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Cite this article: Lescroël A, Schmidt A, Ainley DG, Dugger KM, Elrod M, Jongsomjit D, Morandini V, Winquist S, Ballard G. 2023 High-resolution recording of foraging behaviour over multiple annual cycles shows decline in old Adélie penguins' performance. *Proc. R. Soc. B* **290**: 20222480.
https://doi.org/10.1098/rspb.2022.2480

Received: 12 December 2022
Accepted: 6 March 2023

Subject Category:
Behaviour

Subject Areas:
behaviour, ecology, evolution

Keywords:
behavioural senescence, foraging performance, full annual cycle tracking, longitudinal study, seasonal interactions, within-individual improvement

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High-resolution recording of foraging behaviour over multiple annual cycles shows decline in old Adélie penguins' performance

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Age-related variation in foraging performance can result from both within-individual change and selection processes. These mechanisms can only be disentangled by using logistically challenging long-term, longitudinal studies. Coupling a long-term demographic data set with high-temporal-resolution tracking of 18 Adélie penguins (*Pygoscelis adeliae*, age 4–15 yrs old) over three consecutive annual cycles, we examined how foraging behaviour changed within individuals of different age classes. Evidence indicated within-individual improvement in young and middle-age classes, but a significant decrease in foraging dive frequency within old individuals, associated with a decrease in the dive descent rate. Decreases in foraging performance occurred at a later age (from 12–15 yrs old to 15–18 yrs old) than the onset of senescence predicted for this species (9–11 yrs old). Foraging dive frequency was most affected by the interaction between breeding status and annual life-cycle periods, with frequency being highest during returning migration and breeding season and was highest overall for successful breeders during the chick-rearing period. Females performed more foraging dives per hour than males. This longitudinal, full annual cycle study allowed us to shed light on the changes in foraging performance occurring among individuals of different age classes and highlighted the complex interactions among drivers of individual foraging behaviour.

1. Introduction

Full annual cycle studies in animal ecology are scarce, with most effort severely biased toward the breeding period because of logistical and technical obstacles associated with following wild individual animals across sometimes inhospitable environments [1]. However, full life-cycle approaches are required to better understand a vast array of ecological, evolutionary and conservation questions, from carry-over effects to ageing processes or large-scale habitat use. Longitudinal (as opposed to cross-sectional) studies are also relatively rare and are particularly difficult when they involve recording labile parameters, such as behavioural or physiological traits, repeatedly on the same individuals and over ecologically meaningful periods of time. Longitudinal studies can disentangle

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within-individual variation from selection processes when experimental manipulations cannot be conducted [2–4].

Foraging performance is linked to energy acquisition and ultimately affects growth, self-maintenance and reproduction over time. Variation in this behavioural trait can be attributed to both within-individual variation (e.g. improvement due to growing experience with age, or deterioration due to senescence) and/or to selection processes (e.g. the disappearance of under-performing individuals from the population). Within vertebrate populations, birds, which often carry prey items directly and conspicuously to their offspring and can be individually marked and followed for decades, have been the model of choice to study age variation in foraging behaviour.

Due to their relatively long lifespan and large size, seabirds have been the focus of several, mostly cross-sectional, studies in recent years (see [5] for a review). So far, cross-sectional studies have hypothesized (and mostly confirmed) that foraging performance increases with age, at least in the younger age classes (e.g. [5–7]). This might be due to the selective disappearance of under-performing individuals rather than, or in addition to, learning maturation processes. By contrast to early life improvement, evidence for age-related variation in foraging performance later in life is scarce [8]. Among the recent studies quantifying the effect of true age on the foraging performance of seabirds [5,9–14], only two of these detected signs of foraging senescence [12,14] and all but one [14] were cross-sectional, breeding season-focused studies.

While comparative analyses showed that senescence in survival and reproduction is widespread in terrestrial birds and mammals [15], the onset of senescence might be difficult to detect in the wild because (1) high levels of extrinsic mortality (e.g. through predation) could remove individuals from the population before senescence becomes evident [16]—although ageing theory also predicts that species with high extrinsic mortality deteriorate faster [15]; (2) old individuals could adjust their behaviour to compensate for decreased performance due to physiological decline [9]; and/or (3) a decrease in performance due to senescence might be partially masked by selective disappearance when conducting studies at the population scale [14]. Resolving these issues is possible through the collection of high-temporal-resolution data, encompassing more than just the breeding season (when individuals are more likely to adjust their behaviour to maximize their reproductive output) within a longitudinal framework.

Among seabirds, the Adélie penguin (*Pygoscelis adeliae*) is relatively short-lived and has been shown to increase (either linear or pseudo-threshold, i.e. levelling off at old ages) proxies for daily prey catch rate and prey catch per unit effort with age in a previous cross-sectional study [5]. By coupling a long-term demographic dataset with high-resolution diving data over the full annual cycle on the same individuals over multiple years, we examined how foraging performance changes within individuals of different age classes. We predicted that, within individuals, foraging dive frequency (an index of food intake in this species [16]) would increase from year to year in young individuals, remain stable through middle-age and decrease in old individuals, possibly as a result of behavioural senescence (i.e. a decrease in behavioural performance). To better understand the mechanisms behind age variation in foraging performance, we also examined how diving performance, in terms of descent rate and maximum dive depth, changes within individuals of different age classes. We predicted that diving performance would follow the within-individual pattern of foraging dive frequency as individuals undergo physiological maturation, then decline within old individuals. By following the same individuals over time within each age class, and not just comparing individuals of different age classes, we were able to focus on learning/maturation and senescence processes without the masking effect of selection processes. We also examined the effect of breeding status and period of the annual cycle on the foraging dive frequency and diving performance among both female and male individuals in order to account for potential carry-over effects [1,17].

