

Journal of Animal Ecology



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

Journal:	<i>Journal of Animal Ecology</i>
Manuscript ID	JAE-2023-00365.R1
Manuscript Type:	Research Article
Key-words:	Personality, Demography, Pace-of-Life, Fitness, life history, population growth rate

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A logger on a wandering albatross in flight. Credit Julien Collet

904x595mm (72 x 72 DPI)



Wandering albatrosses at Crozet. Credit Te Papa Museum

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1 Abstract

- 2 1. Differences among individuals within a population are ubiquitous. Those differences are
3 known to affect the entire life cycle with important consequences for all demographic rates
4 and outcomes. One source of among-individual phenotypic variation that has received little
5 attention from a demographic perspective is animal personality, which is defined as con-
6 sistent and heritable behavioral differences between individuals. While many studies have
7 shown that individual variation in individual personality can generate individual differences
8 in survival and reproductive rates, the impact of personality on all demographic rates and
9 outcomes remains to be assessed empirically.
- 10 2. Here, we used a unique, long-term, dataset coupling demography and personality of wander-
11 ing albatross (*Diomedea exulans*) in the Crozet Archipelago and a comprehensive analysis
12 based on a suite of approaches (capture-mark-recapture statistical models, Markov chains
13 models and structured matrix population models). We assessed the effect of boldness on
14 annual demographic rates (survival, breeding probability, breeding success), life-history out-
15 comes (life expectancy, lifetime reproductive outcome, occupancy times), and an integrative
16 demographic outcome (population growth rate).
- 17 3. We found that boldness had little impact on female demographic rates, but was very likely
18 associated with lower breeding probabilities in males. By integrating the effects of boldness
19 over the entire life cycle, we found that bolder males had slightly lower lifetime reproduc-
20 tive success compared to shyer males. Indeed, bolder males spent a greater proportion of
21 their lifetime as non-breeders, which suggests longer inter-breeding intervals due to higher
22 reproductive allocation.
- 23 4. Our results reveal that the link between boldness and demography is more complex than
24 anticipated by the pace-of-life literature and highlight the importance of considering the
25 entire life cycle with a comprehensive approach when assessing the role of personality on

26 individual performance and demography.

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

28 Introduction

29 Demographic rates are not equal between individuals and this variation is typically brought about
30 by phenotypic differences (Hamel et al., 2018). The recognition that different individuals con-
31 tribute differently to population growth motivated the development of, for example, age- (Leslie,
32 1945; Lotka, 1939), stage- (Caswell, 2001; Lefkovich, 1965) and size- (Easterling et al., 2018)
33 structured population models. One source of among-individual phenotypic variation that has re-
34 ceived little attention from a demographic perspective is animal personality, which is defined as
35 consistent and heritable behavioral differences between individuals (Sih et al., 2004). Some indi-
36 viduals are, for example, consistently more aggressive, more explorative, and bolder than others.
37 Those personality differences, because they may dictate how individuals respond towards risks
38 and allocate resources, are expected to correlate with survival rates, reproductive performance,
39 and life-history strategies (Stamps, 2007; Wolf et al., 2007). Many empirical studies have shown
40 behaviourally or personality-associated differential survival and reproductive performance (Ellis
41 et al., 2017; Niemelä et al., 2015; Réale et al., 2009; Santicchia et al., 2018; Smith & Blumstein,
42 2008).

43 Comprehensive assessments of the effect of among-individual differences over the entire life cycle
44 (i.e., over survival and reproductive parameters simultaneously) and on multiple facets of indi-
45 vidual performance are critical to understand the role of personality in shaping demography, but
46 also to assess the selective pressures at play (Santicchia et al., 2018). This is because individual
47 fitness is multidimensional, integrating both performance in survival and reproduction (Mcgraw &
48 Caswell, 1996). Consequently, antagonistic effects (or trade-offs) between demographic rates can
49 arise (Jenouvrier et al., 2018; Sebens et al., 2018), and the expression of a given phenotype can

50 increase one aspect of individual performance while decreasing another (e.g. Van de Walle et al.,
51 2018). In the case of personality, its consistent nature across contexts and situations may lead to
52 trade-offs, for example between survival and reproduction, making the cumulative effect hard to
53 predict. This is because expressing one behaviour can be rewarding in one context or situation, but
54 costly in another (Sih et al., 2004). Those trade-offs are thought to play an important role in the
55 maintenance of among-individual variation in personality at the population level (Sih et al., 2004;
56 Stamps, 2007; Wolf et al., 2007).

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

77 wild populations.

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

97 Here, based on a unique long-term demographic and personality dataset, we investigated the demo-
98 graphic impact of boldness in the wandering albatross. We used a comprehensive approach, investi-
99 gating the effect of boldness over different time scales and levels of organization. At the individual
100 level, we explored 1) short-term consequences with annual demographic rates: survival, breed-
101 ing probability, and breeding success probability. We also explored 2) long-term consequences
102 over the lifetime of individuals through life expectancy and lifetime reproductive outcomes and 3)

103 the relative proportion of lifetime spent in the different reproductive states and the time between
104 breeding events. Finally, at the population level, we computed the effect of boldness on an integrative
105 demographic outcome, namely the population growth rate. We relied on several demographic
106 approaches, including multi-event capture-mark-recapture models, absorbing Markov chains, and
107 structured matrix population models. Following predictions from the pace-of-life syndrome litera-
108 ture, the previously established links between boldness and reproductive success (Patrick &
109 Weimerskirch, 2015), and expected higher vulnerability to bycatch for bolder individuals, we pre-
110 dicted that bolder wandering albatrosses would have lower survival rates, but higher breeding prob-
111 abilities and breeding success. However, it is difficult to make general predictions as to the role of
112 personality on more integrative measures of fitness, (e.g. lifetime reproductive success, population
113 growth rate), as antagonistic effects between parameters over the life cycle (e.g. a trade-off be-
114 tween survival and reproduction) could arise and generate unexpected consequences (Jenouvrier,
115 2013).

116 Materials and Methods

117 We investigated the demographic role of boldness in four steps. First, we estimated the effect
118 of boldness on three annual adult demographic rates (survival, breeding probability, and breed-
119 ing success probability) using Bayesian multi-event capture-mark-recapture models (MECMR).
120 Second, relying on absorbing Markov chains (AMC) and boldness-specific demographic rates cal-
121 culated from the MECMR, we assessed the role of personality on life-history outcomes (expected
122 life expectancy and lifetime reproductive success). Third, to further understand how boldness af-
123 fects individual life histories, we explored transient state transitions (i.e., how individuals transit
124 between the different breeding states within the life cycle during their lifetime) of bold vs shy in-
125 dividuals again within an AMC framework. Specifically, for shy vs bold individuals, we estimated
126 the relative proportion of their lifetime spent in the different reproductive states (e.g. breeder vs
127 non-breeder), as well as their average interval of time between breeding events. Fourth, as an-

128 other integrative demographic outcome, we assessed the overall performance of different boldness
129 scores by calculating the population growth rate (λ) for theoretical populations composed of only
130 individuals of a given boldness value.

131 **Study system and species monitoring**

132 We studied the entire breeding population of wandering albatrosses from Possession Island (46°24'S,
133 52°46'E), in the Crozet Archipelago, south-western Indian Ocean. The breeding season, from egg
134 laying to chick fledging, lasts almost a year (Weimerskirch, 2018) and most breeders take a sab-
135 batical year at sea after a successful breeding event (Tickell, 1968). However, a small proportion
136 of successful breeders can breed the next year, and thus the wandering albatross is considered a
137 quasi-biennial breeder (Barbraud & Weimerskirch, 2012).

