**Age-related variation in reproductive traits in the wandering albatross: Evidence for terminal improvement following senescence**

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ABSTRACT

The processes driving age-related variation in demographic rates are central to understanding population and evolutionary ecology. An increasing number of studies in wild vertebrates find evidence for improvements in reproductive performance traits in early adulthood, followed by senescent declines in later life. However, life history theory predicts that reproductive investment should increase with age as future survival prospects diminish, and that raised reproductive investment may have associated survival costs. These non-mutually exclusive processes both predict an increase in breeding performance at the terminal breeding attempt. Here we use a 30-year study of wandering albatrosses (*Diomedea exulans*) to disentangle the processes underpinning age-related variation in reproduction. Whilst highlighting the importance of breeding experience, we reveal senescent declines in performance are followed by a striking increase in breeding success and a key parental investment trait at the final breeding attempt.

INTRODUCTION

Variation in breeding success forms the basis for natural selection, and therefore understanding the processes driving this variation in natural populations is fundamental to our understanding of ecological and evolutionary dynamics (Clutton-Brock 1988; Gaillard *et al*. 2000). Age-related variation in breeding success is widely documented in long-lived birds and mammals, and the pattern of increasing reproductive performance in early adulthood followed by a plateau and decline in later life is a ubiquitous feature of their demography, central to our understanding of their population dynamics (Gaillard *et al*. 2000; Caswell 2000). Reproductive traits may improve with age if experience enhances competency (Forslund & Pärt 1995). Long-lived species may take several years to acquire the skills necessary to forage efficiently or defend a territory, which may have consequences for reproductive success (Daunt *et al*. 2007). Experience of breeding may also improve competency, particularly in monogamous species in which mate familiarity is important for successful reproduction (Black 1996). In later adulthood, demographic declines with age are typically attributed to senescence, the process of progressive deterioration in physiological function. There is now abundant evidence that both survival probability and reproductive traits decline with age in a wide variety of wild birds and mammals (Nussey *et al.* 2013).

In addition to the constraints associated with developmental processes, lack of experience, and senescence, age-related variation in demographic rates will also be driven by changes in reproductive investment (Forslund & Pärt 1995). Trade-offs between core fitness functions such as reproduction and survival are a cornerstone of life history theory (Stearns 1992). If an increase in reproductive investment contributes to a reduction in subsequent survival probability, we might expect that measures of reproductive investment will be higher on the terminal breeding attempt. Furthermore, classical life history theory predicts that individuals should increase their reproductive effort with age as their future reproductive prospects diminish (Williams 1966). When survival prospects are low, and residual reproductive value approaches zero, individuals are predicted to invest all available resources in their terminal breeding attempt (Clutton-Brock 1984). Given these core predictions of life history theory, we might expect to observe terminal increases in traits associated with reproductive investment in natural populations of long-lived vertebrates. Whilst a few studies have documented age-related increases in measures of reproductive effort through adulthood (e.g. Pärt *et al.* 1992; Descamps *et al.* 2007), evidence for terminal increases in breeding performance or investment remains extremely rare.

In any study of age-related demographic variation, it is important to consider that in addition to the within-individual changes associated with experience, senescence, or terminal effects, variation in the phenotypic composition of successive age classes can also contribute to age-related variation at the population level (Vaupel *et al.* 1979). For example, if individuals with lower than average breeding success also tend to die young, they will be underrepresented in older age classes (van de Pol & Verhulst 2006). This relationship between average breeding success and reproductive lifespan can provide information about the selective effects acting on the population, but it can also mask within-individual changes in reproductive traits (Reid *et al.* 2010). Longitudinal data, following marked individuals throughout their lives, is required to separate these within- and between-individual effects and reveal the processes underlying population-level patterns (Nussey *et al.* 2008). Combining longitudinal data with appropriate analytical methods has made it possible to separate these effects in long-term study populations in the wild (Cam *et al.* 2002; van de Pol & Verhulst 2006; Rebke *et al.* 2010), and permits testing for both gradual within-individual changes with age and more abrupt, terminal shifts (Bouwhuis *et al.* 2009; Nussey *et al.* 2011). Recent studies of wild vertebrates adopting this approach have documented gradual within-individual declines in reproductive traits with age, consistent with senescence, but found either no evidence for terminal changes, or evidence for terminal declines in breeding performance (Coulson & Fairweather 2001; Rattiste 2004; Reed *et al.* 2008; Bouwhuis *et al.* 2009; Dugdale *et al.* 2011; Nussey *et al.* 2011).