2. Methods

(a) Study sites and species

The study was conducted on Ross Island (Ross Sea, Antarctica) at two colonies: Cape Royds (78°33′S, 166°100′E; ~2 500 pairs) and Cape Crozier (77°27′S, 169°12′E; ~300 000 pairs). Adélie penguins exhibit high fecundity (often raising two chicks) and relatively low adult survival for a pelagic seabird (mean life expectancy 12–14 years [18,19], KM Dugger, DG Ainley, G Ballard, A Lescroël, PO'B Lyver, A Schmidt 1996–2019, unpublished data), presumably driven by abundant seasonal food resources and high levels of predation on adults [18,19].

(b) Annual life cycle

Individuals arrive at their breeding colonies in late October/early November, lay (usually two) eggs by mid-November and feed their chicks between mid-December and early February [20]. After fledging young (or sooner in failed breeders), penguins undergo a period of foraging to recover condition before a full moult during which they stay out of the water (mostly on sea ice, rarely on land), fasting for about three weeks [21,22]. Among colonies of the southern Ross Sea, moulting occurs mainly along the Ross Sea continental shelf break, where prey availability is assumed to be high [23,24]. Adélie penguins then shift further north to escape the constant polar night while still staying within the pack ice, reaching the maximum distance from the colony in June–early August [25,26] before adults return towards Ross Island in late August through October.

In this study, we evaluated foraging performance for 6 periods within the annual life cycle of Adélie penguins: incubation (Nov 1–Dec 15), chick-rearing (Dec 16–Jan 31), pre-moult/moult (Feb 1–Apr 14), outgoing migration (Apr 15–May 31), migration maximum (June 1–Aug 15) and returning migration (Aug 16–Oct 31). These periods were based on our best knowledge for the general population (see references above) and could vary per individual; they were used here to divide the annual life cycle into broad periods of ecological significance and similar durations among individuals. Individual variation in the onset and length of these periods will not be addressed in this paper.

(c) Individual tracking

In the 2016/2017 breeding season, a total of 129 known-age, banded birds (mostly past or current breeders) were captured at nest sites at Cape Crozier ($n = 92$) and Cape Royds ($n = 37$) and equipped with geolocating dive recorders (22 × 21 × 15 mm, weight = 4 g, from Atesys, Strasbourg, France, hereafter referred to as GDRs). The GDRs measured light every 60 s, temperature (with a precision of ± 0.5°C) every 30 s and pressure (with a precision of ± 0.3 m) every second for more than a year. GDRs were enclosed in heat-shrink tubing shaped into a leg band attached to the tibiotarsus above the tarsus joint using a 4 mm-wide polyester-coated stainless-steel cable tie to secure the ends of the strap together. The leg band was custom-fitted to each individual so that it could spin freely on the leg, but not slip over the joint [27,28]. Deployments were completed in 5 to 10 min from capture to release. From these 129 birds, 62 (48%) were recaptured in 2017/2018 and re-equipped with a new GDR. In 2018/2019, 38 of these 62 (61%) were recaptured and equipped with a new GDR for a third consecutive year, and 23 (61%) returned in 2019/2020. All 23 birds were thus part of the original 129 and had been equipped over three consecutive years. Excluding incomplete annual files due to tag malfunction, our final dataset included 45 complete annual files from 18 individuals (5 females, 13 males; 12 from Cape Crozier, 6 from Cape Royds) followed over a 3-year period (2016/2017 through 2019/2020). Because birds were first equipped with GDRs at different dates throughout Incubation and chick-rearing in 2016/2017, these two periods were excluded from the analysis for the first year only. Birds were sexed by DNA from a feather sample ($n = 14$) or by a combination of size, behaviour, and timing of colony attendance ([29], $n = 4$).

All penguin survey, capture and handling methods used for data collection followed all relevant guidelines and regulations under the approval and oversight of the Institutional Animal Care and Use Committees of Oregon State University and Point Blue Conservation Science. Additionally, all work was approved and conducted under Antarctic Conservation Act permits issued by the U.S. National Science Foundation and the U.S. Antarctic Program.

(d) Age classes

GDR-equipped birds had been ringed as chicks on the left flipper with a numbered stainless steel band (see [30] for details on band design and effect or lack thereof on foraging behaviour). When first equipped with a GDR, our sample was divided into three age classes: young (4–6 y old, $n = 6$ incl. 3 females), middle-age (7–11 y old, $n = 7$ incl. 2 females and old (12–15 y old, $n = 5$ incl. 0 female). The male-biased sex ratio at older ages in our sample is reflective of the population pattern [17,31].

(e) Breeding status

Each equipped bird was followed throughout the three breeding seasons and assigned a breeding status for each season and the rest of the annual cycle: non-breeder if it was never observed with eggs or chicks, failed breeder if it was observed with either eggs or chicks but did not raise a chick to the crèche stage (when chicks are thermally independent and can be left unattended at the colony), successful breeder if it raised at least one chick to the crèche stage.

