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How does maternal age influence reproductive performance and offspring phenotype in the snow petrel (*Pagodroma nivea*)?

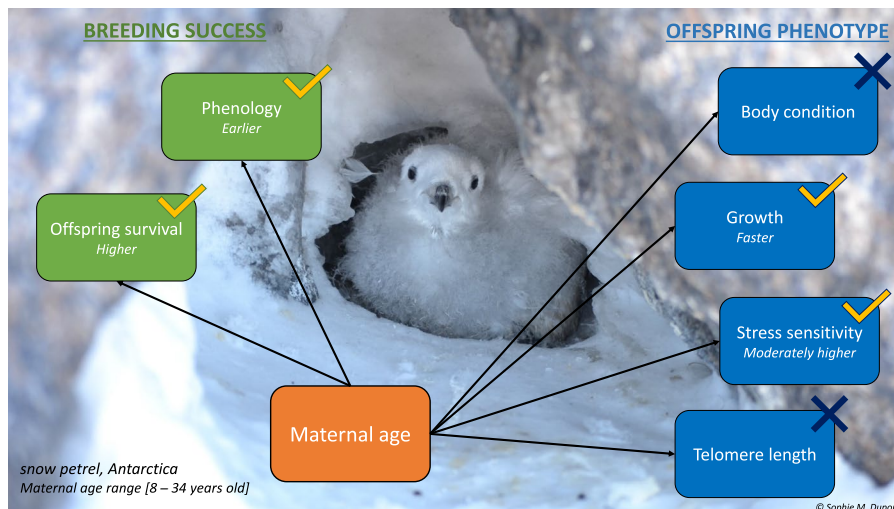
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Abstract

In wild vertebrates, the increase of breeding success with advancing age has been extensively studied through laying date, clutch size, hatching success, and fledging success. However, to better evaluate the influence of age on reproductive performance in species with high reproductive success, assessing not only reproductive success but also other proxies of reproductive performance appear crucial. For example, the quality of developmental conditions and offspring phenotype can provide robust and complementary information on reproductive performance. In long-lived vertebrate species, several proxies of developmental conditions can be used to estimate the quality of the produced offspring (i.e., body size, body condition, corticosterone levels, and telomere length), and therefore, their probability to survive. By sampling chicks reared by known-aged mothers, we investigated the influence of maternal age on reproductive performance and offspring quality in a long-lived bird species, the snow petrel (*Pagodroma nivea*). Older females bred and left their chick alone earlier. Moreover, older females had larger chicks that grew faster, and ultimately, those chicks had a higher survival probability at the nest. In addition, older mothers produced chicks with a higher sensitivity to stress, as shown by moderately higher stress-induced corticosterone levels. Overall, our study demonstrated that maternal age is correlated to reproductive performance (hatching date, duration of the guarding period and survival) and offspring quality (body size, growth rate and sensitivity to stress), suggesting that older individuals provide better parental cares to their offspring. These results also demonstrate that maternal age can affect the offspring phenotype with potential long-term consequences.

Graphical abstract



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Extended author information available on the last page of the article

Keywords Procellariiforms · Maternal effect · Guarding period · Body size · Corticosterone levels · Survival probability

Introduction

In vertebrates, age has a strong influence on individual reproductive performance (Clutton-Brock 1988; Forslund and Pärt 1995). Breeding success usually increases with advancing age up to a point before senescence occurs (Nussey et al. 2013). Multiple hypotheses have been proposed to explain the age-related improvement of reproductive performance (such as the selection, restraint and constraint hypotheses, Williams 1966; Curio 1983; Forslund and Pärt 1995). In birds, an extensive body of literature has focused on laying date, clutch size, hatching success, and fledging success to investigate this age-related improvement of reproductive performance (Pugesek 1983; Cameron et al. 2000; Mauck et al. 2004; Beamonte-Barrientos et al. 2010; Fay et al. 2018; Ivimey-Cook and Moorad 2020; Sarau and Chiaradia 2021). However, most of these studies have failed to measure the condition of the offspring before fledging, mostly due to the constraints associated with the study systems. However, offspring quality could be a robust and relevant additional proxy of parental reproductive performance (Barks and Laird 2020; Barreaux et al. 2022 but see, for instance, Bouwhuis et al. 2015; Schroeder et al. 2015), especially because it correlates with the probability of post-fledging survival. Indeed, there is now increasing evidence that only a small percentage of fledglings will subsequently survive and significantly contribute to future generations through the production of offspring (McCleery et al. 2008; Wilson and Nussey 2010; Cam et al. 2013; Fay et al. 2016, 2018; Vedder and Bouwhuis 2018).

Juveniles are inexperienced, less able to acquire food (Desrochers 1992) and to sustain detrimental conditions (e.g., low food availability, Wiens et al. 2006). Consequently, many often disappear from the population before any breeding attempt (e.g., Alderman et al. 2010; Fay et al. 2015; Naef-Daenzer and Gruebler 2016). In addition, among juveniles that survive until adulthood, their phenotype may constrain them and reduce their probability to successfully breed later in life (e.g., van de Pol et al. 2006). This high individual heterogeneity in performance among individuals is often related to organismal systems (e.g., morphology, behaviour, and physiology), which are at least partly determined during their development (Lindström 1999; Monaghan 2008; Cam and Aubry 2011; Maness and Anderson 2013; Hamel et al. 2018). In that context, assessing not only reproductive success but also the quality of the offspring appears crucial to better evaluate the influence of age on reproductive performance.

When investigating the influence of age on reproductive performance in birds, several components need therefore to be evaluated. Firstly, phenology, parental effort and fledging success are needed to obtain robust estimates of the ability of parents to successfully breed and rear their chick (Clutton-Brock 1988; Newton 1989; Forslund and Pärt 1995; Zhang et al. 2015). Specifically, high parental skills and investment are often related to early breeding, and consequently, high fledging success, especially in seabird species (Bogdanova et al. 2007; Angelier et al. 2007b; Rebke et al. 2010; Sauser et al. 2021). Secondly, several proxies of developmental conditions can be used to assess the quality of the offspring, and therefore, their probability to survive and to recruit into the population (Cam and Aubry 2011; Mumme et al. 2015). Notably, several “key” morphological, physiological, and behavioural systems are important during the developmental period to assess offspring quality (Schoech et al. 2011) and to study the relationship between parental age, developmental constraints and offspring quality.