Here, we reveal the different processes contributing to age-related variation in reproduction using data from a 30-year longitudinal study of an extremely long-lived seabird, the wandering albatross *Diomedea exulans*. We use a mixed-effects model approach to describe the population-level patterns of age-related variation in different reproductive traits (laying date, egg volume, chick weight shortly before fledging, fledging period and breeding success). We go on to decompose the processes driving the patterns in these reproductive traits to quantify the contributions of selection, experience, senescence, and terminal effects. We provide the first evidence, to our knowledge, for a terminal increase in reproductive performance following a gradual age-related decline in a wild vertebrate population.

MATERIALS AND METHODS

Study system and data collection

The wandering albatross *Diomedea exulans* is among the longest-lived vertebrates, potentially reaching an age of over 50 years. Annual survival rates are high, and they are naturally subject to few sources of environmentally-driven mortality (Croxall *et al.* 1990). Demonstrating natal philopatry and very high breeding site fidelity, they are highly monogamous throughout their long reproductive careers; mates usually pair for life and the divorce rate is very low (Jouventin *et al.* 1999). They have an extremely low reproductive rate; a single egg is laid each breeding attempt (mean laying date 22nd December), and both parents incubate the egg and provision the chick for around 80 and 270 days respectively. Since the entire breeding cycle takes >1 year, breeding is typically biennial if successful (Tickell 2000).

The data used in this analysis were collected as part of a long-term study of the wandering albatross at Bird Island, South Georgia (54°00’S, 38°03’W). Data were collected between the 1979/80 and 2009/10 breeding seasons, hereafter referred to as years 1980 to 2010. All birds at the study colony are individually identified by numbered metal leg rings. Nests are visited daily during the pre-laying, hatching and fledging periods, and weekly during incubation and chick rearing. This enables accurate determination of breeding success for each nest; a binary trait defined as nestling survival from a laid egg to fledging. Various other traits underpinning breeding success are also recorded: laying date (days since 1st December) and egg volume (cm3, calculated as 0.00052 x length (mm) x breadth (mm)2 (Hoyt 1979)) are recorded for virtually all nests within a day of laying; chick pre-fledging weight (kg, 260 days after hatching) and fledging period (number of days between hatch and fledge dates) are recorded for surviving chicks.

Chicks have been ringed annually since 1972, and thus much of the population is of known age. Chicks and adult breeders were also ringed in 1959 and 1961-64. Neither year of hatching nor exact year of ringing is known for birds ringed as breeders during these years. Therefore they were assigned a highly conservative minimum age, based on the minimum breeding age (7 years) at the latest possible year of ringing (1964). Ringing year and therefore age is known for all chicks ringed in the late 1950s and early 1960s, but the breeding histories of the early cohorts are incomplete since it is likely they began breeding before regular monitoring began in 1980.

Data analysis

The relationship between age and various reproductive traits was modelled using generalised linear mixed effects models (GLMMs). Breeding success was modelled using a binomial error distribution and logit link. A Gaussian error distribution was used to model laying date, egg volume, chick pre-fledging weight, and fledging period (Zuur *et al.* 2009). All models included individual as a random effect to account for the non-independence of observations, and year as a fixed factor to account for annual variation in environmental conditions. Models with different fixed effects structures were compared using maximum likelihood (ML) estimation, but the models presented were estimated using restricted maximum likelihood (REML) (Zuur *et al.* 2009). All analyses were performed using the *lme4* statistical package in the program R (version 2.14.0).

*Age-related variation in reproductive traits*

Age-related variation in breeding success and other reproductive traits was first examined at the population level. Data were available for both males and females; there were 2270 observations of breeding success from 490 known age females, and 2267 from 493 known age males (see Table S1 for full details of sample sizes). Sexes were initially analysed separately because pairs typically remain together for most of their lives and ages within a pair are highly correlated (r=0.81). Where the number of observations per age-class was less than 10 (females <7 and >39 years; males <8 and >39 years), age classes were collapsed to avoid extreme values biasing results.

Model selection was performed using Akaike Information Criterion (AIC) where the best model is taken to be that with the lowest AIC value (Burnham & Anderson 2002). When model selection resulted in multiple models with an AIC difference of less than two units (∆AIC<2) compared to the model with the lowest AIC, a model averaging approach was used since models where ∆AIC<2 are not considered to be meaningfully different (Burnham & Anderson 2002). These models comprised the top model set (Grueber *et al.* 2011), and predictions from these models were weighted by AIC weights (ω) and summed to give predictions of the average model using the R package *MuMIn* (Barton 2011). The model-averaged estimates were then compared visually with estimates from the best model to see if they differed. r2 measures based on likelihood ratio statistics were used to examine goodness of fit (following Magee 1990).