138 At Possession Island, a capture-mark-recapture program has been undertaken since 1966 (Weimer-
139 skirch, 2018). Fledglings and adults are banded annually using individually-coded stainless-steel
140 leg rings. Birds are monitored, and their reproductive status determined, during the breeding sea-
141 son. Between January and February, i.e., right after egg-laying, nests are visited three to four times
142 to determine the identities of breeding birds. Chicks are ringed in September and October prior
143 to fledging in November-December. Breeding success is determined based on chick survival until
144 fledging. Each year, unmarked individuals found at the colony are also ringed. Sex is based on
145 morphology and genetic assessment (Weimerskirch et al., 2005). We relied on data collected from
146 1966 to 2020 on 11,591 individuals (8,697 males and 2,894 females). Licences and permissions for
147 capture and handling of animals were granted by the Ethic Committee of Institut Polaire Francais
148 (IPEV) and by the Préfet of Terres australes et antarctiques francaises (TAAF) after advice from
149 the Comité de l'Environnement Polaire (CEP).

150 **Personality assessment**

151 Since 2008, boldness of breeding wandering albatrosses has been assessed for 1,746 individuals
152 (931 males and 815 females) through personality tests. During incubation, breeding individuals
153 were approached on foot and their reaction towards human approaches was evaluated on a scale
154 from 0 to 4 (0 = no response, 1 = lifts the head, 2 = stands on tarsus, 3 = vocalizes, and 4 =
155 stands up). The higher the score, the bolder the individual (Patrick et al., 2013). Those scores
156 were then adjusted to control for differences between observers and observation number, and were
157 standardized (mean = 0, sd = 1) prior to analyses. For adult wandering albatrosses, boldness in
158 reaction to human approaches is correlated to that in reaction to a novel object. Boldness is also
159 highly repeatable (Patrick et al., 2013) and assumed as fixed over an individual's life as a previous
160 study did not find evidence of change in boldness with age (Patrick & Weimerskirch, 2015). More
161 information on personality assessment can be found in Patrick et al. (2013).

162 **Life cycle of the wandering albatross**

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

- 172 1. Pre-breeder (**PB**): individuals that have not yet started to breed. Pre-breeders are of age
173 classes one and over.
- 174 2. Successful breeder (**SB**): adults that have bred and successfully fledged a chick in year t . As

175 wandering albatrosses can start to breed (i.e., lay an egg for the first time) at six years-old
176 (Fay et al., 2016), individuals can only reach this state upon age six years-old and older

177 3. Failed breeder (**FB**): adults that have bred, but failed to successfully fledge a chick in year t .

178 As for **SB**, individuals can only reach this state at the age of six years old and older.

179 4. Post-successful breeder (**PSB**): adults during their sabbatical year after having successfully
180 fledged a chick at year $t - 1$. Individuals can only reach this state at the age of seven years
181 old and older.

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

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

187 A capture-mark-recapture model to estimate demographic rates

188 Demographic rates, i.e., survival (α), breeding probability (β) and breeding success probability
189 (γ) were estimated using Bayesian multi-event capture-mark-recapture models (MECMR). Sur-
190 vival and breeding probabilities vary with age in the wandering albatross, but the pattern of age
191 variation differs between survival and breeding probabilities (Fay et al., 2015, 2016; Patrick &
192 Weimerskirch, 2015). Therefore, we estimated survival, breeding probabilities, and breeding suc-
193 cess probabilities for different age classes based on those previous studies. For pre-breeders, we
194 used the same age classes as in Fay et al. (2015): four age classes for survival (age classes 1-2, 3-8,
195 9-13, and 14+), and five age classes for breeding parameters (age classes 6, 7, 8, 9 and 10+). For
196 pre-breeders of age classes 1 through 5 (i.e., juveniles) we set breeding probabilities and breeding
197 success probabilities at 0 due to immaturity (Fay et al., 2016). For adults, we considered three age
198 classes. Wandering albatrosses show signs of survival senescence after age 30 (Pardo et al., 2013).

¹⁹⁹ Thus, for survival, we followed (Fay et al., 2015; Pardo et al., 2013) and used the following age
²⁰⁰ classes: 7-8, 9-30 and 31+, with the age class 31+ consisting of senescent individuals. Breeding
²⁰¹ senescence occurs at age 22 (Patrick & Weimerskirch, 2015), thus for breeding probability and
²⁰² breeding success probability we considered age classes 7-10, 11-21, and 22+.

²⁰³ Survival and breeding probabilities can vary depending on the breeding states of the birds. There-
²⁰⁴ fore, we estimated survival, breeding probabilities, and breeding success for each of the five adult
²⁰⁵ breeding states separately. Due to the computational demands and extended runtime of Bayesian
²⁰⁶ models, we performed an initial model selection using a frequentist approach in E-Surge Version
²⁰⁷ 2.0 (Choquet et al., 2009) to identify constraints in demographic rates between the different breed-
²⁰⁸ ing states (Fig. 1). A step-down model selection was performed using quasi-Akaike Information
²⁰⁹ Criterion (QAIC) as a criterion for model selection. Results from model selection are shown in
²¹⁰ Supplementary Materials S1. From the best-supported model (i.e., lowest QAIC value), survival
²¹¹ rates were found to be similar between breeding states SB and FB, and between PSB and PFB,
²¹² whereas they were different for PB and NB individuals. Breeding probabilities were different for
²¹³ each breeding state. Breeding success probabilities were similar between PSB and PFB, but were
²¹⁴ different for all other reproductive states (PB, SB, FB and NB). For each demographic rate, the
²¹⁵ respective constraints identified from the model selection were then used in the Bayesian MECMR
²¹⁶ framework in a second step. For example, survival rate for SB and FB were constrained to be equal
²¹⁷ in the Bayesian model.

²¹⁸ All demographic rates were modeled following Bernoulli distributions. Survival was modeled as:

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

²¹⁹ where $\text{Alive}_{k,t}$ indicates whether an individual k survived (1) or died (0) from year $t - 1$ to year
²²⁰ t conditional on its previous survival ($\text{Alive}_{k,t-1} = 1$) and $\mu_{\alpha,a,s}$ is the logit transform mean sur-
²²¹ vival rate of individuals of age a and state s . Conditional on being alive, individual k may breed

222 following an additional Bernoulli process:

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

223 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
 224 logit transform mean breeding probability of individuals of age a and state s . Following the same
 225 logic, conditional on breeding, individual i may be successful at fledging a chick following a third
 226 Bernoulli process:

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

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

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

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

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

239 Along with the vital rates, we also estimated detection probability, p_k , which is the probability of
240 observing an individual depending on its reproductive state s . For pre-breeders, we considered
241 6 age classes (1-5, 6, 7, 8, 9, 10+) for detection probability. For recruited individuals, detection
242 probability was assumed fixed for all age classes. We also assumed detection to be equal between
243 SB and FB (set to 1), and between PSB and PFB (set to 0).