Slower growth, smaller body size, and lower body condition are usually associated with higher developmental constraints, and with lower subsequent performance (e.g., post-fledging survival probability; Morrison et al. 2009; Jones et al. 2017; Vernasco et al. 2018; Sauser et al. 2018; Evans et al. 2020). Additionally, organismal-related stress systems are set up during the developmental period, and they are known to determine, at least partly, the ability of individuals to breed and survive when environmental stressors occur (Angelier and Wingfield 2013).

Physiological proxies of stress levels are considered as robust tools to assess not only the constraint that may occur during the developmental period, but also the probability of fledglings to subsequently survive and recruit into the population. When facing a threatening event, corticosterone secretion increases to mobilize energy (e.g., protein catabolism, Sapolsky et al. 2000; Romero 2004) and to promote an emergency response that aims to restore homeostasis and helps the chick surviving the acute stressor (Angelier and Wingfield 2013; Wingfield 2013). In chicks, developmental conditions are associated with short- and long-term modifications of physiological stress sensitivity (Rensel and Schoech 2011; Zimmer et al. 2013; Grace et al. 2017, 2020; Kraft et al. 2019). This stress sensitivity can in turn be related to post-hatching survival and even post-fledging performances (e.g., Harvey et al. 2006; Blas et al. 2007; Breuner et al. 2008; Love et al. 2013).

Finally, short telomere length has been proposed as a relevant proxy of constraining early-life environmental

conditions and of poor fledgling quality. Telomeres are terminal chromosomal complexes composed of highly repeated DNA sequences and proteins. Their length is reduced during each cell division due to the incomplete end-replication (Blackburn 2005). Interestingly, the occurrence of environmental or nutritional constraints at the early stage seems to accelerate this telomere attrition (Monaghan 2014; Angelier et al. 2018; Noguera and Velando 2019; Stier et al. 2020), and parental age could translate into short telomeres if associated with low quality parental cares (e.g., Dupont et al. 2018). This developmental telomere attrition has been already convincingly associated with reduced longevity and fitness in captive and wild animals (Heidinger et al. 2012; Asghar et al. 2015; Wilbourn et al. 2018; Eastwood et al. 2019; Heidinger et al. 2021) and seems to have potential long-lasting fitness consequences (Marasco et al. 2022).

In this study, we investigated the influence of maternal age on reproductive performance and offspring quality in the snow petrel (*Pagodroma nivea*), a long-lived seabird species (average lifespan: ~50 years old, Chastel et al. 1993). In this species, increasing parental age is associated with better breeding performance and reproductive senescence does not occur before very old ages (Angelier et al. 2007a; Berman et al. 2009). We specifically focused on maternal age because known-aged females were more abundant in our study site and because females may have a greater impact on offspring quality than males in this seabird species (Barbraud and Chastel 1999; Barbraud et al. 1999). Breeding pairs produce at most a single chick *per* breeding season, making this species a perfect model to study the influence of age on breeding success and offspring phenotype independently of sibling competition. We followed 56 known-aged females (from 8 to 34 years old, which correspond to young and middle-age classes for this species, Angelier et al. 2007a; Berman et al. 2009) and their chicks and we specifically monitored their reproductive phenology (hatching date), the duration of the guarding period (a component of parental care), and offspring survival at the nest. We also assessed the influence of maternal age on the quality of developmental conditions through morphological (growth, body size and body condition), physiological (corticosterone), and molecular (telomere length) variables. Because no senescent females were monitored, we expected a linear rather than a quadratic relationship between maternal age and measured reproductive outputs. Specifically, we predict that reproductive performance will improve with advancing maternal age. More precisely, we predict that younger snow petrels should lay later as later breeding is usually related to poor reproductive performance (prediction 1). Because the guarding period is supposed to be longer when the chicks grow slowly, we also predict that younger petrels will guard their chick longer if they are less able to feed their chick and sustain its growth (prediction 2). We also predict that

the chicks from younger snow petrels should have a lower probability to survive at the nest (prediction 3). In addition, offspring developmental conditions should also improve with advancing maternal age and younger snow petrels should produce chicks presenting a smaller body size (wing size and tarsus length), with a slower growth and/or a lower body condition (prediction 4). We also predict that offspring physiology will be affected by maternal age. Specifically, developmental energetic constraints are expected to increase the offspring sensitivity to stress. Because younger mothers are expected to be less able to fulfil the energetic needs of their offspring, we then predict that their chicks will present higher basal and stress-induced corticosterone levels (prediction 5). Finally, because telomere attrition is accelerated by increasing developmental constraints, we also predict that younger females should produce chicks with shorter telomeres (prediction 6).

Material and methods

Study species

Our study focused on the snow petrel, a long-lived seabird species with a high survival probability and a low fecundity (only one egg is laid *per* couple and *per* year with no replacement clutch in case of breeding failure, Warham 1990; Chastel et al. 1993). This species provides bi-parental care both during the incubation and the chick-rearing periods (Warham 1990). At 10 days old on average, the chick becomes thermally independent and is left unattended at the nest (Goutte et al. 2011). Both parents forage at sea to feed their chick and to restore their own body reserves (Chastel et al. 1993). The chick fledges approximatively at 47 days old (Brown 1966; Barbraud et al. 1999).

A 56-years-old ongoing mark-recapture program (see Barbraud and Chastel 1999 for details on the monitoring protocol) has been conducted at Ile des Pétrels, Pointe Géologie, Terre Adélie, Antarctica (66° 40' S, 140° 01' E). At this site, all chicks are banded every year since the beginning of the monitoring program. After fledging, juveniles stay at sea for almost a decade until sexual maturity (Chastel et al. 1993; Jenouvrier et al. 2005). During that period, the juvenile survival probability varies between 10–25% (Chastel et al. 1993; Sauser et al. 2018). Then, they return to their hatching colony to breed with a high site fidelity (89.8%, Jouventin and Bried 2001). Thanks to this high philopatry and this long-term banding effort, around a hundred of known-aged reproductive birds could be found at Iles des Pétrels during our study. The sex of individuals was determined through relative size of both pair members (females are 20% smaller than males) and acoustic signals (Barbraud et al. 2000) or

thanks to previous studies, during which molecular sexing was conducted.

