



Research

Cite this article: Robert A, Bolton M, Jiguet F, Bried J. 2015 The survival–reproduction association becomes stronger when conditions are good. *Proc. R. Soc. B* **282**: 20151529. <http://dx.doi.org/10.1098/rspb.2015.1529>

Received: 24 June 2015

Accepted: 1 October 2015

Subject Areas:

ecology

Keywords:

demographic heterogeneity, individual quality, long-lived seabird, multi-event modelling, nest fidelity, *Oceanodroma monteiroi*

Author for correspondence:

Alexandre Robert

e-mail: arobert@mnhn.fr

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2015.1529> or via <http://rspb.royalsocietypublishing.org>.

The survival–reproduction association becomes stronger when conditions are good

Alexandre Robert¹, Mark Bolton², Frédéric Jiguet¹ and Joël Bried^{3,4}

¹Muséum National d'Histoire Naturelle, UMR 7204 Sorbonne Universités-MNHN-CNRS-UPMC, CP51, 55 Rue Buffon, Paris 75005, France

²RSPB Centre for Conservation Science, UK Headquarters, The Lodge, Sandy, Bedfordshire SG19 2DL, UK

³MARE (Marine and Environmental Science Centre), IMAR (Institute of Marine Research) and LARSyS Associated Lab, Departamento de Oceanografia e Pescas, Universidade dos Açores, Horta, Açores 9901–862, Portugal

⁴Cabinet Vétérinaire, 8 Avenue de la Reine Nathalie, Biarritz 64200, France

Positive covariations between survival and reproductive performance (S–R covariation) are generally interpreted in the context of fixed or dynamic demographic heterogeneity (i.e. persistent differences between individuals, or dynamic variation in resource acquisition), but the processes underlying covariations are still unknown. We used multi-event modelling to investigate how environmental and individual features influence S–R covariation patterns in a long-lived seabird, the Monteiro's storm petrel (*Oceanodroma monteiroi*). Our analysis reveals that a strong positive association between individual breeding success and subsequent survival occurs only when conditions are favourable to reproduction (in favourable years, in high-quality nests and in nest-faithful breeders). This finding reflects differences in the main causes of breeding failure and mortality under favourable and unfavourable conditions, which in turn lead to distinct patterns of S–R covariation. We suggest, in particular, that resource-related sources of demographic heterogeneity do not generate a strong S–R covariation, in contrast with hidden and unpredictable sources of variation.

1. Introduction

Patterns of variation and covariation among life-history traits have been intensively studied at the interspecies level [1,2], but covariations occurring within species or populations remain poorly understood (but see [3,4]). At the population-level, the covariation between individual survival and reproductive success or status (hereafter, S–R covariation) primarily reflects the fact that reproduction and survival are not functionally independent, either because they are traded-off by common finite resources, they depend on the same favourable conditions or because one is the direct consequence of the other. At the scale of a single population, four types of processes can generate S–R covariation. First, reproduction costs [5] might result from trade-offs in internal energy reserves [1] or pleiotropic effects of regulators [6]. Second, age variation can affect both survival and reproduction components, related to: (i) the increase in reproductive effort (and breeding success) with age associated with increasing reproductive costs [7], (ii) the growth in body size and/or improvement in experience [8], or (iii) senescence [9]. Third, environmental variation in space or time can lead to similar qualitative responses of survival and reproduction parameters, in relation with, e.g. year-to-year variation in weather [10] or food availability [11] or spatial variation in individual breeding site exposure to predation or adverse meteorological conditions [12]. Fourth, there is a potential fixed variation among individuals, resulting from unobservable differences between individuals, intrinsic and fixed early in life, sometimes referred to as individual quality [13]. Some recent studies have uncovered consistent differences in quality between individuals engendering positive S–R covariation [3,14,15].

Recent works suggested, however, that the above categorization is too simplistic and difficult to use in practice, as the individual, temporal and age components of demographic variation are intermixed. For example, ageing differs among environments [16] and reproductive costs are generally cumulative (thus, expressed along an age axis), especially in long-lived species [17]. Recent results suggested that most of the observed inter-individual differences in life histories are due to dynamic heterogeneity (related to variation in biotic and abiotic conditions, [18,19], but see [20,21]), engendering a labile positive S–R covariation [22]. Furthermore, it is often impossible or meaningless to discriminate intrinsic and environmental effects. Apparent intrinsic heterogeneity can result from, e.g. temporal environmental variation via cohort effects [23] and S–R covariation may result from environmental, unpredictable variations arising in the labile micro-environment of individuals (thus, not consistent in time or space), whose effects are generally impossible to disentangle from the effects of intrinsic dynamic heterogeneity.

Here, we investigate how demographic and behavioural proxies of individual heterogeneity as well as spatial and temporal conditions influence the covariation between breeding performance and subsequent survival in a long-lived seabird, the Monteiro's storm petrel (*Oceanodroma monteiroi*). In this species, a global positive covariation has been found between reproduction status/success of adults and subsequent survival, with a low survival rate in non-breeders, a very high survival rate in successful breeders and an intermediate survival in unsuccessful breeders [24]. Subsequent investigations revealed a significant heterogeneity in breeding success between years, individual nesting sites and breeding pairs as well as higher nest and mate fidelity following successful breeding [25], suggesting that experienced 'high-quality' breeders are faithful to their nest, breed in good quality nests and have a high breeding success.

In this study, we systematically test the relationship between breeding success and subsequent survival for various categories of age, nest quality (defined from achieved fledging success over the 13-year study period), breeding season quality (average fledging success of the population) and nest fidelity. We already know from previous and preliminary analyses that: (i) breeding success (BS) increases with age (see the electronic supplementary material, appendix S1); and that (ii) successful breeding increases the probability of retaining one's nest the next year [25]. We thus consider nest retention as an integrative proxy of a breeder's quality (i.e. the ability for a breeder to have selected a high-quality nest site in a previous year, to have successfully bred in that nest and to have retained its nest). We formulate simple predictions on survival patterns, depending on the main source of variation responsible for the global pattern of positive S–R covariation previously observed. (i) If the S–R covariation arises mainly from age differences, we predict that survival will increase with age but will be similar for same-age unsuccessful (UB) and successful (SB) breeders; (ii) if the S–R covariation comes mainly from breeder 'quality', we predict that the individuals that retain their nest between year t and year $t + 1$ will survive better than those that change nest, but that survival will be the same for UB and SB among the breeders that retained their nest (and, similarly, among those that changed their nest); (iii) finally, if the S–R covariation is essentially related to nest quality, we predict that survival will increase with nest quality, but will be the same for UB and SB for a given nest quality (predictions are summarized in the electronic supplementary material, appendix S1).

