

Variation in the age of first reproduction: different strategies or individual quality?

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Abstract. Although age at first reproduction is a key demographic parameter that is probably under high selective pressure, it is highly variable and the cause of this variability is not well understood. Two non-exclusive hypotheses may explain such variability. It could be the expression of different individual strategies, i.e., different allocation strategies in fitness components, or the consequences of individual difference in intrinsic quality, i.e., some individuals always doing better than others in all fitness components. We tested these hypotheses in the Wandering Albatross investigating relationships between the age at first reproduction and subsequent adult demographic traits. Using finite mixture capture-recapture modeling, we demonstrate that the age at first reproduction is negatively related to both reproductive performances and adult survival, suggesting that individual quality was an important factor explaining variation in the age at first reproduction. Our results suggest that age at first breeding is a good predictor of quality in this long-lived seabird species.

Key words: *capture–mark–recapture; individual heterogeneity; life-history plasticity; reaction norm; trade-off; Wandering Albatross.*

INTRODUCTION

Age at recruitment (i.e., age at first reproduction) is a key demographic trait shaping life-history strategies (Stearns 1976, Gaillard et al. 2005). Variations in this parameter have strong impact for both evolutionary and ecological processes from individual to population level (McGraw and Caswell 1996, Ferrer et al. 2004, Acker et al. 2014). Theoretical works showed that fitness is highly sensitive to changes in age at first reproduction (Stearns 1976) and this result was confirmed by empirical studies (McGraw and Caswell 1996, Oli et al. 2002, Krüger 2005). Intuitively, recruiting as early as possible should be the best strategy. Not only does early recruitment increase the number of lifetime reproductive attempts, it also increases fitness by shortening generation time (McGraw and Caswell 1996). Consequently, early reproduction should be at first glance favored by natural selection (Oli et al. 2002, Martin and Festa-Bianchet 2012). However, because individuals have a limited amount of energy available, life-history theory predicts that the advantages of early breeding could be balanced by associated costs (Stearns 1992). High breeding investment in early life may depress survival probability (Clutton-Brock 1984, Viallefont et al. 1995) and accelerate senescence in old age (Gustafsson and Pert 1990, Nussey et al. 2006, Kim et al. 2011). Such tradeoffs are particularly important in long-lived species because of high residual reproductive value in early life. Indeed, in species with slow life history strategy and thus high

life expectancy, early mortality is very costly since life-time reproductive success varies primarily with breeding longevity (Reid et al. 2003). The high early-life reproductive value in long-lived organisms probably explains why delayed reproduction is generally the rule in these species. Although age at recruitment seems to be under high selective pressure (McGraw and Caswell 1996, Oli et al. 2002, Krüger 2005), long-term studies regularly showed that age at recruitment can be highly variable within wild populations (Reed et al. 2003, Hadley et al. 2006). The variability in the age at first reproduction between populations or between years are usually explained by variations in environmental conditions and food availability, recruitment being often related to body condition (Gaillard et al. 2000, McMahon et al. 2003). However, these environmental effects hardly explain the variations in recruitment age observed between individuals that share the same environment. In such cases, individual variability is expected to arise from intrinsic factors that can be considered independently of environmental effects (Becker and Bradley 2007).

Two non-exclusive intrinsic mechanisms can explain heterogeneity in age at first reproduction. First, allocation strategies among different fitness components may differ between individuals (Roff 1992, Stearns 1992). Individual variations in life-history may emerge when environmental fluctuations are important because the best genotype in one environment is not necessarily the best in another environment (Johnson 2007), or when different strategies provide equivalent solutions to an ecological problem (Shuster and Wade 1991). Some studies suggested that the life-history continuum hypothesis described at the interspecific level may occur at the intraspecific level, with

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some individuals favoring survival compared to others investing more in reproduction (Reid et al. 2010). Empirical studies have reported positive genetic covariance between the age at first reproduction and the later adult performances, providing support for the existence of the fast-slow continuum within populations (Charmantier et al. 2006, Blomquist 2009). In this context, age at first breeding could be linked to individual strategies, early recruitment occurring in individuals investing more in reproduction and late recruitment occurring in individuals favoring survival, resulting in a negative correlation between age at recruitment and survival.

Alternatively, but not exclusively, variations in the age at first reproduction may be explained by individual quality, i.e., “an axis of among-individual heterogeneity that is positively correlated with individual fitness” (Wilson and Nussey 2010). In the wild, the hypothesis of variations in individual quality is supported by observations of individuals having different performance levels that are consistent throughout life (Reid et al. 2003, McCleery et al. 2008, Lee et al. 2013). Positive correlations between life-history traits, e.g., survival and reproduction, are frequently reported although they are not predicted by life-history theory (Cam et al. 2002, Hamel et al. 2009). Such positive correlations between life history traits make sense if individuals vary in their abilities to acquire resources (Van Noordwijk and de Jong 1986). Since recruitment is expected to occur according to a tradeoff between current and future reproduction, variation in individual quality in relation to resource acquisition may strongly affect the recruitment process and age at first reproduction. As a consequence, it is expected that individuals of different quality recruit at different ages (Becker and Bradley 2007). In long-lived species, low quality individuals may recruit at old age, and some may not recruit at all as indicated by the observation of lower survival and recruitment probability for oldest immature age-class (Hadley et al. 2006, Aubry et al. 2009).