Determination of maternal age and reproductive monitoring

During the incubation period of austral summer 2017/2018, we checked the bands of all breeding pairs and this allowed us to know the age of the parents that were banded at the colony as chicks. Because we found more breeding known-aged females than known-aged males, we decided to focus our study on known-aged female snow petrels. This decision also resulted from ecological reasons: female adult snow petrels are smaller than males and they seem to be more energetically constrained during reproduction, and therefore, to have a higher impact on reproductive performance (Barbraud and Chastel 1999; Barbraud et al. 1999; but see Fay et al. 2016; Bouwhuis et al. 2018 in other seabird species). During the incubation period, 56 nests occupied by a known-aged female were identified (range 8–34 years old, which correspond to young and middle-age classes for this species, maximum lifespan: ~50 years old) for this study. All these nests were located in crevices and provided good visibility of the content of the nest from a distance. They were left undisturbed until the hatching period. At that time (early January), these nests were daily checked in order to determine the exact hatching date which is an accurate proxy of the laying date in this species (Goutte et al. 2010). Among the 56 monitored pairs, 45 produced a hatchling (Table 1). After hatching, each of these 45 nests with a chick was observed daily from a distance in order to monitor the age when the chick was left alone by its parents (i.e., age of emancipation), and therefore, to determine the duration of the parental guarding stage (i.e., number of days from hatching until the chick is left unattended at the nest by both parents, $N=42$ because 3 chicks died before emancipation, Table 1). Each

nest was then visited when the chick was 13 days old (i.e., after the end of the guarding period, $N=41$ because 4 of the 45 chicks died before reaching 13 days old, Table 1) and 23 days old (i.e., $N=35$ because 6 chicks died between 13 and 23 days old, Table 1), respectively. When visiting the nest, the presence of a parent in the nest was also monitored (i.e., parents regularly come at the nest to provide food to the chick during the chick-rearing period; 1: present vs 0: absent) because parental presence can affect corticosterone levels and body condition (Dupont et al. 2021). Although one parent was sometimes seen at the nest when the chicks were 13 days old, all the chicks were alone at 23 days old and this variable was therefore not considered when analysing the phenotype of 23-days-old chicks.

Morphometric measurements, body condition and growth

At 13 and 23 days old, each surviving chick was captured by hand at its nest (see Table 1 for sample sizes). Tarsus length and wing length were measured with a calliper (± 0.1 mm) and a ruler (± 1 mm), respectively. All birds were weighed with a spring balance (± 5 g). Body condition was calculated using the scaled mass index (SMI) following Peig and Green (2009). Tarsus length was highly correlated with body mass (tarsus: $r=0.869$; $P<0.001$) and was therefore used to calculate the SMI of growing snow petrels by following this formula: $SMI_i = M_i \times \left(\frac{L_i}{L_0}\right)^b$. The terms M_i and L_i respectively correspond to the body mass and the tarsus length of the individual i . The term L_0 is the arithmetic mean value of tarsus length for the whole study population ($L_0=32.8$ mm). The exponent b corresponds to the slope estimate of a standardized major axis regression of log-transformed body mass on log-transformed tarsus length ($b=2.15$).

Table 1 Biological assumptions of the study and associated model selections

Biological assumption	Dependent variables	Independent variables	<i>n</i>
Effect of maternal age on hatching date	Hatching date	Age	45
Effect of maternal age on the guarding period	Guarding period	Age	42
Effect of maternal age on survival	Survival	Age, hatching date, guarding period	41
Effect of the phenotype of the chick on survival	Survival	Body size, body condition	41
Effect of the physiology of the chick on survival	Survival	Telomere, corticosterone	23
Effect of maternal age on the phenotype of the chick (13)	Body size, body condition	Age, parental presence	41
Effect of maternal age on the phenotype of the chick (23)	Body size, body condition	Age	35
Effect of maternal age on the growth of the chick	Growth, change in body condition	Age	35
Effect of maternal age on the physiology of the chick (13)	Telomere, corticosterone	Age, parental presence, body condition, body size	23

Sample sizes differ because of chick mortality through the study period and because a sub-sample of 13-days-old chicks were monitored for physiological parameters

We then determined the change in body size (wing and tarsus growth) and body condition (SMI) from 13 to 23 days after hatching for the chicks that survived until this age ($N=35$, Table 1). This has been calculated as the difference between body size variables (i.e., wing size and tarsus length) or condition (SMI) measured at day 23 to the data recorded at day 13. To note, if we expressed the change in body size or body condition in terms of percentage, results remain similar. Body mass and body condition were strongly correlated at both ages ($F_{1,39}=149.6$, $P<0.001$; $F_{1,33}=52.4$, $P<0.001$, respectively for 13- and 23-days-old chicks) and analyses of body mass and body condition gave similar results (see Supplementary File, Annex 1). Similarly, results using tarsus length and wing length gave very similar results. Therefore, we only present the results focusing on body condition and tarsus length (as a proxy of body size) in the rest of the manuscript.

Physiological measurements

When chicks were 13 days old, their corticosterone (hereafter CORT) stress response was measured from blood samples by using a well-established protocol (Wingfield et al. 1994). This procedure was conducted on a sub-sample of chicks only, for practical reasons (i.e., bad weather and distance to the station; $N=23$, Table 1). Immediately after capture (i.e., within 3 min, Romero and Reed 2005), an initial blood sample ($\sim 150 \mu\text{L}$) was collected from the alar vein with a 25-gauge needle and heparinized microcapillary tubes. This sample was used to measure baseline CORT levels. A second blood sample ($\sim 150 \mu\text{L}$) was collected 30 min after capture and was used to measure the CORT stress response, i.e., the amount of CORT that is released in the bloodstream following a standardized stress protocol (hereafter “stress-induced CORT levels”). Birds were held in a cloth bag during this 30 min restraint. These blood samples were also used to measure the telomere length of all sampled chicks ($N=23$, Table 1). The corticosterone stress response was not measured when the chicks were 23 days old.