2. Material and methods

(a) Model species

Monteiro's storm petrel is a small (45 g) Procellariiforme endemic to the Azores archipelago (subtropical northeastern Atlantic), where it is known to breed only on two mammal-free islets (Praia and Baixo) situated 5 km apart just off Graciosa Island. Total population size is estimated at 250–300 breeding pairs [26]. Individuals can start breeding when they are 2 years old [27]. Egg laying occurs between late April and early July, and chicks hatch between the second week of June and late July [26]. Like all Procellariiformes, this species is socially monogamous, females lay a single egg per breeding attempt, and both parents participate in incubation and chick-rearing [28].

(b) Data collection and monitoring protocol

We used capture–mark–recapture data collected on Praia Islet (39.8030° N, 27.8570° W; 0.12 km²) between 1994 and 2012, based on banding of adults and chicks. Reproduction and nest/mate fidelity at this locality were monitored only from 2000 onwards. Each nest had a unique identification code. The quality of a nest was defined based on the modelling of achieved fledging success in this nest over the period 2000–2012 (controlling for differences due to breeding pairs and years [25]). Importantly, although most nests (62%) were used by several distinct breeding pairs over the course of the study (13 breeding seasons), it is likely that the nest quality index also reflects breeders' quality. Thus, the nest quality index is partly redundant with our 'breeder quality' index based on nest fidelity (see more discussion in the electronic supplementary material, appendix S1). The nest quality index nevertheless contains distinct information because it is computed over the long term at the population level, while nest fidelity only depends on the behaviour of the focal individual in the previous year. The quantitative nest quality index obtained from [25] was categorized in three distinct groups (L, M and H, for low-, medium- and high-quality nests, respectively; see the electronic supplementary material, appendix S1 for definitions). Three field sessions occurred each year, the first one during the first-half of June (identifying the early breeders during incubation; duration: 8–10 days), the second one in late July–early August (identifying the late breeders during incubation and banding the early-hatched chicks; duration: 3 days) and the last one in early September (banding the late-hatched chicks; duration: 1 day). Breeders were captured/re-captured by hand in their nests during incubation, and nests were checked every 4–5 days (to minimize disturbance) until the two pair mates were identified. Once we had the identity of the two pair mates, the next inspection of the nest occurred during chick-rearing (to ring the chick or to notice that the breeding attempt had failed). Non-breeders were captured/re-captured by hand at the nest and also using a mist-net at night, still during the incubation period of the breeders. Based on these three sessions, the breeding status of each individual in each year t was recorded as NB (non-breeder, i.e. no egg laid), UB (unsuccessful breeder, i.e. failure during incubation or chick-rearing) or SB (successful breeder, i.e. fledged chick). The nest fidelity status of each individual in each year t was recorded as either F (faithful) if it remained in the same nest as during year $t - 1$, or C (changing) if it bred in another nest in year t (see details in the electronic supplementary material, appendix S1).

(c) Multi-event modelling

We used multi-event capture–recapture modelling [29] based on live recaptures of marked adult individuals ($n = 472$ individuals) from 2000 to 2012 ($n = 13$ occasions) to estimate the annual survival probability (S), recapture probabilities (P), as well as the probabilities of moving between different reproductive

Table 1. Comparison among models assuming different annual survival probabilities according to the breeding status of the birds (non-breeder NB, unsuccessful breeder UB, successful breeder SB) in combination with age class (young versus older), nest fidelity (faithful, change or previously non-breeder) and nest quality (low-, medium- or high-quality) states. (The general structure for transition (ψ), recapture (P) and assignment (A) probabilities is [$\psi_{\text{from},t}; P_{t \rightarrow t}; A_{\text{from}}$] (electronic supplementary material, appendix S1). Model selection was performed based on the Akaike information criterion corrected for small sample size and overdispersion (QAICc). Δ QAICc is the difference in QAICc between each model and the best model. The QAICc weight (w) is the amount of evidence in favour of a model; dev and np are the deviance and the number of estimated parameters, respectively. In age models, the threshold between young and older birds is $x = 4$ years. Model indices correspond to those presented in the electronic supplementary material, appendix S2.)

index	model	QAICc	np	dev	w
combination of age class and breeding status models					
1	interaction model (age \times breeding status)	5357.4	59	6858.0	1
2	breeding status model	5362.8	56	6873.6	0.066
3	additive model (age + breeding status)	5363.5	57	6871.6	0.047
4	null model (all equal)	5377.8	54	6898.8	0
5	age model	5378.2	55	6896.6	0
combination of nest fidelity and breeding status models					
21	interaction model (UB _{faithful} versus SB _{faithful} versus all other breeders versus NB)	5549.8	59	7110.2	1
22	breeding status model (all SB versus all UB versus NB)	5551.6	58	7115.2	0.472
32	null model (all breeders versus NB)	5557.7	57	7125.9	0.021
35	nest fidelity model (retention versus change versus previously NB versus NB)	5561.2	59	7124.9	0.004
combination of nest quality and breeding status models					
42	interaction model (UB _{high} versus UB _{medium} versus UB _{low} versus all SB versus NB)	5553.5	78	7060.4	1
51	breeding status model (all SB versus all UB versus NB)	5566.0	76	7082.5	0.002
58	nest quality model (high versus medium versus low versus NB)	5582.4	77	7101.2	0
59	null model (all breeders versus NB)	5592.4	75	7120.0	0

statuses for surviving individuals (ψ) and the probabilities of assignment state (i.e. breeding status, nest fidelity, nest quality status or age) of living individuals by observers. Capture–recapture histories were based on marking and recapture events occurring between June and August of each year. Importantly, survival estimates reported here are actually estimates of ‘apparent survival’ (i.e. mortality and permanent emigration are confounded). Although permanent emigration rates in adult Procellariiformes are presumably extremely low and similar across sexes and breeding status [30], our approach may cause a slight underestimation of survival rates.