In practice, investigating how intrinsic factors affect recruitment is particularly challenging since it requires monitoring known-aged animals individually. Such individual-based data can generally only be obtained by marking individuals at birth. In this case, estimating recruitment into the natal population requires large sample sizes owing to commonly high juvenile mortality and dispersal rate in early life (Clobert et al. 2001). Moreover, obtaining unbiased estimates of age at first reproduction may be challenging due to imperfect age-related detection and uncertainty in the assignment of reproductive status, which are inherent in studies of wild populations. Finally, because the highest variations in recruitment age occur typically in long-lived species delaying their first reproduction, studying the recruitment process necessitates very long-term studies carried out over several decades, which are often complicated to run and difficult to maintain (Clutton-Brock and Sheldon 2010).

In this study, we analyzed a mark–recapture data set of 9,685 known-aged Wandering Albatrosses (*Diomedea*

exulans) born over 48 years to explore the importance of individual quality and individual strategy on the age at first reproduction. To do this, we investigated the relationships between age at first reproduction and breeding success at recruitment, adult breeding probability, adult breeding success, and adult survival. In this long-lived species, recruitment ranges between 6 and 15 yr with a peak around 9–10 yr old (Weimerskirch 1992). According to the *trade-off hypothesis*, we predicted that early recruitment should be associated with high adult breeding performances and low adult survival (Fig. 1). Alternatively, based on the *individual quality hypothesis*, we predicted that early recruitment should be associated with both high breeding performances and high survival (Fig. 1). Finally, we tested the prediction derived from both hypotheses that breeding success at first reproduction should decrease with recruitment age. Note that this last prediction is in contradiction with the common expectation that the breeding success of first time breeder increased with age owing to accumulating competence and experience in early life (Forslund and Pärt 1995).

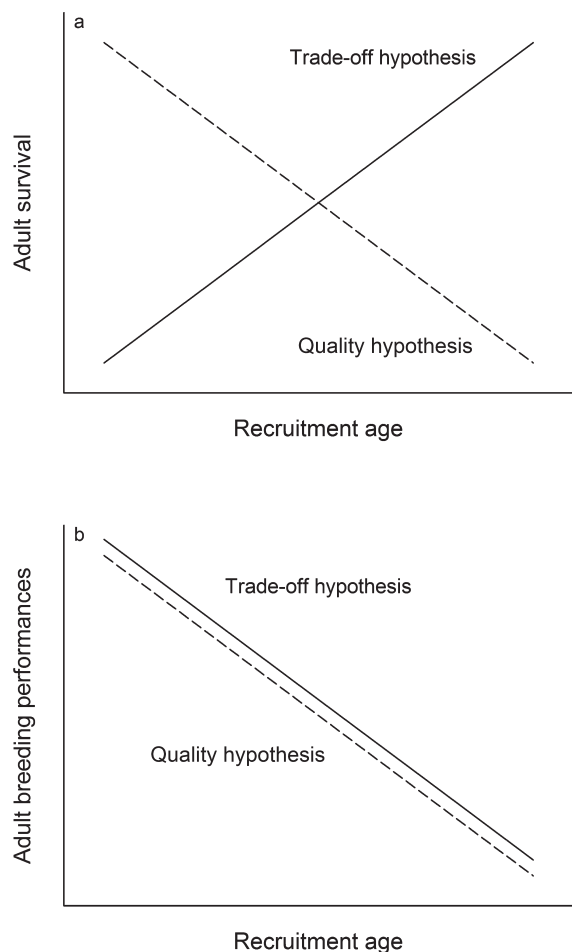


FIG. 1. Variation of (a) adult survival and (b) adult breeding performances as a function of recruitment age predicted by the trade-off hypothesis and by the individual quality hypothesis.

MATERIALS AND METHODS

Study species and field method

We studied the Wandering Albatross population of Possession Island in the Crozet Archipelago (46° S; 52° E), southern Indian Ocean, from 1965 to 2013. Monitoring started in 1960, but all chicks were ringed each year with a stainless steel band just before fledging from 1965. From early to mid-December, pre-breeding adults are checked over the whole island. From mid-January (just after egg laying is resumed) to mid-February at least three visits were made every 10 d to identify the two members of each pair and their breeding status. All new individuals were ringed with a uniquely numbered stainless steel-band. In mid-April June and August, nests were checked and the chick status recorded (alive/dead). During all visits, non-breeding individuals (mainly immatures) were searched for and their identity determined (from ring number) when possible. From mid-September to mid-October, fledglings were ringed. Sex assignments were performed based on both field observations (i.e., sexual size and plumage dimorphism, mating behaviors) and genetic analyses since 1999 (Appendix S1). Wandering Albatrosses show a typical slow life history strategy with high adult survival rates and low productivity (i.e., quasi biennial reproduction and clutch size limited to one egg without replacement laying). Fledglings leave the colony alone, remaining at sea continuously until they return to their colony of birth from 3 yr old at the earliest (Weimerskirch 1992; H. Weimerskirch, unpublished data). Recruitment occurs between 6 and 15 yr old. Females recruit earlier than males but both sexes show increasing recruitment probability until 9–10 yr old followed by a decrease at older age (Fay et al. 2015).

