the underlying cause, prolonged selection could lead to a shift in the relative frequency of personality types at the population level, with further population-level consequences, such as shifts in generation time.

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Conflict of interest

Authors declare no conflicts of interest.

Data availability

Data and codes used to conduct the analyses will be publicly available on USAP-DC repository upon acceptance of the manuscript.

Authors contribution

SJ, SP, CB, HW, and JV conceived the idea and JV, SJ, RS, CB, and SP designed the study. RS and SJ designed the CMR model and RS conducted the CMR analyses with the help of RF. JV conducted the other demographic analyses, with the help from SJ. JV performed results visualization and presentation, and wrote the first draft of the manuscript. HW, CB, SP and KD led the curation of the data, prepared the data, and helped interpret the data. SJ and SP secured funding. All authors contributed to manuscript revision.

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Figures

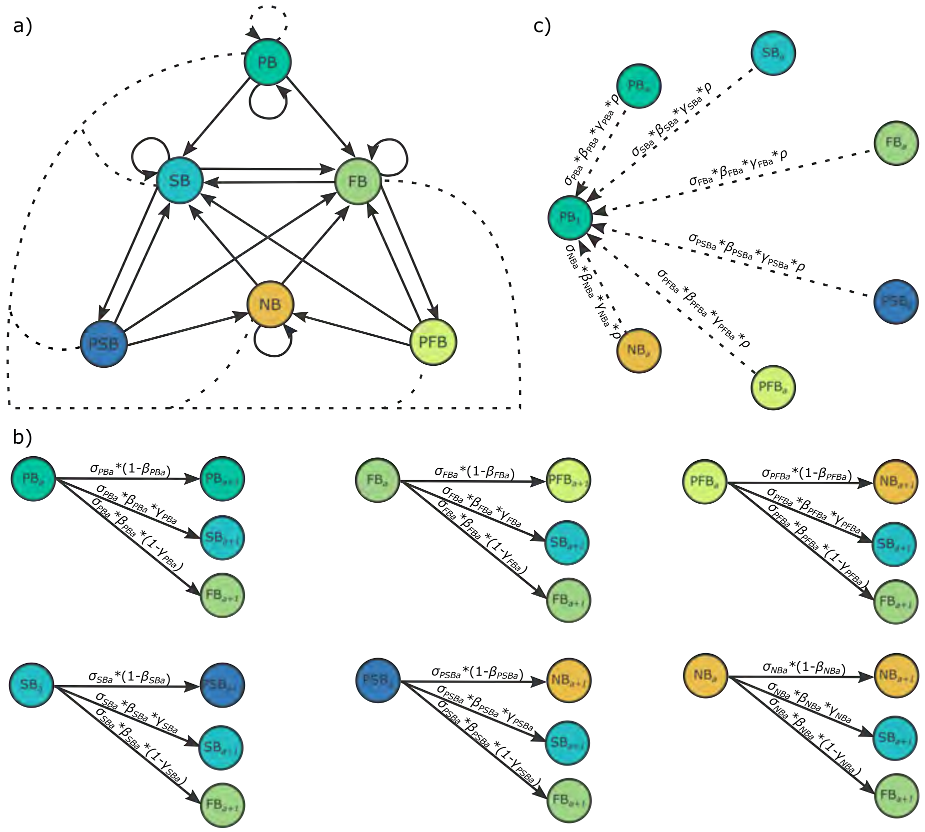

Figure 1: Life cycle graph (a) along with state (b) and fertility (c) transitions for the wandering albatross. In a) are shown annual reproductive state transitions between pre-breeders (PB), successful breeders (SB), failed breeders (FB), post-successful breeders (PSB), post-failed breeders (PFB) and non-breeders (NB). Solid arrows show state transitions, whereas dashed arrows represent fertilities (i.e., the contribution of each state to the pre-breeder state). The life cycle presented is a simplified version; the true life cycle further includes an additive age structure. This means that each annual transition is conditional on age-specific (a) vital rates (α = survival, β = breeding probability, γ = breeding success probability), which are shown in b). From each reproductive state, an individual can transit from year t to year $t + 1$ (or from age a to age $a + 1$) to a non-breeding state (PB, PSB, PFB or NB) or a breeding state (SB or FB) depending on survival and breeding probabilities associated with its state and age a at year t. If the individual breeds, then the individual can transit the next year to either a successful breeder of a failed breeder, depending

on its age and reproductive state-specific breeding success probability. In c) are fertility transitions and represent the contribution of individuals of age a to the first age-class of pre-breeders, PB1, which are fledged chicks. Fledgling production is conditional on the following suite of events: 1) survival, 2) breeding and 3) breeding successfully. The parameter p stands for offspring sex ratio, which here was assumed as 0.5.