244 To maintain the statistical independence among female and male life histories, we built and sepa-
245 rately ran one model per sex. Because personality has only been measured on breeding adults since
246 2008, our analysis focused on testing the impact of personality on demographic rates exclusively
247 in the adult phase of the life cycle. Therefore, we split the juvenile and adult components of the
248 population and estimated their respective demographic rates into separate models. This allowed us
249 to consider the whole life-history dataset during the entire study period (1965-2020) to estimate
250 juvenile demographic rates. Individuals born after 2016 were not considered for the estimation
251 of juvenile demographic rates because their low detection rates between age classes 1 through 5
252 can lead to underestimated survival rates. For adults, we restricted the analyses to the 2008-2020
253 period using the life histories of individuals with a personality score. To further simplify model
254 complexity and reduce runtime, we examined the influence of personality on each demographic
255 adult rates separately. Thus, a total of eight models were built: three models to test the effect of
256 boldness on survival, breeding probability, and breeding success probability for adults of each sex,
257 and two models for juveniles (one for each sex).

258 MECMR analyses were conducted in JAGS (Plummer, 2003) from R (R Core Team, 2021) using
259 the R package “jagsUI” (Kellner, 2021). MECMR models assume a closed population, i.e., there
260 is no emigration or immigration. This is a reasonable assumption in the wandering albatross from
261 Crozet as a previous study have found high philopatry in adults at this colony (Gauthier et al.,
262 2010). By computing male and female models separately, we also assumed that their demographic
263 rates are independent of each other. Further, with such models, survival estimates represent appar-
264 ent survival due to imperfect detection. We used Markov chain Monte Carlo (MCMC) methods for

265 posterior sampling. For each model, we ran 3 parallel chains with 20,000 iterations, a burn-in phase
 266 of 4,000, and a thinning interval of 2 for a total of 24,000 iterations. Convergence was confirmed
 267 by visual examination of the posterior distributions and the Gelman-Rubin statistic, with a R-hat
 268 lower than 1.1 indicating that convergence was reached (Brooks & Gelman, 1998). Evidence for
 269 covariate effects was gauged by the proportion of the posterior distribution that had the same sign
 270 as the posterior mean (referred to as the F-statistics). We followed the Intergovernmental Panel
 271 on Climate Change (IPCC) terminology (IPCC, 2021) to determine the likelihood of an effect and
 272 considered 66–100% as likely, 90–100% as very likely, 95–100% as extremely likely, and 99–100%
 273 as virtually certain.

274 Predictions of boldness-specific demographic rates

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

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

280

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

281

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

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

²⁸⁶ **An absorbing Markov Chain to estimate life-history outcomes**

²⁸⁷ To assess the impact of boldness on life-history outcomes and state occupancy times, we used
²⁸⁸ an Absorbing Markov chain framework, following Caswell (2009) and Roth and Caswell (2018).
²⁸⁹ Specifically, we calculated life expectancy, mean lifetime reproductive success, expected propor-
²⁹⁰ tion of time spent in each reproductive state in an individual's lifetime and breeding return times
²⁹¹ (i.e., expected time required for a breeder to return to breeding) for individuals expressing different
²⁹² boldness scores B .

²⁹³ The life cycle can be formulated as a Markov chain to extract life-history outcomes (Caswell,
²⁹⁴ 2009). A Markov chain model tracks the trajectory of a particle (here, an individual) as it transits
²⁹⁵ among a predefined set of states. In this stochastic process, future movements are solely determined
²⁹⁶ by the current state and are independent from past movements. The transient matrix \mathbf{U} contains
²⁹⁷ live annual transitions between the states and can be extracted directly from the life cycle. In
²⁹⁸ an absorbing Markov chain, an absorbing state (here a death state) is added to the life cycle and
²⁹⁹ individuals reaching such state remain there indefinitely (they become "absorbed"). We built a
³⁰⁰ separate Markov chain models for each boldness score, assuming that all individuals within a
³⁰¹ given boldness score share the same vital rates. Let \mathbf{U}_B be the transient matrix for individuals of
³⁰² boldness score B . The transient matrix includes all the demographic rates predicted for the given
³⁰³ boldness score B (see Section *Predictions of boldness-specific demographic rates*), except for pre-
³⁰⁴ breeders who were assigned average parameter values estimated in the juvenile models given the
³⁰⁵ absence of boldness measurements for this category of individuals. The transition matrix for the
³⁰⁶ absorbing Markov chain can be calculated from \mathbf{U}_B as follows:

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

³⁰⁷

³⁰⁸

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

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

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

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

329 To better understand individual lifetime allocation to reproduction and how this is affected by
 330 boldness, we contrasted for extreme bold *vs* shy individuals the proportion of their adult lifetime
 331 spent in each reproductive state. Starting from each of successful or failed breeder stages (i.e., SB7
 332 to SB31+ and FB7 to FB31+), we divided the total time spent in each adult state (SB, FB, PSB,

333 PFB and NB) by the adult life expectancy (sum of time spent in all adult stages). Then, those
334 proportions were averaged across the initial stages to produce an average occupancy time in each
335 reproductive state for extreme bold and shy individuals.

336 Also, to further understand the role of boldness in breeding, we calculated the time it takes for
337 extreme shy *vs* bold individuals to breed again after either failing or succeeding at fledging a chick.
338 This calculation relied on the estimation of return times, i.e., the time between two visits in a target
339 set of stages, which is described in detail in Roth and Caswell (2018). Briefly, within the absorbing
340 Markov chain framework, we defined a new set of stages as absorbing, i.e., once an individual
341 reached one of those stages, the iterative process stopped and the individual could no longer move
342 between stages in the next time step (it was “absorbed”, as for the death state). Individuals can
343 reach those stages through many different paths. For example, some individuals can reach an
344 absorbing stage after one year, and others after multiple years, depending on the stage transition
345 probabilities. Here, we set breeding stages (SB7 to SB 31+ and FB7 to FB31+) as absorbing and
346 estimated the average time it took before reaching any of those absorbing stages along all possible
347 paths for extreme bold and shy individuals starting as either 1) successful breeders or 2) failed
348 breeders.

349 **A matrix population model to estimate population growth rate**

350 To assess the role of boldness on the overall performance of individuals expressing different bold-
351 ness scores, we used structured matrix population models. For each of 100 simulated boldness
352 scores (B) within the interval -3 and 3, we built one population matrix model \mathbf{A}_B . The population
353 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
354 the vector of parameters θ_B , so that:

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

355 where

$$\mathbf{A}_B = \mathbf{U}_B + \mathbf{F}_B \quad (11)$$

356 with the matrices \mathbf{U}_B representing the annual transitions of live individuals and \mathbf{F}_B representing
357 fertilities (i.e., the production of new individuals) for boldness score B . The full population matrix
358 can be found in Supplementary Materials S3. In each population matrix \mathbf{A}_B , we included 16 age
359 classes for the PB stage, leaving the 16th age class open-ended to account for late recruitment. For
360 adults, we included 25 age classes for each of SB, FB, PSB, PFB and NB stages, starting at age
361 class 7 (pre-breeders can only become breeders between age class 6 at time t and age class 7 at time
362 $t + 1$), and leaving the last age class 31+ open-ended. This resulted in 125 age/stage combinations
363 for adults and a \mathbf{A}_B age and stage matrix of total dimension 141 by 141. Population growth rate
364 was calculated at equilibrium as the dominant eigenvalue of the matrix \mathbf{A}_B . We used Matlab (The
365 MathWorks Inc, 2022) for demographic analyses and relied on occupancy time codes provided in
366 Roth and Caswell (2018). Figures were made in R (R Core Team, 2021).

