

Age-related reproductive performance of the Adélie penguin, a long-lived seabird exhibiting similar outcomes regardless of individual life-history strategy

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Abstract

1. Age-related variation in reproductive performance in long-lived iteroparous vertebrate species is common, with performance being influenced by within-individual processes, such as improvement and senescence, in combination with among-individual processes, such as selective appearance and disappearance. Few studies of age-related reproductive performance have compared the role of these drivers within a metapopulation, subject to varying degrees of resource competition.
2. We accounted for within- and among-individual changes among known-aged Adélie penguins *Pygoscelis adeliae* during 17 years (1997–2013), at three clustered colonies of disparate size, to understand patterns in age-related reproductive success during early and late adulthood.
3. Age at first reproduction (AFR) was lowest, and number of breeding attempts highest, at the largest colony. Regardless of AFR, success improved with early post-recruitment experience. For both oldest and youngest recruitment groups, peak performance occurred at the end of their reproductive life span indicating a possible cost of reproduction. Intermediate recruitment groups reached peak performance in their mid-reproductive life span and with intermediate breeding experience, before decreasing. Breeding success was lowest for the initial breeding attempt regardless of AFR, but we observed subsequent variation relative to recruitment age. Gaining experience by delaying recruitment positively influenced reproductive performance early in the reproductive life span and was most evident for the youngest breeders. Oldest recruits had the highest initial and peak breeding success. Differences in AFR resulted in trade-offs in reproductive life span or timing of senescence but not in the overall number of breeding attempts.
4. Patterns differed as a function of colony size, and thus competition for resources. Early life improvement in performance at the larger colonies was primarily due to within-individual factors and at the largest colony, AFR. Regardless of colony size

late-life performance was positively related to the age at last reproduction, indicating selective disappearance of lower performing individuals.

5. These results highlight that different life-history strategies were equally successful, indicating that individuals can overcome potential trade-offs associated with early- and late-life performance. These results have important implications for understanding the evolution of life-history strategies responsible for driving population change.

KEYWORDS

Adélie penguin, age of first reproduction, breeding experience, individual life-history strategies, *Pygoscelis adeliae*, reproductive performance, senescence

1 | INTRODUCTION

A central tenet of life-history theory is that individuals face trade-offs when partitioning limited resources between growth, maintenance and survival on one hand, and reproduction on the other (Stearns, 1992). Trade-offs between current and future reproduction play an important role in shaping age-specific reproductive performance (Williams, 1966). The commonly observed population-level pattern of age-related variation in reproductive performance is a trajectory in which success increases early, usually reaching a plateau/peak with intermediate experience, and then decreases near the end in an individual's reproductive life span (Balbontín et al., 2007; Bouwhuis et al., 2009; Clutton-Brock, 1988; Forslund & Pärt, 1995). Observed variation in average age-specific reproductive performance (hereafter, performance) at the population level is not simply a product of varying trade-offs but is also driven by complex interactions between processes operating both within- and among individuals (Forslund & Pärt, 1995; van de Pol & Verhulst, 2006). Accordingly, multiple studies have highlighted the importance of accounting for both within- and among-individual processes in order to disentangle those responsible for the observed variation at the population level (reviewed in Bouwhuis & Vedder, 2017 for birds; reviewed in Gaillard et al., 2017 for mammals). The drivers of this variation have important consequences for both population dynamics (Caswell, 2001) and the evolution of life-history strategy (Stearns, 1992).

Accounting for both among- and within-individual processes can produce different age-related reproductive trajectories (see Figure 1; e.g. Aubry et al., 2009; Berman et al., 2009; Bouwhuis et al., 2009; Froy et al., 2017). Within-individual improvements in early adulthood are likely the result of individuals reaching physiological maturity at different rates (Ainley, 1978) or acquiring or becoming more proficient at required skills necessary to reproduce successfully (Balbontín et al., 2007; Curio, 1983), such as foraging (Daunt et al., 2007), mate familiarity (Nisbet & Dann, 2009), or competing for a mate (Perdeck & Cavé, 1992). Meanwhile, within-individual physiological changes, that is, senescence, can be responsible for declines in performance in late adulthood (Hammers et al., 2013; Reed et al., 2008), or terminal investment can result in

increased performance (e.g. Froy et al., 2013, 2017). Abrupt, step-wise changes associated with age-related performance have also been documented (e.g. Berman et al., 2009; Reed et al., 2008). For example, studies have documented much lower performance in first-time breeders compared to more experienced breeders of the same age, as well as much lower performance during the last reproductive attempt (Rattiste, 2004).

Population-level changes in performance are also influenced by among-individual processes (Aubry et al., 2009; Froy et al., 2017). Individuals with low intrinsic quality or those slower to mature, may delay recruitment to the breeding population.

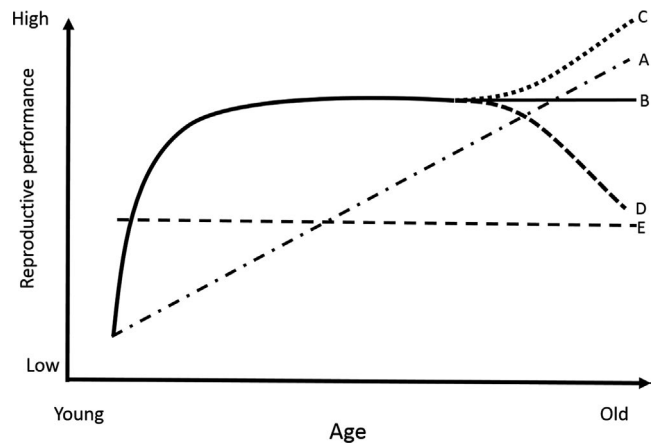


FIGURE 1 Potential trajectories of age-related breeding performance indicating whether an individual successfully produced at least one chick: (A) increases linearly with number of years breeding, that is, experience (individual maturation or population progressive selection of more successful individuals, with no trade-off); (B) Increases with low levels of breeding attempts then reaches a plateau where frequency remains relatively consistent (individual pseudo-threshold response with no senescence); (C) Increases with low levels of breeding attempts, reaches a plateau or peak near-optimum performance with intermediate frequency of breeding, then increases in older age classes (terminal investment); (D) Increases with few early attempts, reaches a plateau or peak near-optimum success with intermediate breeding frequency, then decreases (senescence); (E) remains constant (i.e. no trend)

Their selective appearance could mask within-individual improvements with age during early adulthood (van de Pol & Verhulst, 2006). In late adulthood, the selective disappearance of individuals of lower intrinsic quality may mask the within-individual senescent decline of individuals still in the breeding population (Aubry et al., 2009).

Because breeding behaviours may initiate mechanisms that impede somatic repair (Kirkwood, 1977), which over time can lead to senescence (Charnov, 1997), the age at recruitment into the breeding population (age at first reproduction; AFR) presents different trade-offs and costs that shape subsequent individual reproductive trajectories (Mourocq et al., 2016). These trade-offs, in combination with the selective appearance and disappearance processes, contribute to population-level performance trajectories. Individuals having a young AFR, and which invest heavily early in their reproductive lifetime, may suffer a cost, as well as experience earlier and more pronounced performance declines (senescence) later in life (Nussey et al., 2006). They also may have lower breeding success initially but improve their performance as they gain additional breeding experience. Meanwhile, individuals that delay recruitment may have high success at recruitment, early in their reproductive life, because they have had time to acquire the skills necessary to reproduce successfully (Curio, 1983; Forslund & Pärt, 1995; Perdeck & Cavé, 1992). Thus, we would predict that individuals with more breeding experience should perform better than similarly aged but inexperienced individuals (e.g. Ainley et al., 1983). However, in this scenario, the observed population-level age-related improvement in performance may also result from the selective appearance of new recruits that delayed their first reproduction and exhibit higher success comparable to similarly aged individuals that may have more breeding experience. Therefore, selective appearance of new phenotypes into the breeding population needs to be considered in order to determine if the observed changes are due to within-individual improvement or the selective appearance of new phenotypes.