We conducted three main sets of analyses: the first one combined ‘reproductive performance’ states and ‘nest fidelity’ states, the second one combined ‘reproductive performance’ states and ‘nest quality’ states, whereas the third one combined ‘reproductive performance’ states and ‘age class’ states (see details on each analysis in the electronic supplementary material, appendix S1). We performed these three analyses in parallel because combining reproductive performance, age class, nest quality and nest fidelity states was not possible given limitations of the data and the software currently available for this type of analyses. In all analyses, we considered two steps to model annual state transitions (first, survival, then transition between breeding, quality, fidelity and age states) and two steps to model events (first, recapture, then assignment to a certain or uncertain state) (all matrices are available upon request).

The fit of the most general, starting model to the data was tested by using goodness-of-fit (GOF) tests designed for multistate capture–recapture models, as implemented in program U-CARE version 2.3.2 [31,32] for the JOLLYMoVE model [31]. Model selection was performed using program E-SURGE v. 1.7.1 [33] based on the Akaike information criterion corrected

for small sample size and overdispersion (QAICc). Based on knowledge of the monitoring protocol and species behaviour, we assumed in all cases that the probabilities of assignment A of recaptured individuals to the various states were state-dependent (i.e. different between states), that recapture probabilities P varied additively between years (t) and states (t_o) and that transition probabilities between states varied as a function of the provenance (from) and arrival (t_o) states. Thus, our starting model for model selection on survival structure was [$S_{\text{from},t}; \psi_{\text{from},t}; P_{t \rightarrow t}; A_{\text{from}}$].

3. Results

Results of GOF tests for our most general data structure revealed evidence of moderate lack of fit in the data due to immediate trap-dependence. We incorporated a variance inflation factor ($\hat{c} = 1.31$) to correct for recapture heterogeneities (see detailed GOF results and justifications in the electronic supplementary material, appendix S2).

When assuming that individual state is based only on breeding status (i.e. NB versus UB versus SB), the analysis revealed differences in subsequent survival probabilities between the three states (model 2 versus model 4 in table 1) with estimates ranging from 0.83 ± 0.02 for NB to 0.91 ± 0.02 for UB to 0.98 ± 0.02 for SB (figure 1a).

When pooling breeding statuses (NB, UB and SB), the analysis of age class models did not reveal significant survival differences between age classes (see figure 1b and model 5 in table 1; main results are presented for an age threshold of 4 years, that is, states are defined by separating