367 Results

368 Demographic rates estimation

369 Estimates of average vital rates are provided in Supplementary Materials S4, Table S5 for juveniles
370 and Table S6 for adults. In females, boldness was not likely to affect survival or breeding proba-
371 bility (Fig. 2a,c) as the posterior distribution of ρ was largely centered on zero for both parameters
372 (all $F < 60\%$). Boldness in females was likely associated with lower breeding success ($F = 66.0\%$;
373 Fig. 2e), however the effect was weak. The mean effect of boldness (ρ) on female breeding success
374 was (on the logit scale) -0.019 (95% Credible Interval = [-0.108, 0.072]), which corresponds to a
375 1.8% reduction in the odds of breeding with success for every unit of increase in boldness score.
376 In males, boldness was not likely to affect survival ($F = 49.3\%$; Fig. 2b) or breeding success (F

³⁷⁷ = 52.2%; Fig. 2f). Boldness in males was extremely likely ($F = 98.8\%$) associated with lower
³⁷⁸ breeding probabilities (Fig. 2d). The mean effect of boldness (ρ) on breeding probability was (on
³⁷⁹ the logit scale) -0.078 (95% Credible Interval = [-0.147, -0.0009]), which corresponds to a 7.5% re-
³⁸⁰ duction in the odds of breeding for every unit of increase in boldness score. Posterior distributions
³⁸¹ of ρ for each vital rate and sex can be found in Supplementary Materials S4 Fig. S2.

³⁸² **Life history outcomes, population growth rate and occupancy times**

³⁸³ Boldness had no discernible effect on life expectancy in males and females (Fig. 3a). Lifetime re-
³⁸⁴ productive success was unaffected by boldness score in females (Fig. 3b). In males, lifetime repro-
³⁸⁵ ductive success decreased from a median of 5.8 (95% Confidence Interval = [4.1, 7.9]) fledglings
³⁸⁶ in shy males to a median of 4.9 (95% Confidence Interval = [3.6, 7.5]) fledglings in bold males. In
³⁸⁷ females, there was no detectable decline in population growth rate with increasing boldness score.
³⁸⁸ In males, population growth rates declined with increasing boldness score, from a median of 1.038
³⁸⁹ (95% Confidence Interval = [1.028, 1.045]) for shy to a median of 1.031 (95% Confidence Interval
³⁹⁰ = [1.021, 1.041] for bold individuals (Fig. 3c).

³⁹¹ For males, time spent in the different reproductive states varied between extreme shy and bold
³⁹² individuals (Fig. 4a). Bold males spent 5.8% and 1.8% less time as successful and failed breeders,
³⁹³ respectively, compared to shy males. Bold males also spent 11.8% more time in the non-breeder
³⁹⁴ state. Overall, shy males spent 47.4% of their adult life breeding (52.6% non-breeding) and bold
³⁹⁵ males spent 39.8% of their adult life breeding (60.1% non-breeding). In contrast, for females the
³⁹⁶ time spent in the different reproductive states was similar between shy and bold individuals (Fig.
³⁹⁷ 4b).

³⁹⁸ We found that return times to breeding varied according to the age of the individuals at their
³⁹⁹ previous reproductive state (Fig. 5). Overall, return times were longer after a breeding success.
⁴⁰⁰ Return times to breeding states were on average greater in males compared to females (Fig. 5).
⁴⁰¹ In males, return times to breeding states were longer in older compared to younger individuals

402 regardless of previous reproductive state. Further, in males, return times were longer for bold vs
403 shy individuals, and this difference increased over adult life (Fig. 5a,b). Specifically, it took 0.59
404 years more to return to breeding for a bold male of age class 31+ compared to a bold male of age
405 class 7 after a reproductive failure. This difference was 0.24 years when previous reproductive
406 outcome was success. For shy males, the difference in return time to breeding between age class
407 31+ and age class 7 was 0.11 and 0.31 years when previous reproductive outcome was success or
408 failure, respectively. This means that bolder males take disproportionately longer to breed again
409 as they get older compared to shy males. After age 21, breeding probabilities for males decreased
410 (Supplementary Materials S4; Table S6). This caused return times to increase abruptly up to 21
411 years old as more and more of the state transitions included in the calculation of return times
412 implied breeding probabilities after age 21. For females, the time taken to breed again after a
413 successful reproductive event declined over adult life, which means that older, but successful,
414 females returned to breeding quicker compared to younger females (Fig. 5a). Such a decline with
415 age was not observed for females having failed their previous reproduction (Fig. 5b). A similar
416 pattern was observed in both bold and shy females.

417 Discussion

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

427 comes and overall population growth rates compared to shyer males, whereas female life history
428 outcomes seemed invariable across the shy-bold spectrum.

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

445 We found that boldness had no discernible impact on survival and breeding success, but led to
446 reduced reproductive probabilities in male wandering albatrosses. Overall, our results suggest
447 slightly lower lifetime reproductive success and population growth rates for bolder males, due
448 to reduced breeding probabilities. Most studies assessing the role of personality on reproductive
449 rates focus on breeding success, ignoring reproductive probability. Many species breed every year,
450 with little inter-individual differences in breeding frequencies. Also, tracking individuals between
451 reproductive events poses an important logistical challenge. This may explain why personality
452 impacts on breeding probabilities are less commonly investigated. Yet, long-lived species typically

453 have a conservative strategy characterised by a prioritization of maintenance over reproduction
454 (Gaillard et al., 1998), and breeding can be skipped if it may impair future reproductive prospects
455 (Hamel et al., 2010). In those species, breeding probability can represent an important life-history
456 trait affecting individual fitness and population dynamics (Jenouvrier et al., 2005; Van de Walle
457 et al., 2021).

458 Our results deviate from the pace-of-life syndrome (POLS) hypothesis (Réale et al., 2010), which
459 suggests that the trade-off between survival and reproduction (Stearns, 1989) should be mediated
460 by individual differences in boldness. The POLS hypothesis suggests that due to their expected
461 shorter lifespan, bolder individuals should invest more heavily in reproduction (Réale et al., 2010;
462 Wolf et al., 2007). Instead, we observed no influence of boldness on survival, indicating the ab-
463 sence of antagonistic effects of boldness on survival and reproduction in wandering albatrosses.

464 Expectations from the POLS hypothesis are grounded in the assumption that a slow-fast contin-
465 uum of life histories exists at the individual level. However, the existence of such a continuum is
466 currently being questioned (Royauté et al., 2018), with poor evidence within bird and mammal pop-
467ulations, including the wandering albatross (Van de Walle et al., 2023). Our study thus aligns with
468 Moiron et al. (2020)'s statement that boldness in the wild is generally not associated with lower
469 survival rates and that the shy-bold axis of variation does not correlate with a slow-fast continuum.

470 Laskowski et al. (2021) suggested that the theory on POLS could nevertheless be reconciled if
471 we considered the possibility that boldness can mediate resource acquisition by individuals, and
472 in turn, resource allocation to survival and reproduction. For example, if bolder individuals could
473 acquire more resources, they would be able to allocate more resources to their current reproduc-
474 tion and their maintenance, which would mask the expression of the trade-off. In the wandering
475 albatross, bolder individuals are at the explorative end of the exploitation-exploration continuum,
476 making shorter foraging trips within smaller, but more, foraging patches (Patrick et al., 2017), but
477 it remains unknown whether bold vs shy individuals differ in their foraging success. Answering
478 how boldness affects foraging effort and success would improve our understanding of the mecha-
479 nistic linkages between personality, resource acquisition and allocation, and ultimately individual

480 fitness.