(f) Foraging behaviour

To derive dive statistics and classification, GDR pressure data were processed in R (v. 3.6.0, [32]) with several processes modified from the diveMove package (v. 1.4.5, [33]), according to the methods detailed in Lescroël *et al*. [27]. Throughout this process, each dive (≥3 m) was classified as either 'foraging', 'exploratory' or 'other'. Foraging dive frequency, a metric that predicts body mass gain in this species ([27], also supported in Chinstrap penguins (*Pygoscelis antarcticus*) [34]), was calculated as the number of foraging dives per hour over each period of the annual life cycle for each individual penguin. This was done by summing the number of foraging dives over a given period and dividing by the length of this period in hours. As a measure of diving performance, we calculated the average maximum foraging depth (in metres) per period for each individual and each year. As the initial part of the dive is when penguins have to work the hardest to overcome buoyancy [35], we also calculated descent rate (in metres per second) over the descent phase (from surface to bottom) of each foraging dive as an index of the propulsive force being exerted during a dive.

(g) Removing inter-annual variations: year centring

To disentangle the effect of the time elapsed since initial device attachment (reflecting ageing within age classes and coded as an integer from 1 to 3) from the year-to-year variations generated by environmental fluctuations, we centred individual foraging dive frequency, maximum depth and descent rate of foraging dives within each year by subtracting the yearly average value excluding the Incubation and Chick-rearing periods for which there are no data in 2016/17 [4,14]. This procedure removed year-to-year variation as well as potential biases linked to covariation between time since initial device attachment and year.

(h) Statistics

To examine how foraging dive frequency and maximum foraging depth evolve within individuals of different age classes, we evaluated linear models including either the centred foraging dive frequency or the centred maximum foraging depth as the dependent variable (one value per individual per period for each year, $n = 239$). The additive effects of period, breeding status, age class, time since initial device attachment, sex and colony were included as independent variables, as well as interactions between period and breeding status (to allow for carry-over effects of the breeding status outside of the chick-rearing period) and between age class and time since initial device attachment (to allow for a different evolution of foraging performance within age classes). From these, all possible single-factor and multi-factor models, including a null model (intercept only), were run using the dredge() function of the {MuMIn} package [36] in R. Because (1) our relatively small sample size was balanced between individuals with only one value per individual per period and included the same individuals followed over the same period of time, and (2) including bird ID as a random effect led to singular fits, indicating that models were overfitted [37], we therefore decided not to include bird ID as a random effect.

To better understand the mechanisms behind age variation in foraging performance at the dive scale, we also evaluated linear mixed models with the centred descent rate as the dependent variable (one value per foraging dive, $n = 1\,130\,324$ with unequal number of dives per individual), bird ID as a random effect and maximum depth of the dive, period, breeding status, age class, time since initial device attachment, sex as well as interactions between period and breeding status and between age class and time since initial device attachment as independent variables. We did not have females in our oldest age class, so we could not evaluate whether age effects varied between the sexes (i.e. age by sex interaction) but only evaluated age variation as a consistent effect for both males and females (i.e. as an additive effect in all our models).

To evaluate these models and determine the strength of evidence supporting specific effects, we used an information theoretic approach [38]. Models were ranked and evaluated using the small-sample-size corrected version of Akaike Information Criterion (AICc), ΔAICc (the difference in AICc between each candidate model and the model with the lowest AICc) and Akaike's weights (AICc wt.). We drew inference from all competitive models within 2 ΔAICc of the top model. We determined the strength of evidence supporting specific model effects by examining the unstandardized effect sizes (slope coefficients and differences in means) and the associated 95% confidence intervals (CI). If the 95% CI for a parameter in a competitive model ($\Delta\text{AICc} < 2.0$) included zero, the parameter

Table 1. Model selection results including the difference in AICc between each candidate model and the model with the lowest AICc value (ΔAICc), Akaike weights (weight), the number of parameters (*K*), model deviance, and adjusted R^2 (adj. R^2) for generalized linear models relating foraging performance (number of foraging dives per hour) of Adélie penguins to period of the annual life cycle, breeding status, age class, time since first equipment, sex and colony. Data are from 18 individuals followed over three consecutive full years. Only models with weight > 0.01 as well as the Intercept-only model are reported. $n = 239$ observations.

no.	model	ΔAICc	weight	*K*	deviance	adj. R^2
1	period × breeding status + age class × time + sex	0	0.17	25	718.72	0.61
2	period × breeding status + age class × time + sex + colony	0.05	0.16	26	716.26	0.61
3	period × breeding status + sex	0.33	0.14	20	731.30	0.59
4	period × breeding status + age class + sex	0.58	0.13	22	726.72	0.60
5	period × breeding status + sex + colony	0.64	0.12	21	729.21	0.60
6	period × breeding status + age class + sex + colony	0.79	0.11	23	724.48	0.60
7	period × breeding status + time + sex	2.63	0.04	21	731.20	0.59
8	period × breeding status + age class + time + sex	2.72	0.04	23	726.41	0.60
9	period × breeding status + age class + time + sex + colony	2.86	0.04	24	724.07	0.60
10	period × breeding status + time + sex + colony	2.91	0.04	22	729.05	0.59
11	intercept	194.62	0.00	2	965.40	0.00

was not considered informative [39]. Because we had no females in our oldest age class, all models were also run on a subsample of the data including male individuals only, and results were consistent with the dataset including both sexes.