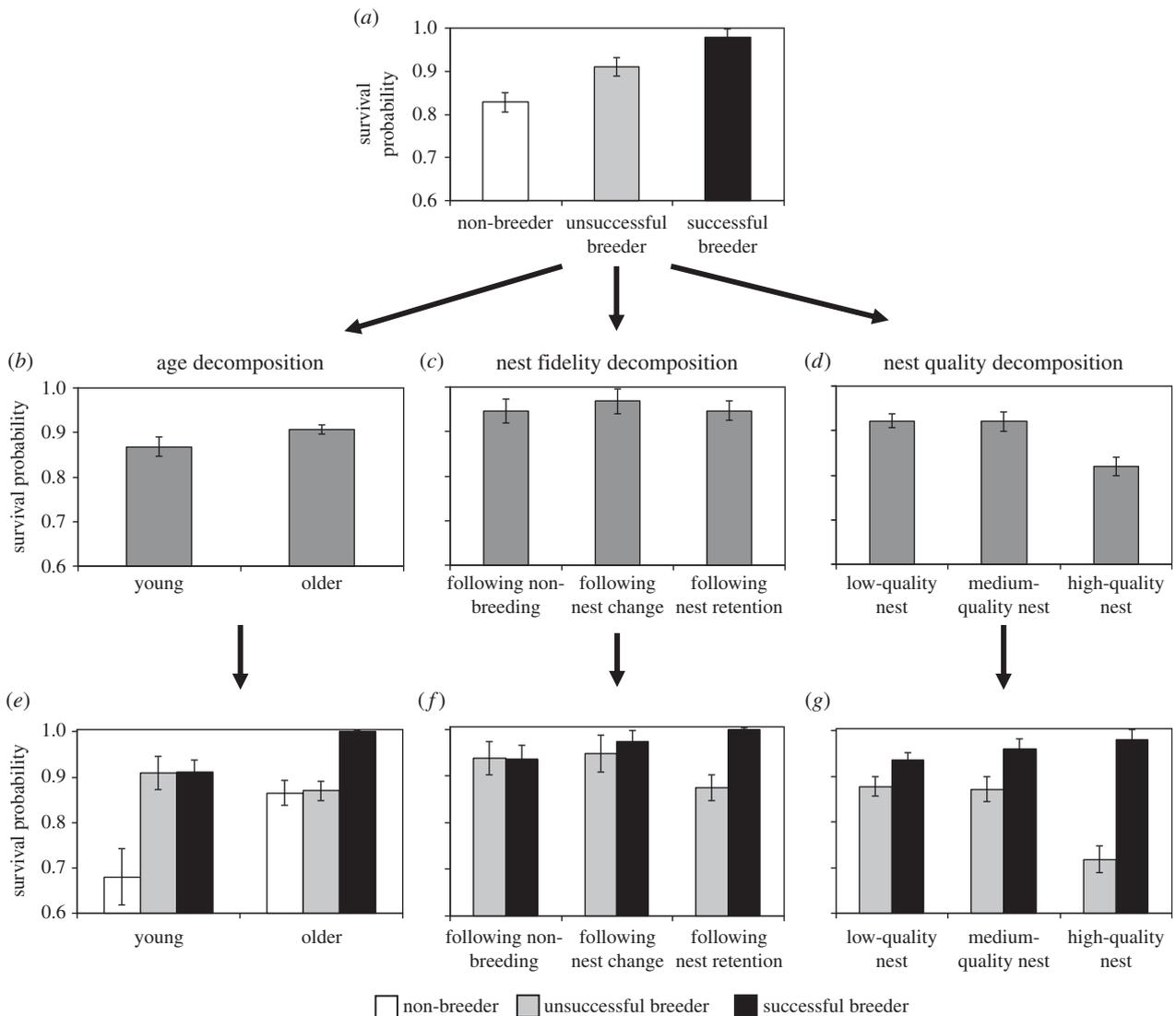


Figure 1. Survival probabilities estimated in the Monteiro's storm petrel population monitored on Praia Islet, Azores (2000–2012). Different survival probabilities were estimated according to the breeding status (a) of the individuals, their age (b), their nest fidelity status (c), the quality of their nest (d) or combinations among these statuses (e–g). Bars are standard errors.

birds less than 4 years old from 4 year-old and older birds, see the electronic supplementary material, appendix S2 for other threshold values). However, when combining information on age class and breeding status, model comparison revealed that, among breeders, there was no survival difference between UB and SB for young (i.e. 2 and 3 year-old adults) birds, whereas the survival probability of SB was higher than that of UB among older breeding adults (model 1 in table 1 and figure 1e).

Similar to the age class model, when pooling breeding statuses, nest fidelity decomposition (figure 1c) suggested no survival differences between individuals that were faithful versus unfaithful to their nest (comparison of models 32 and 35, table 1), but strong survival differences between UB and SB appeared when combining nest fidelity and breeding status (figure 1f). There was no survival difference (between years t and $t + 1$) between UB and SB for individuals that bred in a 'new' nest (i.e. those that changed nest between years $t - 1$ and t , or did not breed in year $t - 1$). By contrast, among the breeders that were faithful to their nest, UB had lower survival (0.87 ± 0.03) than SB (0.99 ± 0.003).

Finally, birds breeding in high-quality nests had slightly lower survival probabilities than birds breeding in low- or medium-quality nests (figure 1d), and that differences in survival between UB and SB become larger for birds breeding in high-quality nests (estimate = 0.71 ± 0.03 for UB and 0.98 ± 0.02 for SB; figure 1g).

In all cases, model comparisons confirmed that the interaction between age class, nest fidelity and nest quality, on the one hand, and breeding outcome, on the other hand, improved the fit of survival models (table 1).

Further analyses using the average breeding success of the population in each year (BS_{mean}) as a temporal covariate indicated that the survival probability of the UB that had retained their nest was strongly negatively related to BS_{mean} (more than 70% of the year-to-year variance in survival was explained by BS_{mean} in faithful UB; figure 2b,c). A qualitatively similar pattern was found for UB breeding in high-quality nests, although the relationship was weaker. By contrast, the survival of NB was (slightly) positively related to BS_{mean} . The survival probabilities of all other categories of individuals were unrelated to BS_{mean} (these results are summarized in table 2 and figure 2, details of