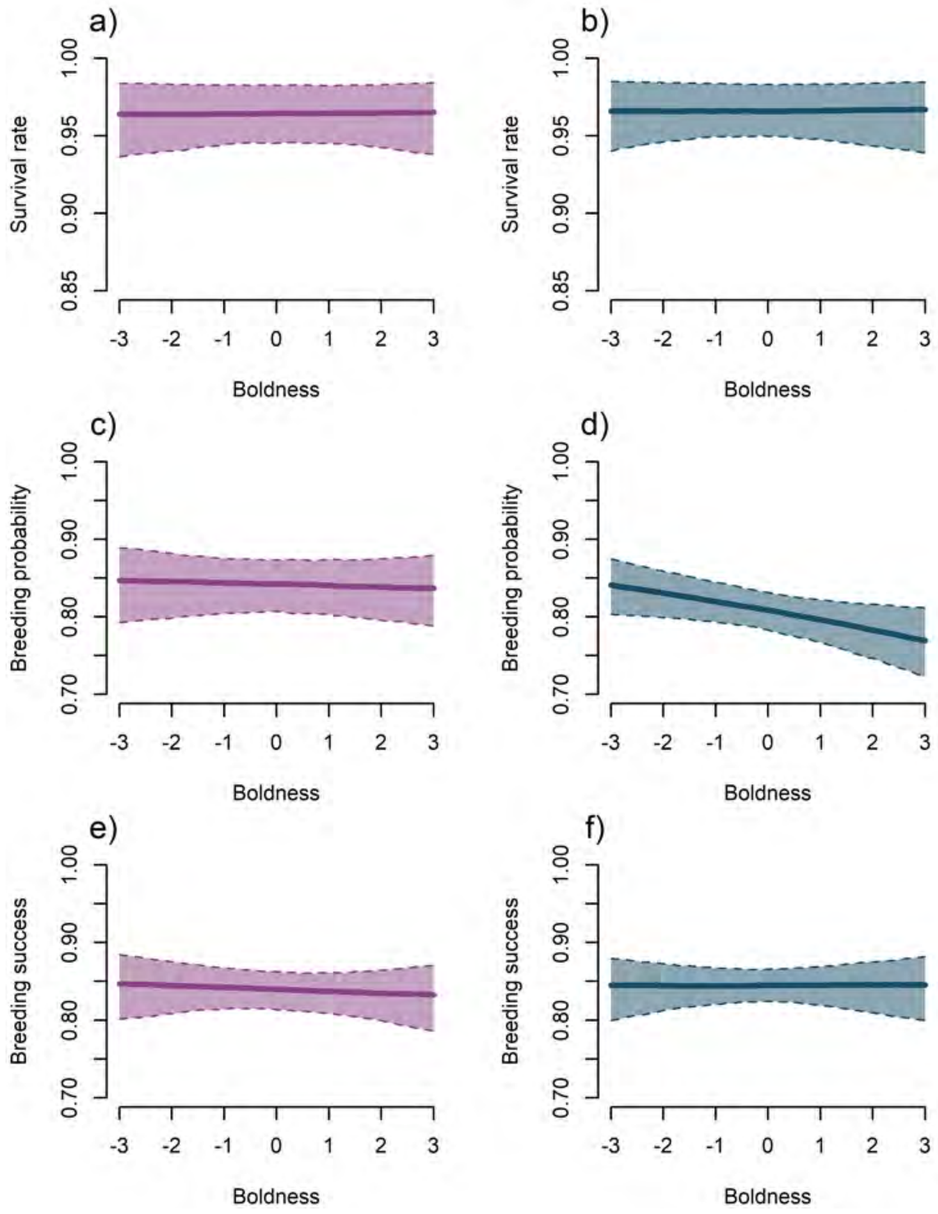

Figure 2: Effect of boldness on adult demographic rates (females: a, c, e; males: b, d, f) wandering albatrosses at Crozet Island from 2008 to 2020. We used the estimate of the impact of boldness on demographic rates from the Capture-Mark-Recapture model to obtain the median prediction line over boldness scores ranging between -3 and 3. The shaded polygons represent the 95% Confidence Intervals over the entire set of posteriors. Predictions for survival are for Successful Breeders (SB) of age 11 and for breeding probability and breeding success probability are for Post-Successful Breeders (PSB) of age 11.