Another hypothesis is that individuals that invest heavily in early adulthood and/or have a younger AFR may incur a survival cost (Ainley et al., 1983) and that their selective disappearance from the breeding population would contribute to age-related declines in success at the population level later in life. This would be particularly true for the longest-living individuals who have the greatest number of breeding attempts over their lifetime (Hammers et al., 2013; Reed et al., 2008). For recruits delaying AFR, particularly those with a short life span, cumulative reproductive costs incurred should be smaller. For these individuals, evidence of senescence should be minimal or even absent.

Alternatively, the heterogeneity in individual quality hypothesis posits that individuals of high intrinsic quality recruit early and go on to exhibit high breeding success late in life (e.g. Zhang et al., 2015). They accomplish this because they incur smaller reproductive costs than lower quality individuals for equal reproductive investment (Nur, 1988). Under this scenario, we would expect early recruits

to incur smaller costs than later recruits, and for senescence to be weak or even absent. Meanwhile, individuals of lower intrinsic quality would delay recruitment, with senescence becoming more pronounced; success should be lower than early recruits with similar number of breeding attempts.

To investigate the complex patterns in early- and late-life age-related breeding strategies that result in success in a long-lived, colonial seabird, we used data from a longitudinal study (1997–2013) of marked individuals in a metapopulation composed of three Adélie penguin colonies on Ross Island, Antarctica, along with a less accessible colony on Beaufort Island (Dugger et al., 2010; LaRue et al., 2013). Colonies were of markedly disparate sizes, which affect intraspecific competition for resources (e.g. longer and deeper foraging dives at largest colony, returning with less food per trip; Ainley et al., 2018; Ballard et al., 2019). We took into account both AFR and post-recruitment breeding experience to model observed patterns in early- and late-life age-specific success at each colony. We describe the early- and late-life performance for different life-history strategies, while accounting for individual heterogeneity and decomposing the observed variation into its constituent processes early and late in the reproduction life span. Herein, breeding performance is a combination of success, that is, chicks raised, and frequency of attempting to breed. This is one of the few studies of a long-lived species that investigates how recruitment age influences performance while taking into account both within- and among-individual changes (see Aubry et al., 2009; Froy et al., 2013, 2017; Reed et al., 2008). To our knowledge, it is the first study to investigate this process for the same species at multiple colonies differing in sizes by orders of magnitude and potentially experiencing different levels of competition for resources and levels of predation.

2 | MATERIALS AND METHODS

2.1 | Study species, study site and data collection

We used breeding history data obtained over 17 years (1997–2013) from uniquely banded known-age (KA) Adélie penguins breeding at Cape Bird (77°13'S, 166°28'E), Cape Crozier (77°31'S, 169°23'E) and Cape Royds (77°34'S; 166°11'E) on Ross Island, Antarctica (Table S1 for sample sizes), along with the less accessible Beaufort Island colony; together they comprise a metapopulation, with episodic levels of interchange (Dugger et al., 2010; LaRue et al., 2013). Colonies differed in size by orders of magnitude (mean annual size, 1981–2012: Cape Royds 2,865, Cape Bird 43,321 and Cape Crozier 153,623 pairs; most recent counts, 3,083, 75,696 and 272,340 respectively; LaRue et al., 2013; Lyver et al., 2014), which affected energetic requirements of foraging (Ballance et al., 2009). All increased in size during the study, with rate positively correlated with colony size (Lyver et al., 2014). We attached uniquely numbered stainless-steel bands to the left flipper of nearly fledged chicks at each colony (Dugger et al., 2006) starting in the austral spring–summer (late October

through January) of 1994–1995 (hereafter year 1994) through 2013. Each year following 1994, we searched for banded birds and upon finding one on a nest with eggs, we marked the nest and recorded the location. Because the youngest breeders in our study were 3 years of age, the time series reported herein begins in 1997. We subsequently monitored each nest to determine reproductive performance and generate known breeding histories for marked individuals.

Adélie penguins exhibit delayed maturity with most individuals recruiting to the breeding population between the ages of 3 and 8 years (Ainley et al., 1983). In our study, as in the latter, we did not observe breeding at <3 years of age, however, banded pre-breeding birds were observed starting at age 2, and most breeding birds were present for at least a year as pre-breeders. From these breeding histories, we determined AFR (age first observed with an egg or chick) for each KA bird, as well as breeding status and outcome for as many years as they were observed.

Adélie penguin chicks are typically left unattended by parents when they are large enough to withstand most South Polar skua *Stercorarius maccormicki* predation, and their growth rate can only be maintained if both parents forage simultaneously. Unattended chicks seek the company of other chicks, forming groups referred to as 'crèches' (Sladen, 1958). Due to the high levels of disturbance required to monitor unmarked chicks in large crèches and the fact that mortality of chicks that enter crèches is relatively low (Ainley et al., 1983), we categorized reproductive performance as a binary response following Lescroël et al. (2009). At the two larger colonies, individuals observed feeding at least one chick after mean crèche date (about the first week of January) were categorized as 'successful' (breeding success = 1) and individuals observed early in the season with an egg(s) and/or chick(s) that were not observed feeding a chick after the mean crèche date were categorized as 'unsuccessful' (breeding success = 0). Because crèches seldom form at Royds, individuals seen feeding chicks 22 days of age, the mean age at which chicks enter the crèche (Davis, 1982), were categorized as 'successful'.

2.2 | Data analysis

We used GLMMs with binomial errors and a logit link (i.e. logistic regression; see Agresti, 2003) using the `lme4` package (Bates et al., 2007) in R (R Core Team, 2018; version 4.0.0) to assess the effects of AFR, breeding experience, and age at last reproduction (ALR; i.e. age when last observed with egg(s) and/or chicks(s)) on the probability of raising at least one chick in a given breeding season. Analyses were necessarily restricted to recruits (i.e. birds that bred at least once) and their subsequent breeding history (3,089 individuals, 9,603 observations).

2.3 | Modelling age-related variation in breeding success

All models included a random effect for individual identity (ID) to account for unobserved heterogeneity in individual quality and

multiple observations per individual over time. Year (i.e. breeding season) was also included as a crossed random effect to account for annual variation in environmental conditions in all models. We also included breeding colony as a fixed effect in each model to account for potential differences in breeding performance relative to colony size or other inherent differences between colonies.

Our initial population-level analysis of the variation in breeding success accounted for the effects of selective appearance only by including AFR as a fixed effect. We considered AFR as a monotonically increasing (or decreasing) factor affecting breeding success (i.e. AFR as a continuous variable corresponding to actual age) and as a categorical variable (AFR_C; Figure S1). Multi-state mark–recapture estimates of age-specific survival probabilities for this metapopulation show differences in annual survival rates among sub-adults (0–1), 2–3, 4, 5–8 and 9+ year olds (K. M. Dugger, D. G. Ainley, G. Ballard, & D. Anderson, unpublished data) consistent with other patterns in age-related survival for this species (Ainley & Demaster, 1980). If age-related patterns in reproductive success have fitness consequences, we would predict similar patterns in the effects of AFR, so we grouped our sample breeding population into four AFR categories that reflected this variation in survival (i.e. 3 years old; 4 years old; 5–8 years old; and 9+ years old). By grouping the older age classes into two categories, we ameliorated the problem of smaller sample sizes for those older ages, which were only present in the later years of our study.