General model

Individual encounter histories were modeled using a multi-event approach (Pradel 2005). The model consisted in seven states (one immature state, five adult states, and the state dead [Fig. 2]), and five events. To consider individuals during the period of immaturity, we defined the Pre-Recruitment state (PrR) after which immature birds can recruit into the breeding population, i.e., lay an egg for the first time into the breeding population. Adult birds can transition into Successful Breeder state (SB), when the chick fledged, Failed Breeder state (FB), when the chick died before fledging, or recruited Non Breeder state (NB), when individuals that have recruited into the population (i.e., bred at least once) were observed as non-breeders at the colony. To model the sabbatical years spent continuously at sea after a year of reproduction, we added two unobservable states (Lebreton and Pradel 2002) corresponding to the two previous breeding states defined: Post Successful Breeder (PSB) and Post Failed Breeder (PFB). Thus, adults that are at sea (i.e., not at colonies for a whole year) are distinguished based on their most recent breeding state, the last time when they were observed at a colony. In our study, state assignment was not always certain since

between 1966 and 1986, state assessment was unknown for a number of breeders; some individuals were classified as breeders but the success or failure was not always ascertained. Multi-event models allowed us to deal with state uncertainty by assessing the likelihood of an individual state given the events (i.e., observations) (Pradel 2005). We considered five events, i.e., five types of observation in the field: 0, not observed; 1, seen as non-breeder; 2, seen as a failed breeder; 3, seen as a successful breeder; 4, seen as a breeder but successful status not ascertained.

Pre-recruitment state and biological constraints

The initial state was constrained to the pre-recruitment state because all birds were banded as chicks. Then, from the first year of life to the fifth, transition probability to the pre-recruitment state was fixed to 1 because no recruitment occurred before 6 yr old. To model the pre-recruitment period, we defined two stages: the *juvenile* stage, which was an unobservable stage, corresponding to the first two years of life spent continuously at sea (i.e., no individual of 1 or 2 yr old were observed at the colony), and the *immature* stage corresponding to non-recruited birds older than 2 yr that started to visit the colony and could be potentially observed. Based on previous results from Fay et al. (2015), the immature stage was decomposed into three age classes: 3–8 yr, 8–13 yr, and >13 yr corresponding to the most parsimonious age structure to model the progressive change of survival rate in early life. Juvenile survival was set to be cohort dependent and both juvenile and immature survivals were assumed to be sex dependent (Fay et al. 2015). Recapture probability of the immature stage was modelled as age dependent to fit the progressive return of individuals at the breeding colony before recruitment. From 6 yr of age, birds may recruit and transition into the mature states SB and FB depending both on sex and age. Recruitment rate was constrained to be constant after age 10 (Fay et al. 2015). For mature birds, following the results of Barbraud and Weimerskirch (2012), survival was assumed sex dependent. Based on Pardo et al. (2014), we distinguished different survival probabilities for breeders and post reproductive breeders on one side and recruited non-breeders on the other side. Transitions were set to be state dependent. Since Wandering Albatrosses are monogamous and both sexes exhibit a quasi-biennial breeding, transitions were constrained to be equal between sexes. Recapture probabilities were assumed state dependent due to lower detection probability for observable non-breeders and failed breeders compared to successful breeders. Details of the models implemented are given in Appendix S2.

Heterogeneity

To model individual heterogeneity in the age at first reproduction and its relation with adult demographic traits, we used finite mixture models (Pledger et al. 2003).