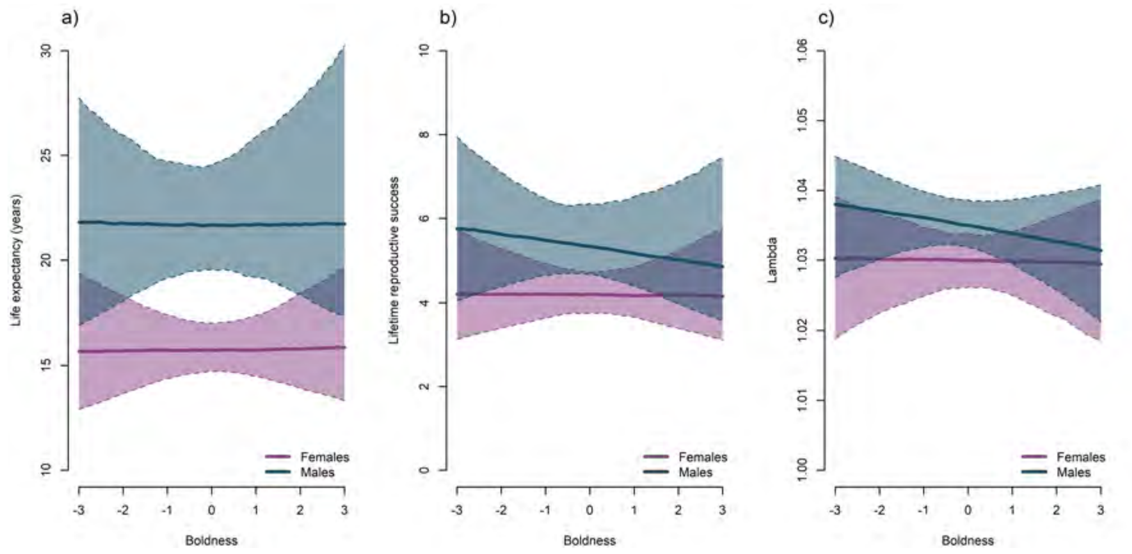

Figure 3: Effect of boldness on life-history outcomes: (a) life expectancy and (b) lifetime reproductive success) and (c) population growth rate (lambda; λ) in wandering albatrosses at Crozet Island. For each simulated boldness score, we randomly sampled 100 values for the intercept and slope of boldness effect and predicted a new value for each demographic rate. Those demographic rates were then inserted into the matrix population models to generate the life-history outcomes. Solid lines represent median effects, whereas the shaded area represent the 95% confidence intervals.

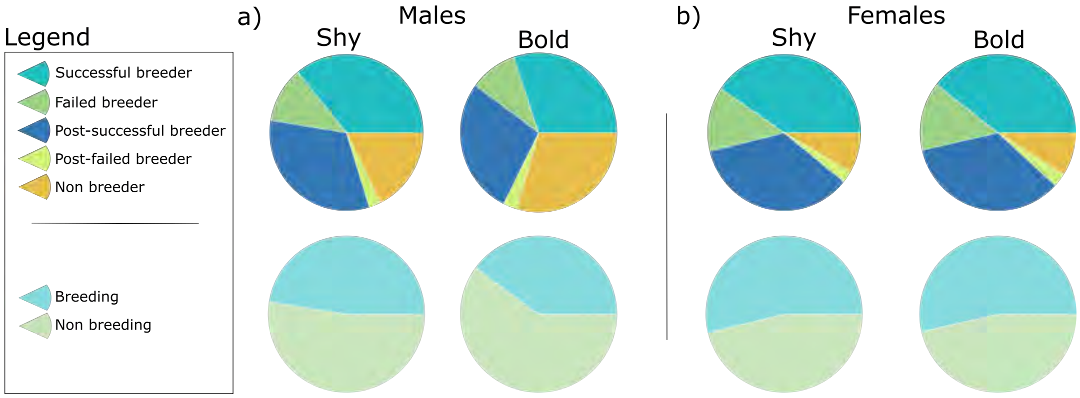

Figure 4: Proportion of time spent by (a) males and (b) females wandering albatrosses in the five adult breeding states (upper panels) and proportion of time spent in breeding and non-breeding states (lower panels) for bold and shy individuals.

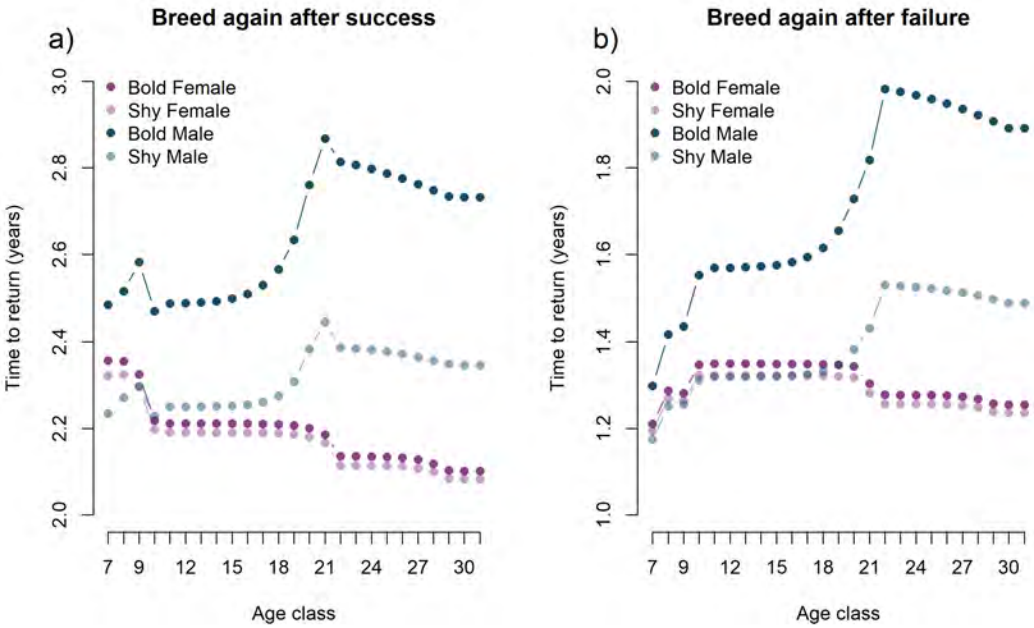

Figure 5: Time to return to a breeding state (i.e. successful breeder, SB, or failed breeder, FB) after a successful (a) or failed (b) breeding attempt in adult wandering albatrosses from Crozet across age classes. Results are shown for males (blue) and females (purple) and for shyer (lighter colors) and bolder (darker colors) individuals.