As another fixed effect, we used breeding experience rather than age per se, to index potential changes in breeding performance of individuals over their life span. Indeed, breeding experience can lead to improved breeding success with age (Ainley et al., 1983; Nol & Smith, 1987; Orell & Belda, 2002), potentially obscuring the influence of recruitment on performance. In addition, some Adélie penguins do not breed every year after recruitment (i.e. taking 'sabbatical' years; see Table S2; Ainley, 1978; Lescroël et al., 2009), making the number of breeding attempts potentially more relevant than true age or the number of years following initial breeding, in terms of potential effect on breeding performance. Thus, we parameterized breeding experience in two ways; learning experience (EXP_L) and true experience (EXP_T; Table 1). Learning experience was defined as the number of breeding seasons following age at first reproduction (i.e. at first reproduction EXP_L = 0 and increased by 1 each year that the bird is observed in the colony until ALR or the end of the study). We defined EXP_T as the number of breeding seasons an individual was previously observed breeding (i.e. observed with at least one egg or chick). Thus, at first reproduction EXP_T = 0 and increased by one following each subsequent confirmed breeding attempt.

Approximately 23% of the records in breeding histories reflected sabbatical years (i.e. former breeders present but not observed breeding; Table S2), which can be an efficient way to increase residual reproduction (i.e. the expected number of offspring produced by an individual at a particular age in future reproductive events; Stearns, 1992). However, we did not feel that those sabbatical years reflected true breeding experience, but rather other important experience. Unlike breeders, non-breeders did not have to repeatedly avoid predation by leopard seals *Hydrurga leptonyx* each time they

TABLE 1 Acronyms and description of life history and extrinsic variables used to model breeding performance of known-age Adélie penguins, 1997–2013, at capes Bird, Crozier and Royds, Ross Island, Antarctica. Success, or the highest measure of performance, was measured as successfully feeding a chick(s) (Y/N) after mean crèche date

Age-related covariate acronyms	Description
AFR _T	Age at first reproduction as a continuous variable (3–14)
AFR _C	Age at first reproduction as a categorical variable ^a
EXP _T	Breeding experience as a continuous variable
EXP _T ²	Breeding experience if quadratic
EXP _L	Breeding experience as a continuous variable with sabbaticals counting as experience
EXP _L ²	Breeding experience with sabbaticals if quadratic
ALR	Age of individual at last reproduction
T1 + T2	Existence of one threshold on breeding experience (between ages 3 and 11)
T1 + T2 + T3	Existence of two thresholds on breeding experience (all combinations between ages 3 and 11)
YBD	Years before death
BA ₁ or BA _L	First breeding attempt OR last breeding attempt (0 = failed; 1 = successful)
Extrinsic variables	
COL	Breeding colony as a categorical variable (i.e. Cape Bird, Crozier and Royds)
ID	Individual band number
YEAR	Breeding season

^aAFR_C levels: 3 years old, 4 years old, 5–8 years old, 9+ years old.

went to forage for their chicks (Ainley et al., 2005), and they did not get experience laying eggs, tending young and synchronizing breeding activities with their mates.

We evaluated linear, quadratic and threshold structures (with a range of breakpoints following Berman et al., 2009; Froy et al., 2017) of EXP_T or EXP_L on breeding success. We included a quadratic (EXP_T²) effect on both parameterizations of EXP because breeding success may increase with increasing EXP to some peak at intermediate levels of experience, followed by a plateau after which breeding success decreases with senescence. The piecewise regression models included both single and double thresholds, between which the slopes were allowed to vary independently in order to detect bi-modal trends that might reflect terminal investment. For both single and double thresholds, we tested breakpoints that depended on the age range observed in each colony. This pattern reflects the improvement in breeding success with early experience, then levels off with middle levels of experience and can either improve or decline with more advanced levels of experience (two breakpoints; Figure 1).

2.4 | Controlling for selective disappearance

Our initial analysis of breeding success (see previous section) within the population accounted for unobserved heterogeneity in quality by including individual ID as a random effect, and selective appearance by including the age at first reproduction. However, this did not explicitly control for potential selective disappearance of individuals. Indeed, heterogeneous survival across individuals (i.e. when 'less fit' phenotypes die earlier) can change the composition of the sample population leading to spurious estimates of age-related breeding success (van de Pol & Verhulst, 2006). To account for this, we reran the top model from our original model set including the additive effect of ALR, in years (i.e. age at last breeding attempt) and another model with the interaction between AFR_C and ALR. We then compared these two models with the top model from our a priori model set. This approach allowed us to explicitly account for heterogeneity in appearance (i.e. variation in AFR) and disappearance (i.e. variation in ALR) from the breeding population. If ALR has an effect on breeding success, this indicates that changes in mean performance associated with ALR are the result of population-level changes driven by selective disappearance of 'less fit' phenotypes.

2.5 | Decomposing within-individual and among-individual processes during early and late adulthood

Although we accounted for heterogeneity among individuals by modelling AFR and ALR in our previous modelling effort, we sought to quantify the relative contributions of within- and between-individual contributions to population-level age-related reproductive performance. To do this we decomposed the observed patterns in breeding success into their constituent processes as they related to early (<10 years of age; selective appearance) and late (only individuals that age at last reproduction could be determined [see more below]; selective disappearance) adulthood. For this analysis, we used the within-group centring approach outlined by van de Pol and Verhulst (2006). We ran two GLMMs for each colony and modelled breeding success in early and late adulthood by including AFR and ALR as fixed effects. Parameter estimates for these terms represent the relative contributions of selective appearance (AFR) and disappearance (ALR), of phenotypically different individuals from the population. The age term used in the models was years since the initial breeding attempt (EXP_L) for early adulthood, and years before death (YBD) for late adulthood (Reed et al., 2008). Parameter estimates for these terms represent the contribution of within-individual changes in breeding success to the population-level averages.

In the analysis for early adulthood, it is critical to account for selective appearance in the breeding population, so only individuals with known AFR were used in this analysis. In the analysis of late adulthood, we only used data of individuals for which the age at last measurement reflected the age at last reproduction (i.e. the last breeding attempt of birds that disappeared from the

population afterwards), because we wanted to test for possible terminal effects. This reduced the dataset to 1826 individuals and 3,811 breeding attempts (BA; Table S1) but allowed us to account for the effects of selective disappearance and identify terminal investment. As we did not know the exact age of death for these individuals, we used disappearance from the breeding colony of >2 years as a proxy for mortality or permanent emigration. However, we assume that selective disappearance primarily reflects mortality rather than emigration because penguins, especially once establishing a territory, show high site fidelity, that is, movement rates of breeders are very low in this metapopulation (Dugger et al., 2010). Even if detection rates were not 100% each year, <1% of birds in our dataset had an interruption of more than two breeding seasons before being subsequently re-sighted, and $\leq 1\%$ of individuals took sabbaticals >2 years (Table S3).

Finally, we included a binary factor for first BA₁ in the early adulthood model to determine how much of the increase in breeding success could be attributed to poor performance by first-time breeders (first BA = 1; subsequent BA = 0). To test for terminal effects, we included a binary factor for the last BA in the late adulthood model (following Bouwhuis et al., 2009), comparing breeding success of individuals on the final BA_L with previous attempts (last BA = 1; previous BA = 0).

2.6 | Model selection

We evaluated all models using an information-theoretic approach (Burnham & Anderson, 2002) and Akaike's Information Criterion corrected for small samples sizes (AIC_c) to determine the model from our a priori model set that best explained variation in reproductive performance patterns. Models with the lowest AIC_c and highest Akaike weight (w_i) were generally considered the best models, but models within 2 AIC_c units (AIC_c ≤ 2.0) were considered competitive (Burnham & Anderson, 2002). We assessed the direction and strength of evidence for each estimated slope parameter (β_i) that appeared in competitive models based on the extent that the 95% confidence intervals (CI) for each β_i overlapped zero (Arnold, 2010). We considered covariates with 95% CI that did not overlap 0 as evidence for having the strongest effect. Covariates in which the 95% CI overlapped 0 by <10% were considered to have less effect, and 'widely' overlapping covariates (i.e. >10% of the interval above or below 0) had no support (see Dugger et al., 2016). All analyses were conducted in R (R Core Team, 2018) and figures were produced using the GGPLOT2 package (Wickham, 2009). We used the *predictSE* function in the AICCMODAVE package (Mazerolle, 2016) to generate predictions \pm standard errors from our top performing models, not accounting for random effects.