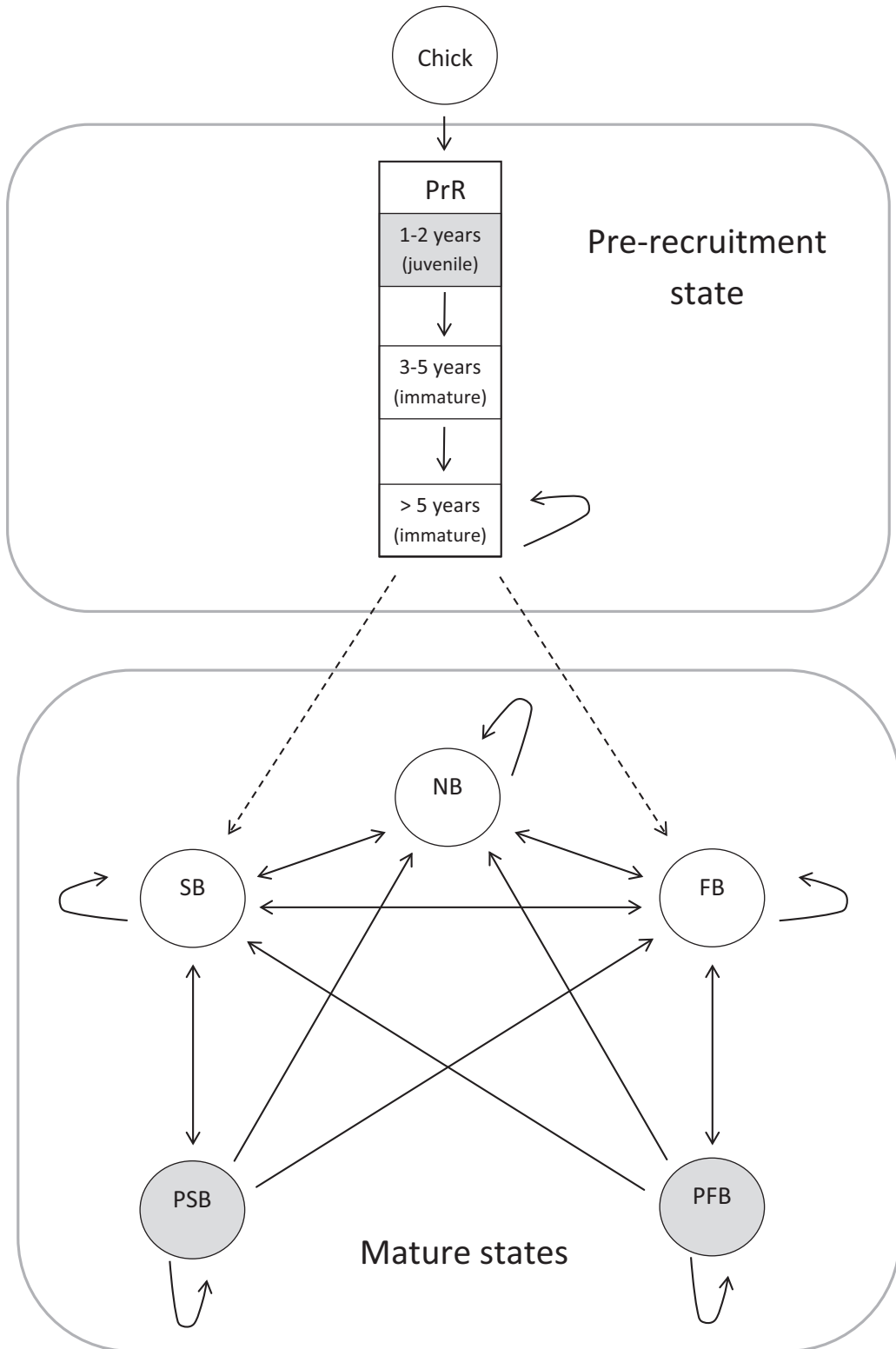


FIG. 2. Life cycle graph representing transitions between observable (white) or unobservable states (gray). All birds are ringed as chicks, thus individuals start in the Pre-Recruitment state (PrR). After fledging, all birds remain at least two years continuously at sea (i.e., juvenile stage). Pre-Recruitment state becomes observable from three years old, when birds start to return to the colony and are now considered as immature. From six years old, birds can pass into the breeding group of the population though recruitment represented by dashed arrows. Then mature birds irrespectively of age can transit between mature states: successful breeder (SB), failed breeder (FB), recruited non breeder (NB), post successful breeder (PSB), and post failed breeder (PFB).

These models allowed us to detect positive or negative correlation between demographic traits and thus to test our predictions. Based on the general model, we considered heterogeneity for adult states for both transition and survival parameters. Each mature state was duplicated (i.e., SB, FB, NB, PSB, PFB) into two groups with specific transition probabilities and adult survival. Individual birds would be split between groups in the likelihood framework based on how they transit between adult states (i.e., breeding frequencies, breeding success) and how they survive. At recruitment, each individual has a probability $\psi_{\text{cst}}^{\text{R} \rightarrow \text{G}1}$ to transition into the group 1 and a probability $\psi_{\text{cst}}^{\text{R} \rightarrow \text{G}2} (= 1 - \psi_{\text{cst}}^{\text{R} \rightarrow \text{G}1})$ to transition into the group 2. These parameters are constant (cst). Once recruited in the breeding population in group G_j ($j = 1, 2$), each individual has transition probabilities $\psi_{\text{state}}^{\text{adG}_j \rightarrow \text{adG}_j}$ and survival probabilities $\phi_{\text{sex, state}}^{\text{adG}_j}$ (Fig. 3). This model has the potential to detect correlations between survival and breeding processes, i.e., breeding probability and breeding success. If individuals differ in their strategies or level of performances, they would be separated in each group according to their pattern of transition between mature states. Thus, $\psi_{\text{cst}}^{\text{R} \rightarrow \text{G}1}$ is the key parameter at the interface between recruitment and adults traits that allowed us to investigate the covariations between age at first reproduction and adult performances. By investigating the age effect on this parameter, we could test if individuals recruiting at different ages adopted different strategies during adulthood or showed differences in quality, i.e., had consistently high or low breeding and survival performances. To summarize, our initial finite mixture model was $\Phi_{a(1 \text{ to } 2), \text{sex}, \text{cohort}, \text{age}(3 \text{ to } 8, >13), \text{sex}, \text{age}(9 \text{ to } 13)}^{\text{pre}}$ for the immature component and $\Phi_{\text{sex, state}}^{\text{adG}1} \Phi_{\text{sex, state}}^{\text{adG}2} \Psi_{\text{state}}^{\text{G}1 \rightarrow \text{G}1} \Psi_{\text{state}}^{\text{G}2 \rightarrow \text{G}2} p_{\text{age}}^{\text{pre}} p_{\text{state}}^{\text{ad}}$ for the adult component, where the pre-recruitment (pre) survival probability (ϕ) was age, sex, and cohort dependent, the

adult (ad) survival probability was sex and state dependent, the probability of transition (Ψ) from pre-recruitment to adult through recruitment (R) was age and sex dependent, the probability of transition into the group 1 (G1) given recruitment was constant, the pre-recruitment capture probability (P) was age dependent, and the adult capture probability was state dependent. In this model notation, symbol “.” indicates interactive effects, “1 to 2” and “3 to 8” indicate that age classes were grouped, and “>13” indicates that age classes were grouped after 13 yrs.