3. Results

(a) Foraging dive frequency

All 6 competitive models included the additive effect of sex and the interaction between period and breeding status. Each of these competitive models explained ≥60% of the variation in foraging dives per hour (table 1). Significantly fewer foraging dives per hour were performed during pre-moult/moult ($\hat{\beta}_{\text{moult}} = -1.40$, s.e. = 0.48, 95% CI[−2.34, −0.46]), Outgoing migration ($\hat{\beta}_{\text{outgoing migration}} = -2.50$, s.e. = 0.48, 95% CI[−3.44, −1.56]) and migration maximum ($\hat{\beta}_{\text{migration maximum}} = -1.73$, s.e. = 0.48, 95% CI[−2.67, −0.79]) compared with incubation. The number of foraging dives per hour did not differ significantly between Incubation and either chick-rearing ($\hat{\beta}_{\text{chick–rearing}} = -0.86$, s.e. = 0.50, 95% CI[−1.85, 0.13]) or returning migration ($\hat{\beta}_{\text{returning migration}} = 0.57$, s.e. = 0.48, 95% CI[−0.37, 1.51]; table 1, model 1; figure 1). During chick-rearing, both failed breeders ($\hat{\beta}_{\text{chick-rearing : failed breeder}} = 1.91$, s.e. = 0.88, 95% CI[0.17, 3.65]) and successful breeders ($\hat{\beta}_{\text{chick-rearing : successful breeder}} = 3.57$, s.e. = 0.66, 95% CI[2.26, 4.88]) performed significantly more foraging dives per hour than non-breeders (table 1, model 1). In addition, over the entire annual cycle, males performed fewer foraging dives per hour ($\hat{\beta}_{\text{male}} = -0.82$, s.e. = 0.19, 95% CI[−1.19, −0.46]) than females (table 1, model 1).

Four of the 6 competitive models included age and time since initial device attachment, but there was slightly more support for an interaction between age and time rather than additive effects (table 1, models 1 & 2), predicting that within individuals, foraging dive frequency would decrease from year to year in old individuals ($\hat{\beta}_{\text{old}} = 1.62$, s.e. = 0.58, 95% CI[0.48, 2.77]; $\hat{\beta}_{\text{time}} = 0.41$, s.e. = 0.25, 95% CI[−0.05, 0.68]; $\hat{\beta}_{\text{old : time}} = -0.60$, s.e. = 0.24, 95% CI[−1.08, −0.12]) compared with young and middle-age individuals, whose performance increased with time (model 1, figure 2). Other competitive models supported the additive effect of age class only (table 1, models 4 & 6), with middle-age individuals ($\hat{\beta}_{\text{middle-age}} = 0.37$, s.e. = 0.18, 95% CI[0.01, 0.72], model 4) performing more foraging dives per hour than young individuals, but little support for differences between old ($\hat{\beta}_{\text{old}} = 0.28$, s.e. = 0.22, 95% CI[−0.14, 0.71], model 4) and young individuals.

The effect of colony on foraging dive frequency was included in 3 of the 6 competitive models (table 1) but examination of the associated 95% CI showed that this covariate was imprecise, suggesting little support for colony differences (e.g. model 2, $\hat{\beta}_{\text{Crozier}} = -0.25$, s.e. = 0.17, 95% CI[−0.59, 0.08]).

(b) Maximum foraging depth

The interaction between period and breeding status was the only strongly supported effect in predicting maximum foraging depth (table 2). Over the annual cycle, foraging depth averaged over all breeding status groups was deeper during the migration maximum ($\hat{\beta}_{\text{migration maximum}} = 14.44$, s.e. = 4.11, 95% CI[6.34, 22.53]) and the returning migration ($\hat{\beta}_{\text{returning migration}} = 11.25$, s.e. = 4.11, 95% CI[3.15, 19.34]) periods compared with other periods (figure 3, model 1). Successful breeders during chick-rearing achieved the deepest foraging depth of all period and breeding status combinations ($\hat{\beta}_{\text{chick-rearing : successful breeder}} = 27.83$, s.e. = 5.72, 95% CI[16.55, 39.11], model 1), diving more than 20 m deeper than the yearly average (2016/2017: 42.3 ± 11.1 m, 2017/2018: 36.5 ± 9.7 m, 2018/2019: 39.5 ± 15.5 m). The maximum dive depth recorded was 179.2 m from a young female during the maximum migration period.

The effect of colony on maximum foraging depth was included in 2 of the 3 competitive models (table 2), predicting that birds from Cape Crozier (the more populous colony) would dive about 3 m deeper than birds from Cape Royds, but the associated 95% CI included zero for one of the