The shape of the age function was determined by comparing a variety of candidate models. Null models included year and individual, but no age term. Linear and polynomial age functions up to 3rd order were compared with threshold models with a range of break points (following Berman *et al.* 2009). These piecewise regression models had a single threshold (between 10 and 37 years) or a double threshold (first threshold 10-25 years; second threshold 16-37 years), between which the slopes were allowed to vary independently. A factor for bill size (from bill length x bill depth, mm at day 260) was included in the models for chick pre-fledging weight to account for the effect of body size, resulting in a proxy for chick condition. Where the best model included a threshold term for age, confidence intervals were placed around the threshold value at the 95% limit (following Ulm & Cox 1989).

*Factors underpinning variation in breeding success during early and late adulthood*

The population-level analysis of breeding success indicated that following an initial increase, breeding success peaked in the mid-teens before a decline or plateau, irrespective of sex or subset of data analysed (see Results). To examine the processes underlying this population-level pattern, the data were split into two phases: early adulthood (<19 years of age) and late adulthood (≥19 years). This cut-off was chosen as it was close to the peak in breeding performance indicated by our population-level models, and the age at which virtually all females had started breeding (99.25% of known age females in this dataset). This made the most of the available data, and allowed us to examine the most biologically relevant processes during the different stages of adulthood.

The within-group centering approach (van de Pol & Verhulst 2006) was used to partition the within-individual and between-individual effects, allowing us to examine the processes underlying the observed population-level changes in breeding success. Two separate GLMMs were fitted, modelling breeding success in early and late adulthood respectively. Age at first or last reproduction (AFR and ALR respectively) were included as fixed covariates in the models in addition to the age term. The parameter estimates for these terms represent the relative contributions of selective appearance and disappearance of phenotypically different individuals into the population. The age term was expressed as years since first bred (YSF) and years before death (YBD) with age at first and last reproduction respectively, and the parameter estimates reflect the contribution of within-individual changes in breeding success to the population average.

In early adulthood it was important to account for the effects of selective appearance into the breeding population, and so the analysis included data from individuals for which we were confident that the age at first measurement reflected the age at first reproduction. Since comprehensive monitoring began in 1980, this was the case for all birds ringed as chicks since 1972. Since virtually all females had started breeding by 19, any effects of selective appearance could be ignored in the late adulthood models. In the late adulthood analysis, data for individuals for which we were confident that age at last measurement reflected age at last reproduction were analysed, allowing us to account for the effects of selective disappearance. This included individuals that have not been observed since 2005; these were assumed to be dead since established breeders show extremely high site fidelity and very few take more than 5 years off between breeding attempts (0.74% of observations in this dataset).

A two-level factor for first breeding attempt (BA) was included in the early adulthood model to examine how much of the within-individual increase could be attributed to low breeding success of first time breeders (first BA=1; subsequent BA=0). Similarly a two-level factor for final breeding attempt was included in the late adulthood models to test for terminal effects (Bouwhuis *et al.* 2009), comparing the breeding success of individuals on their final breeding attempt with previous attempts (last BA=1; previous BA=0). Around 25% of individuals in the dataset changed partner during their lifetimes, comprising ~7% of observed breeding attempts. A two-level factor for partner change was included in the late adulthood models to test whether losing a partner and having to re-pair reduced breeding success (first BA following a partner change=1; other BA=0). Finally, to account for potential effects of the variable time gap between breeding events, and its dependence on the outcome of the previous breeding attempt, we included a covariate for the number of years since the last breeding attempt (YSL), a two-level factor for the success of the previous breeding attempt (previous BA successful=1; unsuccessful=0), and the interaction between these terms, in our late adulthood models. It was not possible to assign these variables for first time breeders, and so these additional terms were not included in our early adulthood models.

To examine whether the age-related variation in breeding success was associated with variation in egg volume or relative laying date (laying date minus mean laying date for that year), they were added to the above early and late adulthood models. The other two reproductive traits, chick pre-fledging weight and fledging period, were only measured in successful breeders, and so we ran GLMMs identical to the breeding success models described above to test for similar age-related variation during early and late adulthood. A factor for bill size was included in the model for chick pre-fledging weight to account for the effect of bill size.

