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Age-related variation in non-breeding foraging behaviour and carry-over effects on fitness in an extremely long-lived bird

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Abstract

1. Senescence has been widely documented in wild vertebrate populations, yet the proximate drivers of age-related declines in breeding success, including allocation trade-offs and links with foraging performance, are poorly understood. For long-lived, migratory species, the non-breeding period represents a critical time for investment in self-maintenance and restoration of body condition, which in many species is linked to fitness. However, the relationships between age, non-breeding foraging behaviour and fitness remain largely unexplored.

2. We performed a cross-sectional study, investigating age-related variation in the foraging activity, distribution and diet of an extremely long-lived seabird, the wandering albatross *Diomedea exulans*, during the non-breeding period. Eighty-two adults aged 8–33 years were tracked with geolocator-immersion loggers, and body feathers were sampled for stable isotope analysis. We tested for variation in metrics of foraging behaviour and linked age-related trends to subsequent reproductive performance.

3. There was an age-related decline in the number of landings (a proxy of foraging effort) during daylight hours, and a decrease in body feather $\delta^{13}C$ values in older males but not females, yet this did not accompany an age-related shift in distributions. Males conducted fewer landings than females, and the sexes showed some spatial segregation, with males foraging further south, likely due to their differential utilization of winds.

4. Although younger (<20 years) birds had higher foraging effort, they all went on to breed successfully the following season. In contrast, among older (20+ years) birds, individuals that landed more often were more likely to defer breeding or fail during incubation, suggesting they have lower foraging success.

5. As far as we are aware, this is the first demonstration of an age-specific carry-over effect of foraging behaviour in the non-breeding period on subsequent reproductive performance. This link between foraging behaviour and fitness in late but not early adulthood indicates that the ability of individuals to forage efficiently outside the breeding period may be an important driver of fitness differences in old age.

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1 | INTRODUCTION

Age-related variation in demographic traits is well documented in long-lived vertebrates (Jones et al., 2008; Nussey, Froy, Lemaitre, Gaillard, & Austad, 2013). Survival and reproductive performance generally increase throughout early life, stabilize during early- to mid-adulthood, and decline in old age due to senescence (Clutton-Brock, 1988; Froy, Phillips, Wood, Nussey, & Lewis, 2013), which is the process of progressive deterioration in physiological and molecular function (Monaghan, Charmantier, Nussey, & Ricklefs, 2008). Identifying the selective forces shaping variation in fitness with old age is key to understanding the evolution of senescence (Nussey et al., 2013), particularly in the context of life-history evolution (disposable soma theory; Kirkwood & Rose, 1991; Lemaître et al., 2015). Life-history theory dictates that animals must allocate acquired energy either for somatic functions such as growth and maintenance, or for reproduction (Cody, 1966), resulting in a trade-off between investment in current or future reproduction, and survival (Stearns, 1992). As individuals are limited in the amount of energy they can extract from their environment across their lifetime (Kirkwood & Rose, 1991), investment in current reproduction comes at a cost to investment in somatic repair; indeed, there is empirical evidence that high allocation to reproduction or growth early in life is associated with earlier or faster senescence (Lemaître et al., 2015; Reed et al., 2008).

Studies of senescence in wild populations have tended to focus on age-related changes in fitness components (Nussey et al., 2013); however, there has been increased emphasis on the proximate drivers, for example physiological, morphological or behavioural traits (Angelier, Shaffer, Weimerskirch, & Chastel, 2006; Lecomte et al., 2010; Nussey et al., 2011; Patrick & Weimerskirch, 2015). As the ability to acquire energy from the surrounding environment determines the resources an individual can allocate between reproduction and self-maintenance, an individual's foraging strategy likely plays a key role in determining its fitness (Daunt, Wanless, Harris, Money, & Monaghan, 2007; Forslund & Pärt, 1995; Stephens & Krebs, 1986). Young individuals generally have inadequate foraging skills and lack experience, and foraging performance improves during early life as they learn how and where to forage (Daunt, Afanasyev, Adam, Croxall, & Wanless, 2007; de Grissac, Börger, Guitteaud, & Weimerskirch, 2016; Yoda, Kohno, & Naito, 2004). This increase in foraging efficiency is likely to be eventually offset by a decrease in muscular or physiological function (MacNulty et al., 2009), often leading to declines in foraging performance (Catry, Phillips, Phalan, & Croxall, 2006; Lecomte et al., 2010; MacNulty et al., 2009). However, there are still comparatively few studies of changes in foraging parameters with old age, and in contrast with demographic traits (Nussey et al., 2013), many fail to find an effect (reviewed in Table 1).

Crucially, little is known about how age shapes the foraging behaviour of wild animals outside the breeding season (see Table 1), likely due to the challenges associated with tracking the movements of individuals of known ages for long periods of time (Phillips, Lewis, González-Solís, & Daunt, 2017). Nevertheless, different stages of the annual cycle are inextricably linked, and there is widespread evidence that carry-over effects (COEs), defined as events in one season that influence individual performance in a subsequent season, drive variation in fitness within wild animal populations (Harrison, Blount, Inger, Norris, & Bearhop, 2011; Marra, Hobson, & Holmes, 1998). Indeed, studies have demonstrated a link between food availability, habitat use, diet, migratory schedules, foraging behaviour and body condition outside the breeding season to subsequent breeding performance in wide range of taxa (e.g., Fayet et al., 2016; Marra et al., 1998; Sorensen, Hipfner, Kyser, & Norris, 2009; reviewed in Harrison et al., 2011). For migratory species which may undertake physically demanding movements to spend winter in more productive areas, the non-breeding period represents a critical time for animals to restore body condition lost during the previous breeding season (Newton, 2010), and repair somatic tissues. For example in birds, feather moult is necessary to maintain flight efficiency, but as it is energetically demanding it usually occurs outside of the breeding period (Payne, 1972; Prince, Weimerskirch, Huin, & Rodwell, 1997). As far as we are aware, the COEs of non-breeding behaviour on subsequent fitness have not been explored in an age-related context. However, it might be expected that older individuals less able to acquire sufficient resources for somatic maintenance during this period would be in poorer physical condition, with negative downstream effects such as breeding failure or reduced survival (Harrison et al., 2011).

Here, we performed a cross-sectional study over 2 years to investigate the links between age, migratory ecology and reproductive success in an extremely long-lived seabird, the wandering albatross *Diomedea exulans*. The life-history traits of wandering albatross are well-established: it has a life span of 50+ years, breeds biennially with a prolonged breeding season (up to a year) and experiences a gradual decline in various indices of reproductive performance from 20 to 25 years onwards (Froy, Lewis, Nussey, Wood, & Phillips, 2017; Froy et al., 2013; Pardo, Barbraud, & Weimerskirch, 2013). A study of changes in foraging behaviour of incubating birds from the south Indian Ocean (Crozet Islands) found that males, but not females, travel further and forage further south with increasing age, and have lower foraging activity (Lecomte et al., 2010). In contrast, no age-related pattern was detected in the foraging behaviour of breeding birds from South Georgia, south Atlantic Ocean (Froy et al., 2015), despite similar patterns of reproductive senescence (Froy et al., 2013). During non-breeding, birds from the Indian Ocean disperse

TABLE 1 Summary of studies that investigate changes in foraging behaviour of wild populations in later life

Species	Site	Season	Behaviour, statistical significance and direction of change	Relationship	Sex-specific	Reference
Vertebrates – Birds						
Audouin's gull *Larus audouinii*	Ebro Delta	Br (I)	Diet (from $\delta^{13}C$ [↑] and $\delta^{15}N$ [↓]).	Linear	NT	Navarro et al. (2010)
Cory's shearwater *Calonectris borealis*	Selvagens Is.	Br (I)	No. landings daylight (*X*) and darkness (↓); time on water and trip duration (*X*).	Factor (26+)	Both	Catry et al. (2011)
Grey-headed albatross *Thalassarche chrysostoma*	South Georgia Is.	Br (I)	Trip duration and mass gain (↓).	Factor (35+)	♂	Catry et al. (2006)
King penguin *Aptenodytes patagonicus*	Crozet Is.	Br (CR)	Dive depth and duration (*X*), PDBA (↓).	Factor (8+)	Both	Vaillant et al. (2012)
			Dive depth, $\delta^{15}N$, trip duration and prey pursuits (↑).		♀	Vaillant et al. (2013)
			Mass gain (↑), $\delta^{13}C$ (*X*).		Both	
Little penguin *Eudyptula minor*	Phillip Is.	Br (CR)	Dive duration and effort[b] (↑), foraging area (↓), distance from shore (↓), dive depth (*X*), $\delta^{13}C$ and $\delta^{15}N$ (*X*)	Factor (11+)	Both	Zimmer et al. (2011) and Pelletier, Chiaradia, Kato, and Ropert-Coudert (2014)
Brünnich's guillemot *Uria lomvia*	Coats Is.	Br (CR)	Dive depth, shape and surface interval (*X*)	n/a	Both	Elliott et al. (2015)
		Br (I + CR)	Dive PDBA (↑)	Quadratic	NT	Cunningham et al. (2017)
Wandering albatross *Diomedea exulans*	Crozet Is.	Br (I)	Foraging latitude (↓) and range (↑), trip duration (*X*), distance travelled (↑), $\delta^{13}C$ (↓), $\delta^{15}N$ (*X*), time on water (*X*) and in flight (↑).	Linear	♂	Lecomte et al. (2010) and Jaeger et al. (2014)
		NB	$\delta^{13}C$ and $\delta^{15}N$ (↓).	Linear	Both	Jaeger et al. (2014)
	South Georgia Is.	Br (I + CR)	Foraging latitude, trip duration, distance travelled, no. landings and time on water (*X*)	n/a	Both	Froy et al. (2015)
Vertebrates – Mammals						
Bottlenose dolphin *Tursiops* cf. *aduncus*	Shark Bay	BR	Time acquiring, travelling and foraging with tool (*X*)	n/a	♀ (♂ NT)	Patterson, Krzyszczyk, and Mann (2016)
Grey wolf *Canis lupus*	Yellowstone	BR	Predatory performance (↓)	Quadratic	Both	MacNulty et al. (2009).
Moose *Alces alces*	Isle Royale	Winter	Habitat use (distance from shore; ↓)	Factor (10+)	Both	Montgomery, Vucetich, Peterson, Roloff, and Millenbah (2013)
Northern elephant seal *Mirounga angustirostris*	Año Nuevo	Post-breeding	Foraging time and distance (*X*)[a], dive structure (*X*)[a]	n/a	♀ (♂ NT)	Hassrick et al. (2013)
		Post-moult	Foraging time and distance (*X*), dive structure (✓)[a]	Linear	♀ (♂ NT)	