Corticosterone assay, molecular sexing, and telomere length

At the end of each nest visit, blood samples were immediately centrifuged in order to separate plasma and blood red cells. Then, all samples were stored at -20°C until subsequent analyses at the Centre d’Etudes Biologiques de Chizé. Plasma CORT concentrations were determined by radioimmunoassay as described previously in Lormée et al. (2003).

The corticosterone was extracted with diethyl-ether in 50 μL of plasma and was then assayed in duplicate with RIA method using H3-corticosterone (Perkin Elmer, US) and rabbit antiserum against corticosterone (Sigma Aldrich,

US). RIA corticosterone assay was validated on snow petrel plasma. One extract was serially diluted in the appropriate assay buffer, its displacement curve was parallel to the standard curve. Inter-assay and intra-assay precisions were respectively 13.78% and 6.91%. Corticosterone lowest detectable concentration was 0.28 ng/mL.

DNA was extracted from blood red cells of the first blood sample collected as part of the stress response by using the DNeasy blood and tissue kit (Qiagen). The sex of each blood sampled chick ($N=23$) was determined by molecular sexing, based on polymerase chain reaction (PCR) amplification of the CHD gene, as detailed by Fridolfsson and Ellegren (1999). This sub-sample of chicks allowed us to check for potential sex-dependent effects of maternal age on our variables of interest.

Telomere length was determined, from the first blood sample collected as part of the stress response, at the Centre d’Etudes Biologiques de Chizé. To do so, the TeloTAGGG Telomere Length Assay (Roche, Mannheim, Germany) has been used as previously described (Dupont et al. 2018; Angelier et al. 2019), with minor modifications. DNA quality was checked by optical density spectrophotometry. Briefly, 4 μg of DNA was digested with restriction enzymes for 16 h at 37°C . Digested DNA samples were then separated with a pulse-field gel electrophoresis (Bio-Rad). Then, all samples were run in a single gel at 3.0 V/cm with an initial switch time of 0.5 s to a final switch time of 7 s for 14 h. After this step, the gel was hybridized with a digoxigenin-labelled probe specific for telomeric sequences, and was visualized with a Chemidoc (Bio Rad). Telomere length was determined using ImageJ by analysing telomere smear densities.

Statistical analyses

All statistical analyses were performed with SAS Studio. Model selections were performed using a second-order Akaike’s Information Criterion (AICc) to select the most parsimonious model (Burnham et al. 2011). AICc were used to compare all possible models and ΔAICc and AICc weight were used to select the most parsimonious model (Burnham et al. 2011). Values for difference in AICc values (ΔAICc) were computed by subtracting the minimum AICc from all candidate model AICc. Differences between AICc values for different models can be used to determine which provides the most adequate description of the data based on the fewest model parameters. ΔAICc values > 2 are a good indicator that the model with the lowest AICc is preferable, whereas ΔAICc values < 2 indicate that models are fairly similar in their ability to describe the data. In that latter case, the model with the fewest number of parameters can be selected and AICc weights provide the likelihood of each competitive

models (Burnham et al. 2011). We used Generalized Linear Models (GLM) with a normal (identity link function) or a binomial distribution (logit link function) depending on the dependent variables of interest. The parameter estimates (Mean \pm SE, and 95% Confidence Intervals) and effect sizes (β) of the best selected models were reported.

Several model selections were conducted to test our biological hypotheses and different sets of models had to be run because of different sample sizes (Table 1) and different data distribution (see Annex 2 for histograms of all response variables). Firstly, we tested whether maternal age was related to hatching date and the length of the guarding period. Secondly, we tested the effect of maternal age, hatching date, and the length of the guarding period on the probability to survive from 13 to 23 days old. We also tested the influence of offspring body size (tarsus length) and body condition on this survival probability. We then tested the relationships between CORT levels (baseline and stress-induced), telomere length and this survival probability. Finally, we tested the influence of maternal age on body size (tarsus length), body condition and the growth of the chicks. We also tested the influence of maternal age, body condition, and body size on corticosterone levels and telomere length. Parental presence was included when relevant (13-days-old chicks) as a previous study found that this variable can affect body condition and corticosterone levels of young chicks (Dupont et al. 2021). Note that the sex of the chicks was not included as an explanatory factor in these analyses because it was available for a limited number of chicks only ($N=23$). We ran additional models including the sex factor with this limited sample size and they gave similar results to our main analyses, suggesting that the sex of the offspring does not affect our results.

Results

Influence of maternal age on hatching date and duration of the guarding period

Hatching date was negatively associated with maternal age (GLM, $\Delta\text{AICc}=4.33$; estimate (mean 95% CI): -0.153 [-0.269 ; -0.037], $\beta=-0.368$; Fig. 1a). More precisely, the chicks from older females hatched earlier than those from younger females. In addition, the duration of the guarding period was also negatively associated with maternal age (GLM, $\Delta\text{AICc}=1.78$; estimate (mean 95% CI): -0.115 [-0.228 ; -0.003], $\beta=-0.305$; Fig. 1b): the chicks from older females were left alone earlier than those from younger females.

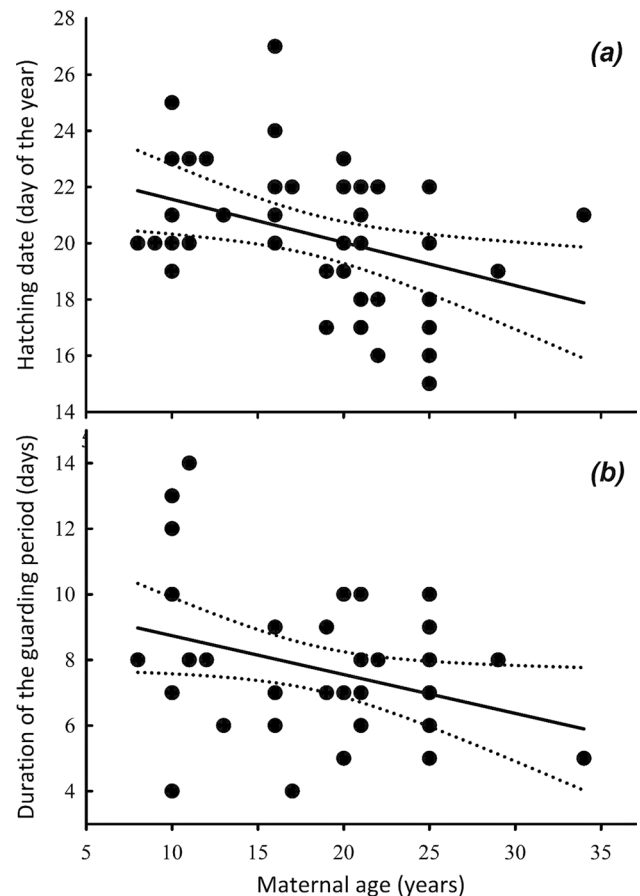


Fig. 1 Influence of maternal age on **a** hatching date and **b** the duration of the guarding period in snow petrels. The solid lines represent the predicted relationships between maternal age and these two variables. The dotted lines represent the 95% confidence intervals for these relationships