RESULTS

Population-level ageing patterns

Female wandering albatrosses showed an increase in breeding success until around 14 years and a more gradual decline thereafter (Fig.1a). Model selection resulted in 27 equivalent models that described the relationship between female age and breeding success, all of which included a threshold at 14 or 15 years (Table S2a). An age function with a single threshold at 14 years had the lowest AIC value (Fig.1a). Model averaging across all models within 2 AIC of the best model resulted in an almost identical age function (Fig.S1a). Likelihood profiles indicated that the 95% confidence interval (CI) for the threshold lies between 13.4 and 15.9 years (Fig.S2a). The best model estimated an increase in breeding success from 43% at 7 years to a peak of 76% at 14 years (β=0.204 ±0.030 SE, z=6.72, p<0.001), followed by a more gradual decline to 53% at 39 years (β=-0.041 ±0.009, z=4.36, p<0.001; model r2=0.10).

Female age explained variation in breeding success much better than male age, based on AIC model comparison. A similar model selection and averaging procedure indicated that a quadratic age function best described the relationship between male age and breeding success (Table S2b; Fig.S3). However, a model with the best female age function had more explanatory power than either a model with the best male age function or a model with both best fitting male and female age functions (∆AIC=+19.216 and +3.256 respectively). When the age functions for both sexes were included in a single model the female terms remained statistically significant (before threshold: β=0.206 ±0.047, z=4.393, p<0.001; after threshold: β=-0.043 ±0.018, z=2.391, p=0.017), and the male terms were statistically non-significant (age: β=0.016 ±0.058, z=0.272, p=0.786; age2: β<-0.001 ±0.001, z=0.313, p=0.754). When models were re-run on a restricted dataset that excluded birds with estimated ages or incomplete breeding histories, model selection returned very similar results (Table S3; Fig.S4).

The other reproductive traits showed variable patterns with female age (Figs.1b-e; Table S2c-f). The best models estimated that laying date advanced and egg volume increased rapidly until 10 and 11 years, respectively (laying date: β=-0.590 ±0.194; egg volume: β=10.249 ±0.695). Both traits then continued to increase more gradually until 27 and 20 years (β=-0.089 ±0.024; β=2.220 ±0.208), after which laying date remained relatively constant (β=0.057 ±0.056) and egg volume declined slightly (β=-0.440 ±0.183) (Figs.1b&1c; Tables S2c&S2d; r2=0.39 & 0.54 respectively). Chick pre-fledging weight (corrected for bill size) declined linearly from 7 years onward (β=-0.014 ±0.005), whereas fledging period decreased until 17 years (β=-0.819 ±0.133), after which it remained fairly constant (β=-0.038 ±0.079) (Figs.1d&1e; Tables S2e&S2f; r2=0.38 & 0.20 respectively). Model averaging across equivalent models resulted in almost identical age functions for all reproductive traits (Figs.S1b-e).

Factors underpinning variation in breeding success

Increases in breeding success in early adulthood appeared to be primarily driven by within-individual improvement, particularly after the first breeding attempt (Table 1). Breeding success was lower on a female’s first breeding attempt, and the effect of years since first bred was positive, indicating that within-individual breeding success continues to increase after the second breeding attempt (Table 1). The effect of age at first reproduction was positive, but did not add to the explanatory power of the model (Table 1). This suggests that within-individual change, rather than selective appearance, is the major driver of the population-level increase in breeding success observed in early adulthood.

Egg volume, but not relative laying date, added to the explanatory power of the early adulthood breeding success model (ΔAIC=+8.272 and -1.849 respectively, when excluded from the model). There was a positive relationship between egg volume and breeding success (β=0.007 ±0.002), and accounting for this effect reduced the estimates for years since first bred (β=0.069 ±0.036), first breeding attempt (β=-0.461 ±0.197) and age at first breeding (β=0.057 ±0.051, compare estimates to Table 1). This suggests that increasing egg volume through early adulthood contributes to the observed increase in breeding success. Early adulthood models of chick pre-fledging weight (corrected for bill size) suggested the fitted terms had little explanatory power (Table 1), although the estimated effects suggest a decline in weights from first to subsequent breeding attempts (Table 1) which is consistent with the population level pattern (Fig.1d). Models of chick fledging period showed an important effect of years since first bred (Table 1), with fledging periods also decreasing through early adulthood as predicted at the population level (Fig.1e).