3 | RESULTS

Mean observed AFR was lower at large Cape Crozier (5.4 ± 0.03 years) than it was at smaller Cape Bird and Cape Royds (both

6.0 ± 0.1 years), and the average number of breeding attempts was highest at Crozier, as well (Crozier: 2.53 ± 0.05 ; Bird: 2.27 ± 0.05 ; Royds: 1.92 ± 0.10). However, within each colony the mean number of breeding attempts per individual was the same, regardless of AFR (Table S4). A post hoc regression analysis using the number of EXP_T as the dependent variable, found no detectable difference between the total number of breeding attempts for birds that we believe were no longer alive at the end of the study, regardless of AFR (all $p > 0.15$). Models including EXP_L were not competitive (all $\Delta AIC_c > 52$). The most supported model indicated that breeding performance changed over an individual's lifetime as a function of an interaction between AFR_C and the quadratic effect of EXP_T, and an additive effect of colony (Table 2; Table S5). This model indicated that the mean population-level probability of success was highest at Cape Crozier (Figure 2). AFR_C was positively associated with success at all three colonies, indicating that individuals delaying recruitment (i.e. selective appearance of new recruits) exhibited high levels of success. The interaction between AFR_C and EXP_T indicated that individuals in the youngest (AFR_C = 3 years old) and oldest (AFR_C 9–17 years old) age categories had the greatest improvement in the probability of success with early additional EXP, compared to individuals in the other two categories. The highest maximum probability of success at all three colonies was observed, regardless of AFR, at intermediate levels of breeding experience (i.e. between four and

TABLE 2 Estimated effects and 95% confidence intervals for each explanatory variable from the best model relating Adélie penguin performance to age at first reproduction (AFR_C; categorical variable), breeding experience (EXP_T), colony (categorical), and AFR_C \times EXP interaction for capes Bird, Crozier, and Royds on Ross Island, Antarctica, 1997–2013

Variable	Estimate	SE	Lower 95% CI	Upper 95% CI
Fixed effects				
Intercept	-0.6188	0.2967	-1.20	-0.04
AFR _C 4	0.3550	0.2121	-0.06	0.77
AFR _C 5–8	0.4250	0.2059	0.02	0.83
AFR _C 9+	0.6154	0.2441	0.14	1.09
EXP _T	85.6137	7.4677	70.98	100.25
EXP _T ²	-45.8254	5.8466	-57.28	-34.37
COL(Crozier)	0.3230	0.0559	0.21	0.43
COL(Royds)	-0.1721	0.1064	-0.38	0.04
AFR _C 4 \times EXP _T	-58.0654	9.2131	-76.12	-40.01
AFR _C 5–8 \times EXP _T	-55.8973	7.2562	-70.12	-41.68
AFR _C 9+ \times EXP _T	-29.3278	8.0563	-45.12	-13.54
AFR _C 4 \times EXP _T ²	24.5152	6.1789	12.40	36.63
AFR _C 5–8 \times EXP _T ²	38.6167	6.4945	25.89	51.35
AFR _C 9+ \times EXP _T ²	28.2475	8.5918	11.41	45.09
Random effects		SD		
Year	0.6261	0.79		
ID	0.0689	0.26		

FIGURE 2 Reproductive performance relative to age at first reproduction (AFR_C: 3, 4, 5–8 and 9+ years old) and number of prior breeding attempts (EXP_T) for Adélie penguins at capes Bird, Crozier and Royds on Ross Island, Antarctica, 1997–2013. Predicted population-level estimates and 95% confidence intervals were obtained for the fixed effects from the best performing GLMM not accounting for year (i.e. random effect of study year) and unobserved individual heterogeneity (i.e. random effect of ID). Data points and bars show the observed mean ± SE breeding success. Rug plots above and below indicate the observed number of successes (1) and failures (0) respectively

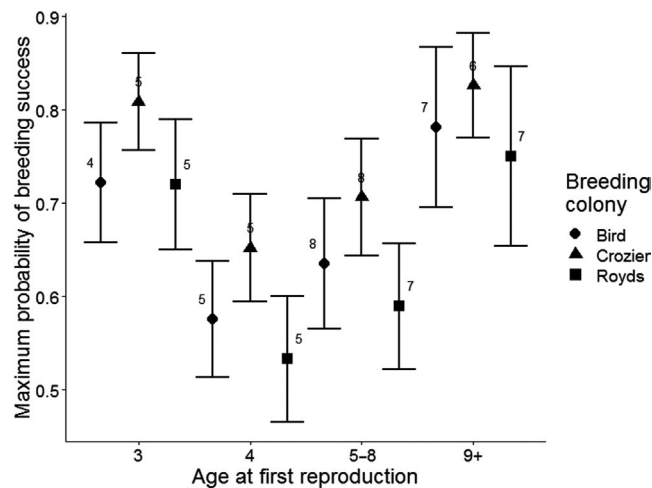
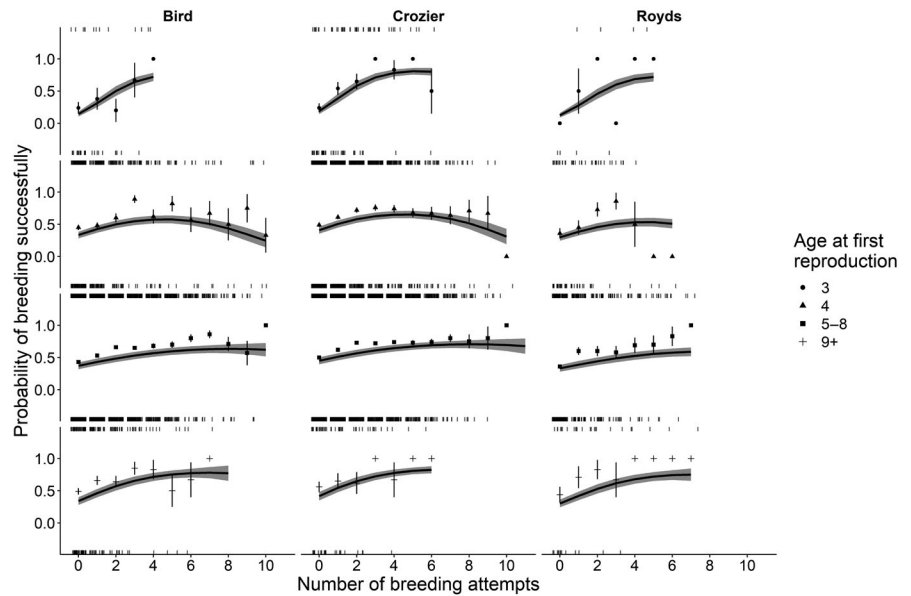


FIGURE 3 Maximum predicted breeding success (±SE) for each age at first reproduction category (AFR: 3, 4, 5–8 and 9+ years old) for Adélie penguins breeding at capes Bird, Crozier and Royds, Ross Island, Antarctica. Labels indicate the average number of breeding attempts associated for each estimate of breeding success for each AFR

eight BAs), and was highest for the oldest and youngest recruitment categories (Figure 3). No other model in the initial candidate set was within 2 ΔAIC_C of the top model so we used this model in further analyses of performance relative to ALR.