Influence of maternal age and offspring phenotype on survival rate

Survival rate from 13 to 23 days after hatching was significantly associated with maternal age but not with the hatching date or the duration of the guarding period (Table 2a, Fig. 2). Specifically, the chicks from older females had a higher survival rate at the nest (estimate (mean, 95% CI): -0.233 [-0.440 ; -0.026], $\beta=0.242$). In addition, this survival probability was not related to offspring body size (tarsus length) and body condition (Table 2b). Regarding physiology, the survival rate was significantly and positively related to offspring telomere length measured at 13 days old (Table 2). More precisely, chicks with longer telomeres had a higher survival probability (estimate (mean, 95% CI): -7.607 [-15.054 ; -0.159], $\beta=0.001$). However, survival rate was not linked with CORT levels (baseline or stress-induced, Table 2c).

Table 2 Influence of (a) maternal age, hatching date, and the duration of the guarding period; (b) body condition and body size of 13-days-old chicks; (c) physiological variables (corticosterone (CORT) levels and telomere length; on the survival of the chick (from 13 to 23 days old)

	Dependent variable	Independent variables	K	AICc	ΔAICc	Weight
a	Survival of the chick	Age	2	31.58	0.000	0.529
		Age, hatching date	3	33.70	2.12	0.184
		Age, guarding duration	3	33.91	2.32	0.166
		Null	1	36.24	4.66	0.052
b	Survival of the chick	Null	1	36.24	0.000	0.300
		Body condition	2	36.53	0.290	0.260
		Body size, body condition	2	36.76	0.522	0.231
		Body size	3	36.96	0.721	0.209
c	Survival of the chick	Telomere	2	15.31	0.000	0.396
		Telomere, baseline CORT	3	15.80	0.491	0.310
		Telomere, stress-induced CORT	3	17.86	2.55	0.110
		Null	1	36.24	20.93	<0.001

The three best models and the null model are represented. Values for difference in AICc values (ΔAICc) were computed by subtracting the minimum AICc from all candidate model AICc. K and weight refer to the number of parameters and to AICc weight, respectively

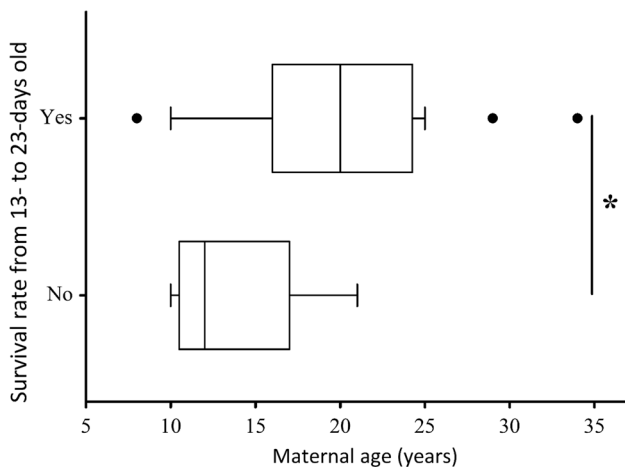


Fig. 2 Influence of maternal age on offspring survival probability from 13 to 23 days after hatching in snow petrel chicks. Box-and-whisker plots represent the data: the top and bottom of the boxes represent the first and last quartiles, respectively; the line across the box represents the median. The whiskers represent the 5th and 95th percentiles, and the circles represent outliers. Significant difference is indicated by an asterisk (* $P < 0.05$)

Influence of maternal age on growth and morphometric measurements in chicks

In 13-days-old chicks, body size was not affected by maternal age or parental presence at the nest (Table 3a, Fig. 3). Although body condition was not affected by maternal age, chicks with a parent in the nests were in better condition than those that were alone in the nest at the time of capture (Table 3b). Tarsus growth was significantly and positively correlated with maternal age (GLM, ΔAICc = 3.57; estimate (mean 95% CI): 0.125 [0.025; - 0.225], β = 0.763; Fig. 4). However, the change in body condition from 13 to 23 days

old was not related with maternal age as the most parsimonious model was the null model (ΔAICc = - 2.20). In 23-days-old chicks, tarsus length was significantly and positively correlated with maternal age (GLM, ΔAICc = 5.11; estimate (mean 95% CI): 0.139 [0.042; - 0.237], β = 0.849; Fig. 3B) but body condition was not significantly associated with maternal age as the most parsimonious model was the null model (ΔAICc = - 2.26).

Influence of maternal age on physiological measurements in 13-days-old chicks

In 13-days-old chicks, baseline CORT levels were not affected by maternal age or by the presence of a parent in the nests (Table 4a). However, baseline CORT levels were significantly and negatively correlated with body condition (estimate (mean 95% CI): - 0.022 [- 0.034; - 0.010], β = - 0.677; Table 4) and slightly but not significantly with body size (tarsus length, estimate (mean 95% CI): - 0.567 [- 1.206; 0.072], β = - 0.318; Table 4a). The selected model for stress-induced CORT levels only included parental presence and maternal age had a lower AICc (ΔAICc = 1.174) and a higher AICc weight (AICc weight = 0.274 vs. 0.153, Table 4b). These two competitive models were therefore considered. In the simplest model, stress-induced CORT levels were negatively correlated with body condition (estimate (mean 95% CI): - 0.108 [- 0.171; - 0.045]). In the more complex model, stress-induced CORT levels were positively associated with maternal age (estimate (mean 95% CI): 0.535 [0.017; 1.052], β = 0.295; Table 4b, Fig. 5), and negatively with body condition (estimate (mean 95% CI): - 0.074 [- 0.139; - 0.009], β = - 0.400; Table 4). Stress-induced CORT levels were also lower when a parent