481 An alternative possibility is that high resource allocation in reproduction by bold males may come
482 at a cost in terms of future reproduction, rather than in survival. Reproduction is costly in the
483 wandering albatross. After a successful breeding attempt, most individuals will take a sabbatical
484 year to replenish body reserves, whereas unsuccessful individuals are more likely to breed again
485 the following year (Barbraud & Weimerskirch, 2012; Tickell, 1968). Therefore, there is an im-
486 plicit trade-off between breeding success and breeding frequency in this species and bolder males
487 may face a stronger trade-off. In addition, boldness being linked with risk-proneness (Réale et al.,
488 2010), it should also dictate the amount of risk individuals are willing to support with regard to
489 reproduction, such as protecting and continuing their reproductive allocation. For example, in a
490 wild population of great tits, shyer individuals were more likely to abandon their nest under risky
491 situations (Cole & Quinn, 2014). Bolder wandering albatross males are also expected to have a
492 higher threshold for nest abandonment (Patrick & Weimerskirch, 2015). Bolder birds in late adult-
493 hood also make longer foraging trips and gain more mass per foraging trip during the breeding
494 season compared to shyer birds (Patrick & Weimerskirch, 2015). Furthermore, breeding success
495 of bolder males declines less rapidly with age than that of shyer males (Patrick & Weimerskirch,
496 2015), suggesting they continue to allocate more to reproduction throughout their life. For those
497 bold males, higher allocation to current reproduction may mean that the sabbatical year is insuf-
498 ficient to replenish body condition, forcing them to spend longer periods of time away from the
499 colony not breeding. Our results support this view as bolder males take more time to come back
500 to breeding after a breeding event and have a stronger increase in inter-breeding intervals with age
501 (i.e., reproductive senescence) compared to shyer males.

502 With the rationale that boldness should correlate with vulnerability to fishery bycatch and higher
503 mortality rates, we expected to find a negative impact of boldness on survival. However, starting in
504 the late 1990s, several mitigation measures were implemented in the French Exclusive Economic
505 Zones (EEZ) of Crozet and Kerguelen Islands to reduce fishery bycatch, such as night settings

506 (albatrosses are diurnal foragers; Bentley et al., 2021), closing period, and the use of scaring
507 line spreading. This probably contributed to lessening the fishery-induced mortality pressure on
508 the population, which could have led to an absence of differential mortality along the shy-bold
509 continuum for male and female wandering albatrosses. This is also coherent with model-based
510 predictions from Barbraud et al. (2012) and Tuck et al. (2015) suggesting that the most vulnerable
511 birds to fishery bycatch were removed from the population around 1990.

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

527 Our results showed that adult personality has relatively little impact on individual performance
528 (life expectancy, lifetime reproductive outcomes) and population growth rate, suggesting either no
529 or only slight selection against boldness in males. The mechanisms that would maintain boldness
530 variation in males despite lower associated reproductive performance are not clear in the wander-
531 ing albatross. Fluctuating selection on personality according to annual variations in environmental

532 pressure is expected in avian populations and can represent a mechanism maintaining genetic varia-
533 tion in personalities (Dingemanse et al., 2004). It is also possible that personality is under selection
534 with opposite selective pressure on adults and juveniles. Indeed, measuring selective pressures at
535 different stages can lead to different conclusions about selective pressures (Grafen, 1988), and fu-
536 ture research priorities include developing methods to measure personality in juveniles. We also
537 acknowledge that boldness represents one dimension of animal personality. Thus, continued ef-
538 forts to monitor boldness, and the consideration of other personality traits, such as e.g. foraging
539 tactics, would help clarify the role of personality in shaping individual fitness in the wild.

540 Drawing definitive conclusions about the selective pressures at play is challenging due to method-
541 ological limitations that may have constrained our ability to detect ongoing selective pressures.
542 Here, we were limited to the period of personality measurements from 2008 to 2020 to assess the
543 role of boldness on adult demographic rates. Despite this representing a very long-term study on
544 personality, it is still relatively short (12 years) in comparison to the wandering albatross lifespan
545 (> 60 years; Weimerskirch, 2018). This has likely limited our statistical power to detect impacts
546 on survival as relatively few individuals have died during the period 2008–2020. As a result, un-
547 certainties around demographic rates were large, which resulted in even larger uncertainties when
548 used in combination to compute life-history outcomes. Further, it is possible that cohort effects
549 might have masked the impact of boldness on individual performance. However, whereas earlier
550 studies have shown an impact of early life condition on juvenile survival (reviewed in Weimer-
551 skirch, 2018) and cohort differences in age at first breeding (Weimerskirch & Jouventin, 1987),
552 so far cohort effects on adult performance has not been reported for this population making such
553 interference effects unlikely.

554 Our comprehensive approach, combining an evaluation of the effect of boldness at different tem-
555 poral scales (annual demographic rates and lifetime outcomes) and on all adult demographic rates,
556 revealed that the link between boldness and demography is not as straightforward as would be ex-
557 pected from the pace-of-life literature. It may be sex-specific and play a more important role in one

558 sex compared to the other. The wandering albatross population at Crozet has a male-biased adult
559 sex ratio (Weimerskirch et al., 2005), which might affect the relative impact of boldness for males
560 and females there (Sun, Barbraud, et al., 2022; Sun, Van de Walle, et al., 2022). Further investi-
561 gations could address the role of the operational sex ratio in mediating the demographic impact of
562 personality in wild populations. Finally, despite the underlying cause, prolonged selection could
563 lead to a shift in the relative frequency of personality types at the population level, with further
564 population-level consequences, such as shifts in generation time.