(Continues)

TABLE 1 (Continued)

Species	Site	Season	Behaviour, statistical significance and direction of change	Relationship	Sex-specific	Reference
Soay sheep *Ovis aries*	St Kilda Is.	Year-round	Home range size and quality (♂=↑ & ♀=↓)	Nonlinear	♀ cf. ♂	Hayward et al. (2015)
Southern elephant seal *Mirounga leonina*	Kerguelen Is.	Year-round	$\delta^{13}C$ (↓)	Linear	Both	Authier, Bentaleb, Ponchon, Martin, and Guinet (2012)
Invertebrates						
European honeybee *Apis mellifera*	Algonquin Park	NA	Rate of food delivery (↓) Trip duration (↑)	Quadratic Linear	♀	Dukas (2008)

Br, Breeding; CR, chick-rearing; NB, non-breeding.

Where age-related changes are statistically significant, the direction of change is shown by an arrow (↑ or ↓), where specified (✓), where not specified. Non-significant changes are shown by a cross (✗).

Factor = differences tested by categorical variable age class (with the oldest age category indicated in parentheses); Linear, nonlinear or quadratic = relationships with age included as a continuous variable, n/a = not applicable. ♂ = only significant in males, ♀ = only significant in females, NT = sex differences not tested, ♀ cf. ♂ = different results in males and females, Both = similar results in males and females.

For nonlinear relationships, the direction is indicated from the middle to oldest age categories.

[a]Foraging time, distance and dive structure = principal component of behavioural variables, [b]dive duration and post-dive duration, PDBA= partial dynamic body acceleration.

throughout the Southern Ocean (Weimerskirch, Delord, Guitteaud, Phillips, & Pinet, 2015; Weimerskirch & Wilson, 2000) and appear to forage further south with age, as documented through changes in stable isotope values of feathers moulted on non-breeding grounds (Jaeger et al., 2014). However, much less is known about age-related changes in the distributions and foraging behaviour of non-breeding birds from South Georgia.

We made serial deployments of geolocator-immersion loggers and sampled feathers for stable isotope analysis to test for age- and sex-related variation in the non-breeding distribution, diet and activity patterns of wandering albatrosses from South Georgia. We also determined whether there was age-related variation in breeding metrics within our sample of tracked birds, and linked age-related changes in foraging behaviour to subsequent reproductive performance. We predicted that old birds would (1) have reduced activity, and forage further south than younger birds, based on the results of previous studies during breeding (Table 1; Catry et al., 2006; Catry, Granadeiro, Ramos, Phillips, & Oliveira, 2011; Lecomte et al., 2010). We also predicted that (2) older birds would have a lower probability of breeding successfully in the following season (Froy et al., 2013), and (3) that age-related trends in foraging behaviour would be linked to lower subsequent breeding success in older birds.

2 | MATERIALS AND METHODS

2.1 | Study site and data collection

Fieldwork was carried out at a long-term wandering albatross study colony on Bird Island, South Georgia (54°00′ S, 38°03′ W), where chicks have been ringed annually since 1972. All of the breeding population (700–800 pairs in recent years) is ringed and the majority (*c.* 80%) of birds are of known age; those with an unknown age were assigned a conservative minimum age of 7 years when first ringed as breeding adults (Weimerskirch, 1992). Regular monitoring of nests has been conducted since 1980, and breeding success is determined from daily visits during the laying, hatching and fledging periods, and weekly visits at other times. Geolocator-immersion loggers (MK3-5 and MK7, 3.5–9 g; BAS, Cambridge, UK) were attached with a cable-tie to the metal rings of breeding adults between February 2004 and January 2009 and retrieved between November 2008 and January 2011, as part of a long-term tracking programme. The data included below correspond to two consecutive non-breeding periods (2008 and 2009) and the subsequent breeding seasons (2009 and 2010). Body feathers for stable isotope analyses were collected from a subset of individuals at device retrieval, and some loggers failed to record immersion data, and thus, sample sizes vary (Table S1). Birds were sexed from field observations (size and plumage dimorphism, copulatory position) or using molecular methods (Froy et al., 2013).

2.2 | Data processing

Light data were processed using the BASTRAK software suite (BAS, Cambridge, UK) providing two positions per day with a mean error

of 186 ± 114 km (Phillips, Silk, Croxall, Afanasyev, & Briggs, 2004). Locations with interruptions around sunrise and sunset and periods around the equinox (3–4 weeks) were excluded, when latitude cannot be estimated reliably. Loggers tested for saltwater immersion every 3 s, storing the sum of positive tests at the end of each 10-min period, providing a value ranging from 0 (continuously dry) to 200 (continuously wet). A wet bout was defined as a 10-min period during which at least one wet event was recorded, and a flight bout as a continuous 10-min period spent entirely dry. For each individual, the non-breeding period was defined as the time from the start of outward migration to return to the colony and was derived from location and immersion data (see Appendix S1 for details). Take-offs and landings are energetically expensive in wandering albatrosses (Shaffer, Costa, & Weimerskirch, 2001; Weimerskirch, Guionnet, Martin, Shaffer, & Costa, 2000), and most prey are detected in flight and caught just after landing (Weimerskirch, Wilson, & Lys, 1997). Consequently, the following activity metrics were chosen to represent foraging effort: the proportion of time spent in flight (proportion of time spent dry), the duration of flight (dry) bouts in hours and the number of landings (wet bouts). Loggers did not record the exact number of landings in a given 10-min interval, so these indices used here should be considered as minimum values (see Appendix S1 for details). Metrics were averaged (flight bout duration) or summed (number of landings) for each individual daylight and darkness period, as albatross activity patterns vary according to photoperiod (Mackley et al., 2010; Phalan et al., 2007).

Stable isotope analysis was carried out on three body feathers per individual, providing information on carbon source (i.e., foraging habitat, δ^{13}C) and trophic level (δ^{15}N) of prey at the time of feather moult (Phillips, Bearhop, McGill, & Dawson, 2009). As wandering albatrosses gradually replace their plumage at the non-breeding grounds (Battam, Richardson, Watson, & Buttemer, 2010; Prince et al., 1997), multiple feathers were analysed to better represent possible shifts in habitat during this period (Jaeger, Blanchard, Richard, & Cherel, 2009). Feathers were prepared following standard procedures and stable isotope ratios were determined by continuous flow mass spectrometry (see Appendix S1 for details). To determine whether there was a relationship between latitude and δ^{13}C, as found in the Indian Ocean (Jaeger, Lecomte, Weimerskirch, Richard, & Cherel, 2010), we calculated the correlation between the average latitude and δ^{13}C values for each bird. We also mapped the distribution of birds with the highest (>−17‰) and lowest (<−19‰) mean δ^{13}C values to visualize isotopic variation in geographic space (see Figure S1).

2.3 | Data analysis

2.3.1 | Age-related variation in fitness

We first compared breeding success and probability between tracked birds and the rest of the monitored population to determine whether our sample of tracked birds was demographically representative. Generalized linear models (GLMs) with a binomial error distribution were run separately for breeding probability and success in each year. The significance of the covariate "treatment" (tracked or untracked) was determined with likelihood ratio tests (LRTs; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We subsequently determined whether there was age-related variation in fitness metrics in our sample of tracked birds, which would permit us to link foraging behaviour to variation in fitness. We constructed separate GLMs with the following parameters as response variables, which took a Gaussian distribution, unless otherwise specified: (1) date of arrival at the breeding colony, (2) breeding probability (binomial), (3) lay date and (4) breeding success (successfully fledged a chick or not, binomial). In each model, the continuous variable age and the factors sex, year and previous breeding outcome (success or incubation failure), as well as the interaction between age and sex to control for differential ageing of males and females (Froy et al., 2013; Pardo et al., 2013), were included as covariates. Models were run separately for the full sample of tracked birds, and for the reduced sample with immersion data. Previous studies have determined that breeding success follows a quadratic relationship with age (Froy et al., 2013; Pardo et al., 2013); however, we could not test this due to sample size considerations. We also ran a GLM investigating the effect of year, sex, age and their interaction on the breeding success of untracked birds. This larger sample size permitted the inclusion of quadratic and cubic relationships with age (see Table S2). For each model set, every possible combination of variables was included and models ranked according to Akaike information criterion (AIC) values, such that the best model was the one with the lowest value (Burnham & Anderson, 2004). If multiple models were within two AIC units of the best-supported model, the most parsimonious model (with fewer parameters) was chosen (Arnold, 2010; Burnham & Anderson, 2004).