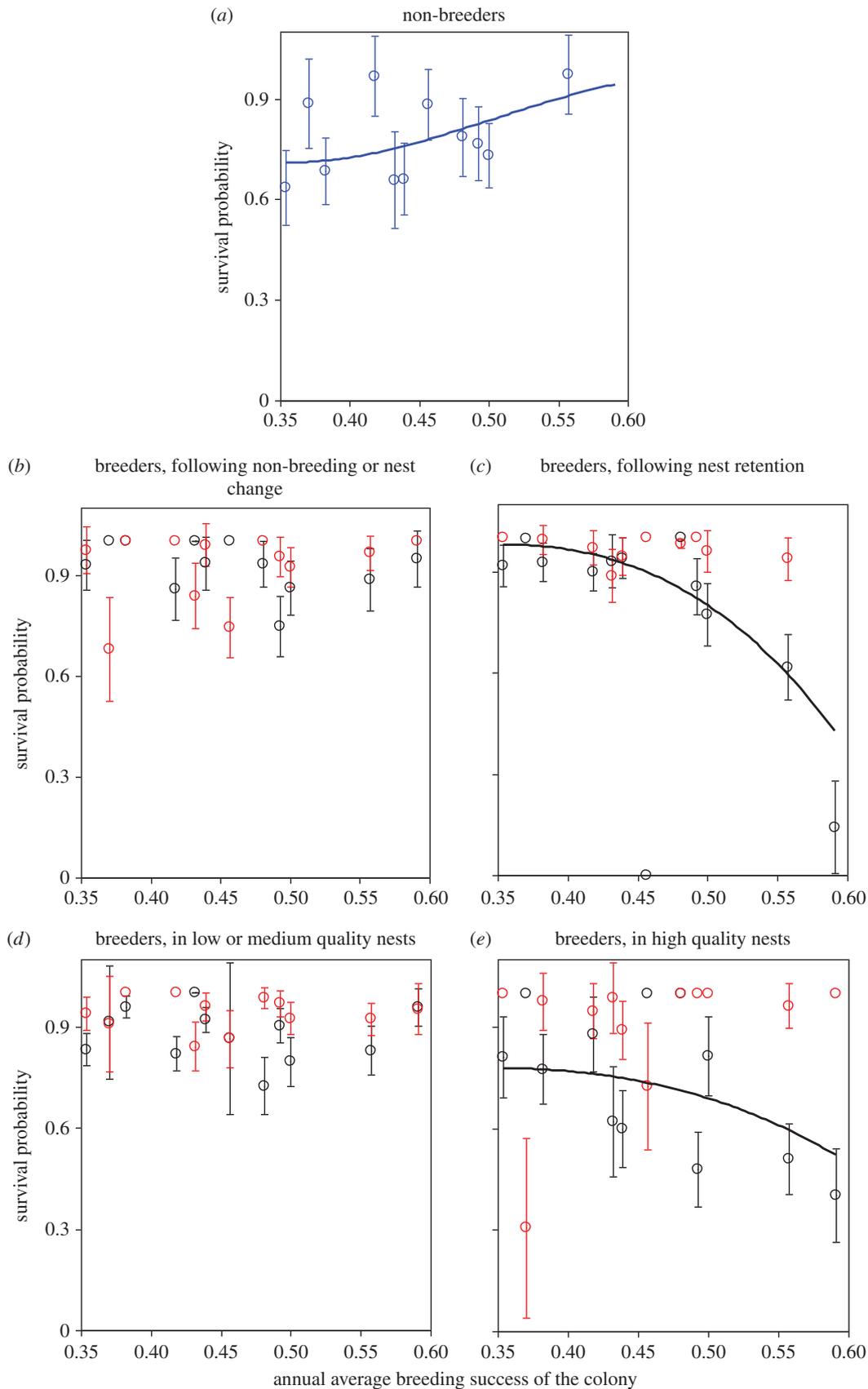


Figure 2. Relationships between survival probabilities and annual average population breeding success (BS_{mean}) estimated for the Monteiro's storm petrel population monitored on Praia Islet, Azores (2000–2012). Different survival probabilities were estimated according to the breeding status of the individuals, their nest fidelity status, the quality of their nest or combinations among these statuses. In panels (b–e), black circles indicate estimates for unsuccessful breeders and red circles indicate estimates for successful breeders. Significant regressions between survival and BS_{mean} are indicated by continuous lines. Bars are standard errors of annual estimates. (Online version in colour.)

time-dependent and covariate models are provided in the electronic supplementary material, appendix S2). All results were qualitatively similar when using an extrinsic

integrative temporal covariate (the North Atlantic Oscillation Index) instead of BS_{mean} (detailed results in the electronic supplementary material, appendix S3).

Table 2. Comparison among models assuming covariation between survival and the mean population breeding success in each year (BS_{mean}) for various categories of individuals. (UB, unsuccessful breeder; NB, non-breeder; faithful, individuals faithful to their nest; high, individuals nesting in high-quality sites. The general structure for transition (ψ), recapture (P) and assignment (A) probabilities is [$\psi_{\text{from,to}}$; $P_{t \rightarrow t}$; A_{from}] (see the electronic supplementary material, appendix S1 for details and notations). Model selection was performed based on the Akaike information criterion corrected for small sample size and overdispersion (QAICc). ΔQAICc is the difference in QAICc between each model and the best model; dev and np are, respectively, the deviance and the number of estimated parameters for each model. The values of R^2 provided correspond to the proportion of temporal variance in survival explained by BS_{mean} , computed through analysis of deviance. Model indices correspond to those presented in the electronic supplementary material, appendix S2. * $p < 0.05$; *** $p < 0.001$.)

index	model	QAICc	np	dev	R^2
best covariate models for non-breeders					
18	S[NB] contrained by BS_{mean}	5546.2	61	7099.7	43.6%*
19	S[NB] contrained by BS_{mean} (quadratic)	5548.0	62	7099.3	45.7%
23	no time variation	5551.6	60	7109.6	n.a.
33	S[NB] different between years	5558.1	71	7087.0	n.a.
best covariate models for nest fidelity models					
16	S[UB _{faithful}] contrained by BS_{mean}	5540.0	61	7091.6	70.8%***
17	S[UB _{faithful}] contrained by BS_{mean} (quadratic)	5540.8	62	7089.8	77.6%***
23	no time variation	5551.6	60	7109.6	n.a.
30	S[UB _{faithful}] different between years	5556.0	71	7084.2	n.a.
best covariate models for nest quality models					
39	S[UB _{high}] contrained by BS_{mean}	5551.6	79	7055.0	20%
40	no time variation	5552.2	78	7058.7	n.a.
43	S[UB _{high}] contrained by BS_{mean} (quadratic)	5553.6	80	7054.7	21.5%
49	S[UB _{high}] different between years	5562.8	89	7040.5	n.a.

4. Discussion

(a) Demographic heterogeneity and S–R covariation

Recent developments in the field of evolutionary demography suggest that inter-individual variations in demographic trajectories (e.g. lifetime reproduction) are shaped by a combination of fixed heterogeneity (individual traits fixed early in life by, e.g. genetic, maternal or cohort effects [21]) and dynamic heterogeneity (related to variations in biotic and abiotic conditions [18,19,34]). Dynamic heterogeneity assumes that individuals have identical traits at birth and that heterogeneity in life-histories comes from the stochastic variation in first-order Markovian transitions among life-history states (i.e. the fact that, e.g. the breeding status of an individual in year t depends on its status in year $t - 1$). While patterns of positive covariation between survival and reproductive performance (S–R covariation) are often interpreted in the context of fixed heterogeneity [3], Orzack *et al.* [22] recently suggested that heterogeneous access to resources in a given breeding season can explain dynamic heterogeneity and labile S–R covariation in the northern fulmar (*Fulmarus glacialis*): poor foraging success in a given year at the individual level results in both poor survival and poor breeding success.

In this study, we did not examine how transitions between life-history states can explain overall differences in lifetime reproductive success, but focused on the S–R covariation. We defined states (based on age, nest quality or proxy of the quality of breeders based on their behaviour), which were determined *a priori* and distinct from the instantaneous breeding success (at year t) and we investigated the relationship between the realized success at year t and subsequent survival in relation

with these individual states as well as with a population level index of breeding success. This protocol allowed us to examine the S–R covariation as a function of intrinsic and environmental conditions more or less favourably associated with breeding success. We predicted similar effects of these conditions on survival and breeding success, engendering S–R covariation at the population level. Instead, we found statistical interactions between reproductive performance and these conditions on survival. Our decomposition of the S–R covariation suggests that the positive association between breeding failure in year t and subsequent mortality (between years t and $t + 1$): (i) occurs mostly in breeders that are faithful to their nest (although survival is globally not affected by nest fidelity, figure 1c,f); (ii) occurs mostly in high-quality nests (figure 1g); and (iii) becomes stronger in years with favourable conditions for reproduction at the population level (see also [24]). We propose below that reproduction failure events related to lack of experience or (fixed or dynamic) limiting resources are only moderately associated with mortality. By contrast, breeding failure related to residual variation (i.e. failure not associated with lack of experience or resources) is strongly associated with mortality. This relationship between survival and reproduction becomes more apparent when resources are plentiful because of sampling bias: when all conditions are favourable for reproduction, mortality does not increase globally, but becomes much more frequent among the few birds that are unsuccessful.