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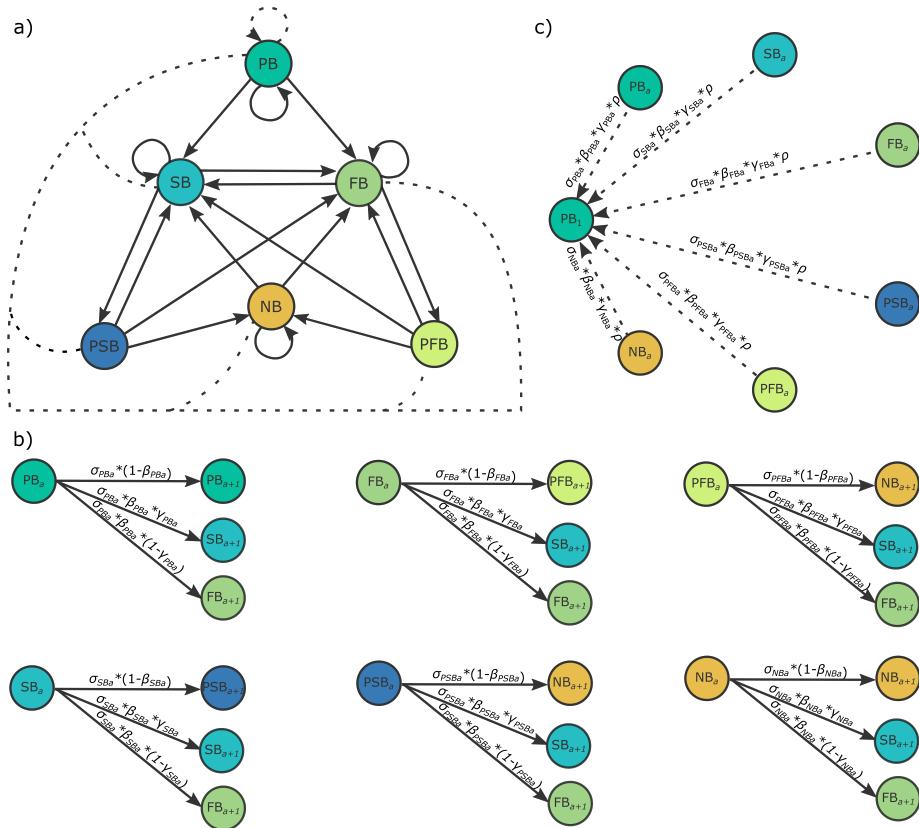
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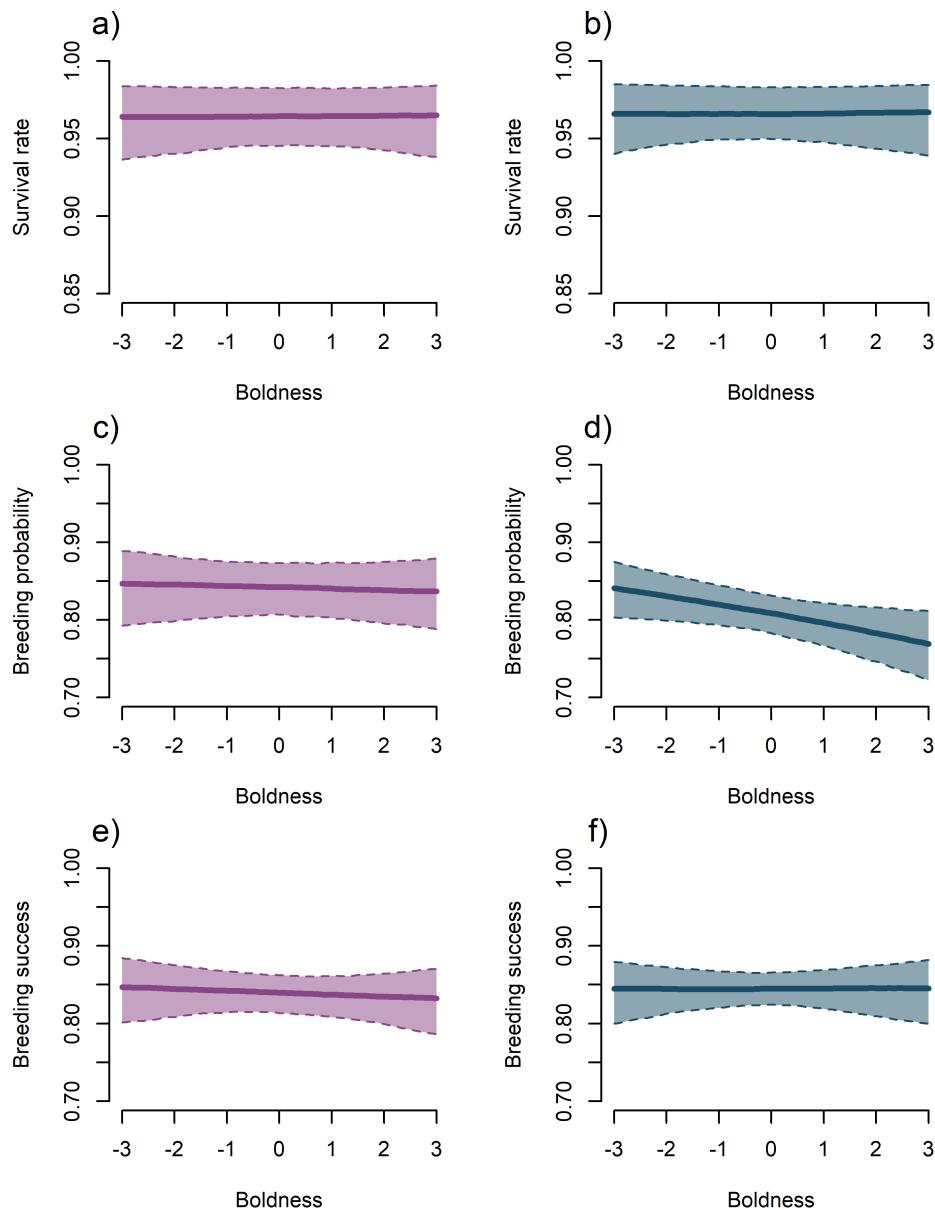
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762 **Figures**



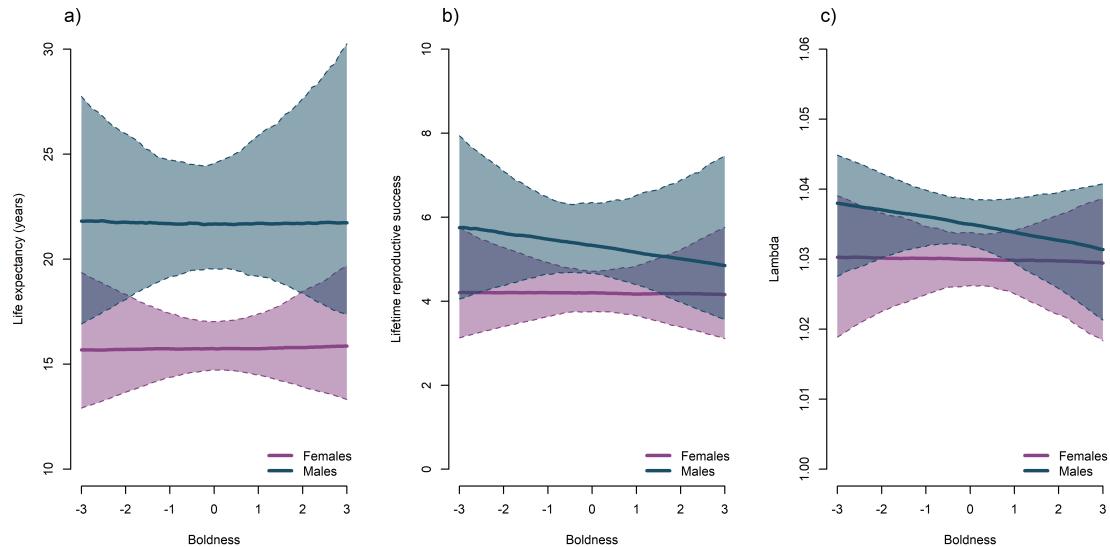
764 **Figure 1:** Life cycle graph (a) along with state (b) and fertility (c) transitions for the wandering
 765 albatross. In a) are shown annual reproductive state transitions between pre-breeder (PB), suc-
 766 cessful breeders (SB), failed breeders (FB), post-successful breeders (PSB), post-failed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