2.3.2 | Age-related variation in non-breeding foraging behaviour

To determine whether albatrosses differed in their spatial distributions with age, sex and year of tracking, we used a randomization procedure which compares spatial distributions between pairwise groups of individuals (Clay et al., 2016). For ease of comparison, birds were split into three age classes which roughly represent the ages at which an increase, plateau and decrease in breeding success occur in this population (Froy et al., 2013): young (6–14 years), middle-aged (15–24 years) and old (25+ years) birds. We created utilization distribution (UD) kernels to represent core (50% UD) and general use areas (95% UD) for each individual using a grid size of 50 km and smoothing factor of 200 km (Phillips et al., 2004), and merged them to assign equal weighting. Bhattacharyya's affinity (BA), a metric of similarity between two distributions ranging from 0 (no similarity) to 1 (identical UDs), was used as a measure of spatial overlap (Fieberg & Kochanny, 2005). We randomly reassigned bird identities and calculated overlap scores for 1,000 iterations, maintaining the same ratios observed. p-values were determined as the proportion of randomized overlaps that were smaller than the observed. This method was validated using another metric of spatial overlap, the UD overlap

index (UDOI, Fieberg & Kochanny, 2005), which produced similar results (Table S3). Kernel analysis and spatial overlaps were run in the R package ADEHABITATHR (Calenge, 2006).

We ran a suite of models investigating changes in foraging behaviour by age and sex, with the following metrics as response variables in separate models: (1) δ^{13}C and (2) δ^{15}N values in feathers; (3) longitude, (4) latitude, (5) distance travelled per day, (6) distance from the colony, and (7) the size of 50% and (8) 95% UDs, generated from the tracking data; and the number of landings during (9) daylight and (10) darkness, flight bout duration during (11) daylight and (12) darkness, and the proportion of time spent in flight during (13) daylight and (14) darkness, from the activity data. A Gaussian distribution was used for all variables except landings, for which Poisson distributions were used. These models also included an offset of the number of daylight or darkness hours to control for seasonal and latitudinal variation in photoperiod. LMs were used to examine variation in the size of home ranges, as there was only one value per individual year. Generalized linear mixed models (GLMMs) were used for all other variables, with bird identity included as a random effect. The area of 50% and 95% UDs and the durations of flight bouts were log transformed, and distance variables were square-root transformed to conform to the assumption of normality, while proportions were logit transformed. Each model included the following covariates: age as a continuous variable (linear, quadratic and cubic), and the categorical variables sex, tracking year, previous breeding outcome and the interaction between age and sex to control for sex-specific differences with age (Lecomte et al., 2010). Model selection was conducted using AIC, as specified above.

2.3.3 | Linking age-related variation in foraging behaviour with fitness

In a third set of models, we investigated the link between non-breeding behaviour and fitness, only considering variables for which there was a significant change with age. We hypothesized that birds that defer breeding or fail during early breeding were in poorer condition on return to the colony than birds that went on to breed successfully (Weimerskirch, 1992). However, as no birds aged <20 years failed, it was not possible to test the influence of age on the relationship between foraging behaviour and subsequent fitness in the full

dataset because of the unbalanced distribution of breeding success with respect to age. As an alternative, we subsampled the dataset to include just individuals aged 20+ years and ran GLMs on each behaviour which showed an age-related trend separately, due to differences in sample sizes between datasets (Table S1). The probability of successful breeding (1 = chick fledged and 0 = egg failure or breeding deferral; the single individual that failed in chick-rearing was excluded as this was more likely to reflect factors other than body condition at return) was included as the response variable, taking a binomial distribution. The mean individual value of each foraging metric was included as a covariate along with age, and their two-way interaction. Where we previously found a significant effect of sex on that behaviour, the covariate sex was also included. The most parsimonious model was chosen through model selection, as above. For all models conducted, we checked for collinearity between covariates using generalized variance inflation factors (GVIF; Zuur et al., 2009). All analyses were conducted in R v. 3.3.1 (R Core Team, 2014), and all linear models were run using the R package LME4 (Bates et al., 2015). Unless otherwise reported, data are presented as a mean ± standard error (SE).

3 | RESULTS

3.1 | Age-related variation in fitness

We tracked the non-breeding migrations of 82 adults and obtained immersion and stable isotope data for 49 and 48 individuals, respectively (Table S1). There was a significant relationship between age and subsequent breeding success in both the full sample of tracked birds (Table 2, Figure 1a) and the reduced sample with immersion data (Figure 1b), but no effect of age on arrival date, breeding probability or laying date (Table 2). Birds aged 20+ years were more likely to fail (Figure 1a, Table 2). For the rest of the monitored population not tracked as part of our study, there was a significant quadratic effect of age on breeding success, with lower breeding success in younger (<15 years) and older birds (30+ years) (Figure 1c, Table S2; Froy et al., 2013). We found no interaction between age and sex in either tracked or untracked birds (Tables 2 and S2).

In neither year did we find a significant difference in breeding probability (2009: $\chi^2_1 = 0.13$, $p = .717$; 2010: $\chi^2_1 = 2.92$, $p = .087$)

TABLE 2 Summary of the most parsimonious models explaining variation in the arrival date at the colony and in subsequent breeding parameters for non-breeding wandering albatrosses

| | | Predictor variables | | | | | |
Response	N	Age	Sex	Age:Sex	Year	Previous breed	ΔAICc
Arrival date	69	–	X	–	–	–	0.00
Breeding probability	82	–	–	–	X	–	0.42
Lay date	32	–	–	–	–	–	0.00
Breeding success	73	X	–	–	X	X	0.00

Previous breed = a factor denoting previous breeding outcome (success or fail); N = number of individuals; X = predictor variables retained and − = not retained, in the most parsimonious models; ΔAICc = change in Akaike information criterion, corrected for small sample sizes, from the best-supported model.
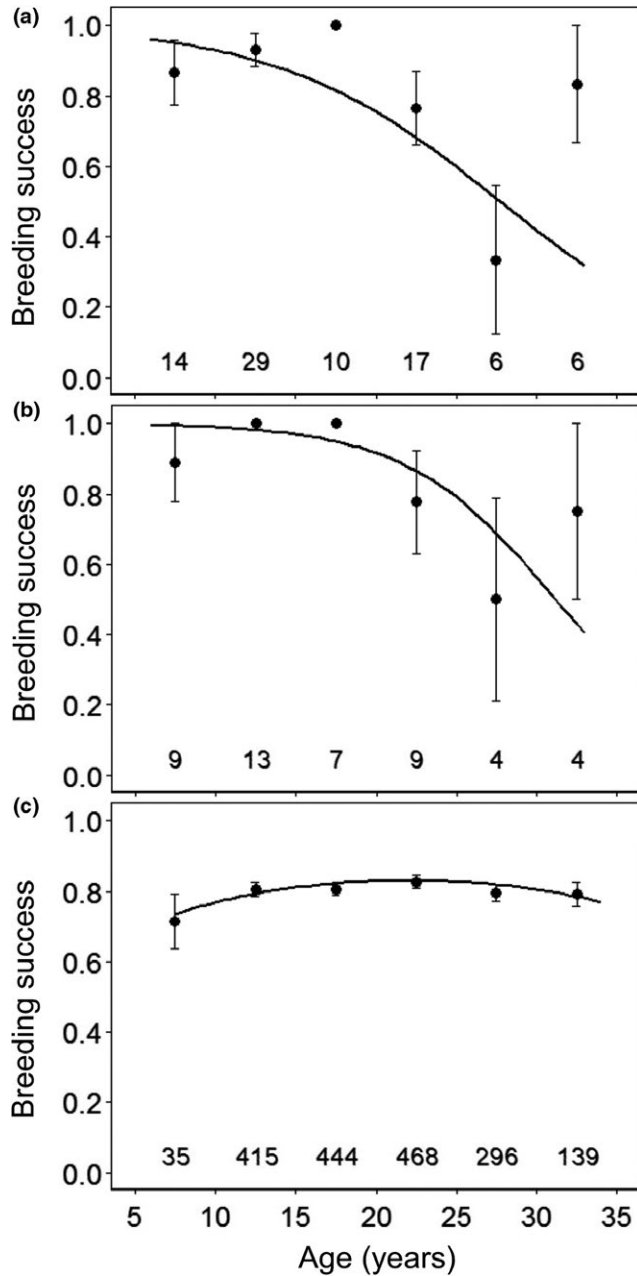
FIGURE 1 Relationship between age and breeding success for wandering albatrosses from Bird Island, South Georgia, for the 2009 and 2010 seasons together, for: (a) all birds tracked with geolocator-immersion loggers (*n* = 82), (b) tracked birds with immersion data (*n* = 46) and (c) untracked birds (*n* = 1,797). The solid black line shows the ageing pattern predicted by the most parsimonious model. For ease of plotting, the mean ± *SE* breeding success is shown for each 5-year age bin, along with the sample size

or success (2009: χ_1^2 = <0.01, *p* = .970; 2010: χ_1^2 = 0.20, *p* = .659) between tracked and untracked birds. A greater proportion of tracked birds attempted to breed in 2009 (0.94 ± 0.04) than in 2010 (0.77 ± 0.07) (Table 2), reflecting annual differences at the population level (breeding probability of untracked birds ± *SE* in 2009: 0.93 ± 0.01; 2010: 0.87 ± 0.01). Breeding success was also significantly higher in 2009 (0.87 ± 0.05) than in 2010 (0.77 ± 0.08)

(Table 2), also reflecting annual differences at the population level (2009: 0.87 ± 0.01; 2010: 0.73 ± 0.01), and was higher for previously successful breeders (0.89 ± 0.04) than birds which failed during incubation the previous season (0.75 ± 0.16) (Table 2). While females returned to the breeding colony significantly later than males (mean ± *SD*: 1 December ± 8 days and 26 November ± 5 days, respectively), there were no sex differences in breeding probability, laying date or breeding success (Table 2).