Estimation of adult breeding performances

Since our model had full state-dependent transitions, we did not have direct access to breeding probability and breeding success estimates after recruitment. Both were calculated from the outputs of the multievent modeling. For a given state, breeding probability is the probability to be in success plus the probability to be in failure. The breeding success is the ratio between the probability to be in success and the probability to reproduce (with success or not). The 95% confidence intervals for these derived estimates were obtained with a bootstrap method as described in Appendix S3.

Model selection and goodness-of-fit

All models were run using program E-SURGE (Choquet et al. 2009b). Model selection was done using Akaike information criteria (AIC; Burnham and Anderson 2002). A model averaging approach was used to estimate demographic parameters when models had a $\Delta\text{AIC} < 2$ since they were not considered meaningfully different (Burnham and Anderson 2002). Model selection was done for parameters modelling the breeding success at recruitment ($\psi^{\text{R} \rightarrow \text{BS}}$), and group assignment ($\psi^{\text{R} \rightarrow \text{G}_j}, j = 1, 2$). To investigate the relation between the

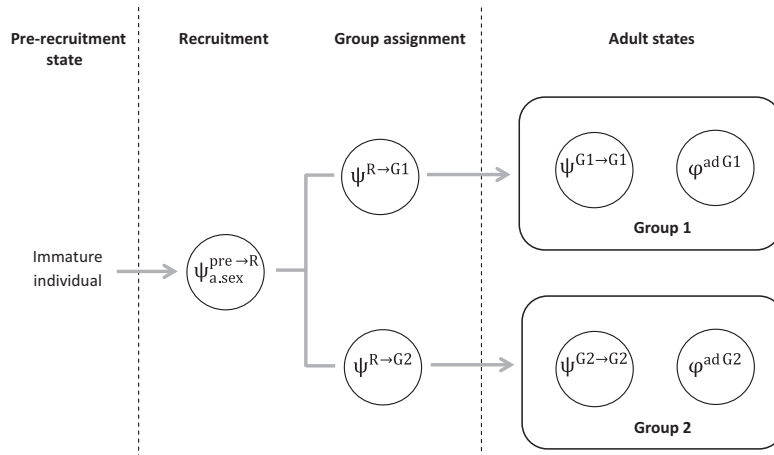


FIG. 3. Graph summarizing the finite mixture model used. Immature individuals recruit differently according to their age and sex ($\psi_{a, \text{sex}}^{\text{pre} \rightarrow \text{R}}$), and may transition into group 1 or 2 ($\psi^{\text{R} \rightarrow \text{G}_j}, j = 1, 2$) based on how they transit between adult states ($\psi^{\text{adG}_j \rightarrow \text{adG}_j}$) and how they survive (ϕ^{adG_j}), where Ψ is the probability of transition and ϕ is the survival probability.

age at first reproduction and both breeding success at recruitment and adult performances, we used a logistic model: $\text{logit}(\psi) = \beta_0 + \beta_1 \times x_i$, where ψ is a demographic parameter, β_0 is an intercept parameter, β_1 is a slope parameter, and x_i is the age of individual i at recruitment. We tested linear, quadratic and log inverse relationships for breeding success at recruitment, and both linear and quadratic effects for group assignment. There is no test available to assess the goodness-of-fit (GOF) of multi-event models. Hence, we performed GOF tests using program U-CARE (v.2.3.2, Choquet et al. 2009a) on a simplified data set that distinguished solely successful breeders from failed breeders and assigned randomly a reproductive status, i.e., failed or successful, to each individual for which no information was available (Pradel 2005). A variance inflation factor (\hat{c}) was taken into account by correcting AIC for extra-binomial variation.

RESULTS

Goodness of fit tests ($\chi^2 = 1003.4$, $df = 749$, $P < 0.001$ for females and $\chi^2 = 1263.8$, $df = 898$, $P < 0.001$ for males) indicated that the general JMV model did not fit the data correctly (see Table S1 for detailed comments). We thus used a variance inflation factor ($\hat{c} = 1.37$) for model selection. Results suggest that the breeding success at recruitment varied with age without significant differences between sexes. Individuals that recruited at 6 yr old appeared to be significantly less successful than those recruiting at older ages (Table S2 SM1 vs SM3: $\Delta\text{AIC} = 3$, Fig. 4). For individuals recruiting at 7 yr old and older, we found, based on multi-model inference accounting for uncertainty in model selection (AIC weight), that the breeding success at recruitment was negatively related to