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



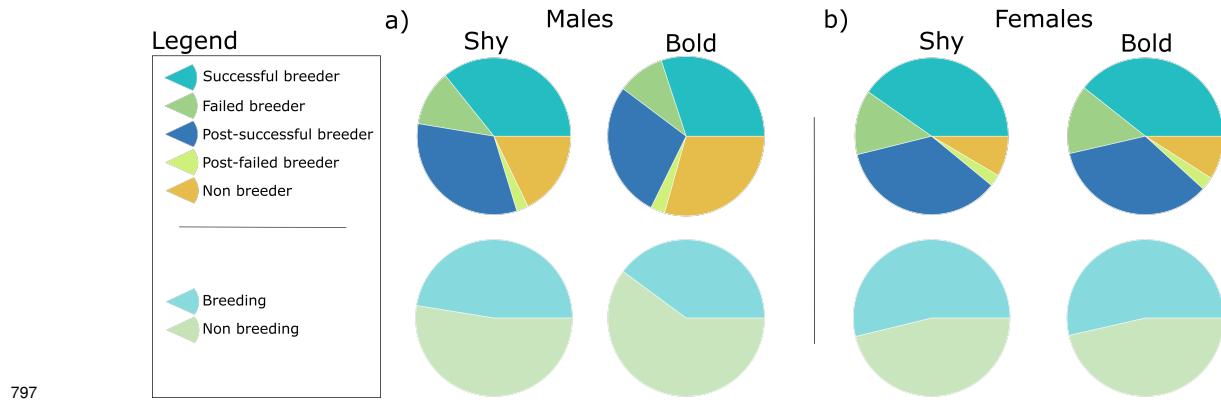
781

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

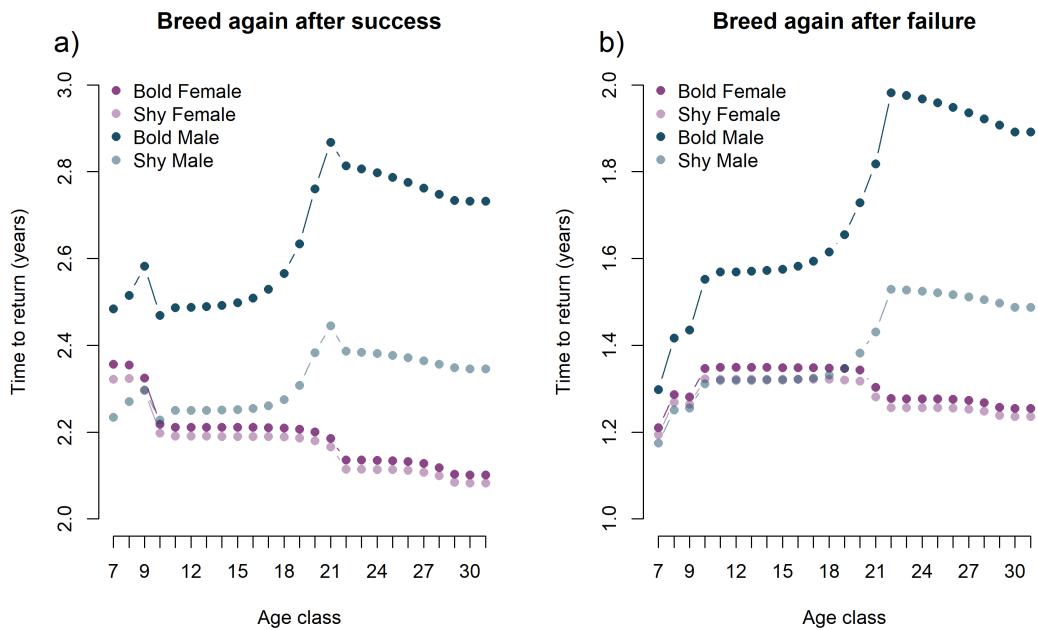


789

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



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



801

802 **Figure 5:** Time to return to a breeding state (i.e. successful breeder, SB, or failed breeder, FB)
 803 after a successful (a) or failed (b) breeding attempt in adult wandering albatrosses from Crozet
 804 across age classes. Results are shown for males (blue) and females (purple) and for shyer (lighter
 805 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 _{α,J+SB/FB/PFB/PFB/NFB/NFB/NFB/NFB/a_{α,A}}	PB*a _{β,J+SB/FB/PFB/PFB/NFB/NFB/a_{β,A}}	PB*a _{γ,J+SB/FB/PFB/PFB/NFB/NFB/a_{γ,A}}	28048.070	45612.850
1	PB*a _{α,J+SB FB/PFB/PFB/NFB/NFB/a_{α,A}}	-	-	28048.683	28214.683
2	PB*a _{α,J+SB FB/PFB/NFB/NFB/a_{α,A}}	-	-	28050.786	28208.786
3	PB*a_{α,J+SB FB/PFB/PFB/NFB/NFB/a_{α,A}}	-	-	28052.739	28202.739
4	PB*a _{α,J+SB FB/PFB/PFB/NFB/NFB/a_{α,A}}	-	-	28066.092	28208.092
5	PB*a_{α,J+SB FB/PFB/PFB/NFB/NFB/a_{α,A}}	-	-	28054.073	28200.073
6	PB*a _{α,J+SB FB/PFB/PFB/NFB/NFB/a_{α,A}}	-	-	30018.822	30164.822
7	PB*a _{α,J+SB FB/PFB/PFB/NFB/NFB/a_{α,A}}	-	-	28059.200	28205.200
8	PB*a _{α,J+SB FB/PFB/PFB/NFB/NFB/a_{α,A}}	PB*a _{β,J+SB FB/PFB/PFB/NFB/NFB/a_{β,A}}	-	28056.239	28202.239
9	PB*a _{α,J+SB FB/PFB/PFB/NFB/NFB/a_{α,A}}	PB*a_{β,J+SB FB/PFB/PFB/NFB/NFB/a_{β,A}}	PB*a _{γ,J+SB FB/PFB/PFB/NFB/NFB/a_{γ,A}}	28054.701	28196.701
10	PB*a _{α,J+SB FB/PFB/PFB/NFB/NFB/a_{α,A}}	PB*a _{β,J+SB FB/PFB/PFB/NFB/NFB/a_{β,A}}	PB*a _{γ,J+SB FB/PFB/PFB/NFB/NFB/a_{γ,A}}	28055.850	28197.850
11	PB*a _{α,J+SB FB/PFB/PFB/NFB/NFB/a_{α,A}}	PB*a _{β,J+SB FB/PFB/PFB/NFB/NFB/a_{β,A}}	PB*a_{γ,J+SB FB/PFB/PFB/NFB/NFB/a_{γ,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. $a_{\theta, \text{stage}}$ 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* $\mathbf{a}_{\alpha,J+SB/FB/PFB/NSB/NFB}*\mathbf{a}_{\alpha,A}$	PB* $\mathbf{a}_{\beta,J+SB/FB/PFB/NSB/NFB}*\mathbf{a}_{\beta,A}$	PB* $\mathbf{a}_{\gamma,J+SB/FB/PFB/NSB/NFB}*\mathbf{a}_{\gamma,A}$	32104.722	32276.722
1	PB* $\mathbf{a}_{\alpha,J+SB/FB/PFB/NSB/NFB}*\mathbf{a}_{\alpha,A}$	-	-	32104.839	32266.839
2	PB* $\mathbf{a}_{\alpha,J+SB/FB/PFB/NSB/NFB}*\mathbf{a}_{\alpha,A}$	-	-	32108.431	32262.431
3	PB* $\mathbf{a}_{\alpha,J+SB/FB/PFB/NSB/NFB}*\mathbf{a}_{\alpha,A}$	-	-	32108.775	32254.775
4	PB*$\mathbf{a}_{\alpha,J+SB/FB/PFB/NSB/NFB}*\mathbf{a}_{\alpha,A}$	PB*$\mathbf{a}_{\beta,J+SB/FB/PFB/NSB/NFB}*\mathbf{a}_{\beta,A}$	PB*$\mathbf{a}_{\gamma,J+SB/FB/PFB/NSB/NFB}*\mathbf{a}_{\gamma,A}$	32111.920	32249.920
5	PB* $\mathbf{a}_{\alpha,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\alpha,A}$	-	-	32113.586	32247.586
6	PB* $\mathbf{a}_{\alpha,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\alpha,A}$	-	-	34084.327	34218.327
7	PB* $\mathbf{a}_{\alpha,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\alpha,A}$	-	-	32148.653	32282.653
8	PB* $\mathbf{a}_{\alpha,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\alpha,A}$	PB* $\mathbf{a}_{\beta,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\beta,A}$	PB* $\mathbf{a}_{\gamma,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\gamma,A}$	32116.704	32250.704
9	PB* $\mathbf{a}_{\alpha,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\alpha,A}$	PB*$\mathbf{a}_{\beta,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\beta,A}$	-	32118.206	32248.206
10	PB* $\mathbf{a}_{\alpha,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\alpha,A}$	PB* $\mathbf{a}_{\beta,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\beta,A}$	PB* $\mathbf{a}_{\gamma,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\gamma,A}$	32122.504	32248.504
11	PB* $\mathbf{a}_{\alpha,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\alpha,A}$	PB* $\mathbf{a}_{\beta,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\beta,A}$	PB* $\mathbf{a}_{\gamma,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\gamma,A}$	32126.606	32252.606
12	PB* $\mathbf{a}_{\alpha,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\alpha,A}$	PB* $\mathbf{a}_{\beta,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\beta,A}$	PB*$\mathbf{a}_{\gamma,J+SB/FB/PFB/PFB/NSB/NFB}*\mathbf{a}_{\gamma,A}$	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 (λ , 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%)