## 3.2 | Age-related variation in foraging behaviour

3.2.1 | Spatial distributions

The tracked birds dispersed across the Southern Ocean with core areas mainly in the southwest Atlantic and southeast Pacific Oceans: around the Patagonian Shelf break, in the Drake Passage and in the Humboldt Current off the coast of southern Chile (Figure 2). They also used waters around the Prince Edward Islands in the southwest Indian Ocean and around the Chatham Rise, east of New Zealand.

We found no effect of age on any spatial variable (Tables 3 and 4); indeed, there was no evidence of spatial segregation by age class for males and females pooled (Figure 2, Table 3), nor when tested separately (Table S4). However, males and females were more spatially segregated than expected by chance (Figure 3, Table 3). Females migrated further east than males (by 32.4°) and so were more likely to use the Indian Ocean, whereas males were more likely to use the Pacific Ocean (Figures 3 and 4f); yet, there was no difference between males and females in the median distance from the colony (Table 4). Females used waters on average 2.5° further north (Table 4, Figure 4g), and sexual segregation of core areas appeared to be driven predominantly by latitudinal differences (Figure 3). Males used a region in the southern Humboldt Current and the Drake Passage, whereas females were more likely to use the Patagonian Shelf and the Brazil-Falklands Confluence. Birds were distributed further from the colony in 2008 (3,728 ± 283 km) than in 2009 (2,926 ± 254 km), and previously failed breeders were distributed further east than previously successful breeders (by 32.9°), but there were no differences in any other spatial metrics by year or by previous breeding outcome (Tables 3 and 4, Figure S2).

3.2.2 | Stable isotopes

Despite large variability in δ^{13}C values, there was a significant interaction between age and sex, whereby males exhibited an age-related decline in δ^{13}C feather values from 20+ years onwards (modelled change of −1.37 ± ‰ from 9 to 33 years), but females did not (Table 4, Figure 4a). Although we found no correlation between the average δ^{13}C values and latitude of each bird (Pearson's correlation *r* = .27, *df* = 47, *t* = 1.89, *p* = .06), birds with high (>−17‰) δ^{13}C values appeared to use more northerly waters (around the Subtropical Front) and forage closer to the coast
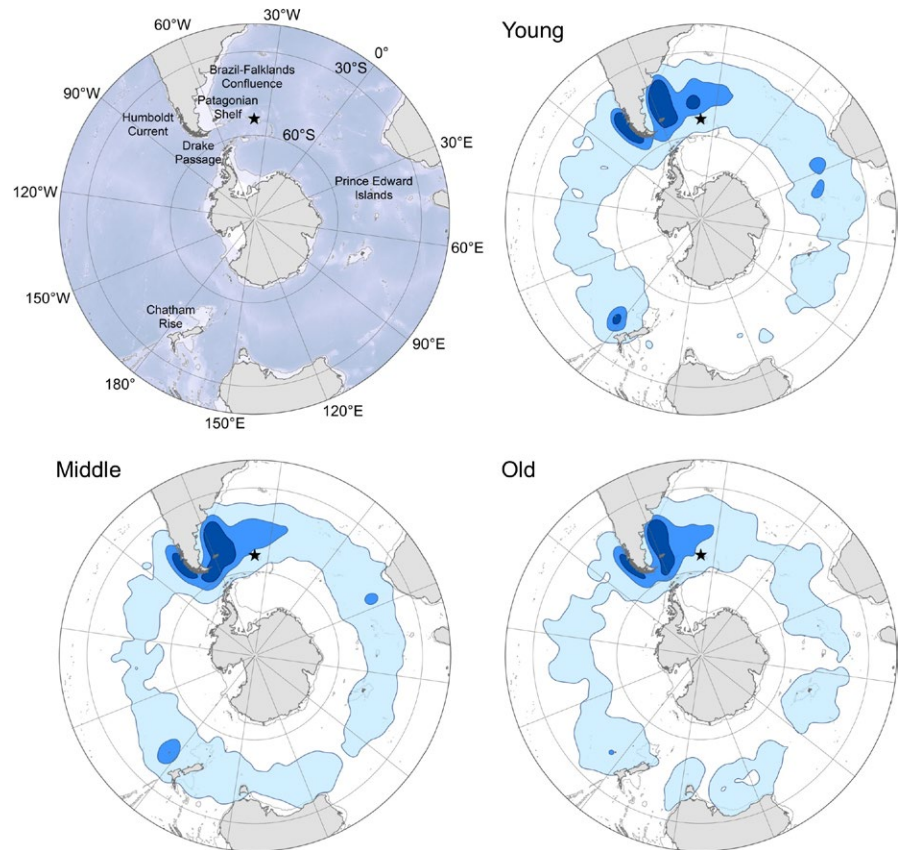
FIGURE 2 Map of study region and core (25% and 50%) and general use (95%) utilization distributions (UDs) of young (6–14 years, *n* = 27), middle-aged (15–24 years, *n* = 29) and old (25+ years, *n* = 17) wandering albatrosses tracked with geolocator-immersion loggers from Bird Island (black star), South Georgia during non-breeding

TABLE 3 Observed and randomized spatial overlap (Bhattacharyya's affinity, BA) of core (50%) and general use (95%) utilization distributions (UDs) of wandering albatrosses, compared between age classes, sex and tracking year

Class	50%			95%		
	Observed	Randomized	*p*	Observed	Randomized	*p*
Age (both sexes)	—	—	—	—	—	—
Y vs. M	0.45	0.43 ± 0.03	.95	0.86	0.87 ± 0.02	.14
M vs. O	0.44	0.42 ± 0.03	.91	0.85	0.85 ± 0.03	.53
Y vs. O	0.42	0.40 ± 0.04	.79	0.84	0.84 ± 0.03	.46
Sex (all ages)	0.38	0.44 ± 0.02	**.002**	0.81	0.89 ± 0.02	**<.001**
Year	0.42	0.44 ± 0.02	.13	0.87	0.89 ± 0.01	.14

Y, young (6–14 years); M, middle-aged (15–24 years); O, old (25+ years).
Randomized overlaps are shown as a median ± interquartile range. *P* represents the proportion of randomized overlaps that were smaller than the observed. Significant differences (*p* < .05) are shown in bold.

(within the 1,000 m isobath) (Figure S1), whereas birds with low (<−19‰) δ^{13}C values appeared to forage further south in association with the Polar Front, and in deeper, pelagic waters. In contrast, we found no differences in δ^{15}N values with age nor sex (Table 4, Figure 4b).

3.2.3 | Activity patterns

There was a significant linear decrease with age in the number of landings during daylight (modelled change of −0.63 landings per day [15%] from 9 to 33 years), for both males and females (Table 4, Figure 4c), but there was no effect of age on the other five metrics (Table 4). Males landed less often than females during both daylight (by 0.27 landings per day) and darkness (by 0.35 landings per day)

(Table 4, Figure 4c,e), yet there were no sex differences in the length of flight bouts or proportion of time spent flying (Table 4). Birds tracked in 2009 conducted a greater number of landings during daylight than in those tracked in 2008 (by 0.23 landings per day), yet there were no differences in any other activity metrics by year nor by previous breeding outcome (Table 4).

3.3 | Linking age-related variation in foraging behaviour with fitness

As all birds <20 years bred successfully the following season (Figure 1b), we investigated the relationship between the two foraging metrics that showed a decrease with age (δ^{13}C and number of landings during daylight) and the probability of successful breeding

TABLE 4 Summary of the most parsimonious models explaining variation in the foraging behaviour of non-breeding wandering albatrosses

Category	Response variable	N	Covariates								ΔAICc
			Age	Age^2	Sex	Age:Sex	Age^2:Sex	Year	Previous breed	
Moulting habitats	δ^{13}C (‰)	48	X	X	X	X	X	—	—	0.99
	δ^{15}N (‰)		—	—	—	—	—	—	—	1.84
Space use	Latitude (°)	82	—	—	X	—	—	—	—	1.80
	Longitude (°)		—	—	X	—	—	—	X	0.00
	Distance travelled per day (km)		—	—	—	—	—	—	—	0.00
	Distance to colony (km)		—	—	—	—	—	X	—	1.57
	Area of 50% UD (km^2)		—	—	—	—	—	—	—	0.17
	Area of 95% UD (km^2)		—	—	—	—	—	—	—	0.00
Activity patterns	No. landings light	49	X	—	X	—	—	X	—	0.00
	No. landings dark		—	—	X	—	—	—	—	0.00
	Flight bout length light (hrs)		—	—	—	—	—	—	—	0.85
	Flight bout length dark (hrs)		—	—	—	—	—	—	—	0.48
	Proportion time in flight light		—	—	—	—	—	—	—	0.00
	Proportion time in flight dark		—	—	—	—	—	—	—	0.00

All are (generalized) linear mixed effects models ([G]LMMs) with bird identity included as a random effect, except for the area of 50% and 95% utilization distributions (UDs) which are linear models (LMs).