(b) Resource-based versus residual variation

Population genetics theory [35] and evolutionary demography theory [36] predict that different demographic components will exhibit quantitatively different homeostatic responses to

environmental variation, the magnitude of the response being dependent on the effect of a proportional change in the demographic component on the population growth rate. As a consequence, in long-lived vertebrates, changes in environmental conditions are expected to affect annual breeding success more than adult survival [36,37]. In long-lived seabirds, such contrasting demographic responses have been shown to be mediated by adaptive behaviours [38]. For example, Cubaynes *et al.* [39] showed in the red-footed booby (*Sula sula*) that skipping breeding is more likely to occur in El-Niño years, characterized by an increase in local sea surface temperature and fewer resources available for seabirds [40]. Thus, when climatic or oceanic conditions are unfavourable for reproduction at the population level: (i) population-level adult survival is not expected to be affected (here we found only a weak positive correlation between BS_{mean} and the survival probability of non-breeders, figure 2a); and (ii) many breeding failures are caused by food shortages [40,41] and the survival probability of unsuccessful breeders is not expected to be more impacted than the survival of successful breeders by such shortages. Similarly, if breeding failures occur due to the low quality of the nests, breeding failures are not expected to be related to adult mortality (in petrels, for instance, the bulk of adult mortality occurs at sea [42], thus independently of nest quality).

By contrast, when conditions are favourable for reproduction and average breeding success is high, breeding failures are more likely to be related to punctual events not correlated in space or time than to chronic experience or resource-related problems. We refer to this variation as residual, not environmental variation, because it may be caused by either environmental or intrinsic processes. In theoretical studies, temporal environmental variation is generally modelled by considering that, at a given time, all individuals in the population face similar environmental conditions [20], although the response to these conditions can vary between individuals, depending on fixed traits ([43], discussion in [20]). This assumption is of course not a true biological assumption but rather a convenient way to model environmental dynamics. In reality, the individuals of a given population face a variety of conditions (although the effect of environmental variations arising in the micro-environments of individuals can generally not be disentangled from the effects of intrinsic sources of variations). In adult Monteiro's storm petrels, any intrinsic (e.g. catastrophic failure of organ systems) or micro-environmental incident (injury, disease, attack by a predator) leading to delayed mortality should also reduce the ability of birds to successfully fledge their offspring. Furthermore, direct mortality during the breeding season will generally lead to breeding failure given that apart from very few exceptions [44], a single adult cannot raise a chick successfully in Procellariiformes [45]. Thus, those few individuals whose breeding attempts fail despite favourable breeding conditions are (generally) those that died during or after the breeding season.

(c) Age variation

Our results also confirm the importance of the age component in S–R covariation patterns. Survival and reproduction parameters are expected to vary with age, especially in young, inexperienced birds and at old ages [46]. In young ages, an increase in reproductive success with age is expected in relation with improved experience [47] or increased reproductive effort [7], potentially leading to age-related covariation of breeding performance

with survival [8]. Here, we revealed a change in the magnitude of the S–R covariation with age, though using only two age classes (figure 1e). In particular, among breeders (i.e. excluding non-breeders), the positive S–R covariation observed at the population level does not occur in younger adults, which is consistent with the expectation that inexperienced birds will modulate their breeding effort to maximize their survival and future reproduction [48], especially if environmental conditions are unfavourable [39]. Interestingly, Lescroël *et al.* [14] recently uncovered the reverse pattern in the Adélie penguin (*Pygoscelis adeliae*), in which the selective disappearance of poor survivors/breeders leads to a more homogeneous pool of experienced breeders, thus decreasing the S–R covariation with age.

At old ages, classical theories of senescence predict that both survival and reproduction should be affected by senescence [7], although selection for optimal resource allocation may lead to the opposite pattern for reproduction [49]. Here, we were not able to test or control directly for potential senescence effects for statistical reasons. However, we found that high-quality nests (which are by definition associated with a higher probability of successful breeding than other nests) are associated with an increased probability of 'failure and mortality' relative to other nests (figure 1g). Although our data do not allow us to test this hypothesis formally, this pattern could be explained by some reproduction and mortality costs of senescence among the oldest breeders breeding in high-quality nests.

5. Conclusion

Our results in Monteiro's storm petrel reveal that, at the individual level, a positive association between breeding success and survival appears clearly when conditions are favourable. In agreement with evolutionary demography expectations and seabird behavioural ecology, this result suggests that the main causes of breeding failure and mortality are not the same under favourable and unfavourable conditions, which in turn leads to distinct patterns of S–R covariation. We suggest in particular that unpredictable, invisible sources of demographic variation, which are generally treated as noise (e.g. demographic stochasticity) are a major component of the positive S–R covariation observed in many species. We predict that applying similar decomposition of the survival-breeding performance association with some other long-lived species would lead to similar results. Overall, our results confirm the importance and complexity of demographic heterogeneity [18,20] in shaping covariation patterns. Understanding these patterns and underlying processes has profound implications for evolutionary demography [21,34], population dynamics modelling [50] and extinction risk assessment [51].

Ethics. The Regional Environmental Directorate from the Azores (DRA) allowed us to conduct fieldwork.

Data accessibility. Demographic data are available at Dryad: <http://dx.doi.org/10.5061/dryad.7pk05>.

Authors' contributions. M.B. and J.B. collected data, A.R. designed the study, performed modelling work, analysed output data and wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Competing interests. We declare we have no competing interests.