Age-related variation in breeding success in late adulthood at the population level appeared to be principally driven by within-individual declines with age, alongside declines following a partner change (Table 2, Figs.2a&2b). There was also evidence for an important increase in breeding success at the final breeding attempt (Table 2, Fig.2a). The effect of age at last reproduction was negative but it did not add to the explanatory power of the late adulthood model, suggesting that selective disappearance may be of lesser importance in the observed population-level declines with age (Table 2). Years before death, last breeding attempt and partner change all contributed substantially to explaining variation in breeding success in late adulthood (all ΔAIC>3, Table 2). On average, individuals showed a gradual decline in breeding success with age in late adulthood, followed by an increase on their final breeding attempt (Fig.2a). They also showed reduced breeding success following a partner change (Fig.2b). These effects were independent of effects of the gap since an individual’s last breeding attempt and the outcome of that previous attempt, as these terms were included in our model (Table 2). We went on test whether the observed terminal increase in breeding success was itself age dependent, by adding the interaction between last breeding attempt and age at last breeding to the model. Although the interaction predicts a small increment in the size of the terminal increase as animals age, inclusion of the interaction did not provide meaningful additional explanatory power to the model (ΔAIC=+0.962 when interaction excluded from model).

Egg volume and relative laying date did not appear to be important predictors of breeding success in late adulthood (ΔAIC =-1.887 and +1.623, respectively) and their inclusion did not meaningfully influence other parameter estimates in our model. As for early adulthood models, there was little evidence that any variables other than bill size had meaningful explanatory power in the late adulthood models of chick pre-fledging weight (Table 2). However, there was evidence for important effects of years before death and last breeding attempt in the late adulthood model of chick fledging period (both ΔAIC>4, Table 2). Fledging period declined gradually with age but then increased on the terminal breeding attempt (Fig.2c), as observed for breeding success (Fig.2a).

DISCUSSION

In our study population of wandering albatrosses, breeding success showed the classic population-level pattern of increase through early adulthood followed by decline in late life (Fig.1a). Statistical dissection of the within- and between-individual processes underpinning this pattern revealed independent contributions of breeding experience, senescence, and terminal effects. There was little evidence that selective appearance or disappearance contributed to the population-level ageing pattern. Breeding experience was key during early adulthood, with individuals showing reduced success on their first breeding attempt, independent of age. Changes in breeding success in late adulthood were more complex, reflecting within-individual senescent declines, the negative effects of partner loss, and increased breeding success on the final breeding attempt. A senescent decline was also apparent among successful breeders, with fledging period declining as individuals approached death, and similarly increasing on the terminal event. Such a terminal increase in reproductive performance is consistent with predictions of life history theory, but has not to our knowledge been previously documented in a long-lived, wild vertebrate.

There was strong support for age-related variation in breeding success at both the population and individual levels (Fig.1a&2). Breeding success, egg volume and fledging period all improved through early adulthood (Fig.1a,1c&1e), highlighting the importance of development and experience. Age at first reproduction did not explain any additional variation in breeding success, indicating that pre-breeding experience is insufficient, and experience of breeding itself is key in a species with such complex parental care. First time breeders fledged a smaller proportion of chicks (Table 1), which may be related to their inability to accurately assess the delicate trade-off that arises during incubation, when individuals must remain foraging at sea long enough to regain body condition, but return to land before their mate is forced to desert the egg (Weimerskirch 1995; Pardo *et al.* 2012). Mate familiarity is likely to be important for accurately assessing the partner’s state at departure and likely fasting capability (Black 1996), which is also highlighted by the continued improvement in performance observed after the second breeding attempt (Table 1). In contrast with some studies (e.g. Naves *et al.* 2007), this effect was also evident in late adulthood, as females showed reduced breeding success on their first attempt with a new partner (Fig.2b).

Female wandering albatrosses showed a decline in breeding success with age in late adulthood, followed by a striking increase in breeding success on the terminal breeding event before disappearance from the colony (Fig.2a). This pattern was mirrored among successful breeders, with decreases in the duration of the fledging period with age followed by an increase at the end of life. These results add to a growing body of literature documenting reproductive senescence in long-lived seabirds (Reed *et al.* 2008; Berman *et al.* 2009; Lecomte *et al.* 2010; Rebke *et al.* 2010; Pardo *et al.* 2012). A recent cross-sectional study of a different wandering albatross population found no evidence for age-related declines in baseline physiology, but did find that older individuals showed different at-sea distributions, lower sea surface activity levels, and elevated corticosterone (Lecomte *et al.* 2010). This may indicate that foraging ability or efficiency is compromised in older individuals, as has also been suggested by data from other albatross species (Catry *et al.* 2006). Physiological deterioration negatively influencing foraging behaviour is likely to have a considerable impact on the resources these birds have available to allocate between reproduction and survival. However, longitudinal investigation must build on this cross-sectional work if we are to develop a full understanding of the behavioural and physiological mechanisms underpinning age-related declines in reproductive performance in long-lived seabirds.