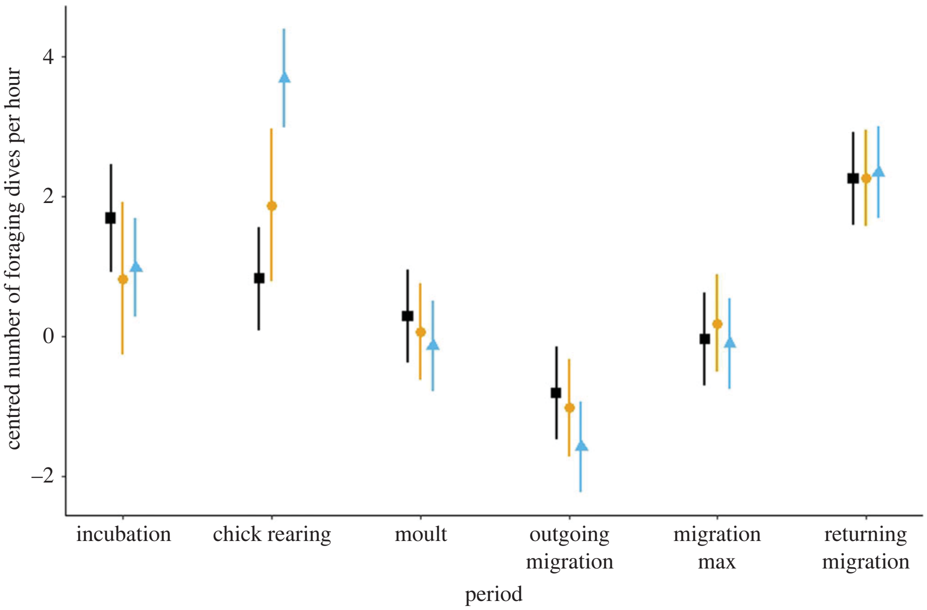

Figure 1. Predicted changes in the foraging performance of Adélie penguins (expressed as the mean centred number of foraging dives per hour with associated 95% CI) according to the period of their annual cycle and breeding status (squares: non breeders, circles: failed breeders, triangles: successful breeders).

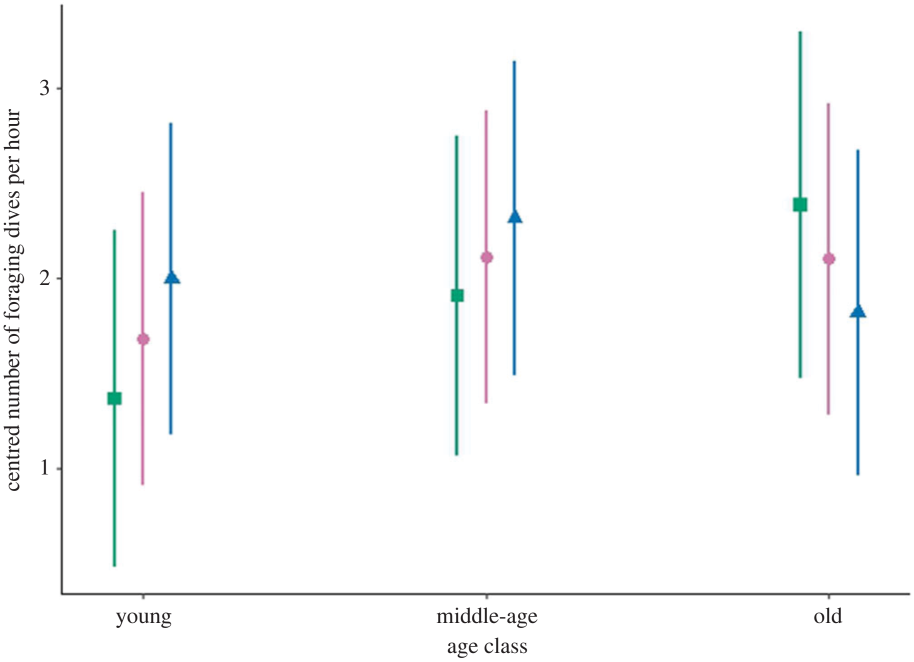

Figure 2. Predicted changes in the foraging performance of Adélie penguins (expressed as the mean centred number of ureforaging dives per hour with associated 95% CI) according to age class and time since initial device attachment (squares: year 1, circles: year 2, triangles: year 3).

models ($\hat{\beta}_{\text{Crozier}} = 2.83$, s.e. = 1.47, 95% CI[−0.07, 5.73], model 1; $\hat{\beta}_{\text{Crozier}} = 2.91$, s.e. = 1.48, 95% CI[0.01, 5.82], model 2), indicating only weak support for inter-colony differences. Sex was uninformative ($\hat{\beta}_{\text{male}} = -1.31$, s.e. = 1.46, 95% CI[−4.18, 1.56]).

(c) Descent rate

The top model for predicting descent rate included the effect of an interaction between age class and time since initial device attachment, the effect of an interaction between period and breeding status, and an effect of maximum depth and sex (table 3, model 1). Thus, descent rate increased with time within middle-age individuals ($\hat{\beta}_{\text{middle-age : time}} = 0.033$, SE = 0.001, 95% CI[0.031, 0.035]), but decreased with time in old individuals ($\hat{\beta}_{\text{old : time}} = -0.012$, s.e. = 0.001, 95% CI[−0.014, −0.010]; figure 4). Descent rate was lowest for failed breeders in most periods compared with non-breeders and successful breeders ($\hat{\beta}_{\text{failed breeder}} = -0.092$, s.e. = 0.004, 95% CI[−0.099, −0.085]; figure 5). Descent rate also increased linearly with maximum dive depth ($\hat{\beta}_{\text{max dive depth}} = 0.00682$, s.e. = 0.00001, 95% CI[0.00679,