Supplementary materials S1:

E-Surge model selection

We conducted a preliminary model selection in E-Surge to determine the best breeding state structure to use in the Bayesian MECMR models. We performed a step-down procedure. We started from the most general model (which we termed the ”umbrella” model), which assumed that survival rates, breeding probabilities and breeding success probabilities all differed in each reproductive state. Then, we varied the constraints on the breeding state structure for survival while maintaining the umbrella model structure for breeding probability and breeding success probability.

In this preliminary analysis, we also explored the possibility of contrasting demographic parameters between non-breeders depending on their previous breeding success (NSB = Non-breeder after a successful breeding event, NFB = Non-breeder after a failed breeding event). Therefore, we tested 6 adult breeding states. After the model selection, all best performing models had equal demographic rates between NSB and NFB. Thus, we grouped NSB and NFB into a single breeding state (NB) in the Bayesian model to simplify the model structure and improve computational efficiency.

Across models with different breeding state structures for survival, we selected the best model using AIC corrected by overdispersion (quasi-AIC, QAIC) as a criterion, where lower QAIC values indicate better model fit. We then varied the constraints on breeding probability while maintaining the best structure for survival and the umbrella structure for breeding success probability. We kept only the best model based on QAIC from this second round. Finally, we varied the constraints on breeding success probability while maintaining the best structures for survival and breeding probability and selected the best model based on QAIC. When multiple models performed similarly (i.e., differed by two QAIC points or less), we selected the model with fewer parameters.

We performed model selection on females (Table S1) and males (Table S2) separately. The best-supported model structures from E-Surge differed between females and males. For females, survival rates were different between post-breeders (PSB and PFB) and non-breeders (NSB and NFB), whereas survival rates were the same between PB and NB in males. As for breeding probability, the best supported model for females included an additional group separation between FB and PSB for breeding probability. The best model structure was the same in males and females otherwise. We decided to keep only one model structure for both sexes to ensure analytical consistency between sexes. We retained the best supported model structure for females as it included fewer constraints with a more general formulation.

Table S1: E-Surge MECMR model selection results for females to estimate the demographic parameters survival, breeding probability, and breeding success probabilities. $a_{\theta,stage}$ indicates the age structure for the corresponding demographic parameter described in Section in the main text. The subscript θ indicates the estimated demographic parameter (α for survival, β for breeding probability, and γ for breeding success probability) and $stage$ indicates juveniles (J) or adults (A). “/” indicates group separation and means that the parameters are constrained to be equal within this group. “+” indicates additive effects and “*” indicates interactive effects. “–” indicates that the model structure is the same as the umbrella model. The selected model structure appears in bold.

Model rank	Survival	Breeding probability	Breeding success probability	Deviance	QAIC
Umbrella	PB*a$_{\alpha,J}$+SB/FB/PSB/PFB/NSB/NFB*a$_{\alpha,A}$	PB*a$_{\beta,J}$+SB/FB/PSB/PFB/NSB/NFB*a$_{\beta,A}$	PB*a$_{\gamma,J}$+SB/FB/PSB/PFB/NSB/NFB*a$_{\gamma,A}$	28048.070	45612.850
1	PB*a$_{\alpha,J}$+SB FB/PSB/PFB/NSB/NFB*a$_{\alpha,A}$	-	-	28048.683	28214.683
2	PB*a$_{\alpha,J}$+SB FB/PSB PFB/NSB/NFB*a$_{\alpha,A}$	-	-	28050.786	28208.786
3	**PB*a$_{\alpha,J}$+SB FB/PSB PFB/NSB NFB*a$_{\alpha,A}$**	-	-	28052.739	28202.739
4	PB*a$_{\alpha,J}$+SB FB/PSB PFB NSB NFB*a$_{\alpha,A}$	-	-	28066.092	28208.092
5	**PB*a$_{\alpha,J}$+SB FB/PSB PFB/NSB NFB*a$_{\alpha,A}$**	**PB*a$_{\beta,J}$+SB/FB/PSB/PFB/NSB NFB*a$_{\beta,A}$**	-	28054.073	28200.073
6	**PB*a$_{\alpha,J}$+SB FB/PSB PFB/NSB NFB*a$_{\alpha,A}$**	PB*a$_{\beta,J}$+SB FB/PSB/PFB/NSB/NFB*a$_{\beta,A}$	-	30018.822	30164.822
7	**PB*a$_{\alpha,J}$+SB FB/PSB PFB/NSB NFB*a$_{\alpha,A}$**	PB*a$_{\beta,J}$+SB/FB/PSB PFB/NSB/NFB*a$_{\beta,A}$	-	28059.200	28205.200
8	**PB*a$_{\alpha,J}$+SB FB/PSB PFB/NSB NFB*a$_{\alpha,A}$**	PB*a$_{\beta,J}$+SB/FB PSB/PFB/NSB/NFB*a$_{\beta,A}$	-	28056.239	28202.239
9	**PB*a$_{\alpha,J}$+SB FB/PSB PFB/NSB NFB*a$_{\alpha,A}$**	**PB*a$_{\beta,J}$+SB/FB/PSB/PFB/NSB NFB*a$_{\beta,A}$**	PB*a$_{\gamma,J}$+SB/FB/PSB/PFB/NSB NFB*a$_{\gamma,A}$	28054.701	28196.701
10	**PB*a$_{\alpha,J}$+SB FB/PSB PFB/NSB NFB*a$_{\alpha,A}$**	**PB*a$_{\beta,J}$+SB/FB/PSB/PFB/NSB NFB*a$_{\beta,A}$**	PB*a$_{\gamma,J}$+SB/FB/PSB PFB/NSB/NFB*a$_{\gamma,A}$	28055.850	28197.850
11	**PB*a$_{\alpha,J}$+SB FB/PSB PFB/NSB NFB*a$_{\alpha,A}$**	**PB*a$_{\beta,J}$+SB/FB/PSB/PFB/NSB NFB*a$_{\beta,A}$**	**PB*a$_{\gamma,J}$+SB/FB/PSB PFB/NSB NFB*a$_{\gamma,A}$**	**28056.497**	**28194.497**