Previous breed = a factor denoting previous breeding outcome (success or fail); N = number of individuals; X = predictor variables retained and − = not retained, in the most parsimonious models; ΔAICc = change in Akaike information criterion, corrected for small sample sizes, from the best-supported model. Both the cubic relationship with age and its interaction with sex were not significant for all models and so are not shown.
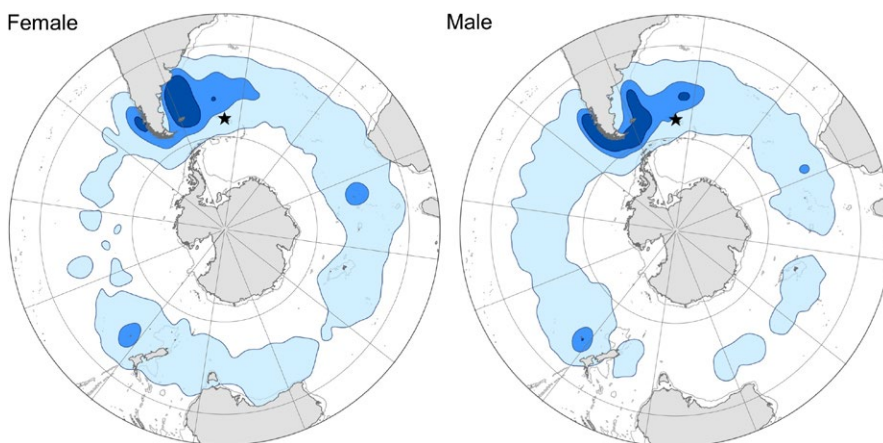
Female   Male

FIGURE 3 Sex differences in core (25% and 50%) and general use (95%) utilization distributions (UDs) of female and male wandering albatrosses tracked with geolocator-immersion loggers from Bird Island (black star), South Georgia during non-breeding

in the following season, just in birds aged 20+ years. There was a significant effect of the average number of landings during daylight on subsequent breeding outcome, such that older individuals with a higher landing rate were more likely to defer breeding or fail during incubation (Table 5, Figure 5). The interaction between the number of landings and age was not significant, nor was the effect of sex on subsequent breeding outcome. There was no effect of the average body feather carbon isotope value on subsequent breeding

outcome, nor were the interaction with age and the effect of sex significant (Table 5).

4 | DISCUSSION

This study is the first to investigate the relationship between age and foraging behaviour outside the breeding season in a
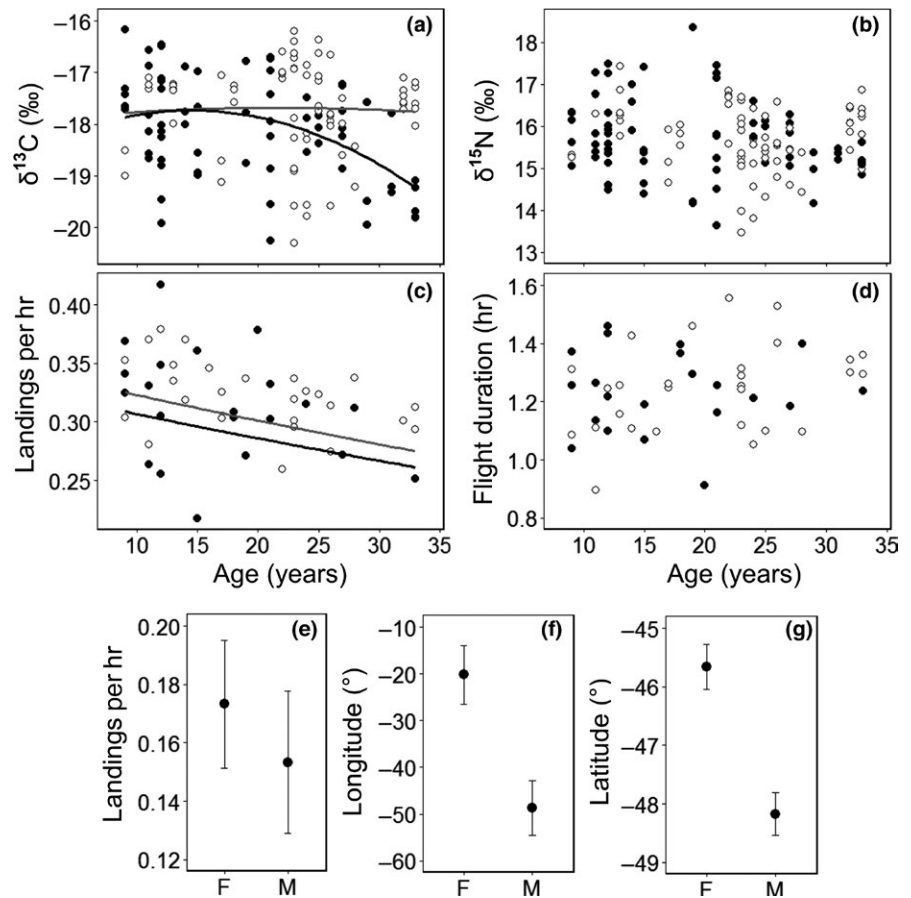
FIGURE 4 The effects of age and sex on non-breeding foraging metrics of wandering albatrosses from Bird Island, South Georgia. Variables shown are (a) $\delta^{13}C$ and (b) $\delta^{15}N$ values in body feathers; and (c) the number of landings per hour during daylight, (d) the average flight bout duration during daylight, (e) the number of landings per hour during darkness, (f) longitude and (g) latitude from geolocator-immersion loggers. (a–d) show age and sex effects. Best fit lines show significant relationships with age predicted by the most parsimonious models, separately for males (black) and females (grey) where there was a significant effect of sex. For ease of plotting, the median value for each individual is represented as a dot, with male and females as filled and closed circles, respectively. (e–g) show just sex effects, which are modelled means ± *SE* for males (M) and females (F)

TABLE 5 Summary of the five best-supported generalized linear models (GLMs) investigating the effect of age and foraging metrics (number of landings during daylight and $\delta^{13}C$; tested separately) on subsequent reproductive performance (next outcome; 1 = chick fledged, 0 = failed in incubation or deferred breeding) in non-breeding wandering albatrosses aged 20+ years, as no birds <20 years failed; X = predictor variables retained, and — = not retained, in the most parsimonious models; ΔAICc = change in Akaike information criterion, corrected for small sample sizes, from the best-supported model. The most parsimonious models are shown in bold

| | Covariates | | | | | |
Response variable	Age	No. landings	Age: No. landings	Sex	AICc	ΔAICc
(a)						
Next outcome	—	**X**	—	—	**25.1**	**0.00**
	—	X	—	X	25.8	0.76
	X	X	—	—	27.7	2.64
	X	X	—	X	28.2	3.18
	—	—	—	—	30.1	5.07
	Covariates					
Response variable	Age	$\delta^{13}C$	Age: $\delta^{13}C$ (‰)	Sex	AICc	ΔAICc
(b)						
Next outcome	—	—	—	—	**37.3**	**0.00**
	—	—	—	X	37.9	0.63
	—	X	—	—	38.3	1.01
	X	—	—	—	39.3	1.97
	—	X	—	X	39.7	2.42

long-lived, migratory species, and to demonstrate an age-specific COE of foraging effort on subsequent reproductive performance. Specifically, older birds of both sexes made fewer landings (a proxy of foraging effort) and older males had lower body feather $\delta^{13}C$ values. Although we were not able to test for a link between foraging behaviour and fitness in younger individuals, we found that older birds with a higher number of landings were less likely to breed successfully in the following season. These results emphasize that the ability to forage efficiently outside the breeding season may be an important driver of fitness differences in old age.
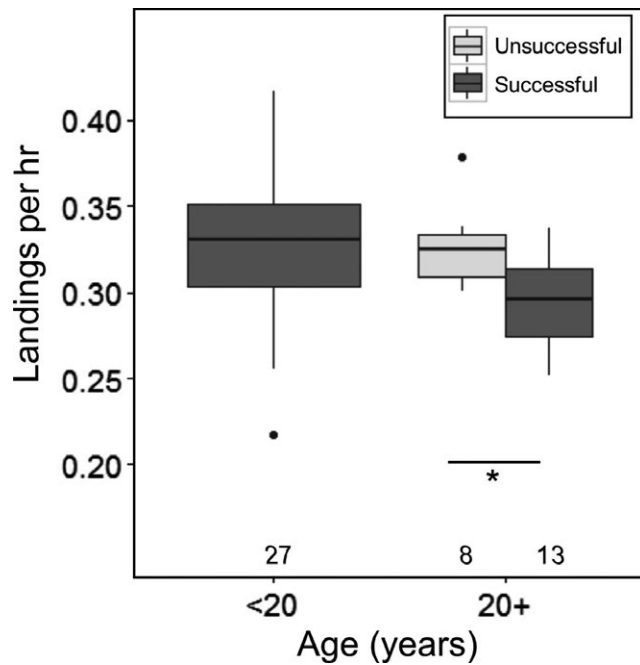
FIGURE 5 The relationship between the number of landings per hour during daylight and subsequent reproductive performance for wandering albatrosses aged 20+ years tracked with geolocator-immersion loggers from Bird Island, South Georgia. Successful = chick fledged; Unsuccessful = failed in incubation or deferred breeding. Birds <20 years were not modelled as they all bred successfully the following season, but are included here for illustrative purposes. The number of individuals for each category is given at the bottom of the plot. Two outliers are shown by black points.*$p < .05$

4.1 | Age-related variation in fitness

In our sample of tracked birds, we found an age-related decline in breeding success (also see Froy et al., 2013, 2017), which allowed us to confidently link age-related variation in foraging behaviour to variation in fitness. Breeding probability and success of tracked and untracked birds did not differ, indicating that our sample was representative of population-level processes. However, we tracked few young birds (none with immersion data) that failed, suggesting the sampled individuals might have been of above-average phenotypic quality. As our study focusses predominantly on the proximate drivers of reproductive declines in older birds, this does not detract from our main conclusion, but did limit our ability to fully document the processes driving improvements in breeding performance in younger individuals (Daunt, Wanless, et al., 2007; Froy et al., 2015).