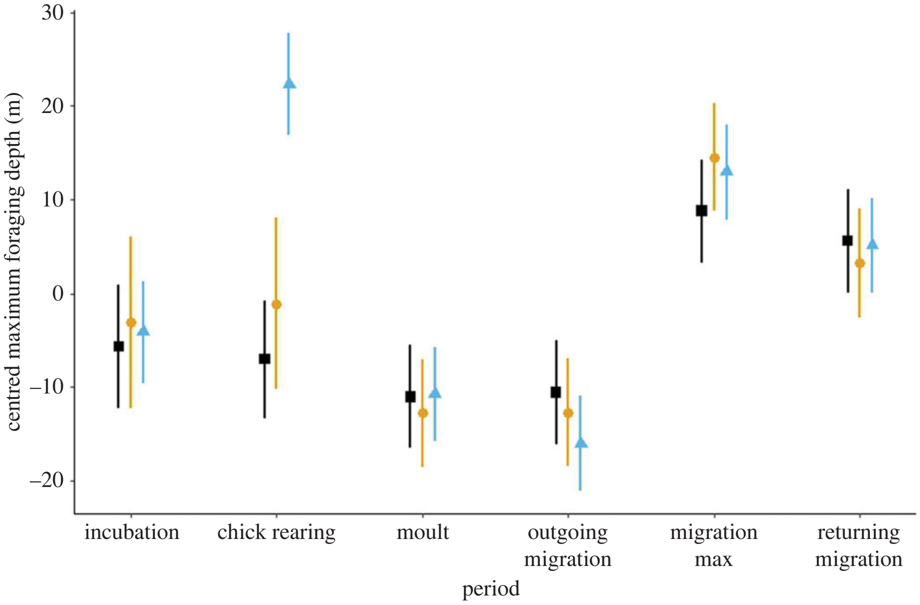

Figure 3. Predicted changes in the centred maximum foraging depth of Adélie penguins (mean ± 95% CI) according to the period of their annual cycle and breeding status (squares: non breeders, circles: failed breeders, triangles: successful breeders).

Table 2. Model selection results including the difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAICc), Akaike weights (weight), the number of parameters (K), model deviance and adjusted R^2 (adj. R^2) for generalized linear models relating the maximum foraging depth of Adélie penguins to period of the annual life-cycle, breeding status, age class, time since first equipment, sex and colony. Data are from 18 individuals followed over three consecutive full years. Only models with weight > 0.01 as well as the intercept-only model are reported. $n = 239$ observations.

no.	model	ΔAICc	weight	K	deviance	adj. R^2
1	period × breeding status + colony	0	0.27	20	1754.62	0.55
2	period × breeding status + sex + colony	1.52	0.13	21	1753.73	0.55
3	period × breeding status	1.60	0.12	19	1758.60	0.54
4	period × breeding status + age class + colony	2.10	0.10	22	1751.89	0.55
5	period × breeding status + time + colony	2.39	0.08	21	1754.60	0.55
6	period × breeding status + sex	3.33	0.05	20	1757.95	0.54
7	period × breeding status + age class	3.65	0.04	21	1755.87	0.54
8	period × breeding status + age class + sex + colony	3.66	0.04	23	1751.00	0.55
9	period × breeding status + time + sex + colony	3.94	0.04	22	1753.72	0.54
10	period × breeding status + time	3.98	0.04	20	1758.60	0.54
11	period × breeding status + age class + time + colony	4.55	0.03	23	1751.89	0.55
12	period × breeding status + age class + sex	5.39	0.02	22	1755.18	0.54
13	period × breeding status + time + sex	5.74	0.02	21	1757.95	0.54
16	intercept	168.33	0.00	2	1962.75	0.00

0.00684) and was lower in males ($\hat{\beta}_{\mathrm{male}} = -0.101$, 95% CI[−0.172, −0.029]) compared to females.

4. Discussion

This study reports on the first longitudinal, high-resolution recording of a seabird's foraging behaviour over multiple full annual cycles. The study design allowed us to detect the first evidence of behavioural senescence in Adélie penguins. Consistent with our predictions, we observed within-individual improvement in young birds, but also during middle age, and highlighted a significant decrease in foraging performance with time in old individuals. We suggest this decrease in the number of foraging dives performed per hour, concomitant with a decrease in the descent rate of these dives, indicated a decrease in the physical condition of old birds. During descent, penguins have to swim vigorously to overcome buoyancy and reach the depths where their prey occur. If penguins descend quickly, they can spend more time at depth, pursuing prey, before depleting their oxygen stores. This ultimately might mean that older birds, descending slower as they age, have less time to spend in dive phases where prey acquisition occurs. In previous cross-sectional

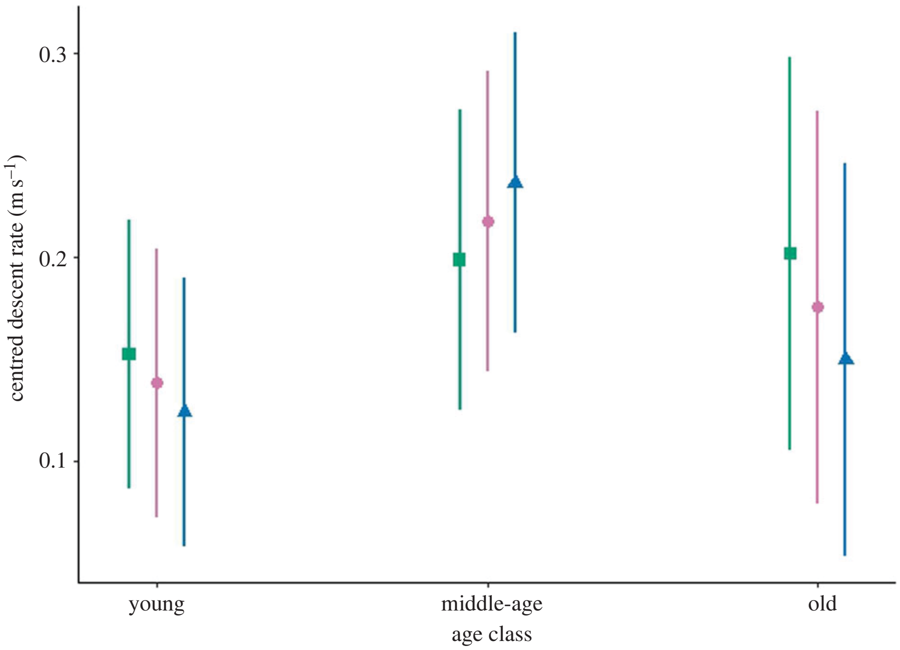

Figure 4. Predicted changes in the centred descent rate of Adélie penguins during foraging dives (mean ± 95% CI) according to age class and time since initial device attachment (squares: year 1, circles: year 2, triangles: year 3).