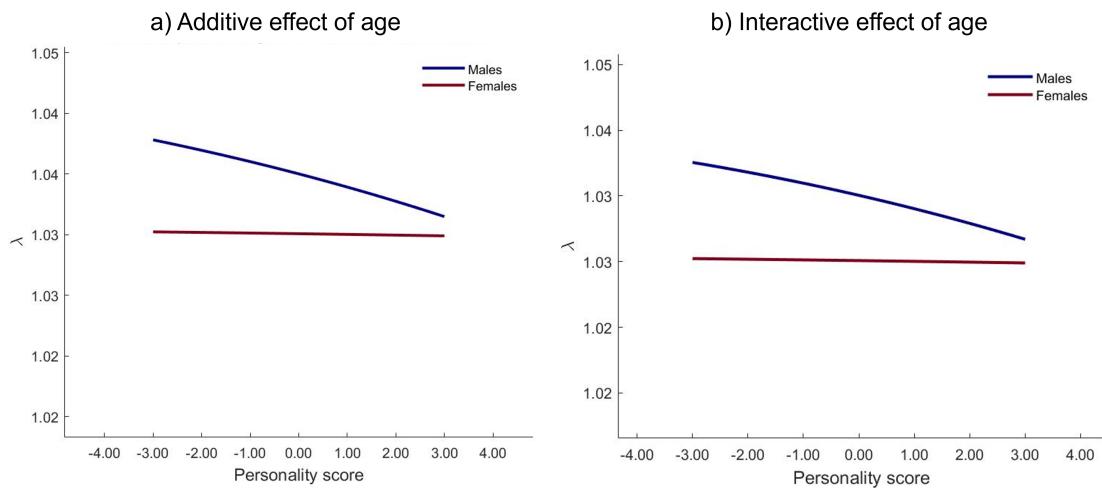


Figure S1: Effect of boldness on population growth rate (λ) when considering either (a) an additive or (b) interactive effect of age and boldness on male breeding success.

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

Age classes	Vital rate estimate	
	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 and 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

Vital rate	Female					Male				
	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]

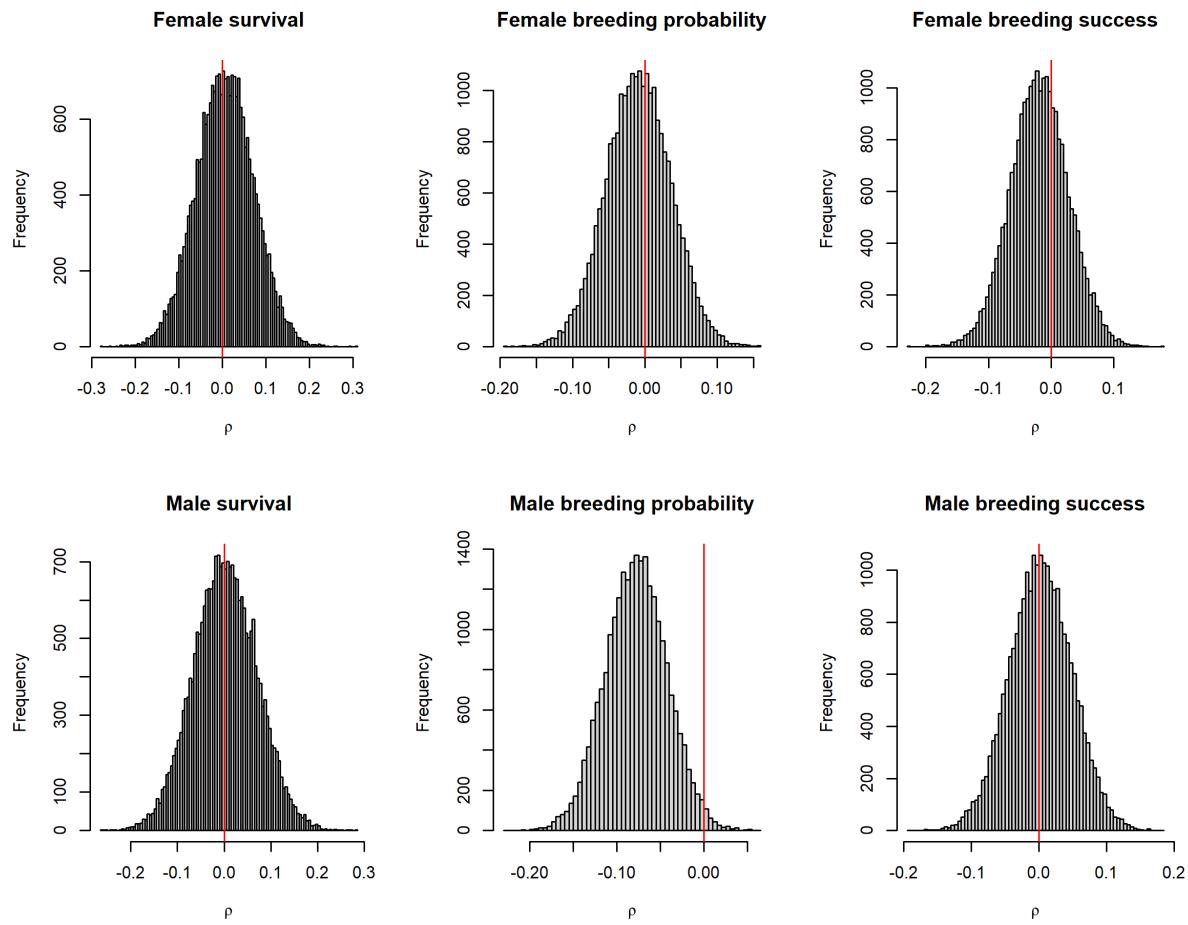


Figure S2: Posterior distributions for the effect of boldness on demographic rates in wandering albatrosses from Crozet obtained through MECMR models.