

Research



Cite this article: Angelier F, Chastel O, Lendvai AZ, Parenteau C, Weimerskirch H, Wingfield JC. 2020 When do older birds better resist stress? A study of the corticosterone stress response in snow petrels. *Biol. Lett.* **16**: 20190733.

<http://dx.doi.org/10.1098/rsbl.2019.0733>

Received: 4 October 2019

Accepted: 4 December 2019

Subject Areas:

ecology, evolution, behaviour

Keywords:

age, stress, corticosterone, parental effort, seabirds

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Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.4782564>.

When do older birds better resist stress? A study of the corticosterone stress response in snow petrels

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Life-history theory predicts that, to optimize their fitness, individuals should increase their reproductive effort as their residual reproductive value decreases. Accordingly, several studies have shown that individuals downregulate their glucocorticoid stress response (a proxy of reproductive investment in vertebrates) as they age, and as the subsequent reproductive value decreases. However, and surprisingly, results appear inconsistent, suggesting that the environmental context or the individual state may affect the relationship between age and reproductive effort. Here, we tested for the first time this hypothesis, and more specifically, whether this attenuation of the corticosterone stress response with advancing age depends on the energetic status of individuals. We compared the influence of age on the corticosterone stress response between fasting and non-fasting breeding snow petrels (*Pagodroma nivea*), an extremely long-lived bird. As expected, we found that the corticosterone stress response was attenuated in old petrels, but only when they were not fasting. Interestingly, this pattern was not apparent in fasting petrels, suggesting that old birds downregulate their corticosterone stress response and increase their parental investment only when they are in good body condition. At the ultimate level, old individuals may maintain a strong corticosterone stress response when fasting because the survival costs of increased stress resistance and parental effort might then outweigh their reproductive benefits.

1. Introduction

When the value of the current reproduction is high relative to the value of future reproduction and survival, life-history theory predicts that individuals should increase their reproductive effort to optimize their fitness [1]. According to this theory, the reproductive effort is supposed to increase with advancing age because, as organisms age, their future reproductive opportunities decline [2]. The study of this question can benefit from an eco-physiological approach because the reproductive effort is driven by several flexible physiological mechanisms that govern resource allocations and mediate life-history decisions [3].

Among these physiological mechanisms, the glucocorticoid stress response is of special interest [4]. Corticosterone (the primary glucocorticoid in birds) secretion increases when stressors occur, and importantly, elevated circulating plasma corticosterone levels are known to promote immediate survival at the expense of reproduction in vertebrates. Importantly, this corticosterone stress response is flexible and can be modulated according to individual state or environmental conditions [4–7]. Therefore, investigating the influence of age on this corticosterone stress response can allow ecologists to understand the modulation of parental investment with age [8].

A limited number of studies have examined this question, and interestingly, the relationship between age and the corticosterone stress response appears inconsistent [9,10]. Some studies found that the corticosterone stress response decreases with age [5,8–13] whereas this relationship was not found in others [14,15]. Even more surprisingly, the relationship between age and the corticosterone stress response is not consistent within the same species [11,12,14,16]. These results show that individuals do not always downregulate their corticosterone stress response as they age, suggesting that such increased resistance to stress with advancing age may strongly depend on the ecological context.

Under poor environmental conditions, resources are limited and the trade-off between parental effort and parent survival is likely to be exacerbated. Therefore, the influence of age on parental investment, and the corticosterone stress response, should logically depend on the environmental situation [17]. First, this increase in parental effort is expected to be magnified when individuals reach an age when the residual reproductive value becomes null or close to null ('the terminal investment hypothesis', [1]). According to this theory, the negative relationship between age and the corticosterone stress response should be reinforced when parent's integrity is compromised as it is the case under harsh environmental conditions (illness, poor energetic condition). Second, recent state-dependent models suggest that individuals may not benefit from increasing parental effort with advancing age when such an increase in parental effort is associated with a high risk of mortality or severe physiological damage. Instead, old individuals should adopt a prudent strategy to limit further damage, and thus increase their residual reproductive life ('the terminal restraint hypothesis', [10,17]. Under this scenario, the negative relationship between age and the corticosterone stress response should be reinforced when the costs of increased parental effort are reduced, i.e. under good environmental conditions.

In this study, we propose to test these hypotheses in a long-lived species by comparing the influence of age on the corticosterone stress response between fasting and non-fasting birds. To do so, we caught known-age snow petrels, *Pagodroma nivea* (from 9 to 46 years old), either immediately after a foraging trip or after a few days of fasting on the nest. Fasting birds are more energetically constrained than non-fasting ones, and therefore, we expect that the influence of age on the corticosterone stress response will differ between non-fasting and fasting petrels. Specifically, we predict that (1) old snow petrels will downregulate their corticosterone stress response relative to young individuals; (2a) this age-related downregulation will be amplified in fasting birds relative to non-fasting birds because energetically constrained individuals should increase their parental effort to insure a final successful reproductive event (the terminal investment hypothesis); (2b) alternatively, this age-related downregulation could be reduced in fasting birds relative to non-fasting birds because energetically constrained individuals could reduce their investment in order to limit further damage to the organism, and thus, to increase their residual reproductive life.