Table 3. Model selection results including the difference in AICc between each candidate model and the model with the lowest AICc value (ΔAICc), Akaike weights (weight), the number of parameters (*K*), model deviance, and marginal *R*-squared value (marg. R^2 [40]) for generalized linear mixed models (with bird ID as random effect) relating the descent rate of Adélie penguins during foraging dives according to maximum depth of the dive, age class, time since first equipment and sex. Models were fitted with maximum likelihood for model selection (here) then the top model was fitted with restricted maximum likelihood for parameter estimation. Data are from 18 individuals followed over three consecutive full years. Only models with weight > 0.01 as well as the Intercept-only model are reported. $n = 1\ 130\ 324$ observations.

no.	model	ΔAICc	weight	*K*	deviance	marg. R^2
1	maximum depth + age class × time + period × breeding status + sex	0	0.92	27	969 025	0.23
2	maximum depth + age class × time + period × breeding status	4.99	0.08	26	969 026	0.21
3	intercept	264 198.36	0.00	3	1,233,016	0.00

studies (e.g. [5]), where no evidence for senescence was found, such ontogenetic change in performance may have been concealed by the selective disappearance (i.e. increased mortality over time) of underperforming individuals [14].

According to the positive relationship between age at onset of senescence and generation time [15], and the Adélie penguin generation time (estimated between 9.55 [41] and 13.3 yrs. [42]), an onset of senescence in annual fitness is predicted between 9 and 11 years of age for this species. However, depending on the birds' age at first reproduction, reproductive performance showed either no decrease with age or a decrease from 12–14 years of age [43]. Here, we showed a decrease in foraging performance from 12–15 through 15–18 years of age, suggesting an onset of senescence at a later age than predicted by theoretical relationships, and beyond the average life expectancy for this species in the wild. As the rate and onset of senescence can be highly variable among populations (e.g. when populations experience different rates of extrinsic mortality [44]) and also among individuals within populations (e.g. [45]), further studies in different populations and/or contrasted environmental conditions can help clarify the effects of senescence. Decades of continuous monitoring are required to build such longitudinal datasets, especially in systems where relatively few individuals reach senescent age due to high rates of predation on juveniles and adults [16,46].

We also found evidence for higher foraging performance in middle-age birds compared to young birds, consistent with previous findings [5]. This aligns with results from cross-sectional data on black-browed and grey-headed albatrosses (*Thalassarche melanophris* and *T. chrysostoma*) that showed improvement in foraging competency into mature age classes [12]. Our present results indicated that part of this difference was attributable to within-individual improvement, which extends past early life. In a longitudinal study on little penguins (*Eudyptula minor*), a similar pattern of increasing foraging performance (measured during the breeding season) from young to middle age then decreasing performance in old ages (greater than 10 yrs) was observed, mostly driven by within-individual ontogenetic changes during early and late life [14]. Although the selective disappearance of poorly performing individuals might also play a role in the differences among age classes, it is likely a more influential mechanism during the first weeks of juvenile life at sea, when

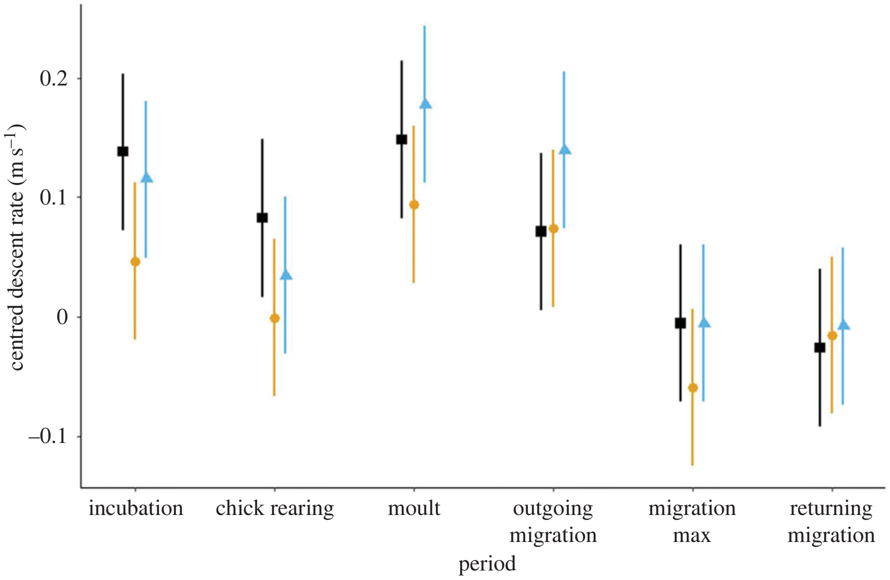

Figure 5. Predicted changes in the centred descent rate of Adélie penguins during foraging dives (mean ± 95% CI) according to the period of their annual cycle and breeding status (squares: non breeders, circles: failed breeders, triangles: successful breeders).

acute survival bottlenecks are most likely [47], and/or during the first reproductive event [48], and late in life [14].