Table S2: E-Surge MECMR model selection results for females to estimate the demographic parameters survival, breeding probability, and breeding success probabilities. $a_{\theta,stage}$ indicates the age structure for the corresponding demographic parameter described in Section in the main text. The subscript θ indicates the estimated demographic parameter (α for survival, β for breeding probability, and γ for breeding success probability) and $stage$ indicates juveniles (J) or adults (A). "/" indicates group separation and means that the parameters are constrained to be equal within this group. "+" indicates additive effects and "*" indicates interactive effects. "–" indicates that the model structure is the same as the umbrella model. The selected model structure appears in bold.

Model rank	Survival	Breed probability	Breeding success probability	Deviance	QAIC
Umbrella	PB*a$_{\alpha,J}$+SB/FB/PSB/PFB/NSB/NFB*a$_{\alpha,A}$	PB*a$_{\beta,J}$+SB/FB/PSB/PFB/NSB/NFB*a$_{\beta,A}$	PB*a$_{\gamma,J}$+SB/FB/PSB/PFB/NSB/NFB*a$_{\gamma,A}$	32104.722	32276.722
1	PB*a$_{\alpha,J}$+SB FB/PSB/PFB/NSB/NFB*a$_{\alpha,A}$	-	-	32104.839	32266.839
2	PB*a$_{\alpha,J}$+SB FB/PSB PFB/NSB/NFB*a$_{\alpha,A}$	-	-	32108.431	32262.431
3	PB*a$_{\alpha,J}$+SB FB/PSB PFB/NSB NFB*a$_{\alpha,A}$	-	-	32108.775	32254.775
4	**PB*a$_{\alpha,J}$+SB FB/PSB PFB NSB NFB*a$_{\alpha,A}$**	-	-	32111.920	32249.920
5	**PB*a$_{\alpha,J}$+SB FB/PSB PFB NSB NFB*a$_{\alpha,A}$**	**PB*a$_{\beta,J}$+SB/FB/PSB/PFB/NSB NFB*a$_{\beta,A}$**	-	32113.586	32247.586
6	**PB*a$_{\alpha,J}$+SB FB/PSB PFB NSB NFB*a$_{\alpha,A}$**	PB*a$_{\beta,J}$+SB FB/PSB/PFB/NSB/NFB*a$_{\beta,A}$	-	34084.327	34218.327
7	**PB*a$_{\alpha,J}$+SB FB/PSB PFB NSB NFB*a$_{\alpha,A}$**	PB*a$_{\beta,J}$+SB/FB/PSB PFB/NSB/NFB*a$_{\beta,A}$	-	32148.653	32282.653
8	**PB*a$_{\alpha,J}$+SB FB/PSB PFB NSB NFB*a$_{\alpha,A}$**	PB*a$_{\beta,J}$+SB/FB PSB/PFB/NSB/NFB*a$_{\beta,A}$	-	32116.704	32250.704
9	**PB*a$_{\alpha,J}$+SB FB/PSB PFB NSB NFB*a$_{\alpha,A}$**	**PB*a$_{\beta,J}$+SB/FB PSB/PFB/NSB NFB*a$_{\beta,A}$**	-	32118.206	32248.206
10	**PB*a$_{\alpha,J}$+SB FB/PSB PFB NSB NFB*a$_{\alpha,A}$**	**PB*a$_{\beta,J}$+SB/FB PSB/PFB/NSB NFB*a$_{\beta,A}$**	PB*a$_{\gamma,J}$+SB/FB/PSB/PFB/NSB NFB*a$_{\gamma,A}$	32122.504	32248.504
11	**PB*a$_{\alpha,J}$+SB FB/PSB PFB NSB NFB*a$_{\alpha,A}$**	**PB*a$_{\beta,J}$+SB/FB PSB/PFB/NSB NFB*a$_{\beta,A}$**	PB*a$_{\gamma,J}$+SB/FB/PSB PFB/NSB/NFB*a$_{\gamma,A}$	32126.606	32252.606
12	**PB*a$_{\alpha,J}$+SB FB/PSB PFB NSB NFB*a$_{\alpha,A}$**	**PB*a$_{\beta,J}$+SB/FB PSB/PFB/NSB NFB*a$_{\beta,A}$**	**PB*a$_{\gamma,J}$+SB/FB/PSB PFB/NSB NFB*a$_{\gamma,A}$**	**32126.911**	**32248.911**