Funding. This study was funded by grants from the Fundação para a Ciência e a Tecnologia (PRAXIS/C/BIA/13194/98, POCTI-BIA-13194/98 and PTDC/BIABDE/67286/2006) and FEDER (Programme COMPETE, ref. no. FCOMP-01-0124-FEDER-007061), and also received support from the Programmes 'MARE' (Life contract B4-3200/98-509),

'OGAMP' (Interreg IIIB-MAC/4.2/A2), 'MARMAC' (Interreg IIIB/FEDER/MARMAC/003-4/2005-6 and Interreg IIIB-05/MAC/4.2/A4), MoniAves (Programme launched by the Regional Environment Directorate from the Azores) coordinated by R. S. Santos and the French ANR (grant no. ANR-12-ADAP-0006). IMAR-DOP-UAç is funded by FCT and DRCT-Azores (Research Unit No. 531 and Associate Laboratory No. 9-ISR-Lisbon).

Acknowledgements. We thank the Regional Environment Directorate from the Azores (DRA) for allowing us to conduct fieldwork, and DRA, M. Melo and R. Oliveira for transportation to the islet. V. C. Neves, R. Medeiros, A. Campos, B. Hothersall, L. Aguiar, M. Laranjo, M. C. Magalhães, M. Villafane, P. A. Crochet, M. P. Dubois, M. Antunes, R. Fontaine, P. Visicchio and M. Andris provided field assistance.

References

1. Stearns SC. 1992 *The evolution of life histories*. New York, NY: Oxford University Press.
2. Bielby J, Mace GM, Bininda-Emonds ORP, Cardillo M, Gittleman JL, Jones KE, Orme CDL, Purvis A. 2007 The fast-slow continuum in mammalian life history: an empirical reevaluation. *Am. Nat.* **169**, 748–757. (doi:10.1086/516847)
3. Cam E, Link WA, Cooch EG, Monnat JY, Danchin E. 2002 Individual covariation in life-history traits: seeing the trees despite the forest. *Am. Nat.* **159**, 96–105. (doi:10.1086/324126)
4. Reid JM, Bignal EM, Bignal S, McCracken DI, Monaghan P. 2003 Environmental variability, life-history covariation and cohort effects in the red-billed chough *Pyrrhocorax pyrrhocorax*. *J. Anim. Ecol.* **72**, 36–46. (doi:10.1046/j.1365-2656.2003.00673.x)
5. Roff DA. 1992 *The evolution of life histories; theory and analysis*. New York, NY: Chapman & Hall.
6. Harshman LG, Zera AJ. 2007 The cost of reproduction: the devil in the details. *Trends Ecol. Evol.* **22**, 80–86. (doi:10.1016/j.tree.2006.10.008)
7. Hamilton WD. 1966 The moulding of senescence by natural selection. *J. Theor. Biol.* **12**, 12–45. (doi:10.1016/0022-5193(66)90184-6)
8. Mauck RA, Huntington CE, Doherty PF. 2012 Experience versus effort: what explains dynamic heterogeneity with respect to age? *Oikos* **121**, 1379–1390. (doi:10.1111/j.1600-0706.2012.20271.x)
9. Beauplet G, Barbraud C, Dabin W, Küssener C, Guinet C. 2006 Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. *Oikos* **112**, 430–441. (doi:10.1111/j.0030-1299.2006.14412.x)
10. McDonald PG, Olsen PD, Cockburn A. 2004 Weather dictates reproductive success and survival in the Australian brown falcon *Falco berigora*. *J. Anim. Ecol.* **73**, 683–692. (doi:10.1111/j.0021-8790.2004.00842.x)
11. Davis SE, Nager RG, Furness RW. 2005 Food availability affects adult survival as well as breeding success of parasitic jaegers. *Ecology* **86**, 1047–1056. (doi:10.1890/04-0989)
12. Montgomerie RD, Weatherhead PJ. 1988 Risks and rewards of nest defence by parent birds. *Q. Rev. Biol.* **63**, 167–187. (doi:10.1086/415838)
13. Wilson AJ, Nussey DH. 2010 What is individual quality? An evolutionary perspective. *Trends Ecol. Evol.* **25**, 207–214. (doi:10.1016/j.tree.2009.10.002)
14. Lescoërl A, Dugger K, Ballard G, Ainley D. 2009 Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. *J. Anim. Ecol.* **78**, 798–806. (doi:10.1111/j.1365-2656.2009.01542.x)
15. Hamel S, Côté SD, Gaillard JM, Festa-Bianchet M. 2009 Individual variation in reproductive costs of reproduction: high-quality females always do better. *J. Anim. Ecol.* **78**, 143–151. (doi:10.1111/j.1365-2656.2008.01459.x)
16. Vleck CM, Haussmann MF, Vleck D. 2007 Avian senescence: underlying mechanisms. *J. Ornith.* **148**, 611–624. (doi:10.1007/s10336-007-0186-5)
17. Aubry LM, Koons DN, Monnat J-Y, Cam E. 2009 Consequences of recruitment decisions and heterogeneity on age-specific breeding success in a long-lived seabird. *Ecology* **90**, 2491–2505. (doi:10.1890/08-1475.1)
18. Tuljapurkar S, Steiner UK, Orzack SH. 2009 Dynamic heterogeneity in life histories. *Ecol. Lett.* **12**, 93–106. (doi:10.1111/j.1461-0248.2008.01262.x)
19. Steiner UK, Tuljapurkar S, Orzack SH. 2010 Dynamic heterogeneity and life history variability in the kittiwake. *J. Anim. Ecol.* **79**, 436–444. (doi:10.1111/j.1365-2656.2009.01653.x)
20. Plard F, Bonenfant C, Delorme D, Gaillard JM. 2012 Modeling reproductive trajectories of roe deer females: fixed or dynamic heterogeneity? *Theor. Popul. Biol.* **82**, 317–328. (doi:10.1016/j.tpb.2012.03.006)
21. Cam E *et al.* 2013 Looking for a needle in a haystack: inference about individual fitness components in a heterogeneous population. *Oikos* **122**, 739–753. (doi:10.1111/j.1600-0706.2012.20532.x)
22. Orzack SH, Steiner UK, Tuljapurkar S, Thompson P. 2011 Static and dynamic expression of life history traits in the northern fulmar *Fulmarus glacialis*. *Oikos* **120**, 369–380. (doi:10.1111/j.1600-0706.2010.17996.x)
23. Albon SD, Clutton-Brock TH, Langvatn R. 1992 Cohort variation in reproduction and survival: implications for population demography. In *The biology of deer* (ed. RD Brown), pp. 15–21. Berlin, Germany: Springer Verlag.
24. Robert A, Paiva VH, Bolton M, Jiguet F, Bried J. 2012 The interaction between reproductive cost and individual quality is mediated by oceanic conditions in a long-lived bird. *Ecology* **93**, 1944–1952. (doi:10.1890/11-1840.1)
25. Robert A, Paiva VH, Bolton M, Jiguet F, Bried J. 2014 Nest fidelity is driven by multi-scale information in a long-lived seabird. *Proc. R. Soc. B* **281**, 20141692. (doi:10.1098/rspb.2014.1692)
26. Bolton M, Smith AL, Gómez-Díaz E, Friesen VL, Medeiros RB, Roscales JL, Furness RW. 2008 Monteiro's storm-petrel *Oceanodroma monteiroi*: a new species from the Azores. *Ibis* **150**, 717–727. (doi:10.1111/j.1474-919X.2008.00854.x)
27. Bried J, Bolton M. 2005 An initial estimate of age at first return and breeding in Madeiran storm petrels *Oceanodroma castro*. *Atlantic Seabirds* **7**, 71–74.
28. Warham J. 1990 *The petrels. Their ecology and breeding systems*. London, UK: Academic Press.
29. Pradel R. 2005 Multievent: an extension of multistate capture–recapture models to uncertain states. *Biometrics* **61**, 442–447. (doi:10.1111/j.1541-0420.2005.00318.x)
30. Bried J, Jouventin P. 2002 Site and mate choice in seabirds: an evolutionary approach. In *Biology of marine birds* (eds EA Schreiber, J Burger), pp. 263–305. Boca Raton, FL: CRC Press.
31. Pradel R, Wintrebert CLM, Gimenez O. 2003 A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture–recapture model. *Biometrics* **59**, 43–53. (doi:10.1111/1541-0420.00006)
32. Choquet R, Lebreton J-D, Gimenez O, Reboulet AM, Pradel R. 2009 U-CARE: utilities for performing goodness of fit tests and manipulating capture–recapture data. *Ecography* **32**, 1071–1074. (doi:10.1111/j.1600-0587.2009.05968.x)
33. Choquet R, Rouan L, Pradel R. 2009 Program E–SURGE: a software application for fitting multievent models. *Environ. Ecol. Stat.* **16**, 847–868. (doi:10.1007/978-0-387-78151-8_39)
34. Steiner UK, Tuljapurkar S. 2012 Neutral theory for life histories and individual variability in fitness components. *Proc. Natl Acad. Sci. USA* **109**, 4684–4689. (doi:10.1073/pnas.1018096109)
35. Wagner GP, Booth G, Bagheri-Chaichain H. 1997 A population genetic theory of canalization. *Evolution* **51**, 329–347. (doi:10.2307/2411105)
36. Gaillard J-M, Yoccoz NG. 2003 Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* **84**, 3294–3306. (doi:10.1890/02-0409)
37. Eberhardt LL. 2002 A paradigm for population analysis of long-lived vertebrates. *Ecology* **83**, 2841–2854. (doi:10.1890/0012-9658(2002)083[2841:APFAO]2.0.CO;2)
38. Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW. 2005 Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* **20**, 187–193. (doi:10.1016/j.tree.2005.01.010)
39. Cubaynes S, Doherty Jr PF, Schreiber EA, Gimenez O. 2011 To breed or not to breed: a seabird's response