The increase in breeding success and chick fledging period observed at the terminal breeding attempt (Fig.2a) is, to our knowledge, unique in the literature on reproductive ageing in wild vertebrates. Although some studies have found results consistent with terminal allocation (Weladji *et al.* 2010), most studies have failed to test for such terminal effects. The handful of recent studies that have done so in wild populations have either found evidence for a terminal decline (Coulson & Fairweather 2001; Rattiste 2004; Reed *et al.* 2008; Nussey *et al.* 2011), or no effect at all (Bouwhuis *et al.* 2009; Dugdale *et al.* 2011). What remains unclear is the mechanism underpinning these terminal increases in reproductive traits. The reduced survival of successful breeders may reflect a high cost of investing in reproduction, an adaptive increase in effort as a response to declining survival prospects, or a combination of both. Below we discuss the potential role of these two non-mutually exclusive mechanisms.

Long-lived seabirds such as the wandering albatross possess many life history characteristics that might lead us to predict adaptive changes in reproductive investment in response to changes in residual reproductive value (RRV). Classical predictions of increasing reproductive effort with age are difficult to test in wild animals (Clutton-Brock 1984), but some studies have documented age-related increases using proxies for reproductive effort, such as feeding rate, weight loss, and breeding frequency (e.g. Pärt *et al.* 1992; Descamps *et al.* 2007). Manipulative studies have also shown that individuals are able to increase their reproductive effort when faced with an immune challenge (e.g. Bonneaud *et al.* 2004; Velando *et al.* 2006; Cotter *et al.* 2011; Bowers *et al.* 2012). This indicates that animals are able to use information about their future survival prospects to inform allocation decisions, adjusting their reproductive effort in response to cues about their physiological state. Given that wandering albatrosses are subject to few sources of environmentally-driven mortality, intrinsic cues about their state are likely to be highly informative of their future survival prospects and RRV. Since the senescent declines observed in breeding success and chick fledging period (Figs.2a&2c) are likely indicative of a physiological decline, individuals may be able to respond by adaptively increasing their reproductive investment if their condition drops below a threshold. Regardless of whether death is inevitable below the threshold, or is in part a consequence of the costs of increased reproductive allocation, they will have made a terminal investment.

An alternative explanation would be that variation in breeding success does not reflect an adaptive increase in effort in response to declining survival prospects, but rather unrelated, stochastic factors lead to variation in breeding success, and that successful breeding is associated with a survival cost. The lack of strong evidence indicating that the terminal increases are more likely to occur at older ages could be taken in support of such a state- or RRV-independent survival cost of reproduction. However, it should be noted that chronological age in adulthood may provide only a weak reflection of parameters associated with physiological state (e.g. Bize *et al.*2009; Lecomte *et al.*2010), and thus an individual’s actual or perceived RRV. Importantly, the terminal effect observed in breeding success was paralleled by an increase in chick fledging period (Fig.2c), which is only measured in successful breeders and reflects the duration of parental provisioning of their offspring after hatching. This supports the idea that the terminal increase in breeding success reflects an increase in parental investment prior to disappearance from the breeding colony, rather than stochastic variation in breeding success coupled with a survival cost of reproduction. Ultimately, without data on relevant markers of physiological state or intrinsic damage, we are unable to test whether the observed terminal increases in reproductive investment are independent of individual state or RRV or not.

We have provided a comprehensive dissection of the within- and among-individual processes associated with age-dependent variation in reproductive traits at the population level in this extremely long-lived species. However, convincingly disentangling the relative roles of the two mechanisms that could be responsible for the observed terminal increase in parental investment would be challenging in a manipulated laboratory system, let alone in an unmanipulated natural population. Regardless of the underlying mechanism, our results provide compelling evidence for a negative covariance between reproductive success and survival during adulthood in a long-lived vertebrate. It has been suggested that the chance of detecting survival costs of reproduction may be lower in long-lived species, where variance in survival is low compared to variance in reproduction (Hamel *et al.* 2010). Previous studies on the survival costs of successful reproduction in seabirds have produced mixed results (e.g. Golet *et al.* 1998; Weimerskirch *et al.* 2001; Townsend & Anderson 2007). Indeed, support for antagonistic associations between vital rates in later adulthood remains quite rare in wild populations of long-lived vertebrates, despite being predicted under classical life history theory. The terminal increases in reproductive traits observed here are likely to have important and as yet under-appreciated consequences for the population dynamics of this seabird, as they suggest that any factor influencing one adult demographic rate would have knock-on consequences for another vital rate.