Supplementary materials S2 :

Preliminary analysis of non-linear effects of boldness on demographic parameters with respect to age

We conducted a preliminary analysis to evaluate the potential non-linear impact of boldness on demographic parameters across age classes. In each of the six adult models (one model per demographic rate per sex), rather than considering the effect of boldness on demographic rates as additive, we added an interaction term between boldness and age. Then, we compared the performance of models considering age as additive or interactive using the Watanabe Akaike Information Criterion (Hooten & Hobbs, 2015). Lower WAIC values suggest better model performance. Based on WAIC values, adding an interactive effect of age did not improve model fit for five out of six models (Table S3). Model for male breeding success performed better when including an interaction with age. The model suggests that boldness leads to higher breeding success for younger and older age classes, and lower breeding success for males of intermediate age class. Although this result is consistent with findings by Patrick and Weimerskirch (2015), the F-statistics, which is the percentage of the posterior distribution that diverges from zero, was low for all age classes (Table S4), providing little support for a differential impact of boldness with age. Further, we tested how including differential impact of boldness with age on male breeding success would change our results by comparing the slope of the relationship between boldness and population growth rate (lambda, Figure 3c in the main text). We found that the relationship was quasi-identical (Figure S1). Overall, our preliminary analyses provide little support for the inclusion of an age interaction in our models. For parsimony reasons and to limit model complexity, we opted for additive linear effects of age and boldness on demography rates in our analyses.

Table S3: Comparison of model performance based on Watanabe Information Criterion (WAIC). In bold are models with lowest WAIC values

	Female survival	Female breeding probability	Female breeding success	Male survival	Male breeding probability	Male breeding success
Model	WAIC	WAIC	WAIC	WAIC	WAIC	WAIC
Interactive effect of age	8835.9	8875.0	8823.7	12003.8	12013.2	**11995.2**
Additive effect of age	**8834.5**	**8849.1**	**8815.5**	**11995.2**	**12006.3**	12015.8

Table S4: Effect size of boldness on male breeding probability for the three age classes when considering an interaction term between boldness and age in the model

Age class	Effect size (F-statistics)
7-8	0.255 (88.3%)
9-30	-0.053 (79.4%)
31+	0.039 (72.5%)

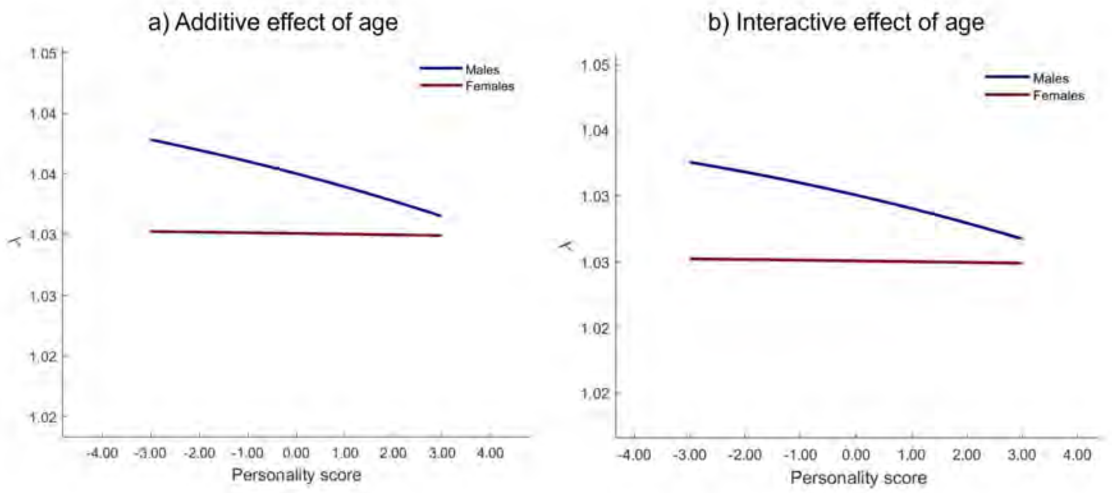

Figure S1: Effect of boldness on population growth rate (λ) when considering either (a) an additive of (b) interactive effect of age and boldness on male breeding success.