2. Material and methods

Incubating snow petrels were studied in 2010 (January 8–21) on Pointe Géologie Archipelago, Terre Adélie (66°40' S, 140°01' E), Antarctica. In snow petrels, the incubation period lasts for

about 45 days and both partners alternate incubation spells lasting 5–9 days. Incubating snow petrels lose a significant portion of their body mass during an incubation shift, and after their incubation duty, birds forage in Antarctic waters to restore their body condition while their partner is incubating the egg and fasting on the nest [18]. We selected 75 known-aged snow petrel nests and marked all incubating birds with a black spot of dye on their head. Their partners were unmarked allowing us to subsequently recognize both partners. Then, we checked every nest twice a day to monitor the presence and absence of both partners. Of these petrels, some individuals were caught and blood sampled just after their return from the sea (hereafter called 'non-fasting birds', $N=29$) or after 4 days of fast on the nest (hereafter called 'fasting birds', $N=28$).

Birds were captured by hand at their nest and all birds were bled according to the standardized capture/restraint stress protocol previously used in this species [11,14,16]. Immediately after capture (i.e. within 3 min), an initial blood sample (300 μ l) was collected from the alar vein with a 1-ml heparinized syringe and a 25-gauge needle to measure baseline corticosterone levels (hereafter called 'baseline' sample). After collection of the initial blood samples, birds were placed into cloth bags, and a subsequent sample (300 μ l) was collected 30 min after capture (hereafter called 'stress induced' sample). All birds were weighed to the nearest 2 g using a spring balance and their skull length was measured to the nearest 0.5 mm. Body condition was calculated as the residuals between body mass and skull length ($F_{1,55} = 15.21$, $p < 0.001$, $r = 0.458$). Blood samples were centrifuged and both plasma and red cells were stored at -20°C until laboratory analyses. The sex was determined by molecular sexing and plasma concentrations of corticosterone were determined by radioimmunoassay [14]. All samples were run in one assay (intra-assay variation, 7.07%).

All analyses were performed with SAS statistical software (v. 9.3; SAS Institute). We used a generalized linear model (GLM) to test the influence of age on body condition, baseline and stress-induced corticosterone levels in fasting and non-fasting petrels (dependent variable: body condition or corticosterone levels, independent factors: age, sex, fasting and their interactions). Because the influence of age on physiological variables may follow a curvilinear pattern [10,11], we also included the age^2 variable and the $\text{age}^2 \times \text{fasting}$ interaction in the models. Corticosterone data were log-transformed to meet the normality assumption.

3. Results

Body condition and baseline corticosterone levels were not affected by sex (body condition: $F_{1,53} = 0.67$, $p = 0.418$; baseline corticosterone: $F_{1,53} = 0.09$, $p = 0.772$), age (body condition: $F_{1,54} = 2.13$, $p = 0.150$; baseline corticosterone: $F_{1,54} = 0.24$, $p = 0.625$) or any interaction (all $p > 0.100$). However, fasting individuals had lower body condition and higher baseline corticosterone levels than non-fasting individuals ($F_{1,55} = 48.10$, $p < 0.001$; $F_{1,55} = 4.28$, $p = 0.043$). There was no significant influence of age^2 or the ' $\text{age}^2 \times \text{fasting}$ ' interaction on baseline corticosterone levels (all $p > 0.250$).

Stress-induced corticosterone levels were not affected by sex ($F_{1,52} = 0.60$, $p = 0.443$) and fasting ($F_{1,53} = 0.06$, $p = 0.811$). Stress-induced corticosterone levels were significantly affected by age ($F_{1,53} = 6.80$, $p = 0.012$) and the ' $\text{age} \times \text{fasting}$ ' interaction ($F_{1,53} = 5.06$, $p = 0.029$), demonstrating that the relationship between age and stress-induced corticosterone levels significantly differed between fasting and non-fasting birds (figure 1). All the other interactions had no significant effect on stress-induced corticosterone levels (all $p > 0.250$). Specifically, stress-induced corticosterone levels of non-

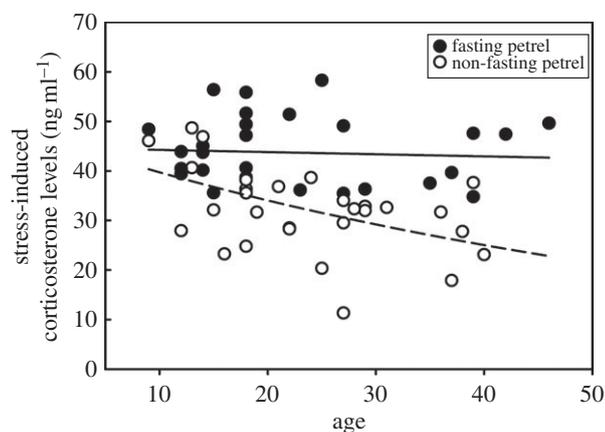


Figure 1. Relationship between age and stress-induced corticosterone levels in non-fasting (white dots, dashed line) and fasting (black dots, solid line) known-aged snow petrels ($n = 57$).

fasting birds were negatively correlated with age ($\chi^2 = 7.78$, $p = 0.005$; figure 1) but this relationship was not significant for fasting birds ($\chi^2 = 0.10$, $p = 0.757$; figure 1). There was no significant influence of age^2 or the ‘ $\text{age}^2 \times \text{fasting}$ ’ interaction on stress-induced corticosterone levels (all $p > 0.250$).