Table 3 Influence of maternal age and parental presence in the nest on (a) body size and (b) body condition in 13-days-old snow petrel chicks

	Dependent variable	Independent variables	K	AICc	Δ AICc	Weight
a	Body size (13 days old) (<i>tarsus length</i>)	Null	1	117.46	0.000	0.552
		Parental presence	3	119.43	1.98	0.205
		Age	2	119.70	2.25	0.179
		Age, parental presence	4	121.78	4.33	0.063
b	Body condition (13 days old)	Parental presence	2	111.19	0.000	0.725
		Age, parental presence	3	113.47	2.28	0.232
		Null	1	117.46	6.27	0.032
		Age	2	119.41	8.22	0.012

The three best models and the null model are represented. Values for difference in AICc values (Δ AICc) were computed by subtracting the minimum AICc from all candidate model AICc. K and weight refer to the number of parameters and to AICc weight, respectively

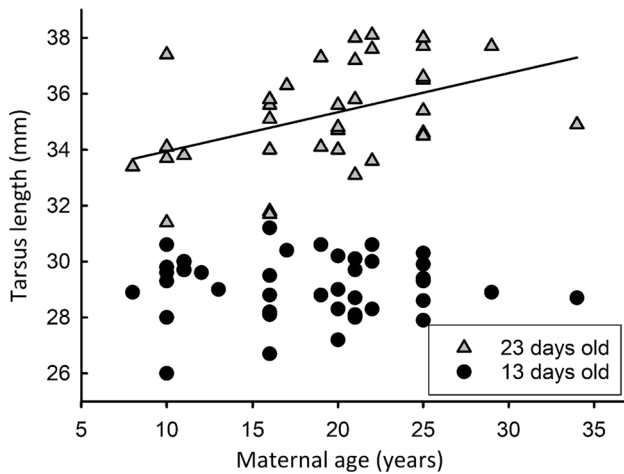


Fig. 3 Influence of maternal age effect on offspring body size in 13-days-old (fill circles) and 23-days-old (fill triangles) snow petrel chicks. The solid line represents the positive/significant relationship between maternal age and offspring tarsus length in 23-days-old chicks

was present in the nest (estimate (mean 95% CI): -9.874 [-18.888 ; -0.859], $\beta=0.894$; Table 4b, Fig. 5). However, stress-induced CORT levels were not linked with body size (Table 4b). Telomere length was not significantly associated with maternal age or body condition (Table 4c). However, telomere length was negatively correlated with tarsus length (estimate (mean 95% CI): -0.357 [-0.693 ; -0.020], $\beta=-0.404$; Table 4c).

Discussion

In this study, we showed that maternal age had an important and significant influence on reproductive behaviour and offspring performance. Specifically, older females bred and left their chick alone earlier. Importantly, we also showed that maternal age had an impact on offspring morphology

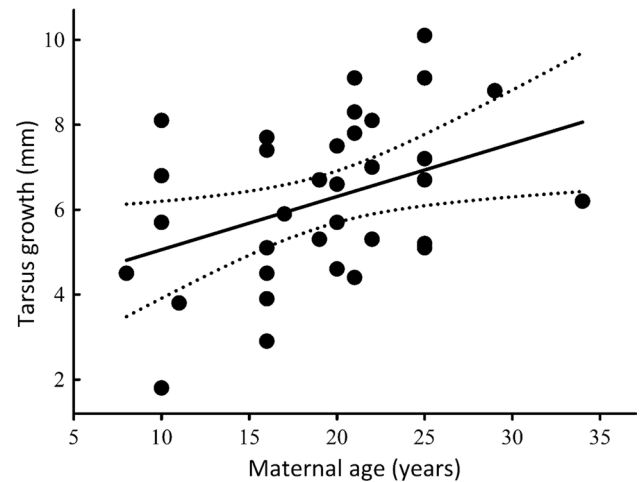


Fig. 4 Influence of maternal age on tarsus growth from 13 to 23 days old in snow petrel chicks. The solid line represents the relationship between maternal age and tarsus growth. The dotted lines represent the 95% confidence intervals for this relationship

and physiology, and ultimately, on chick survival. Importantly, these morphological effects were not found in young chicks (13 days old), and the influence of maternal age on growth seems to become apparent after that age only as the chicks grow and require an increasing amount of food/energy. After 13 days, chicks from older females were larger, heavier, grew faster, and had a higher survival probability at the nest. Moreover, 13-days-old chicks had a higher sensitivity to stress, as shown by moderately higher stress-induced corticosterone levels. Altogether, these results demonstrate not only that younger mothers have lower reproductive performances, but also that maternal age affects the offspring phenotype with potential long-term consequences.

Importantly, our parental sample size was only composed of young and middle-aged females (<35 years old). Therefore, it was not possible to detect sign of senescence on reproductive output in this study (Berman et al. 2009).

Table 4 Influence of maternal age, body size, body condition, and parental presence in the nest (for corticosterone levels only) on (a) baseline and (b) stress-induced corticosterone levels and (c) telomere length in 13-days-old snow petrel chicks

	Dependent variable	Independent variables	K	AICc	ΔAICc	Weight
a	Baseline corticosterone	Body condition, body size	3	90.92	0.000	0.334
		Body condition	2	91.38	0.453	0.267
		Parental presence, body condition	3	93.58	2.66	0.089
		Null	1	97.61	6.68	0.012
b	Stress-induced corticosterone	Age, parental presence, body condition	4	168.38	0.000	0.274
		Body condition	2	169.55	1.17	0.153
		Parental presence, body condition	3	169.73	1.35	0.139
		Null	1	176.94	8.56	0.004
c	Telomere	Body size	2	63.42	0.000	0.357
		Body condition, body size	3	65.02	1.60	0.160
		Age, body size	3	65.21	1.80	0.145
		Null	1	65.23	1.81	0.144

The three best models and the null model are represented. Values for difference in AICc values (ΔAICc) were computed by subtracting the minimum AICc from all candidate model AICc. K and weight refer to the number of parameters and to AICc weight, respectively