Supplementary materials S3 :

Matrix model

The matrix model can be visualized in the Excel file Population_Matrix_WA.xlsx

Supplementary materials S4 :

Supplementary Tables and Figures

Table S5: Estimation of average demographic rates for juvenile (pre-breeders) wandering albatrosses at Crozet Island from 1966 to 2020. Demographic rates were estimated for males and females independently using Bayesian multi-event capture-mark-recapture (MECMR) models. In the models, demographic rates were estimated for each age-class. We assumed equal survival rates for age classes 1-2, age classes 3-8, age classes 9-13 and age classes 14+. We assumed null breeding probabilities and breeding success probabilities for juveniles of age classes 1 through 5 and different breeding probabilities and breeding success probabilities for age classes 6, 7, 8, and 9. For age classes 10+ we assumed equal breeding probabilities and breeding success probabilities. In brackets are the 95% Credible Intervals

	Vital rate estimate	
Age classes	Female	Male
	Survival (α)	
1-2	0.74 [0.72, 0.76]	0.78 [0.76, 0.81]
3-8	0.96 [0.95, 0.97]	0.94 [0.93, 0.95]
9-13	0.92 [0.90, 0.94]	0.97 [0.96, 0.98]
14+	0.92 [0.90, 0.95]	0.93 [0.91, 0.95]
	Breeding probability (β)	
1-5	0.00	0.00
6	0.02 [0.01, 0.02]	0.01 [0.00, 0.01]
7	0.10 [0.09, 0.12]	0.04 [0.03, 0.05]
8	0.28 [0.26, 0.30]	0.15 [0.13, 0.16]
9	0.37 [0.34, 0.40]	0.25 [0.23, 0.27]
10+	0.23 [0.22, 0.26]	0.27 [0.26, 0.29]
	Breeding success probability (γ)	
1-5	0.00	0.00
6	0.56 [0.41, 0.72]	0.41 [0.20, 0.70]
7	0.65 [0.60, 0.71]	0.69 [0.60, 0.79]
8	0.69 [0.65, 0.73]	0.70 [0.66, 0.76]
9	0.74 [0.71, 0.78]	0.67 [0.63, 0.72]
10+	0.74 [0.71, 0.78]	0.71 [0.69, 0.74]

Table S6: Estimation of median demographic rates for adult wandering albatrosses at Crozet Island from 2008 to 2020. demographic rates were estimated for males and females independently using Bayesian multi-event capture-mark-recapture (MECMR) models. In the models, demographic rates were estimated for each combination of reproductive state and age class. For survival, we assumed equal probabilities for age classes 7-8, 9-30 an 30+. For breeding probabilities and breeding success probabilities, we assumed equal probabilities for age classes 7-10, 11-21 and 22+. Definitions: SB = successful breeder, FB = failed breeder, PSB = post-successful breeder, PFB = post-failed breeder and NB = non-breeder. In brackets are the 95% Credible Intervals

	Female					Male				
Vital rate	SB	FB	PSB	PFB	NB	SB	FB	PSB	PFB	NB
Survival (α)										
Age classes										
7-8	0.96 [0.90, 0.99]	0.96 [0.90, 0.99]	0.68 [0.31, 0.94]	0.68 [0.31, 0.94]	NA	0.91 [0.72, 0.98]	0.91 [0.72, 0.98]	0.68 [0.15, 0.97]	0.68 [0.15, 0.97]	NA
9-30	0.96 [0.95, 0.98]	0.96 [0.95, 0.98]	0.97 [0.94, 0.99]	0.97 [0.94, 0.99]	0.95 [0.91, 0.98]	0.97 [0.95, 0.98]	0.97 [0.95, 0.98]	0.97 [0.95, 0.99]	0.97 [0.95, 0.99]	0.97 [0.95, 0.98]
31+	0.90 [0.86, 0.94]	0.90 [0.86, 0.94]	0.95 [0.90, 0.99]	0.95 [0.90, 0.99]	0.86 [0.74, 0.95]	0.94 [0.90, 0.98]	0.94 [0.90, 0.98]	0.95 [0.90, 0.98]	0.95 [0.90, 0.98]	0.94 [0.91, 0.97]
Breeding probability (β)										
Age classes										
7-10	0.02 [0.01, 0.04]	0.79 [0.70, 0.86]	0.77 [0.69, 0.85]	0.81 [0.57, 0.96]	0.53 [0.24, 0.81]	0.03 [0.01, 0.06]	0.77 [0.66, 0.87]	0.77 [0.62, 0.88]	0.75 [0.44, 0.93]	0.60 [0.09, 0.96]
11-21	0.03 [0.02, 0.04]	0.79 [0.73, 0.84]	0.84 [0.81, 0.87]	0.59 [0.43, 0.74]	0.63 [0.54, 0.73]	0.02 [0.01, 0.03]	0.77 [0.72, 0.81]	0.81 [0.78, 0.83]	0.55 [0.42, 0.68]	0.48 [0.42, 0.53]
22+	0.07 [0.05, 0.08]	0.81 [0.74, 0.86]	0.85 [0.82, 0.88]	0.72 [0.53, 0.89]	0.66 [0.57, 0.75]	0.05 [0.04, 0.06]	0.72 [0.66, 0.77]	0.78 [0.75, 0.81]	0.44 [0.32, 0.56]	0.29 [0.25, 0.32]
Breeding success probability (γ)										
Age classes										
7-10	0.50 [0.15, 0.85]	0.87 [0.79, 0.92]	0.75 [0.67, 0.82]	0.75 [0.67, 0.82]	0.75 [0.36, 0.94]	0.61 [0.20, 0.92]	0.86 [0.75, 0.94]	0.81 [0.68, 0.91]	0.81 [0.68, 0.91]	0.65 [0.11, 0.96]
11-21	0.65 [0.47, 0.80]	0.78 [0.72, 0.83]	0.84 [0.82, 0.86]	0.84 [0.82, 0.86]	0.74 [0.66, 0.81]	0.73 [0.53, 0.87]	0.77 [0.72, 0.82]	0.84 [0.82, 0.87]	0.84 [0.82, 0.87]	0.79 [0.73, 0.85]
22+	0.43 [0.30, 0.55]	0.68 [0.61, 0.74]	0.82 [0.79, 0.84]	0.82 [0.79, 0.84]	0.81 [0.73, 0.88]	0.52 [0.38, 0.66]	0.71 [0.65, 0.77]	0.82 [0.80, 0.85]	0.82 [0.80, 0.85]	0.76 [0.69, 0.82]