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TABLES

Table 1) Estimated fixed effects (estimates and standard errors) from generalised linear mixed models of breeding success (1327 observations from 393 individuals), chick pre-fledging weight (681 observations, 309 individuals), and fledging period (774 observations, 324 individuals) for wandering albatrosses in early adulthood (<19 years). All models also included female identity as a random effect and year of measurement as a fixed factor. The effect of removing each parameter on the model AIC is shown (∆AIC). Positive ∆AIC values indicate the term improved model fit, and those parameters whose removal increased AIC by >2 are highlighted in bold.

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Breeding success** | | |  | **Chick pre-fledging weight** | | |  | **Fledging period** | | |
|  | Estimate | Std Error | ∆AIC |  | Estimate | Std Error | ∆AIC |  | Estimate | Std Error | ∆AIC |
| Years Since First bred | **0.091** | **0.036** | **4.395** |  | –0.017 | 0.023 | –1.386 |  | **–0.786** | **0.223** | **10.765** |
| Age at First Reproduction | 0.085 | 0.050 | 0.786 |  | 0.020 | 0.035 | –1.672 |  | –0.461 | 0.381 | –0.487 |
| First Breeding Attempt | **–0.550** | **0.191** | **5.590** |  | –0.024 | 0.140 | –1.969 |  | 0.502 | 1.425 | –1.867 |
| Bill Size | Not fitted | | |  | **0.377** | **0.021** | **265.843** |  | Not fitted | | |

Table 2) Estimated fixed effects (estimates and standard errors) from generalised linear mixed models of breeding success (498 observations from 116 individuals), chick pre-fledging weight (214 observations, 90 individuals), and fledging period (251 observations, 95 individuals) for wandering albatrosses in late adulthood (≥19 years). All models also included female identity as a random effect and year of measurement as a fixed factor. The effect of removing each parameter on the model AIC is shown (∆AIC). Positive ∆AIC values indicate the term improved model fit, and those parameters whose removal increased AIC by >2 are highlighted in bold.

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | **Breeding success** | | |  | **Chick pre-fledging weight** | | |  | **Fledging period** | | |
|  | Estimate | Std Error | ∆AIC |  | Estimate | Std Error | ∆AIC |  | Estimate | Std Error | ∆AIC |
| Years Before Death | **0.071** | **0.031** | **3.282** |  | 0.007 | 0.025 | –1.898 |  | **0.590** | **0.246** | **4.238** |
| Age at Last Reproduction | –0.024 | 0.019 | –0.474 |  | –0.007 | 0.015 | –1.128 |  | –0.131 | 0.143 | –1.112 |
| Last Breeding Attempt | **0.810** | **0.299** | **5.429** |  | 0.182 | 0.218 | –1.722 |  | **6.267** | **2.162** | **7.331** |
| Partner Change | **–0.944** | **0.398** | **3.781** |  | 0.336 | 0.331 | –0.725 |  | –1.545 | 3.272 | –1.728 |
| Years Since Last Bred | 0.177 | 0.222 | –2.761 |  | 0.042 | 0.170 | –3.722 |  | 0.656 | 1.489 | –1.704 |
| Previous Breeding Success | –0.113 | 0.694 | –3.818 |  | –0.308 | 0.537 | –3.215 |  | –6.343 | 5.161 | –2.217 |
| Years Since Last Bred x Previous Breeding Success | 0.103 | 0.328 | –1.903 |  | 0.071 | 0.255 | –1.895 |  | 2.523 | 2.404 | –0.776 |
| Bill Size | Not fitted | | |  | **0.441** | **0.038** | **115.059** |  | Not fitted | | |

FIGURES

Figure 1) The relationship between female age and reproductive traits in the wandering albatross. Points show trait averages for each age. The solid line shows the ageing pattern predicted by the best model (as determined by AIC comparison, see Table S2), with dotted lines showing standard errors around this prediction. Plots are for the following reproductive traits: (a) breeding success; (b) laying date; (c) egg volume; (d) chick pre-fledging weight; (e) fledging period. In cases where a threshold age function was the best fit to the data, the bar just above the x-axis reflects the estimated 95% confidence intervals for each threshold (see also Fig.S2).