3.1 | Accounting for selective disappearance of individuals

To account for selective disappearance, we reran the best model identified from our initial analysis ($p(\text{breeding success}) = \text{AFR}_C * \text{EXP}_T + \text{COL}$), including the additive effect of a monotonically increasing trend in ALR ($p(\text{breeding success}) = \text{AFR}_C * \text{EXP}_T + \text{COL} + \text{ALR}$) as well as another

TABLE 3 Estimated effects and 95% confidence intervals for each explanatory variable in the second-best model, which accounted for selective disappearance affecting performance for individuals breeding at capes Bird, Crozier and Royds on Ross Island, Antarctica

Variable	Estimate	SE	Lower 95% CI	Upper 95% CI
Fixed effects				
Intercept	-0.8245	0.3111	-1.43	-0.21
AFR _C 4	0.3387	0.2123	-0.08	0.75
AFR _C 5–8	0.3633	0.2080	-0.04	0.77
AFR _C 9+	0.4674	0.2523	-0.03	0.96
EXP _T	80.5741	5.6292	69.54	91.61
EXP _T ²	-44.7278	5.6233	-55.75	-33.76
COL(Crozier)	0.3329	0.0562	0.22	0.44
COL(Royds)	-0.1648	0.1066	-0.37	0.04
ALR	0.0265	0.0115	0.00	0.05
AFR _C 4 × EXP _T	-58.8163	6.1157	-70.80	-46.83
AFR _C 5–8 × EXP _T	-56.3158	5.8761	-67.83	-44.80
AFR _C 9+ × EXP _T	-29.1425	7.3097	-43.47	-14.82
AFR _C 4 × EXP _T ²	24.0023	6.2730	-11.71	36.30
AFR _C 5–8 × EXP _T ²	38.2823	5.8699	26.78	49.79
AFR _C 9+ × EXP _T ²	28.3367	7.5578	-13.52	43.15
Random effects		SD		
Year	0.6386	0.2663		
ID	0.0709	0.7991		

model with the interaction between AFR_C and ALR. The additive effect of ALR was supported (ΔAIC_C = -2.07) and the positive relationship between ALR and success indicated the selective disappearance of 'less fit' phenotypes (Table 3); those with above average performance tended to live longer.

TABLE 4 Fixed effect estimates and standard errors (SE) from GLMM predicting breeding success for Adélie penguins during (a) early and (b) late adulthood. The effect of removing each parameter on the model AIC is shown (Δ AIC). Positive Δ AIC values indicated that the term improved model fit, and those parameters whose removal increased or decreased AIC by >2 are highlighted in bold. All models included year and individual ID as random effects

(a)	n	Estimate	SE	Δ AIC	Estimate	SE	Δ AIC	Estimate	SE	Δ AIC
		Years since first breeding attempt			Age at first reproduction			Outcome first breeding attempt		
Bird	1,215	0.07	0.03	5.95	0.05	0.03	0.56	-0.22	0.12	1.39
Crozier	1,573	0.08	0.02	10.23	0.10	0.03	9.83	-0.42	0.10	15.31
Royds	247	0.09	0.09	-1.14	0.14	0.08	0.82	-0.98	0.34	6.67
(b)	n	Estimate	SE	Δ AIC	Estimate	SE	Δ AIC	Estimate	SE	Δ AIC
		Years before death			Age at last reproduction			Outcome of last breeding attempt		
Bird	729	0.07	0.06	-0.80	0.06	0.03	2.14	-0.05	0.19	-1.95
Crozier	989	-0.14	0.04	8.63	0.15	0.02	35.85	-0.18	0.14	-0.42
Royds	108	0.04	0.23	-2.10	0.18	0.08	2.51	0.05	0.56	-2.12

3.2 | Decomposing selective appearance and disappearance during early and late adulthood

The effect of years since first BA was positive at all three colonies, indicating that success progressively improved within individuals during early adulthood at each of the colonies (Table 4a). This played a particularly important role in early breeding at both Bird and Crozier (both Δ AIC > 5) compared to the smaller Royds (Table 4a). The relationship between AFR and success was also positive at all three colonies, indicating that individuals who delayed their initial breeding attempt performed better than those that began breeding earlier (Table 4a), and was particularly important at Crozier, the largest colony (Δ AIC = 9.83). The relationship between success and the outcome of the first BA was negative at all three colonies, indicating individuals tended to perform poorly on their first breeding attempt. This was the most important factor explaining success at both Crozier and Royds, indicating that most of the within-individual improvement occurred on the second breeding attempt and not thereafter.

The relationship between breeding success and YBD was inconsistent among the colonies. A negative relationship at Crozier indicated that success increased as individuals approached death, while positive relationships at the other two colonies indicated that success decreased as individuals approached death (Table 4b). There was a positive relationship between ALR and success at all three colonies, indicating selective disappearance of low-performing individuals. Thus, those individuals with lower-than-average success had reduced life spans, while high-performing individuals continued to breed successfully. The effect of the outcome of the last BA on success was inconsistent between colonies. At the two larger colonies there was a negative relationship, indicating that success decreased in the final breeding attempt. However, at Royds the relationship was positive indicating that success increased in the final breeding attempt, supporting the terminal investment hypothesis.

4 | DISCUSSION

4.1 | Age-related reproduction performance trajectories

We found support for a quadratic trajectory of performance relative to AFR and breeding experience (Clutton-Brock, 1988; Newton, 1989; Sæther, 1990). Regardless of AFR, performance improved with subsequent experience immediately following first reproduction (also reported by Ainley et al., 1983). Performance reached a peak with an intermediate delay in breeding (~5 BA), followed by a decrease for individuals recruiting at older ages (Figure 2). In the youngest and oldest recruiting categories, breeding effectively ceased following peak performance (Figure 2). Meanwhile, performance for the 5–8-year-old recruitment group peaked late in the reproductive life span (range: 6–8 BA), appearing to reach a consistent threshold at similar levels throughout their remaining reproductive years. Although general trajectories were similar among colonies, the increase in performance early in the reproductive life span was strongest (steepest slopes) for the youngest and oldest AFR categories at Bird and Crozier (Figure 2; Table 4a). This is likely due to both within- and among-individual processes that contributed to early improvement at the medium and large colonies. These results support the constraint hypothesis (Curio, 1983; Forslund & Pärt, 1995), that is, that individuals improve skills or behaviours early in their reproductive life span. As another example, older, more experienced European Shags *Phalacrocorax aristotelis* delivered more food to their chicks, regardless of foraging conditions, than less experienced pairs, resulting in higher chick survival (Daunt et al., 2007). Interestingly, we recently confirmed the Ainley et al. (1983) hypothesis that foraging competency increases with age (Lescroël et al., 2019), indicating a possible mechanism to explain the positive relationship between AFR and success observed early in the reproductive life span.

A possible additional explanation for this improvement is that performance is linked to prior breeding experience. Indeed, previous work on a variety of species (see Clutton-Brock, 1988; Newton, 1989; Sæther, 1990), including Adélie penguins (Ainley et al., 1983; Polito et al., 2010), found that as females gain foraging and breeding experience, they begin to initiate breeding earlier, lay larger eggs, and lay large (two-egg) clutches. Given that eggs from earlier and larger clutches have higher probabilities of survival (Davis & McCaffrey, 1986), even after controlling for age (Ainley et al., 1983), the observed increase in early performance may be driven by an increase in competency in a number of life-history aspects. However, improvement in performance gradually diminished or plateaued after five to seven BA (Ainley et al., 1983; Lescroël et al., 2019; Polito et al., 2010). This indicated a threshold at which additional breeding attempts do not provide further success or trade-offs counteract additional increases in performance.