4. Discussion

According to our prediction, we found that old individuals have an overall dampened corticosterone stress response when compared to young parents (prediction 1). Several explanations have been proposed for this age-dependent relationship [5,8–11]. First, a strong stress response could be detrimental to survival [4], and therefore, only birds with a weak stress response would survive long enough to reach old ages (selection). Second, birds may secrete less and less corticosterone in response to stress as they are repeatedly handled, and therefore, as they age (habituation, [6]). Third, birds could actively downregulate their corticosterone stress response in order to adjust their parental investment to their residual reproductive value (the brood value hypothesis, [5]). Here, we found that the corticosterone stress response is dampened with advancing age in the non-fasting birds but not in fasting birds, supporting the idea that the stress response is flexible and can be actively downregulated by individuals according not only to their age but also to their energetic state [4,7]. Importantly, this also suggests that habituation and selection processes might play a minor role only in shaping the corticosterone stress response of this species although individual survival data would be necessary to fully test these hypotheses.

Our study provides a functional basis to explain the reason why this relationship between age and the corticosterone stress response appears inconsistent among studies [9,10]. It demonstrates that this dampened stress response with advancing age is dependent on the individual state (i.e. energetic condition). According to previous studies [5], a dampened stress response is thought to mediate an increased parental investment. Therefore, our study suggests that individuals increase their parental investment as they age only when they are not energetically constrained. Actually, we predicted that this age-related downregulation should be amplified in fasting birds relative to non-fasting birds if energetically constrained birds increase their parental

effort to insure a final successful reproductive event (‘the terminal investment hypothesis’, prediction 2a). However, our results did not support this hypothesis since we actually found the opposite pattern.

We suggest instead that old birds refrain from increasing their parental investment when they are more advanced in their incubation shift, and when their energetic condition reaches a lower threshold (prediction 2b). Petrels are very long-lived birds with an extremely high annual survival probability and they are expected to refrain from investing resources into reproduction if physiological damage impairs survival and future reproductive opportunities [17]. Therefore, petrels may increase their parental investment as they age to a given extent only. Thus, older individuals would better resist stress when their body condition moderately deteriorates because the survival costs (i.e. immediate mortality or physiological damages) of such resistance would remain very low and minor relative to its reproductive benefit. However, this stress resistance of older birds would progressively decrease as the degree of environmental constraint increases, and as their body condition gets worse, because the survival cost of maintaining parental effort might then outweigh its reproductive benefit. This hypothesis is indeed supported by a few studies that reported such interactive effect of age and environmental conditions on reproductive performances and proxies of parental investment (i.e. laying date and clutch size, [19,20]).

Importantly, we compared birds returning from the sea after a foraging trip (non-fasting petrels) and birds that had been fasting on their nest for 4 days (fasting petrels). These two groups differed in their body condition because fasting petrels were more advanced in their incubation shift. Petrels are known to maintain incubation behaviour until they reached a low threshold in body condition, which is associated with a rise in corticosterone levels, a decrease in prolactin levels, and ultimately with nest desertion [14,16]. In our study, all fasting and non-fasting petrels were incubating at the time of capture, meaning that they did not reach this low threshold in body condition. Our study, therefore, examined the impact of the moderate changes in body condition that occur during incubation shifts on the regulation of the corticosterone stress response. Although most studies have used age as a proxy of residual reproductive value, we demonstrate here the additional importance of individual internal state (body condition). There is increasing evidence that, for a given age, individuals differ in their survival probability and their reproductive performance. Therefore, the residual reproductive value of individuals can be only weakly correlated with their age in some species. Future studies should now rely on long-term and individual-based population monitoring to fully explore the link between resistance to stress and the residual reproductive value.

Ethics. Licences and permissions were granted by the Ethic Committee of the Institut Polaire Francais (IPEV) and by the Préfet de Terres Australes et Antarctiques Francaises (MP/09/13/04/09).

Data accessibility. Data are available as electronic supplementary material.

Authors’ contributions. F.A. and J.C.W. collected field data. F.A., O.C. and J.C.W. designed the study. F.A. analysed the data and drafted the manuscript. C.P. ran the hormone assays. All authors contributed to the analyses and interpretation of the data. All authors revised the article for important intellectual content. All authors gave final approval for publication and agree to be held accountable for the content of the article.

Competing interests. We declare we have no competing interests.
Funding. The project was supported by the French Polar Institute (IPEV, Prog. 109 to H.W.) and the 7th research programme of the

European Community FP7/2007–2013 (Marie-Curie Fellowship, grant no. 237034 to F.A.). A.Z.L. was supported by the National Research Development and Innovation Office (OTKA K113108).

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