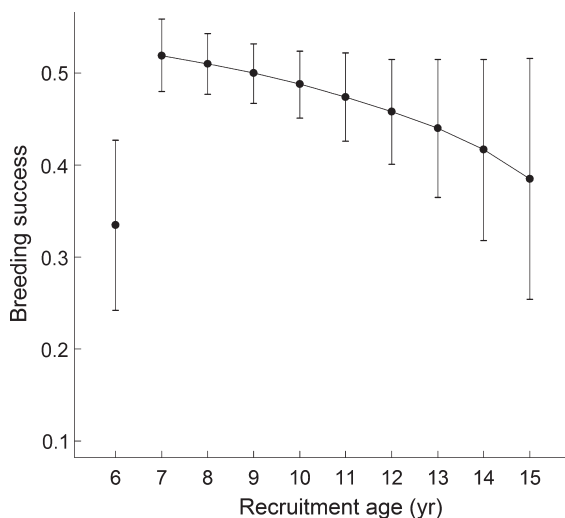


FIG. 4. Breeding success probability at first breeding event in relation to recruitment age for Wandering Albatrosses from Crozet Island from 1965 to 2012. Estimates (mean \pm SE) came from the model averaging over all the models presented in Table 1.

TABLE 1. Testing for individual heterogeneity in Wandering Albatrosses from Crozet Island from 1965 to 2012.

No.	Model	k	QDev	QAIC
M1	$\psi^{R \rightarrow G1}(\text{nul})$	119	79703.91	79941.91
M2	$\psi^{R \rightarrow G1}(\text{cst})$	143	79383.53	79669.53
M3	$\psi^{R \rightarrow G1}(\text{sex})$	144	79381.08	79669.08
M4	$\psi^{R \rightarrow G1}(a_{6-15})$	153	79370.81	79676.81
M5	$\psi^{R \rightarrow G1}(a_{6-15}^{\text{linear}})$	144	79377.36	79665.36
M6	$\psi^{R \rightarrow G1}(a_{6-15}^{\text{quadratic}})$	145	79375.06	79665.06

Notes: M1 (nul) and M2 (cst) test, respectively, for absence or presence of individual heterogeneity. M3 to M6 test for individual heterogeneity as a function of sex and age at first reproduction (a). Results include the number of mathematical parameters (k), the relative deviance corrected by the overdispersion factor (QDev), and Akaike information criterion value corrected by the overdispersion factor (QAIC).

recruitment age. Model averaged estimates indicated that breeding success at recruitment declined from 0.519 ± 0.039 at 7 yr old to 0.385 ± 0.131 at 15 yr old (Fig. 4).

Using finite mixture models, we found strong support for individual heterogeneity (Table 1, M1 vs M2: $\Delta\text{AIC} = 272$). We found a positive covariation between adult survival, breeding probability and breeding success. Individuals from the first group (1, higher quality individuals) had high breeding probabilities whatever their previous state, i.e., post-success, failed or non-breeder, associated with a high survival probability (0.973 ± 0.003). In contrast, individuals from the second group (2, lower quality individuals) had lower breeding frequency with breeding probabilities varying between 0.315 ± 0.026 and 0.944 ± 0.010 depending on the previous state (Fig. 5a), and lower survival probability (0.959 ± 0.003). Furthermore, given reproduction, breeding success was higher for individuals from the first group than for those from the second group (Fig. 5b), except for observed non breeders but this latter state represented less than 7% of all adults. Average breeding success weighted by the proportion of individuals in each state was 0.735 for individuals in the first group and 0.684 for individuals in the second. On average, $36.1\% \pm 0.5\%$ of birds belonged to the first group and $63.9\% \pm 0.5\%$ to the second group with no clear evidence for differences between sexes (Table 1, M2 vs. M3: $\Delta\text{AIC} = 0.45$). Allowing this proportion to vary as a function of age at recruitment improved significantly our model (Table 1, M2 vs. M5 and M6: $\Delta\text{AIC} = 4$), suggesting a negative relationship between the age at first reproduction and adult performances (survival, breeding probability, breeding success). The probability to be in the first group declined rapidly after 8 yr old, both linear and quadratic trends being equivalently supported (Fig. 6). This negative relationship was consistent both between years and cohorts suggesting that this pattern was independent of environmental conditions (Fig. S1).