Similar to Ainley et al. (1983) we documented that individuals recruiting at 3 and 4 years of age generally reached maximum performance earlier (range: 4–5) than individuals that initiated breeding at 5 years or older (range: 6–8; Figure 3). Outcomes for individuals that began breeding at 3 years and 9+ years ceased after maximum performance, indicating either a survival cost or a truncated reproductive life span and could explain the general relationship of increased breeding success with age (Figure S2). We found that individuals who recruited at 4 years of age reached a peak after an intermediate number of BAs before experiencing a decline in success. The later recruits exhibited a less pronounced decrease later in life, possibly indicating a threshold effect or senescence being masked due to the shortened time-series and selective disappearance (but see below). Individuals in the oldest and the youngest AFR_C categories (AFR_C = 9+ and 3) both had the highest maximum performance (Figure 2) and reached maximum at similar points in their respective reproductive life spans (approximately their third BA; Figure 2). This presents an interesting contrast, in which individuals that recruit early optimize success through early improvement, as predicted by the constraint hypothesis, while the oldest recruits follow the delayed breeding hypotheses entering the breeding population with sufficient experience to achieve high success from the first breeding attempt. Meanwhile individuals electing to first breed at intermediate ages balanced lower probabilities of performance by having a prolonged reproductive life span, similar to what has been observed in Black-legged Kittiwakes (*Rissa tridactyla*; Aubry et al., 2009). This may also represent a difference in life-history tactics between sexes. Ainley et al. (1983) found that earliest recruits (i.e. 3 years old) were all females, while males generally recruited at older ages, a finding recently supported by a subset of our own data (D. G. Ainley, K. M. Dugger, & G. Ballard, unpublished data). Young females may be able to take advantage of older, more experienced males that have lost their previous mate owing to mortality (Ainley et al., 1983). Another possible explanation for the high probability of success late in life is that this performance peak is the result of terminal investment (Williams, 1966). The latter posits an age-related increase in effort that corresponds with an increase in investment resulting in increased performance (e.g. Froy et al., 2013; Pärt et al., 1992).

4.2 | Accounting for selective appearance and disappearance

After we explicitly decomposed variation in reproductive performance into its components, we found that early improvement observed in all three colonies was due in part to within-individual success with experience. The negative relationship between the outcome of the first breeding attempt and success (Table 4a) indicates that this improvement in performance was not influenced by the low success observed for all AFR categories on their initial BA. Presumably this reflected genuine individual improvements and/or selective appearance of high-performing individuals. The fact that this was the most important factor affecting performance in early adulthood at both Crozier and Royds indicates that at the largest and smallest colonies within-individual improvements were extremely important to early-life breeding performance when controlling for selective appearance (Table 4a). This was particularly so during the second breeding attempt, similar to the finding that after an initial year of breeding, performance did not improve (Ainley et al., 1983). This is in line with the proposed benefits of individual development and experience postulated for birds (Forslund & Pärt, 1995). Age-related improvements in foraging capability, rather than breeding itself, is one possible explanation for this improvement (see Daunt et al., 2007; Lescroël et al., 2019), as indicated by a recent study at medium-sized Cape Bird that found little connection between foraging performance and breeding experience (Lescroël et al., 2020). Otherwise, simply having the experience of previous attempts has been linked to breeding success (Nol & Smith, 1987; Orell & Belda, 2002), presumably because certain necessary skills can only be gained by actual breeding effort (Ainley et al., 1983). Adélie penguins must learn to coordinate timing with their mates and modify their behaviours due to the constraints associated with central place foraging. The latter is a particular issue in regard to colony size, especially at large Cape Crozier, and competition for prey. As noted above, foraging requires greater energetic investment with lower return at the largest colony. In combination with improved foraging capabilities, this could help explain the improvement we detected early in the reproductive life span. At Crozier, improved performance early in life was also driven by the selective appearance of new recruits that had high reproductive performance on their initial breeding attempt (Table 4a). These individuals by-passed breeding opportunities, but not the requirement to deal with foraging competition, and achieved high levels of success when they recruited to the breeding population (e.g. Boulinier & Danchin, 1997). Delaying reproduction likely allows individuals to increase other skills, including prospects for higher quality nesting sites (Schmidt et al. In review), a pattern also documented as important in Black-legged Kittiwakes (Danchin et al., 1998). Another skill individuals at the largest colony must develop is the ability to avoid leopard seals (Ainley et al., 2005), which are more abundant and thus more of an issue at Crozier than at the two smaller colonies.

Breeding trajectories, however, were not the same across the different AFR categories or colonies. AFR was younger at the largest

colony than at the two smaller colonies, which could be due to different tactics employed by the different sexes. We were unable to investigate this, but as noted above, the earliest recruits tend to be females, while males generally recruited later at Crozier (Ainley et al., 1983; Morandini et al., in review). In addition, females suffered higher mortality, likely related to their earlier AFR, resulting in a male-biased sex ratio at older ages (Ainley & Demaster, 1980), indicating that young females may be able to find experienced older males that had lost a previous mate, which might not be occurring at the two smaller colonies. Selective appearance of delayed breeders also contributed to improvements early in the breeding life span at all three colonies, which could be due to improvements in foraging ability (Lescroël et al., 2019), particularly late in the breeding season when individuals at the larger colonies have to find sufficient food (Ballard et al., 2019).

The relationship between breeding success and YBD was inconsistent (Table 4b), such that only at the largest colony it was negative. In fact, all of the late-life metrics of performance at Royds, the smallest colony, indicated reproductive performance improved late in life due to a combination of continued individual improvement, high individual success in the final breeding attempt and selective disappearance of lower quality individuals. Similarly, high-performing individuals also outlived lower performing individuals in Cassin's auklets *Ptychoramphus aleuticus* and gained substantial benefits via double brooding (Johns et al., 2018). While the Adélie penguin does not double brood, owing to their very short seasonal window for breeding, they may be advantaged by living in an especially productive environment. Less limited to resources may allow it, as a long-lived species, flexibility in how individuals allocate resources, as a means of balancing reproductive costs against future survival. Individuals delaying reproduction until 9+ years of age reached maximum breeding success levels sooner than birds that recruited at ages 5–8, and these birds had a longer period of elevated performance throughout intermediate levels of experience. Thus, they balanced trade-offs between early breeding and late-life performance. Similar to Black-legged Kittiwakes (Aubry et al., 2009), the earliest and latest individuals to initiate breeding exhibited similar performance. Both the three and 9(+)-year-old penguin recruits failed to survive their peak reproductive period and the 4-year-old recruits exhibited only a visible decrease in performance (Figure 2). These results are interesting in that they may provide insights into the simultaneous evolution of differing reproductive strategies and senescence within one population.

5 | CONCLUSIONS

Our study is one of relatively few long-term studies of known-aged, known-breeding history, long-lived individuals that can provide insights into various hypotheses proposed to explain different age-related natural-history strategies, and appropriately control for both individual- and population-level changes driving these patterns.

On average birds began breeding earlier at the largest colony, possibly a reflection of increased prey resources or social facilitation. Depending on circumstances, we found evidence for a variety of recruitment life-history strategies, that is, constraint, selection and senescence hypotheses. Most interestingly, we were able to disentangle the costs and benefits associated with different life-history strategies, highlighting a range within a metapopulation. A younger age at first reproduction did not always translate into subsequent increased successful reproductive outcomes, indicating that in this system attempting to reproduce results in increased survival costs to the youngest but not oldest recruits. Such would be an example of how different strategies may be equally successful in a short, highly seasonal, but resource replete breeding environment, such as the Ross Sea. These results highlight the importance of longitudinal datasets and their utility for providing deeper understanding of the evolution of fundamental life-history strategies that are responsible for driving population change.

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AUTHORS' CONTRIBUTIONS

P.J.K. analysed the data; P.J.K. and K.M.D. led writing the manuscript, with significant contributions from A.L. and D.G.A. All authors contributed to the ideas, data collection, design methodology, contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.s7h44j15w> (Kappes et al., 2020).