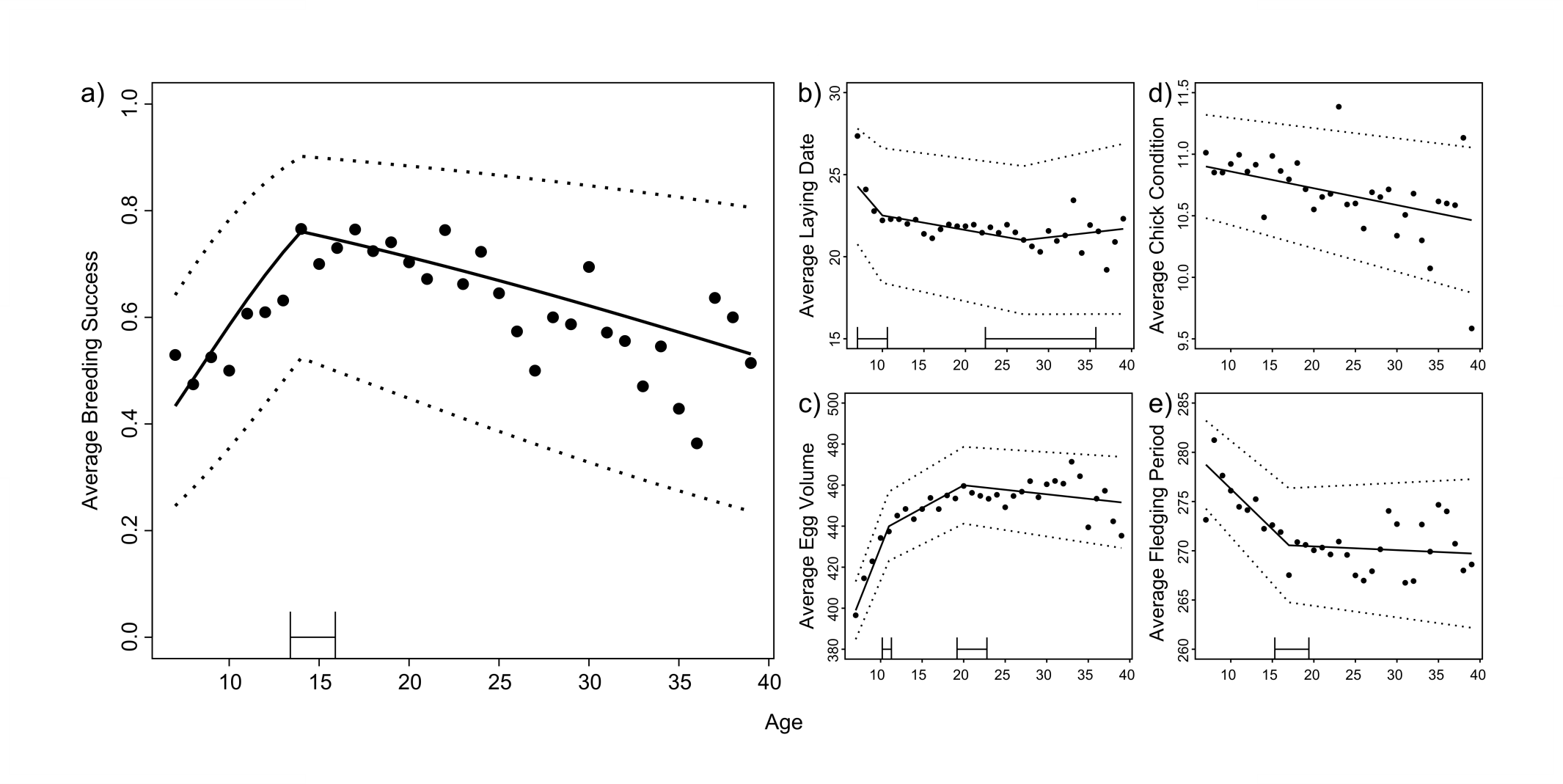


Figure 2) Factors influencing reproductive performance in late adulthood (≥19 years) in the wandering albatross. (a) and (c) show senescent declines in breeding success and fledging period, respectively, followed by an improvement on the final breeding attempt. Points show grouped trait averages for years before death, and the lines show the prediction (±standard error) of a model including the effect of years before death, a factor for final breeding attempt, female identity as a random effect, and year of measurement as a fixed factor. (b) shows proportions from the raw data averages (with standard error bars) illustrating the effect of partner change on breeding success. 