4.2 | Age- and sex-related variation in foraging behaviour

With increasing age, male but not female wandering albatrosses had lower δ^{13}C values in body feathers. Previous tracking studies at the Crozet Islands revealed an unexpected foraging pattern, in that older males foraged further south than females (Lecomte et al., 2010), but

this was not apparent in birds from South Georgia during breeding (Froy et al., 2015). Our isotope data corroborate those from Crozet in terms of the decrease in δ^{13}C values with age in the non-breeding season (Jaeger et al., 2014). However, there was no latitudinal shift in distribution of the tracked birds from South Georgia with age, in contrast to our prediction. As we found no correlation between average δ^{13}C and latitude (matching results for breeding birds; Ceia et al., 2015), we suggest that changes in δ^{13}C might reflect different habitat preferences or diets of older males, as depletion in ^{13}C can also reflect greater reliance on offshore than inshore, or pelagic than benthic prey (Phillips, Bearhop, et al., 2009). It has been hypothesized that old males forage further south to take advantage of stronger winds, thereby reducing flight costs (Jaeger et al., 2014; Lecomte et al., 2010). However, unlike birds from the Indian Ocean, adults from South Georgia appear not to shift their distribution with age during any part of the annual cycle (this study, Froy et al., 2015); this may be due to differences in wind regimes and in the availability and productivity of habitats in the two regions (Phillips, Wakefield, Croxall, Fukuda, & Higuchi, 2009).

While we found no evidence of spatial segregation between age classes, there was some segregation of males and females, and males also landed less often than females. Sexual segregation is well documented in breeding seabirds, particularly those with large sexual size dimorphism, but is considerably less frequent during the non-breeding season (Phillips, McGill, Dawson, & Bearhop, 2011; but see Jaeger et al., 2014; Clay et al., 2016). Nor have many studies documented sex differences in the activity patterns of seabirds outside the breeding season. Male wandering albatrosses are 20% larger than females (Shaffer, Weimerskirch, & Costa, 2001), and their higher wing loading makes them more efficient at foraging in windier latitudes (Shaffer, Weimerskirch, et al., 2001; Weimerskirch, Salamolard, Sarrazin, & Jouventin, 1993). Also, due to their larger size, males may out-compete females at profitable prey patches, such as scavenging opportunities around demersal longline vessels (Xavier et al., 2004). As such, the lower landing rate of males could indicate that they eat fewer but larger prey items, or could be linked to their use of different marine habitats. Females were distributed further north and spent more time off the Patagonian Shelf as far north as the Brazil-Falklands Confluence, whereas males were more likely to forage in the Drake Passage and Humboldt Current. Wandering albatrosses are bycaught in pelagic longline fisheries in the southwest Atlantic and the lower survival of females has been attributed to sex differences in bycatch rates as a result of greater overlap with vessels during breeding (Jiménez et al., 2016). We emphasize that females may also be at much greater risk than males as a result of their more northerly distribution during the non-breeding season, a period representing a considerable portion of their adult lives.

Most foraging activity of albatrosses takes place during daylight (Mackley et al., 2010; Phalan et al., 2007), and birds probably do not land unless prey capture is very likely (Weimerskirch et al., 1997). The number of landings in our study may be slightly underestimated

by the low resolution of our activity loggers. Regardless, the 15% decrease in the number of landings conducted per day during daylight, from youngest to oldest birds, represents a notable reduction in foraging effort, particularly as take-offs and landings are energetically costly (Shaffer, Costa, et al., 2001). During the non-breeding period, birds must undergo a partial moult of flight feathers which reduces flight and foraging efficiency (Prince et al., 1997). While we did not investigate seasonal variation in activity patterns, moult is likely to be an important driver of time and activity budgets (Cherel, Quillfeldt, Delord, & Weimerskirch, 2016), and the timing and duration of moult are likely to have important downstream effects on fitness (Dawson, Hinsley, Ferns, Bonser, & Eccleston, 2000; Prince et al., 1997).

4.3 | Links with fitness: foraging senescence or experience with age?

Old animals are expected to suffer from deterioration in muscular or physiological condition (Nussey et al., 2013), which is reflected in reduced foraging activity or ability (Catry et al., 2006; MacNulty et al., 2009). However, reduced activity may not necessarily indicate a decrease in foraging success (i.e., foraging senescence), if animals are able to increase their efficiency with age (Catry et al., 2011; Weimerskirch, Gault, & Cherel, 2005). As expected, older birds were less active; however, in contrast to our prediction that less active individuals would have a lower probability of breeding successfully, reduced foraging activity was linked to higher fitness. We therefore infer that reduced activity is not a direct indication of poor foraging ability, but that birds able to limit their foraging effort are likely to be more efficient. Whether this trend results from selective mortality of poor foragers or from individual improvements with age is unclear (see below).

There is increasing evidence that non-breeding behaviour influences subsequent breeding outcome, particularly in migratory species (e.g., Inger et al., 2010; Marra et al., 1998). In seabirds, increased activity has been linked to higher past reproductive effort (Fayet et al., 2016), or to decreased probability of breeding, later laying and lower subsequent breeding success (Daunt, Afanasyev, Silk, & Wanless, 2006; Shoji et al., 2015). This suggests that individuals may compensate for poor condition by increasing their foraging effort, but with repercussions for reproduction the following season. Reproductive performance is likely to be mediated by pre-breeding body condition; indeed, wandering albatrosses with lower mass on return to the colony are less likely to breed (Weimerskirch, 1992). In our study, the few birds that deferred breeding or bred unsuccessfully were all 20+ years old. The larger individual variability in foraging effort of young and middle-aged birds suggests that there is little direct fitness cost of high activity. In contrast, older individuals with higher foraging activity appeared to pay a price for greater effort. As our study included young individuals with low foraging activity, but lacked old birds with high foraging activity, it is likely that, over the course of their lives, there is selection against birds with consistently high effort (Daunt, Afanasyev, et al., 2007; Fay, Barbraud, Delord, & Weimerskirch,

2016). Similarly, we speculate that if individuals are in poor condition, it may be optimal to increase effort allocated to self-maintenance at the risk of breeding failure (McNamara, Houston, Barta, Scheuerlein, & Fromhage, 2009), supported by evidence that breeding albatrosses maintain a high level of physiological fitness into old age (Lecomte et al., 2010). Ultimately, the inability of animals to recover body condition between breeding attempts could increase the cost of reproduction, leading to a positive feedback loop, as suggested by a recent conceptual study (Senner, Conklin, & Piersma, 2015).

As our study is cross-sectional, the observed patterns in behaviour could have arisen through two principal mechanisms: within-individual increases in foraging experience or selective mortality of particular phenotypes (Forslund & Pärt, 1995). Young albatrosses must reach a threshold mass to recruit into the breeding population, and the improvement in foraging efficiency is likely to be an important determinant of breeding success in early life (Froy et al., 2013; Weimerskirch, 1992). While increased foraging experience in old age is poorly documented (except see Zimmer, Ropert-Coudert, Kato, Ancel, & Chiaradia, 2011; Vaillant et al., 2013), it has been suggested that where changes in behaviour have not accompanied declines in physiological or metabolic function, increased foraging experience can mask senescence effects (Elliott et al., 2015; Hassrick, Crocker, & Costa, 2013). Ultimately, as senescence is a within-individual process, longitudinal datasets are needed to disentangle selective mortality from within-individual changes (Froy et al., 2013; Nussey, Coulson, Festa-Bianchet, & Gaillard, 2008; van de Pol, Verhulst, Pfister, & DeAngelis, 2006), as well as the influence of intrinsic quality (Daunt et al., 2006).

Our study emphasizes that the ability of individuals to garner resources during the non-breeding period is an important driver of fitness differences, and that this interacts with the effects of age. To follow the behaviour of individuals over extended time periods is logistically challenging (MacNulty et al., 2009), but those studies that manage to do so over consecutive seasons should greatly improve our understanding of the factors influencing senescence in the wild.

AUTHOR CONTRIBUTIONS

T.A.C., E.J.P., A.M. and R.A.P. conceived the ideas and designed the methodology; R.A.P. oversaw the data collection; T.A.C. and R.A.R.M. processed the data; T.A.C. and E.J.P. analysed the data and T.A.C. led the writing of the manuscript. All authors contributed to drafts and gave final approval for publication.

DATA ACCESSIBILITY

Movement, activity and stable isotope data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cr266nb (Clay, Pearmain, McGill, Manica, & Phillips, 2018). Movement data have been uploaded to the BirdLife International Seabird Tracking Database (http://seabirdtracking.org/mapper/?dataset_id=1405).

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REFERENCES

Angelier, F., Shaffer, S. A., Weimerskirch, H., & Chastel, O. (2006). Effect of age, breeding experience and senescence on corticosterone and prolactin levels in a long-lived seabird: The wandering albatross. *General and Comparative Endocrinology*, *149*, 1–9. https://doi.org/10.1016/j.ygcen.2006.04.006

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *The Journal of Wildlife Management*, *74*, 1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

Authier, M., Bentaleb, I., Ponchon, A., Martin, C., & Guinet, C. (2012). Foraging fidelity as a recipe for a long life: Foraging strategy and longevity in male southern elephant seals. *PLoS ONE*, *7*, e32026. https://doi.org/10.1371/journal.pone.0032026

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., … Grothendieck, G. (2015) *lme4: Linear mixed-effects models using "Eigen" and S4*. R package version 1.1-7. Retrieved from http://cran.r-project.org/web/packages/lme4/index.html.