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REFERENCES

- Agresti, A. (2003). *Categorical data analysis*. John Wiley & Sons.
- Ainley, D. G. (1978). Activity patterns and social-behavior of non-reeding Adélie penguins. *Condor*, 80, 138–146.
- Ainley, D. G., Ballard, G., Karl, B. J., & Dugger, K. M. (2005). Leopard seal predation rates at penguin colonies of different size. *Antarctic Science*, 17, 335–340. <https://doi.org/10.1017/S0954102005002750>
- Ainley, D. G., & Demaster, D. P. (1980). Survival and mortality in a population of Adélie Penguins. *Ecology*, 61, 522–530. <https://doi.org/10.2307/1937418>
- Ainley, D. G., Dugger, K. M., La Mesa, M., Ballard, G., Barton, K. J., Jennings, S., Karl, B. J., Lescroel, A., Lyver, P. O., Schmidt, A., & Wilson, P. (2018). Post-fledging survival of Adélie penguins at multiple colonies: Chicks raised on fish do well. *Marine Ecology Progress Series*, 601, 239–251. <https://doi.org/10.3354/meps12687>
- Ainley, D. G., LeResche, R. E., & Sladen, W. J. L. (1983). *Breeding biology of the Adélie Penguin*. University of California Press.
- Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management*, 74, 1175–1178. <https://doi.org/10.1111/j.1937-2817.2010.tb01236.x>
- Aubry, L. M., Koons, D. N., Monnat, J. Y., & Cam, E. (2009). Consequences of recruitment decisions and heterogeneity on age-specific breeding success in a long-lived seabird. *Ecology*, 90, 2491–2502. <https://doi.org/10.1890/08-1475.1>
- Balbontin, J., Hermosell, I. G., Marzal, A., Reviriego, M., De Lope, F., & Møller, A. P. (2007). Age-related change in breeding performance in early life is associated with an increase in competence in the migratory barn swallow *Hirundo rustica*. *Journal of Animal Ecology*, 76, 915–925. <https://doi.org/10.1111/j.1365-2656.2007.01269.x>
- Ballance, L. T., Ainley, D. G., Ballard, G., & Barton, K. (2009). An energetic correlate between colony size and foraging effort in seabirds, an example of the Adélie penguin *Pygoscelis adeliae*. *Journal of Avian Biology*, 40, 279–288. <https://doi.org/10.1111/j.1600-048X.2008.04538.x>
- Ballard, G., Schmidt, A. E., Toniolo, V., Veloz, S., Jongsomjit, D., Arrigo, K. R., & Ainley, D. G. (2019). Fine-scale oceanographic features characterizing successful Adélie penguin foraging in the SW Ross Sea. *Marine Ecology Progress Series*, 608, 263–277. <https://doi.org/10.3354/meps12801>
- Bates, D., Sarkar, D., Bates, M. D., & Matrix, L. (2007). *The lme4 package*. R package version, 2, 74.
- Berman, M., Gaillard, J.-M., & Weimerskirch, H. (2009). Contrasted patterns of age-specific reproduction in long-lived seabirds. *Proceedings of the Royal Society B: Biological Sciences*, 276, 375–382. <https://doi.org/10.1098/rspb.2008.0925>
- Boulinier, T., & Danchin, E. (1997). The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology*, 11, 505–517. <https://doi.org/10.1007/s10682-997-1507-0>
- Bouwhuis, S., Sheldon, B. C., Verhulst, S., & Charmantier, A. (2009). Great tits growing old: Selective disappearance and the partitioning of senescence to stages within the breeding cycle. *Proceedings of the Royal Society B: Biological Sciences*, 276, 2769–2777. <https://doi.org/10.1098/rspb.2009.0457>
- Bouwhuis, S., & Vedder, O. (2017). Avian escape artists? Patterns, processes and costs of senescence in wild birds. In R. P. Shefferson, O. R. Jones, & R. Salguero-Gómez (Eds.), *The evolution of senescence in the tree of life* (pp. 156–174). Cambridge University Press.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel selection: A practical information theoretic approach*. Springer Verlag.
- Caswell, H. (2001). *Matrix population models* (2nd ed.). Sinauer Associates.
- Charnov, E. L. (1997). Trade-off-invariant rules for evolutionary stable life histories. *Nature*, 387, 393–394. <https://doi.org/10.1038/387393a0>
- Clutton-Brock, T. H. (1988). *Reproductive success: Studies of individual variation in contrasting breeding systems*. University of Chicago Press.
- Curio, E. (1983). Why do young birds reproduce less well? *Ibis*, 125, 400–404. <https://doi.org/10.1111/j.1474-919X.1983.tb03130.x>
- Danchin, E., Boulinier, T., & Massot, M. (1998). Conspecific reproductive success and breeding habitat selection: Implications for the study of coloniality. *Ecology*, 79, 2415–2428. [https://doi.org/10.1890/0012-9658\(1998\)079\[2415:CRSABH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2415:CRSABH]2.0.CO;2)
- Daunt, F., Wanless, S., Harris, M. P., Money, L., & Monaghan, P. (2007). Older and wiser: Improvements in breeding success are linked to better foraging performance in European shags. *Functional Ecology*, 21, 561–567. <https://doi.org/10.1111/j.1365-2435.2007.01260.x>
- Davis, L. S. (1982). Créching behaviour of Adélie penguin chicks (*Pygoscelis adeliae*). *New Zealand Journal of Zoology*, 9, 279–286. <https://doi.org/10.1080/03014223.1982.10423856>
- Davis, L. S., & McCaffrey, F. T. (1986). Survival analysis of eggs and chicks of Adélie penguins (*Pygoscelis adeliae*). *The Auk*, 103, 379–388. <https://doi.org/10.1093/auk/103.2.379>
- Dugger, K. M., Ainley, D. G., Lyver, P. O., Barton, K., & Ballard, G. (2010). Survival differences and the effect of environmental instability on breeding dispersal in an Adélie penguin meta-population. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 12375–12380. <https://doi.org/10.1073/pnas.1000623107>
- Dugger, K. M., Ballard, G., Ainley, D. G., & Barton, K. J. (2006). Effects of flipper bands on foraging behavior and survival of Adélie penguins (*Pygoscelis adeliae*). *The Auk*, 123, 858–869. <https://doi.org/10.1093/auk/123.3.858>
- Dugger, K. M., Forsman, E. D., Franklin, A. B., Davis, R. J., White, G. C., Schwarz, C. J., Burnham, K. P., Nichols, J. D., Hines, J. E., Yackulic, C. B., Doherty, P. F., Bailey, L., Clark, D. A., Ackers, S. H., Andrews, L. S., Augustine, B., Biswell, B. L., Blakesley, J., Carlson, P. C., ... Sovern, S. G. (2016). The effects of habitat, climate, and Barred Owls on long-term demography of Northern Spotted Owls. *Condor*, 118, 57–116. <https://doi.org/10.1650/CONDOR-15-24.1>
- Forslund, P., & Pärt, T. (1995). Age and reproduction in birds - hypotheses and tests. *Trends in Ecology & Evolution*, 10, 374–378. [https://doi.org/10.1016/S0169-5347\(00\)89141-7](https://doi.org/10.1016/S0169-5347(00)89141-7)
- Froy, H., Lewis, S., Nussey, D. H., Wood, A. G., & Phillips, R. A. (2017). Contrasting drivers of reproductive ageing in albatrosses. *Journal of Animal Ecology*, 86, 1022–1032. <https://doi.org/10.1111/1365-2656.12712>
- Froy, H., Phillips, R. A., Wood, A. G., Nussey, D. H., & Lewis, S. (2013). Age-related variation in reproductive traits in the wandering albatross: Evidence for terminal improvement following senescence. *Ecology Letters*, 16, 642–649. <https://doi.org/10.1111/ele.12092>
- Gaillard, J.-M., Garratt, M., & Lemaître, J.-F. (2017). Senescence in mammalian life history traits. In R. P. Shefferson, O. R. Jones, & R. Salguero-Gómez (Eds.), *The evolution of senescence in the tree of life* (pp. 126–155). Cambridge University Press.
- Hammers, M., Richardson, D. S., Burke, T., & Komdeur, J. (2013). The impact of reproductive investment and early-life environmental conditions on senescence: Support for the disposable soma hypothesis. *Journal of Evolutionary Biology*, 26, 1999–2007. <https://doi.org/10.1111/jeb.12204>
- Johns, M. E., Warzybok, P., Bradley, R. W., Jahncke, J., Lindberg, M., & Breed, G. A. (2018). Increased reproductive investment associated with greater survival and longevity in Cassin's auklets. *Proceedings*