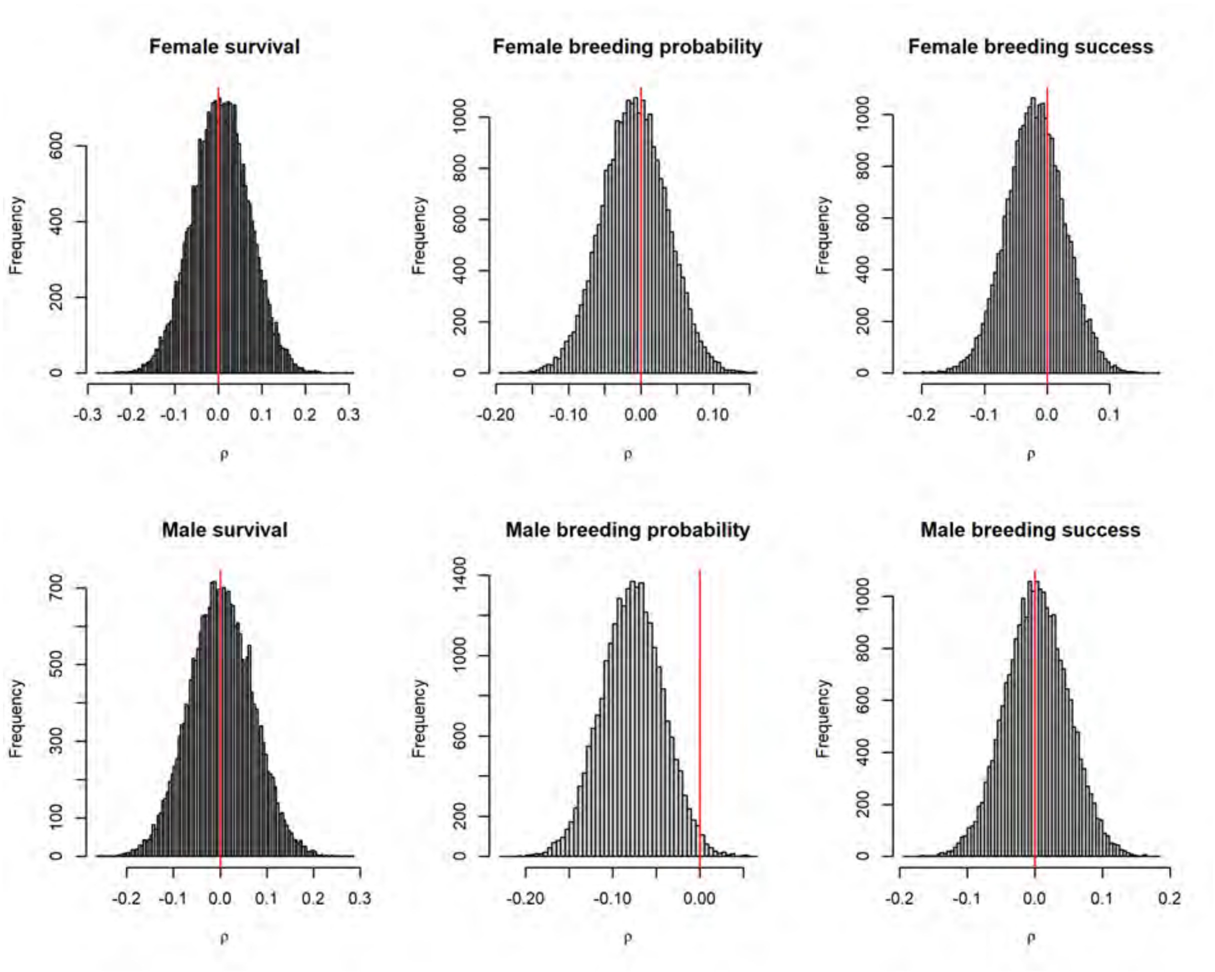
Female survival
Female breeding probability
Female breeding success
Male survival
Male breeding probability
Male breeding success

Figure S2: Posterior distributions for the effect of boldness on demographic rates in wandering albatrosses from Crozet obtained through MECMR models.