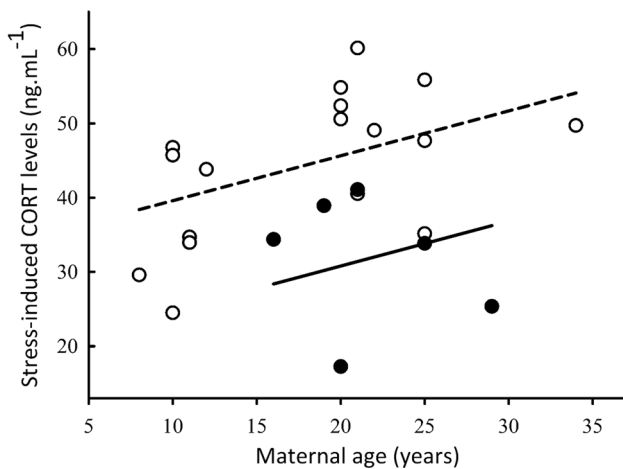


Fig. 5 Influence of maternal age effect on offspring stress-induced CORT levels in 13-days-old snow petrel chicks. Filled and open symbols represent alone chicks and attended chicks, respectively. The solid and the broken lines represent the relationships between maternal age and offspring stress-induced CORT levels for alone and attended chicks, respectively

In addition, we specifically focused on adult females in this study and we did not consider the potential importance of paternal age. This decision resulted from practical reasons because we found more known-aged females than known-aged males in our study colony, but also from ecological reasons because female snow petrels are smaller than males. As such, they seem to be more constrained in their ability to deliver food to the offspring and they have a higher impact on reproductive performance than male snow petrels (Barbraud and Chastel 1999; Barbraud et al. 1999).

Reproductive phenology, duration of the guarding period and offspring survival

Consistent with our prediction 1, we found that younger female snow petrels reproduced later. Accordingly, numerous studies have also reported that laying date or hatching date are negatively affected by parental age (Perrins 1970; Curio 1983; de Forest and Gaston 1996; Cam and Monnat 2000; Verhulst and Nilsson 2008; Blas et al. 2009; Bauer et al. 2018; Reséndiz-Infante and Gauthier 2020). In birds, and more specifically snow petrels, laying date and reproductive phenology are influenced by environmental conditions (Barbraud and Chastel 1999; Barbraud and Weimerskirch 2006; Dickey et al. 2008; Verhulst and Nilsson 2008; Moe et al. 2009; Descamps et al. 2011; Sauser et al. 2021) and internal state (body condition: Bêty et al. 2003; Descamps et al. 2011; stress physiology: Goutte et al. 2010). In the snow petrel, Barbraud et al. (2000) found that laying date was tightly connected to the duration of the pre-laying exodus, during which females forage at sea to improve their body condition. This suggests that younger females may be less able to acquire food and to build as quickly as older females the body reserves, which are required for egg laying.

In addition, we also reported that younger females guarded their chick for a longer period (prediction 2). To our knowledge, our study is the first to demonstrate that maternal age affects the duration of the guarding period in an altricial species. In petrels, the duration of the guarding phase is related to the environmental condition and to the quality of the parents (Amundsen 1995; Tveraa and Christensen 2002; Varpe et al. 2004), but also to the chick’s needs in terms of food provisioning and protection (Varpe et al. 2004; but see Goutte et al. 2011). Leaving a chick unattended can be beneficial because both parents can forage simultaneously

at sea, increasing therefore chick provisioning (quantity and frequency, Catry et al. 2006). However, this may also entail some costs because the chick is left unguarded and is therefore more susceptible to inclement weather and/or predation (Weathers et al. 2000; Catry et al. 2006). Older females may be better at provisioning their chick during the first days after hatching and their chicks may therefore reach earlier a body condition/size that allow them to thermoregulate. This could explain why older females guarded their chick for shorter periods. Unfortunately, our data did not allow us to test this hypothesis as the first morphometric measurements were recorded at day 13 (i.e., maximum length of the guarding period) for all the chicks and not at the end of the guarding period. This hypothesis is however not supported by the available data because we did not find any difference in body size and body condition at day 13. Instead, older females may be more experienced and better at estimating when the chick can be left alone without any major risk for its survival. Alternatively, older females may be in poorer condition, and as a consequence, they may have to leave the nest unguarded at an earlier age to replenish their body reserves (Tveraa et al. 1998). However, this explanation is quite unlikely because previous studies have not found a relationship between age and body condition in this species (Angelier et al. 2007a, 2020; Goutte et al. 2010).

In line with our prediction 3, we found a strong positive correlation between offspring survival at the nest and maternal age, as previously reported in multiple bird species including the snow petrel (Angelier et al. 2007a; Sergio et al. 2007). Although our sample size was too small to detect a link between phenology and offspring survival, our study confirms that offspring survival is linked to parental age, probably through the timing of reproduction, as previously found in numerous altricial species (Blas et al. 2009; Culina et al. 2020) including the snow petrel (Sauser et al. 2021).

Offspring growth, body size, and body condition

According to our fourth prediction, we found that younger mothers had smaller chicks (i.e., at 23 days old) compared to older ones, highlighting therefore that maternal age has an important impact on their offspring developmental conditions. Specifically, we found that the chicks from younger females grew slower and reached a lower body size 23 days after hatching (wing and tarsus length). Importantly, this impact of maternal age on body size was not apparent 13 days after hatching. This suggests that young females can sustain their offspring needs at the beginning of the developmental period, when the chick is small and cannot ingest large meals. However, the provisioning effort of young females may not be sufficient later as the chick becomes larger and requires increasing amounts of food, explaining the influence of maternal age on growth and body size when

offspring reaches 23 days old. In other words, small differences in provisioning effort that are not apparent on day 13 may accumulate through the chick-rearing period, and become significant at a later stage only (i.e., day 23).

In our study, the condition of snow petrel chicks was not related to maternal age, suggesting that chicks from young females did not suffer from nutritional stress. Interestingly, we however found that the chicks from younger females grew slower and were smaller at 23 days old. This suggests that snow petrel chicks may maintain their body condition (a major determinant of post-fledging survival, Sauser et al. 2018) at the expense of their body size, which is at least partly developmentally determined (Barbraud et al. 1999). This contrasts with other studies, which have suggested that developing seabirds may prioritize growth at the expense of their condition and their survival (e.g., Harris 1966). Interestingly, body size is closely associated with adult performance in this species: smaller snow petrels feed their chick less often and seem to be less efficient foragers (Barbraud et al. 1999, 2019). Therefore, chicks from younger females may have lower post-fledging survival probabilities and reproductive performance later in life, although these hypotheses need to be explicitly tested in the future.