- of the Royal Society B: Biological Sciences, 285, 20181464. <https://doi.org/10.1098/rspb.2018.1464>
- Kappes, P. K., Dugger, K. M., Lescroël, A., Ainley, D. G., Ballard, G., Barton, K. J., Lyver, P. O., & Wilson, P. R. (2020). Data from: Age-related reproductive performance of the Adélie Penguin, a long-lived seabird exhibiting similar outcomes regardless of individual life-history strategy. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.s7h44j15w>
- Kirkwood, T. B. (1977). Evolution of ageing. *Nature*, 270, 301–304. <https://doi.org/10.1038/270301a0>
- LaRue, M. A., Ainley, D. G., Swanson, M., Dugger, K. M., Lyver, P. O., Barton, K., & Ballard, G. (2013). Climate change winners: Receding ice fields facilitate colony expansion and altered dynamics in an Adélie Penguin metapopulation. *PLoS One*, 8, e60568. <https://doi.org/10.1371/journal.pone.0060568>
- Lescroël, A., Ballard, G., Massaro, M., Dugger, K., Jennings, S., Pollard, A., Porzig, E., Schmidt, A., Varsani, A., Grémillet, D., & Ainley, D. (2019). Evidence of age-related improvement in the foraging efficiency of Adélie penguins. *Scientific Reports*, 9, 1–13. <https://doi.org/10.1038/s41598-019-39814-x>
- Lescroël, A., Dugger, K. M., Ballard, G., & Ainley, D. G. (2009). Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. *Journal of Animal Ecology*, 78, 798–806. <https://doi.org/10.1038/s41598-019-39814-x>
- Lescroël, A., Lyver, P. O., Jongsomjit, D., Veloz, S., Dugger, K. M., Kappes, P., Karl, B. J., Whitehead, A. L., Pech, R., Cole, T. L., & Ballard, G. (2020). Inter-individual differences in the foraging behavior of breeding Adélie penguins are driven by individual quality and sex. *Marine Ecology Progress Series*, 636, 189–205. <https://doi.org/10.3354/meps13208>
- Lyver, P. O., Barron, M., Barton, K. J., Ainley, D. G., Pollard, A., Gordon, S., McNeill, S., Ballard, G., & Wilson, P. R. (2014). Trends in the breeding population of Adélie Penguins in the Ross Sea, 1981–2012: A coincidence of climate and resource extraction effects. *PLoS One*, 9, e91188. <https://doi.org/10.1371/journal.pone.0091188>
- Mazerolle, M. J. (2016). *AICcmodavg: Model selection and multimodel inference based on (Q) AIC (c)*. R package version, 2.1-0. CRAN R Project.
- Mourocq, E., Bize, P., Bouwhuis, S., Bradley, R., Charmantier, A., de la Cruz, C., Drobnik, S. M., Espie, R. H. M., Herenyi, M., Hotker, H., Kruger, O., Marzluff, J., Moller, A. P., Nakagawa, S., Phillips, R. A., Radford, A. N., Roulin, A., Torok, J., Valencia, J., ... Griesser, M. (2016). Life span and reproductive cost explain interspecific variation in the optimal onset of reproduction. *Evolution*, 70, 296–313. <https://doi.org/10.1111/evo.12853>
- Newton, I. (1989). *Lifetime reproduction in birds*. Academic Press.
- Nisbet, I. C. T., & Dann, P. (2009). Reproductive performance of little penguins *Eudyptula minor* in relation to year, age, pair-bond duration, breeding date and individual quality. *Journal of Avian Biology*, 40, 296–308. <https://doi.org/10.1111/j.1600-048X.2008.04563.x>
- Nol, E., & Smith, J. N. M. (1987). Effects of age and breeding experience on seasonal reproductive success in the song sparrow. *Journal of Animal Ecology*, 56, 301–313. <https://doi.org/10.2307/4816>
- Nur, N. (1988). The cost of reproduction in birds: An examination of the evidence. *Ardea*, 55, 155–168.
- Nussey, D. H., Kruuk, L. E. B., Donald, A., Fowlie, M., & Clutton-Brock, T. H. (2006). The rate of senescence in maternal performance increases with early-life fecundity in red deer. *Ecology Letters*, 9, 1342–1350. <https://doi.org/10.1111/j.1461-0248.2006.00989.x>
- Orell, M., & Belda, E. J. (2002). Delayed cost of reproduction and senescence in the willow tit *Parus montanus*. *Journal of Animal Ecology*, 71, 55–64. <https://doi.org/10.1046/j.0021-8790.2001.00575.x>
- Pärt, T., Gustafsson, L., & Moreno, J. (1992). "Terminal investment" and a sexual conflict in the collard flycatcher (*Ficedula albicollis*). *The American Naturalist*, 140, 868–882. <https://doi.org/10.1086/285445>
- Perdeck, A. C., & Cavé, A. J. (1992). Laying date in the Coot: Effects of age and mate choice. *Journal of Animal Ecology*, 61, 13–19. <https://doi.org/10.2307/5504>
- Polito, M. J., Miller, A. K., Trivelpiece, S. G., & Trivelpiece, W. Z. (2010). Maturation increases early reproductive investment in Adélie Penguins *Pygoscelis adeliae*. *Ibis*, 152, 38–47. <https://doi.org/10.1111/j.1474-919X.2009.00971.x>
- R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.r-project.org/>
- Rattiste, K. (2004). Reproductive success in presenescent common gulls (*Larus canus*): The importance of the last year of life. *Proceedings of the Royal Society of London Series B: Biological Sciences*, 271, 2059–2064. <https://doi.org/10.1098/rspb.2004.2832>
- Reed, T. E., Kruuk, L. E. B., Wanless, S., Frederiksen, M., Cunningham, E. J. A., & Harris, M. P. (2008). Reproductive senescence in a long-lived seabird: Rates of decline in late-life performance are associated with varying costs of early reproduction. *The American Naturalist*, 171, E89–E101. <https://doi.org/10.1086/524957>
- Sæther, B. (1990). Age-specific variation in reproductive performance of birds. In D. M. Power (Ed.), *Current ornithology* (pp. 251–283). Plenum Publishing Corporation.
- Schmidt, A., Ballard, G., Lescroël, A., Dugger, K., Jongsomjit, D., Elrod, M., & Ainley, D. (In review). The influence of subcolony-scale nesting habitat on reproductive success of Adélie penguins. *Scientific Reports*.
- Sladen, W. J. (1958). *The Pygoscelid penguins: I. Methods of study. II. The Adélie penguin*. HMSO.
- Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.
- van de Pol, M., & Verhulst, S. (2006). Age-dependent traits: A new statistical model to separate within- and between-individual effects. *The American Naturalist*, 167, 766–773. <https://doi.org/10.1086/503331>
- Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York Inc. <https://ggplot2-book.org/>
- Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist*, 100, 687–690. <https://doi.org/10.1086/282461>
- Zhang, H., Vedder, O., Becker, P. H., & Bouwhuis, S. (2015). Age-dependent trait variation: The relative contribution of within-individual change, selective appearance and disappearance in a long-lived seabird. *Journal of Animal Ecology*, 84, 797–807. <https://doi.org/10.1111/1365-2656.12321>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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