Battam, H., Richardson, M., Watson, A. W. T., & Buttemer, W. A. (2010). Chemical composition and tissue energy density of the cuttlefish (*Sepia apama*) and its assimilation efficiency by *Diomedea* albatrosses. *Journal of Comparative Physiology B*, *180*, 1247–1255. https://doi.org/10.1007/s00360-010-0497-3

Burnham, K. P., & Anderson, D. R. (Eds.). (2004). *Model selection and multimodel inference*. New York, NY: Springer. Retrieved from http://link.springer.com/10.1007/b97636

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*, 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Catry, P., Granadeiro, J. P., Ramos, J., Phillips, R. A., & Oliveira, P. (2011). Either taking it easy or feeling too tired: Old Cory's Shearwaters display reduced activity levels while at sea. *Journal of Ornithology*, *152*, 549–555. https://doi.org/10.1007/s10336-010-0616-7

Catry, P., Phillips, R. A., Phalan, B., & Croxall, J. P. (2006). Senescence effects in an extremely long-lived bird: The grey-headed albatross *Thalassarche chrysostoma*. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 1625–1630. https://doi.org/10.1098/rspb.2006.3482

Ceia, F. R., Ramos, J. A., Phillips, R. A., Cherel, Y., Jones, D. C., Vieira, R. P., & Xavier, J. C. (2015). Analysis of stable isotope ratios in blood of tracked wandering albatrosses fails to distinguish a δ^{13}C gradient within their winter foraging areas in the southwest Atlantic Ocean. *Rapid Communications in Mass Spectrometry*, *29*, 2328–2336. https://doi.org/10.1002/rcm.7401

Cherel, Y., Quillfeldt, P., Delord, K., & Weimerskirch, H. (2016). Combination of at-sea activity, geolocation and feather stable isotopes documents where and when seabirds moult. *Frontiers in Ecology and Evolution*, *4*, 3.

Clay, T. A., Manica, A., Ryan, P. G., Silk, J. R. D., Croxall, J. P., Ireland, L., & Phillips, R. A. (2016). Proximate drivers of spatial segregation in non-breeding albatrosses. *Scientific Reports*, *6*, 29932. https://doi.org/10.1038/srep29932

Clay, T. A., Pearmain, E. J., McGill, R. A. R., Manica, A., & Phillips, R. A. (2018) Data from: Age-related variation in non-breeding foraging behaviour and carry-over effects on fitness in an extremely long-lived bird. *Dryad Digital Repository*, https://https://doi.org/10.5061/dryad.cr266nb

Clutton-Brock, T. H. (1988). *Reproductive success. Studies of individual variation in contrasting breeding systems*. Chicago, IL: University of Chicago Press.

Cody, M. L. (1966). A general theory of clutch size. *Evolution*, *20*, 174–184. https://doi.org/10.1111/j.1558-5646.1966.tb03353.x

Cunningham, J. T., Le Vaillant, M., Gaston, A. J., Ropert-Coudert, Y., Kato, A., Jacobs, S. R., & Elliott, K. H. (2017). Reduced activity in middle-aged thick-billed murres: Evidence for age related trends in fine-scale foraging behaviour. *Animal Behaviour*, *126*, 271–280. https://doi.org/10.1016/j.anbehav.2017.02.010

Daunt, F., Afanasyev, V., Adam, A., Croxall, J. P., & Wanless, S. (2007). From cradle to early grave: Juvenile mortality in European shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. *Biology Letters*, *3*, 371–374. https://doi.org/10.1098/rsbl.2007.0157

Daunt, F., Afanasyev, V., Silk, J. R. D., & Wanless, S. (2006). Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behavioral Ecology and Sociobiology*, *59*, 381–388. https://doi.org/10.1007/s00265-005-0061-4

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

Dawson, A., Hinsley, S. A., Ferns, P. N., Bonser, R. H. C., & Eccleston, L. (2000). Rate of moult affects feather quality: A mechanism linking current reproductive effort to future survival. *Proceedings of the Royal Society of London B: Biological Sciences*, *267*, 2093–2098. https://doi.org/10.1098/rspb.2000.1254

Dukas, R. (2008). Life history of learning: Performance curves of honeybees in the wild. *Ethology*, *114*, 1195–1200. https://doi.org/10.1111/j.1439-0310.2008.01565.x

Elliott, K. H., Hare, J. F., Le Vaillant, M., Gaston, A. J., Ropert-Coudert, Y., & Anderson, W. G. (2015). Ageing gracefully: Physiology but not behaviour declines with age in a diving seabird. *Functional Ecology*, *29*, 219–228. https://doi.org/10.1111/1365-2435.12316

Fay, R., Barbraud, C., Delord, K., & Weimerskirch, H. (2016). Variation in the age of first reproduction: Different strategies or individual quality? *Ecology*, *97*, 1842–1851. https://doi.org/10.1890/15-1485.1

Fayet, A. L., Freeman, R., Shoji, A., Kirk, H. L., Padget, O., Perrins, C. M., & Guilford, T. (2016). Carry-over effects on the annual cycle of a migratory seabird: An experimental study. *Journal of Animal Ecology*, *85*, 1516–1527. https://doi.org/10.1111/1365-2656.12580

Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: The importance of the utilization distribution. *The Journal of Wildlife Management*, *69*, 1346–1359. https://doi.org/10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2

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

Froy, H., Lewis, S., Catry, P., Bishop, C. M., Forster, I. P., Fukuda, A., ... Phillips, R. A. (2015). Age-related variation in foraging behaviour in the wandering albatross at South Georgia: No evidence for senescence. *PLoS ONE*, 10, e0116415. https://doi.org/10.1371/journal.pone.0116415

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

de Grissac, S., Börger, L., Guitteaud, A., & Weimerskirch, H. (2016). Contrasting movement strategies among juvenile albatrosses and petrels. *Scientific Reports*, 6, 26103. https://doi.org/10.1038/srep26103

Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R., & Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*, 80, 4–18. https://doi.org/10.1111/j.1365-2656.2010.01740.x

Hassrick, J. L., Crocker, D. E., & Costa, D. P. (2013). Effects of maternal age and mass on foraging behaviour and foraging success in the northern elephant seal. *Functional Ecology*, 27, 1055–1063. https://doi.org/10.1111/1365-2435.12108

Hayward, A. D., Moorad, J., Regan, C. E., Berenos, C., Pilkington, J. G., Pemberton, J. M., & Nussey, D. H. (2015). Asynchrony of senescence among phenotypic traits in a wild mammal population. *Experimental Gerontology*, 71, 56–68. https://doi.org/10.1016/j.exger.2015.08.003

Inger, R., Harrison, X. A., Ruxton, G. D., Newton, J., Colhoun, K., Gudmundsson, G. A., ... Bearhop, S. (2010). Carry-over effects reveal reproductive costs in a long-distance migrant. *Journal of Animal Ecology*, 79, 974–982. https://doi.org/10.1111/j.1365-2656.2010.01712.x

Jaeger, A., Blanchard, P., Richard, P., & Cherel, Y. (2009). Using carbon and nitrogen isotopic values of body feathers to infer inter- and intra-individual variations of seabird feeding ecology during moult. *Marine Biology*, 156, 1233–1240. https://doi.org/10.1007/s00227-009-1165-6

Jaeger, A., Goutte, A., Lecomte, V. J., Richard, P., Chastel, O., Barbraud, C., ... Cherel, Y. (2014). Age, sex, and breeding status shape a complex foraging pattern in an extremely long-lived seabird. *Ecology*, 95, 2324–2333. https://doi.org/10.1890/13-1376.1

Jaeger, A., Lecomte, V. J., Weimerskirch, H., Richard, P., & Cherel, Y. (2010). Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators' foraging areas in the Southern Ocean. *Rapid Communications in Mass Spectrometry*, 24, 3456–3460. https://doi.org/10.1002/rcm.4792

Jiménez, S., Domingo, A., Brazeiro, A., Defeo, O., Wood, A. G., Froy, H., ... Phillips, R. A. (2016). Sex-related variation in the vulnerability of wandering albatrosses to pelagic longline fleets. *Animal Conservation*, 19, 281–295. https://doi.org/10.1111/acv.12245

Jones, O. R., Gaillard, J. M., Tuljapurkar, S., Alho, J. S., Armitage, K. B., Becker, P. H., ... Clutton-Brock, T. (2008). Senescence rates are determined by ranking on the fast-slow life-history continuum. *Ecology Letters*, 11, 664–673. https://doi.org/10.1111/j.1461-0248.2008.01187.x

Kirkwood, T. B. L., & Rose, M. R. (1991). Evolution of senescence: Late survival sacrificed for reproduction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 332, 15–24. https://doi.org/10.1098/rstb.1991.0028

Lecomte, V. J., Sorci, G., Cornet, S., Jaeger, A., Faivre, B., Arnoux, E., ... Weimerskirch, H. (2010). Patterns of aging in the long-lived wandering albatross. *Proceedings of the National Academy of Sciences*, 107, 6370–6375. https://doi.org/10.1073/pnas.0911181107

Lemaître, J.-F., Berger, V., Bonenfant, C., Douhard, M., Gamelon, M., Plard, F., & Gaillard, J.-M. (2015). Early-late life trade-offs and the evolution of ageing in the wild. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20150209. https://doi.org/10.1098/rspb.2015.0209

Mackley, E. K., Phillips, R. A., Silk, J. R. D., Wakefield, E. D., Afanasyev, V., Fox, J. W., & Furness, R. W. (2010). Free as a bird? Activity patterns of albatrosses during the nonbreeding period. *Marine Ecology Progress Series*, 406, 291–303. https://doi.org/10.3354/meps08532

MacNulty, D. R., Smith, D. W., Vucetich, J. A., Mech, L. D., Stahler, D. R., & Packer, C. (2009). Predatory senescence in ageing wolves. *Ecology Letters*, 12, 1347–1356. https://doi.org/10.1111/j.1461-0248.2009.01385.x

Marra, P. P., Hobson, K. A., & Holmes, R. T. (1998). Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science*, 282, 1884–1886. https://doi.org/10.1126/science.282.5395.1884

McNamara, J. M., Houston, A. I., Barta, Z., Scheuerlein, A., & Fromhage, L. (2009). Deterioration, death and the evolution of reproductive restraint in late life. *Proceedings of the Royal Society B: Biological Sciences*, 276, 4061–4066. https://doi.org/10.1098/rspb.2009.0959