Importantly, foraging dive frequency and foraging depth were most affected by the different periods of the annual life cycle, with dive frequency greatest at the times of highest energetic demand, i.e. the breeding season and, interestingly, during the returning migration. During the returning migration period, penguins exhibited both a high number of foraging dives per hour and deeper foraging depths (see also [49]). This pattern is consistent with increasing daylight availability in the spring [50] and with pre-breeding hyperphagia typical of capital breeders [51] which, for Adélie penguins, likely is necessary to build large deposits of fat needed for fasting during territory establishment, laying and incubation [20]. These results further highlight the important ecological role of pre-breeding foraging areas and the seasonal interaction (or carry-over effect) affecting body condition at the onset of the breeding season.

Breeding status was also associated with variation in foraging performance. Successful breeders achieved the greatest annual foraging dive frequency during chick rearing, when food becomes depleted or less available near the big colonies [52,53] and breeders are constrained to return to their colony regularly to feed their chick(s). Successful breeders mitigate food availability by using a greater portion of the 'foraging volume' by diving deeper than non-breeders or failed breeders. In fact, we have shown that 'higher-quality' breeders dive deeper than 'lower-quality' breeders towards the end of the breeding season, when chick needs are greater and food availability near the colony is lower [54]. Undoubtedly, this comes at greater energetic cost, as parents providing more food to their chicks exhibit greater body mass loss during the breeding season [55]. This cost might be partially mitigated by accessing prey of higher energy density, i.e. fish, which generally occur deeper than krill [53,56]. Parents that start the breeding season in good condition with the greatest body mass can afford to lose more mass proportionally than individuals with less initial body mass [55], highlighting again, the importance of late-winter conditions for subsequent breeding output. The lower descent rate of failed breeders throughout most of the annual cycle also points towards potential differences in 'individual quality' between successful and failed breeders [48,54].

Contrary to studies focusing only on the breeding season, we found that throughout the annual cycle female Adélie penguins performed a greater number of foraging dives per hour, and although they dived to similar depths to males, females also exhibited higher descent rates during foraging dives. During the breeding season, both sexes bring back similar amounts of food to their chicks but male and female foraging areas appear spatially segregated. Females travel further from the colony on longer trips while making shallower dives, maximizing net energy gain per energy spent, while males exploit waters closer to the colony by diving deeper, thus allowing them to maximize net energy gain per unit time and to spend more time defending their territories at the colony [5,54]. Over the full annual cycle, sex differences in foraging performance and diving behaviour could be explained by differences in energetic requirements (e.g. for egg-formation in females, which is initiated before reaching the breeding grounds [57]) and/or in size (smaller females might be less buoyant and therefore able to descend faster). Although more studies would be required, the higher overall foraging performance of females could come with a cost and might help explain their earlier age at first reproduction [43] and their higher mortality rate compared to males [18]. This would contrast with other vertebrate species (especially mammals) in which males usually incur greater physiological costs for maintaining higher levels of foraging performance [58–60].

This longitudinal, full annual-cycle study allowed us to elucidate changes in foraging performance within ageing individuals of different age classes and highlighted the complex interactions between intrinsic drivers in determining individual foraging behaviour and its fitness consequences. Although this study was limited to individuals that had entered the breeding population, future studies could expand knowledge on the ontogenetic development of foraging behaviour by focusing on the first few months or years after fledging, a phase of seabirds' life history that still remains very much a mystery.

Ethics. All penguin survey, capture and handling methods used for data collection were performed following all relevant guidelines and regulations under the approval and oversight of the Institutional Animal Care and Use Committees of Oregon State University and Point Blue Conservation Science. Additionally, fieldwork was conducted under Antarctic Conservation Act permits (ACA 2017-005) issued by the U.S. National Science Foundation and the U.S. Antarctic Program, and Assurance of Compliance with NSF Requirements on Humane Care and Use of Vertebrate Animals.

Data accessibility. Data collected are available at the PenguinScience file sharing site hosted by Point Blue Conservation Science (via https://data.pointblue.org/apps/penguin_science/; see AllData/gdr_datashare). Processed data and code are available on GitHub (https://github.com/pointblue/ADPE_longitudinal_foraging). Code for processing raw pressure data can be found at https://github.com/pointblue/gdr_data_processing.

Authors' contributions. A.L.: conceptualization, formal analysis, funding acquisition, investigation, methodology, supervision, validation, visualization, writing—original draft, writing—review and editing; A.S.: data curation, formal analysis, investigation, methodology, project administration, software, validation, writing—review and editing; D.G.A.: conceptualization, funding acquisition, validation, writing—review and editing; K.M.D.: conceptualization, funding acquisition, methodology, writing—review and editing; M.E.: investigation, writing—review and editing; D.J.: investigation, writing—review and editing; V.M.: investigation, writing—review and editing; S.W.: investigation, writing—review and editing; G.B.: conceptualization, funding acquisition, investigation, methodology, resources, software, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. We are grateful for financial support provided by the National Science Foundation (grants OPP-1543498 & 1935870) and NASA (grant no. 80NSSC19K0189).

Acknowledgements. Logistical support for work in Antarctica was provided by the US Antarctic Program. Data were collected using protocols approved by Point Blue Conservation Science and Oregon State University Institutional Animal Care and Use Committees. Arvind Varsani from Arizona State University kindly performed the molecular sexing of the study birds. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is Point Blue Conservation Science Contribution no. 2450.

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