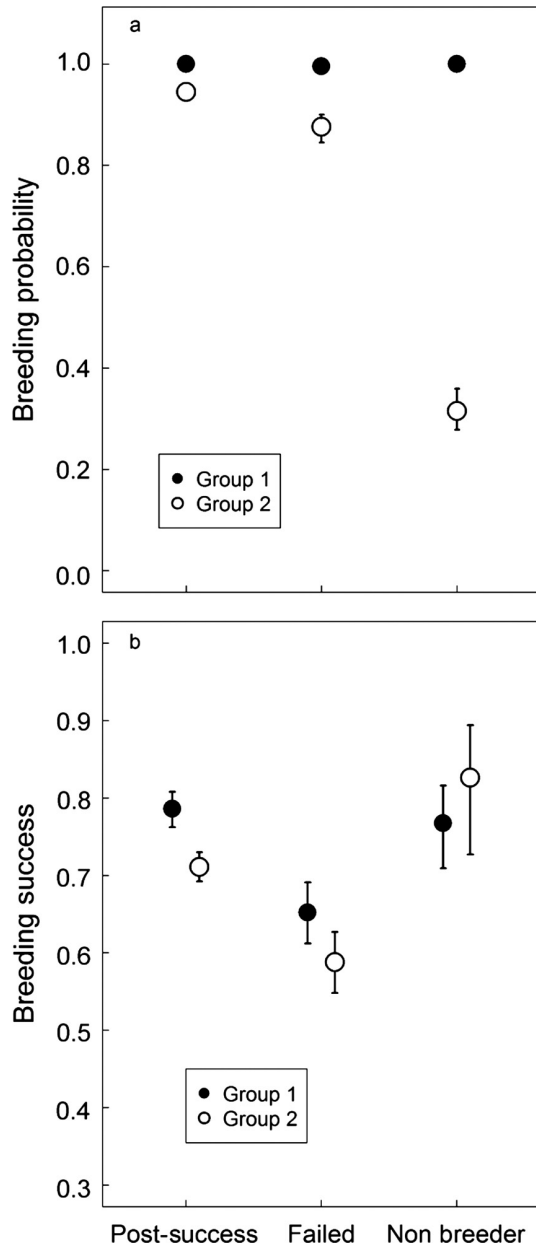


FIG. 5. Heterogeneity in (a) breeding probability and (b) breeding success probability considering the previous breeding state for adult Wandering Albatrosses from Crozet Island from 1965 to 2012. Estimates were calculated from the outputs of M6 (Table 1) and $\pm 95\%$ confidence intervals were obtained with a bootstrap method.

DISCUSSION

Our study suggested that individual quality was an important factor to explain variations in the age at first reproduction. Age at recruitment was negatively related to both reproductive and survival adult performances, as predicted by the *individual quality hypothesis*. The *trade-off hypothesis* was not supported by our analyses, since age at recruitment was negatively related to adult survival performances.

Heterogeneity in adult demographic traits

Our results provide strong support for individual heterogeneity in adult demographic traits with positive covariations between reproductive rate, breeding success and survival. Such positive covariations at the intra-population level are not predicted by life-history theory, although they have been reported in a number of taxa and interpreted as a consequence of variability in individual quality (Cam et al. 2002, Hamel et al. 2009). Theoretically, positive correlations between life-history traits at the individual level could be explained by variations in the ability of individuals to find resources (Van Noordwijk and de Jong 1986). Thus, variations are expected to derived from between-individual phenotypic differences, which are often difficult to define consistently (Moyes et al. 2009).

In our model, individual heterogeneity was modelled through two classes where adults had their proper demographic parameters. Importantly, although our model used two classes, the results should not be interpreted as providing evidence of the existence of two classes (Pledger et al. 2003). Rather, individual quality may be viewed as a continuous variable, similarly to “frailty” (Vaupel et al. 1979), that we partly captured with our model through two classes. The detection of a strong individual heterogeneity within each group supports this interpretation. For example, the breeding success of individuals from the failed-breeder state was still lower than those from the post-success state in both groups. This result suggests that within each group, failed breeders may be individuals of lower quality since they had higher probability to fail again compared to birds being successful in their last breeding attempt.

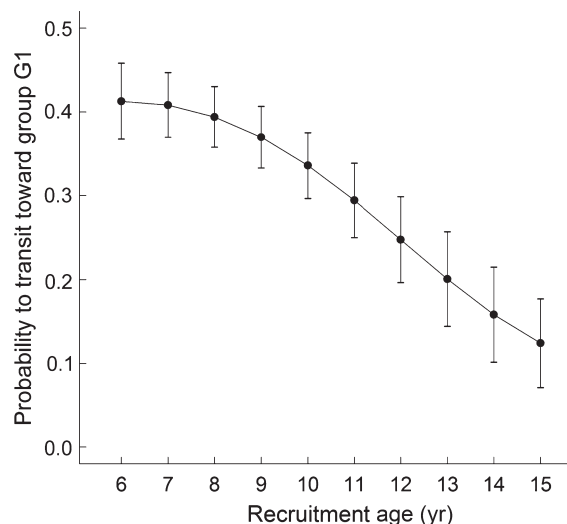


FIG. 6. Heterogeneity in relation to the age at first reproduction: transition probability into group 1 (\pm SE) in relation to recruitment age. Estimates were derived from model averaging of M5 and M6 (Table 1).

Recruitment age and adult performances

In accordance with the hypothesis of individual quality, we found a negative relationship between recruitment age and adult performances. Individuals that recruited early had both higher breeding performances and higher adult survival than those that recruited at advanced ages. Previous studies have suggested that individual recruiting early in life are not a random subgroup of the population and could be individuals of higher quality (Viallefont et al. 1995, Oli et al. 2002, Zhang et al. 2015). Early recruiting females red deer *Cervus elaphus* calved earlier in the season and produced heavier offspring at birth (Nussey et al. 2006), and Common Terns *Sterna hirundo* recruiting at younger ages showed a stronger increase in body mass and a better improvement of breeding performance in early life (Becker et al. 2008). Recruitment age has also been linked to long-term adult performances. It was reported that young recruits produced more offspring over their life span (red squirrel *Tamiasciurus hudsonicus* [Descamps et al. 2006], European badger *Meles meles* [Dugdale et al. 2011], Blue-footed Boobie *Sula nebouxii* [Kim et al. 2011], bighorn sheep *Ovis canadensis* [Martin and Festa-Bianchet 2012]) and that late recruitment was associated with higher adult mortality rate (Green Woodhoopoe *Phoeniculus purpureus* [Hawn et al. 2007], Black-legged Kittiwake *Rissa tridactyla* [Aubry et al. 2011], Lesser Black-backed Gull *Larus fuscus* [Bosman et al. 2013]). In our study, we reported positive correlation between early recruitment and four life history traits. Early first-time breeders had higher breeding success at recruitment, higher reproductive rate and breeding success after recruitment, and higher adult survival probability.