Monaghan, P., Charmantier, A., Nussey, D. H., & Ricklefs, R. E. (2008). The evolutionary ecology of senescence. *Functional Ecology*, 22, 371–378. https://doi.org/10.1111/j.1365-2435.2008.01418.x

Montgomery, R. A., Vucetich, J. A., Peterson, R. O., Roloff, G. J., & Millenbah, K. F. (2013). The influence of winter severity, predation and senescence on moose habitat use. *Journal of Animal Ecology*, 82, 301–309. https://doi.org/10.1111/1365-2656.12000

Navarro, J., Oro, D., Bertolero, A., Genovart, M., Delgado, A., & Forero, M. G. (2010). Age and sexual differences in the exploitation of two anthropogenic food resources for an opportunistic seabird. *Marine Biology*, 157, 2453–2459. https://doi.org/10.1007/s00227-010-1509-2

Newton, I. (2010). *Bird migration*. Collins New Naturalist. UK: Collins

Nussey, D. H., Coulson, T., Delorme, D., Clutton-Brock, T. H., Pemberton, J. M., Festa-Bianchet, M., & Gaillard, J.-M. (2011). Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. *Ecology*, 92, 1936–1947. https://doi.org/10.1890/11-0308.1

Nussey, D. H., Coulson, T., Festa-Bianchet, M., & Gaillard, J.-M. (2008). Measuring senescence in wild animal populations: Towards a longitudinal approach. *Functional Ecology*, 22, 393–406. https://doi.org/10.1111/j.1365-2435.2008.01408.x

Nussey, D. H., Froy, H., Lemaitre, J.-F., Gaillard, J.-M., & Austad, S. N. (2013). Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. *Ageing Research Reviews*, 12, 214–225. https://doi.org/10.1016/j.arr.2012.07.004

Pardo, D., Barbraud, C., & Weimerskirch, H. (2013). Females better face senescence in the wandering albatross. *Oecologia*, 173, 1283–1294. https://doi.org/10.1007/s00442-013-2704-x

Patrick, S. C., & Weimerskirch, H. (2015). Senescence rates and late adulthood reproductive success are strongly influenced by personality in a long-lived seabird. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20141649. https://doi.org/10.1098/rspb.2014.1649

Patterson, E. M., Krzyszczyk, E., & Mann, J. (2016). Age-specific foraging performance and reproduction in tool-using wild bottlenose dolphins. *Behavioral Ecology*, 27, 401–410. https://doi.org/10.1093/beheco/arv164

Payne, R. B. (1972). Mechanisms and control of molt. In D. S. Farner, & J. R. King (Eds.), *Avian biology*, Vol. 3 (pp. 103–155). New York, NY: Academic Press. https://doi.org/10.1016/B978-0-12-249402-4.50012-7

Pelletier, L., Chiaradia, A., Kato, A., & Ropert-Coudert, Y. (2014). Fine-scale spatial age segregation in the limited foraging area of an inshore

seabird species, the little penguin. *Oecologia*, *176*, 399–408. https://doi.org/10.1007/s00442-014-3018-3

Phalan, B., Phillips, R. A., Silk, J. R., Afanasyev, V., Fukuda, A., Fox, J. W., … Croxall, J. P. (2007). Foraging behaviour of four albatross species by night and day. *Marine Ecology Progress Series*, *340*, 271–286. https://doi.org/10.3354/meps340271

Phillips, R. A., Bearhop, S., McGill, R. A., & Dawson, D. A. (2009). Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. *Oecologia*, *160*, 795–806. https://doi.org/10.1007/s00442-009-1342-9

Phillips, R. A., Lewis, S., González-Solís, J., & Daunt, F. (2017). Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Marine Ecology Progress Series*, *578*, 117–150. https://doi.org/10.3354/meps12217

Phillips, R. A., McGill, R. A. R., Dawson, D. A., & Bearhop, S. (2011). Sexual segregation in distribution, diet and trophic level of seabirds: Insights from stable isotope analysis. *Marine Biology*, *158*, 2199–2208. https://doi.org/10.1007/s00227-011-1725-4

Phillips, R. A., Silk, J. R., Croxall, J. P., Afanasyev, V., & Briggs, D. R. (2004). Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series*, *266*, 265–272. https://doi.org/10.3354/meps266265

Phillips, R. A., Wakefield, E. D., Croxall, J. P., Fukuda, A., & Higuchi, H. (2009). Albatross foraging behaviour: No evidence for dual foraging, and limited support for anticipatory regulation of provisioning at South Georgia. *Marine Ecology Progress Series*, *391*, 279–292. https://doi.org/10.3354/meps08028

van de Pol, M., Verhulst, S., Pfister, A. E. C. A., & DeAngelis, E. D. L. (2006). Age-dependent traits: A new statistical model to separate within- and between-individual effects. *The American Naturalist*, *167*, 766–773.

Prince, P. A., Weimerskirch, H., Huin, N., & Rodwell, S. (1997). Molt, maturation of plumage and ageing in the wandering albatross. *The Condor*, *99*, 58–72. https://doi.org/10.2307/1370224

R Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org.

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*, 89–101. https://doi.org/10.1086/524957

Senner, N. R., Conklin, J. R., & Piersma, T. (2015). An ontogenetic perspective on individual differences. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20151050. https://doi.org/10.1098/rspb.2015.1050

Shaffer, S. A., Costa, D. P., & Weimerskirch, H. (2001). Behavioural factors affecting foraging effort of breeding wandering albatrosses. *Journal of Animal Ecology*, *70*, 864–874. https://doi.org/10.1046/j.0021-8790.2001.00548.x

Shaffer, S. A., Weimerskirch, H., & Costa, D. P. (2001). Functional significance of sexual dimorphism in Wandering Albatrosses, *Diomedea exulans*. *Functional Ecology*, *15*, 203–210. https://doi.org/10.1046/j.1365-2435.2001.00514.x

Shoji, A., Aris-Brosou, S., Culina, A., Fayet, A., Kirk, H., Padget, O., … Guilford, T. (2015). Breeding phenology and winter activity predict subsequent breeding success in a trans-global migratory seabird. *Biology Letters*, *11*, 20150671. https://doi.org/10.1098/rsbl.2015.0671

Sorensen, M. C., Hipfner, J. M., Kyser, T. K., & Norris, D. R. (2009). Carry-over effects in a Pacific seabird: Stable isotope evidence that pre-breeding diet quality influences reproductive success. *Journal of Animal Ecology*, *78*, 460–467. https://doi.org/10.1111/j.1365-2656.2008.01492.x

Stearns, S. (1992). *The evolution of life histories*. Oxford, UK: Oxford University Press.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton, NJ: Princeton University Press.

Vaillant, M. L., Bohec, C. L., Prud'Homme, O., Wienecke, B., Maho, Y. L., Kato, A., & Ropert-Coudert, Y. (2013). How age and sex drive the foraging behaviour in the king penguin. *Marine Biology*, *160*, 1147–1156. https://doi.org/10.1007/s00227-013-2167-y

Vaillant, M. L., Wilson, R. P., Kato, A., Saraux, C., Hanuise, N., Prud'Homme, O., … Ropert-Coudert, Y. (2012). King penguins adjust their diving behaviour with age. *Journal of Experimental Biology*, *215*, 3685–3692. https://doi.org/10.1242/jeb.071175

Weimerskirch, H. (1992). Reproductive effort in long-lived birds: Age-specific patterns of condition, reproduction and survival in the wandering albatross. *Oikos*, *64*, 464–473. https://doi.org/10.2307/3545162

Weimerskirch, H., Delord, K., Guitteaud, A., Phillips, R. A., & Pinet, P. (2015). Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year, and their fitness consequences. *Scientific Reports*, *5*, 8853. https://doi.org/10.1038/srep08853

Weimerskirch, H., Gault, A., & Cherel, Y. (2005). Prey distribution and patchiness: Factors in foraging success and efficiency of wandering albatrosses. *Ecology*, *86*, 2611–2622. https://doi.org/10.1890/04-1866

Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S. A., & Costa, D. P. (2000). Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society B: Biological Sciences*, *267*, 1869–1874. https://doi.org/10.1098/rspb.2000.1223

Weimerskirch, H., Salamolard, M., Sarrazin, F., & Jouventin, P. (1993). Foraging strategy of wandering albatrosses through the breeding season: A study using satellite telemetry. *The Auk*, *110*, 325–342.

Weimerskirch, H., & Wilson, R. P. (2000). Oceanic respite for wandering albatrosses. *Nature*, *406*, 955–956. https://doi.org/10.1038/35023068

Weimerskirch, H., Wilson, R. P., & Lys, P. (1997). Activity pattern of foraging in the wandering albatross: A marine predator with two modes of prey searching. *Marine Ecology Progress Series*, *151*, 245–254. https://doi.org/10.3354/meps151245

Xavier, J. C., Trathan, P. N., Croxall, J. P., Wood, A. G., Podesta, G., & Rodhouse, P. G. (2004). Foraging ecology and interactions with fisheries of wandering albatrosses (*Diomedea exulans*) breeding at South Georgia. *Fisheries Oceanography*, *13*, 324–344. https://doi.org/10.1111/j.1365-2419.2004.00298.x

Yoda, K., Kohno, H., & Naito, Y. (2004). Development of flight performance in the brown booby. *Proceedings of the Royal Society B: Biological Sciences*, *271*, S240–S242. https://doi.org/10.1098/rsbl.2003.0157

Zimmer, I., Ropert-Coudert, Y., Kato, A., Ancel, A., & Chiaradia, A. (2011). Does foraging performance change with age in female little penguins (*Eudyptula minor*)? *PLoS ONE*, *6*, e16098. https://doi.org/10.1371/journal.pone.0016098

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Berlin, Germany: Springer. https://doi.org/10.1007/978-0-387-87458-6

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