- to extreme climatic events. *Biol. Lett.* **7**, 303–306. (doi:10.1098/rsbl.2010.0778)
40. Schreiber EA. 2002 Climate and weather effects on seabirds. In *Biology of marine birds* (eds E Schreiber, A Burger), pp. 179–215. Boca Raton, FL: CRC Press.
41. Inchausti P, Guinet C, Koudil M, Durbec J-P, Barbraud C, Weimerskirch H, Cherel Y, Jouventin P. 2003 Inter-annual variability in the breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the Kerguelen sectors of the Southern ocean. *J. Avian Biol.* **34**, 170–176. (doi:10.1034/j.1600-048X.2003.03031.x)
42. Warham J. 1996 *The behaviour, population biology and physiology of the petrels*. London, UK: Academic Press.
43. McNamara JM, Houston AI. 1996 State-dependent life histories. *Nature* **12**, 215–221. (doi:10.1038/380215a0)
44. Brown CR, Adams NJ. 1984 Female wandering albatross *Diomedea exulans* raising a chick on its own at Marion Island. *Cormorant* **12**, 103–104.
45. Lack D. 1966 *Population studies of birds*. Oxford, UK: Clarendon Press.
46. Chantepie S, Teplitsky C, Pavard S, Sarrazin F, Descaves B, Lecuyer P, Robert A. In press. Age-related variation and temporal patterns in the survival of a long-lived scavenger. *Oikos*. (doi:10.1111/oik.02216)
47. Forslund P, Pärt T. 1995 Age and reproduction in birds: hypotheses and tests. *Trends Ecol. Evol.* **10**, 374–378. (doi:10.1016/S0169-5347(00)89141-7)
48. McCleery RH, Perrins CM, Sheldon BC, Charmantier A. 2008 Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. *Proc. R. Soc. B* **275**, 963–970. (doi:10.1098/rspb.2007.1418)
49. Cichon M. 2001 Diversity of age-specific reproductive rates may result from ageing and optimal resource allocation. *J. Evol. Biol.* **14**, 180–185. (doi:10.1046/j.1420-9101.2001.00243.x)
50. Saether B, Bakke O. 2000 Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**, 642–653. (doi:10.1890/0012-9658(2000)081[0642:ALHVAC]2.0.CO;2)
51. Acker P, Robert A, Bourget R, Colas B. 2014 Heterogeneity of reproductive age increases the viability of semelparous populations. *Funct. Ecol.* **28**, 458–468. (doi:10.1111/1365-2435.12187)