Individual quality is assumed to be related to the ability of individuals to find resources (Van Noordwijk and de Jong 1986). Such variations may affect the body condition of non-recruited individuals, which is a determining factor for the decision to engage or not into the breeding population (Martin and Festa-Bianchet 2012). Indeed, individuals should recruit when their condition allows them to avoid any cost of reproduction. This is particularly important in long-lived species where survival is strongly canalized against temporal variability (Sæther and Bakke 2000). In such context, delayed recruitment is interpreted as a life-history adaptation that maximizes fitness under given constraints (McNamara and Houston 1996). This theoretical hypothesis was largely developed into the reaction norm literature (Stearns and Koella 1986) and is supported by empirical studies. For example, early reproducers were larger for their age in African elephant *Loxodonta africana* (Lee et al. 2013) and bighorn sheep *Ovis canadensis* (Martin and Festa-Bianchet 2012), suggesting that immature individuals delaying recruitment are individuals that have not accumulate enough resources to reach breeding condition. Concordant results have been provided for Wandering Albatross with breeders being heavier than non-recruited birds at the same age, and only individual attaining a certain mass threshold being able to reproduce

(Weimerskirch 1992). Low quality individuals recruiting later in life are thus expected to make “the best of a bad job.”

Although this adaptive interpretation, equivalent to the restraint hypothesis, is robustly based on theoretical and empirical evidence, delayed recruitment of low quality individuals may also be due to constraints (Curio 1983). Beyond adaptive decision, low quality individuals could suffer from poorer access to breeding territories or nest sites due to competition (Camacho et al. 2013) and/or have limited access to mating because of a lack of attractiveness due to condition-dependent expression of secondary sexual character (Andersson 1994).

Breeding success at recruitment

Contrary to the predictions from the *individual quality hypothesis* and from the *trade-off hypothesis*, we found that the breeding success of 6-yr-old first-time breeders was lower than those that recruited later. In long-lived species, breeding success for first time breeders is often expected to increase with age owing to age-related improvements of competence (Forslund and Pärt 1995). As individuals become older, they improve their foraging efficiency, arrive earlier at the breeding grounds, acquire higher quality territories and lay earlier in the breeding season; all having positive effects on breeding success (foraging efficiency [Limmer and Becker 2009], quality territory [Pärt 2001], timing [Verhulst and Nilsson 2009]). In accordance with these expectations, studies focusing on breeding success at recruitment documented increasing breeding success of first-time breeders with age (Goshawks *Accipiter gentilis* [Krüger 2005], Black-legged Kittiwake *Rissa tridactyla* [Aubry et al. 2009]). However, for Wandering Albatrosses, this improvement was only observed between age 6 and 7. For those recruiting after 6 yr of age, as predicted by our tested hypothesis, model selection supported a decreasing breeding success with recruitment age. This pattern concerned most of the recruitments since 98% of birds recruit after 6 yr old (Fay et al. 2015). In such long-lived species with a long immature stage, first-time breeders may have the same foraging skills as experienced breeders, birds starting to breed only when they have attain a mass threshold, and good foraging skills. Also, Wandering Albatrosses are very long lived and have overall a very high breeding success compared to most other species, making them extreme cases. It appears that the more a species delays reproduction, the less breeding success increases with age at first reproduction (Newton et al. 1981, Krüger 2005, Aubry et al. 2009, Blas et al. 2009, this study). However, this age related pattern has rarely been investigated and seems difficult to detect. The negative relationship that we showed between recruitment age and breeding success was not found in a previous study on the same population (Weimerskirch 1992) and was here rather subtle even with large sample sizes. This might be explained by the conservative strategy adopted by young individuals in long-lived species. If each individual recruits when it

reaches a condition at which costs of reproduction can be avoided, between individual differences in breeding success in the first reproductive event could be attenuated. Indeed, lower quality individuals could offset their intrinsic inferiority by delaying their first reproduction for longer, increasing in this way their experience and body condition.

CONCLUSION

Our study suggests that variability in individual quality may be an important factor explaining variations in recruitment age. Intrinsic individual differences associated with a conservative reproductive strategy could explain the high variability of recruitment age in the Wandering Albatross, leading to strong relationships between this trait and adult demographic rates. Finally, although there is increasing evidence of individual demographic heterogeneity in wild populations, very few studies assessed the impact of individual heterogeneity on demographic processes. More studies are needed to better understand the ecological effects of trait variations within species, and the different pattern occurring between species.

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