Offspring sensitivity to stress

As previously reported in this species (Dupont et al. 2021), we reported that the presence of a parent in the nest may mitigate the stress sensitivity of its chick. Specifically, snow petrel chicks had lower stress-induced CORT when a parent was present in the nest at the time of capture, 13 days after hatching (see Dupont et al. 2021 for further details).

In addition, we found that stress-induced CORT levels seem to be affected by maternal age in our study although the effect size could be considered as moderate ($\beta = 0.295$). Specifically, chicks from older females have higher stress-induced CORT levels, suggesting that they have a higher adrenocortical stress sensitivity (prediction 5). Elevated stress-induced CORT levels are classically associated with a poor body condition and with nutritional stress in chicks (Kitaysky et al. 2001; Pravosudov and Kitaysky 2006; Love and Williams 2008; Angelier et al. 2022). Our result on stress-induced CORT levels is therefore surprising because we did not find any relationship between maternal age and offspring body condition. Interestingly, this pattern is not equivocal since other studies report no or opposite effects of nutritional stress or poor body condition on stress-induced CORT levels (Wada et al. 2009). For example, in the tufted puffin (*Fratercula cirrhata*), chicks are known to suppress Hypothalamic–Pituitary–Adrenal (HPA) axis activity and to have therefore lower stress-induced CORT levels when facing nutritional stress (Kitaysky et al. 2005). Then, the observed reduced CORT stress sensitivity in 13-days-old

snow petrels produced by young females may be interpreted as a way to protect the chick against the detrimental effect of elevated circulating CORT levels (reviewed in Sapolsky et al. 2000). However, it remains unclear why older females produce chicks with higher stress-induced CORT levels. In laboratory bird species, the corticosterone stress response increases with age as the chicks develop (Wada et al. 2007, 2009) and higher stress-induced corticosterone levels could therefore reflect a more developed HPA axis, and therefore a more advanced developmental state, in the chicks from older mothers. Finally, and importantly, CORT levels were unrelated to offspring survival, questioning therefore the relevance of this physiological marker of fitness in snow petrel chicks. Further studies are definitely needed to better understand how stress-induced CORT levels relate to developmental constraints and offspring survival.

Importantly, there is increasing evidence that the adrenocortical stress response is repeatable among life-history stages (Wada et al. 2008; Grace and Anderson 2014; Vitousek et al. 2014; Small and Schoech 2015; Jimeno et al. 2017), meaning that snow petrel chicks from older females may also have higher stress-induced CORT levels later in life. Although the potential benefits of mounting a strong stress response remains debated (Breuner et al. 2008; Angelier and Wingfield 2013; Vitousek et al. 2018), having elevated stress-induced CORT levels may promote survival under some situations (Angelier et al. 2009). Our study shows for the first time that maternal age can affect offspring CORT stress sensitivity and future studies are now needed to fully understand the fitness consequences of such phenotypic plasticity.

Offspring telomere length

Contrary to our sixth prediction and to other studies (e.g., Asghar et al. 2015; Dupont et al. 2018; Eisenberg 2019), we did not find any relationship between maternal age and offspring telomere length. Other studies also failed to find such an effect of parental age on offspring telomere in vertebrates (e.g., Noguera et al. 2018; Belmaker et al. 2019; van Lieshout et al. 2021), suggesting that the influence of parental age on the telomere length of the progeny varies between species and depends if we consider maternal age or paternal age. Indeed, previous studies in humans have suggested that paternal age could have a stronger impact on telomere length than maternal age (Eisenberg et al. 2017). Therefore, maternal age might only be related to offspring telomere length if paternal and maternal age are strongly correlated although this hypothesis has never been explicitly tested in wild vertebrates to our knowledge. In our study, we also did not find any strong relationship between body condition and telomere length in 13-days-old chicks. We however found a negative association between telomere length and

tarsus length at this age, suggesting that growth may affect telomere attrition and telomere length in snow petrel chicks. Indeed, developmental constraints experienced by the chicks have been shown to affect the allocation of resources to both growth and telomere maintenance (Boonekamp et al. 2014; Vedder et al. 2017; Monaghan and Ozanne 2018). However, in our study, most of the effects of maternal age on body size were not apparent when the chicks were 13 days old and they appeared at an older age (e.g., 23 days old). This could explain why we did not find any strong relationship between telomere length and maternal age in our study. In future studies, it would be relevant to measure telomere length several times during the development to test whether the influence of maternal and paternal age on telomere length exacerbates as the chick grows. Actually, we aimed to sample the chicks 32 days after hatching in our study, but the colony was no longer accessible later in the season because of successive heavy snowstorms.

Finally, we found that telomere length was a reliable predictor of survival in snow petrel chicks: 13-days-old chicks with shorter telomere had a lower survival probability until 23 days old. This link between telomere length and survival at early stage has already been found in an increasing number of studies (Quque et al. 2021), and our result supports the idea that telomere length is a relevant proxy of individual quality both at juvenile and adult stages (Angelier et al. 2019; Bichet et al. 2020).

Conclusion

Our study shows that maternal age had an important influence on reproductive performance and offspring morphology and physiology in an Antarctic long-lived bird species. Further studies should now aim to examine the influence of both maternal and paternal ages on offspring physiology to better understand how they contribute to offspring quality. Such studies should also investigate the consequence of such physiological modifications on the lifelong performance of the offspring (recruitment and reproduction).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00442-023-05451-5>.

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Data availability All data produced from this study will be provided as a supplementary file.

Code availability Not applicable.

Declarations

Conflict of interest Authors have no conflicts of interest to declare.

Ethics approval Ethics approval were waived by the Ethic Committee of Institut Polaire Français (IPEV) and by the Préfet of Terres australes et antarctiques françaises (TAAF) after advices from the Comité de l'Environnement Polaire (CEP).

Consent to participate Not applicable.

Consent for publication Not applicable.

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