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"Home alone!" influence of nest parental attendance on offspring behavioral and hormonal stress responses in an Antarctic seabird, the snow petrel (*Pagodroma nivea*)

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ABSTRACT

In altricial species, parents brood their chicks constantly before leaving them unattended sometimes for extended periods when they become thermally independent. During this second phase, there is sometimes important inter-individual differences in parental attendance and the fitness costs and benefits of parental strategies have previously been extensively investigated. However, the impact of parental presence on offspring behaviors and stress physiology has been overlooked. Here, we examined the influence of parental presence on offspring hormonal and behavioral stress sensitivities in snow petrel chicks. We demonstrated for the first time in a wild bird species that attended chicks had lower stress-induced corticosterone levels and a lower probability to show defensive behavior compared to the alone chicks. This reduced stress sensitivity is certainly explained by the well-known link between corticosterone and nutritional status, and by the recent delivery of meals to the attended chicks and the improvement of their nutritional status. It may also be explained by the parental protection against predators or inclement weather, or/and by the psychosocial comfort of parental presence for the offspring. Overall, these results suggest that the presence of a parent in the nest reduces offspring stress sensitivity in wild birds. Further studies would now be required to disentangle the impact of nutritional status and parental presence on stress sensitivity and to better understand the potential impact of parental presence and circulating corticosterone levels on growth and cognitive development in wild birds.

1. Introduction

In most vertebrates, parents provide important cares to their offspring after birth or hatching, allowing them to grow, which is important for survival to independence (Clutton-Brock, 1991). The offspring of altricial species are fully dependent on their parents for heat and resources (Starck and Ricklefs, 1998), and the quality of parental care has a huge impact on their growth and survival until fledging (Clutton-Brock, 1991). After the brooding period, offspring can be left unattended for extended periods of time (Tveraa et al., 1998). Parents can then fulfil the nutritional needs of the growing chicks by increasing their chick-provisioning activity, i.e. their time spent away from the nest (Catry et al., 2010). Although high foraging and chick-provisioning activities are beneficial to the chick in terms of growth, they are also associated with a low parental attendance at the nest, which can entail important costs for the chick (Tveraa et al., 1998; Catry et al., 2010). For example, low parental nest attendance can increase the risk of nest predation and parents often increase nest attendance under high nest predation risk (Lima, 2009). Low or infrequent parental nest attendance can also increase the offspring vulnerability to weather events and jeopardize chick's survival, especially in the case of extreme events (Dupont et al., 2020). Finally, parental absence could also entail a psychosocial stress for the offspring because of the breaking of the parent-offspring bond, as previously shown in mammals (Enríquez et al., 2011). For all these reasons, parental nest attendance is often adjusted to environmental conditions, and variations in parental attendance may have an influence on offspring behavior and physiology, and on their ability to cope with stressful events. Specifically, the frequent delivery of meal to the offspring, the energetic status of the offspring (fed vs. fasting), the psychosocial comfort and the protective role of parental presence for the chicks may lead to lower stress levels and lower stress sensitivity. However, to our knowledge this question has never been

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examined in wild altricial birds.

In response to stressful situations, individuals activate a suite of physiological and behavioral adjustments that aims to restore homeostasis (Gormally and Romero, 2020). These organismal stress-coping mechanisms promote an adaptive response that helps the individual survive the acute stressor, but also comes at a cost for developing organisms because they entail important energetic costs (Angelier and Wingfield, 2013) and can lead to reduced performance (Eyck et al., 2019). In birds, these stress responses involve the activation of the hypothalamic-pituitary-adrenal (HPA) axis, and the resulting secretion of corticosterone (Sapolsky et al., 2000). Circulating corticosterone levels classically increase in response to food shortage, experimental food removal or short-term and long-term fasting (Astheimer et al., 1992; Angelier et al., 2015; Krause et al., 2017; Cornelius et al., 2018). Very young chicks often show a hypo-sensitivity to stress to avoid the detrimental effect of corticosterone on physiology and survival (Rensel et al., 2010). However, at older ages (i.e. a few days after hatching), this corticosterone stress response becomes fully operational (Rensel et al., 2010) and it is clearly associated with the energetic status of the organism (satiety and body condition, Astheimer et al., 1992) and unfed chicks often show high circulating corticosterone levels (Angelier et al., 2015; Krause et al., 2017; Cornelius et al., 2018). Elevated corticosterone levels promote begging behavior and the mobilization of energy through protein catabolism (Kitaysky et al., 2003), but is also associated with cognitive impairment and delayed growth (Nowicki et al., 2002; Kitaysky et al., 2003; Wada and Breuner, 2008). In addition to metabolic effects (Sapolsky et al., 2000), these stress responses also involve an immediate behavioral fight or flight response, which is associated with the expression of defensive or fleeing behaviors (Wingfield, 2003). This behavioral response aims to increase survival when stressors occur, but it also entails energetic costs that may be detrimental to growth, especially when nutritional conditions are not optimal (Gormally and Romero, 2020).

In this study, we investigated the influence of parental presence on these physiological and behavioral proxies of offspring stress sensitivity in a long-lived Antarctic bird species, the Snow petrel (*Pagodroma nivea*). We specifically tested the influence of parental presence on offspring behavioral (defensive behavior) and physiological stress responses (corticosterone levels). We predict that attended chicks should have a lower sensitivity to stress (corticosterone stress response, defensive behavior) relative to alone chicks mainly because of the well-known effect of satiety and energetic status (fed vs. fasting) on the regulation of the HPA axis (Astheimer et al., 1992), but also because parental presence might provide a psychosocial comfort to the chick and may provide protection against predator and inclement weather. We also expect that parental presence will be associated with a better chick body condition because of recent parental food delivery (full stomach).

2. Material and methods

2.1. Study system

Our study focused on breeding Snow petrels and their chicks during the austral summer 2017/2018 at Ile des Pétrels, Terre Adélie, Antarctica (66°40′S, 140°01′E). Snow petrels are seabirds with biparental care. Both parents alternate brooding the single chick. Once the chick becomes thermally independent, it is left unattended at the nest (~10 days after hatching, Goutte et al., 2011) and both parents forage at sea to provision their chick. The duration of foraging trips during the chick-rearing period can last several days (~70 h, Barbraud et al., 1999). After a foraging trip, parents stay at the nest with their thermally independent chick for a few hours to deliver a meal to the offspring (Barbraud et al., 1999).

In early-January, 84 of snow petrel nests were checked daily to determine the hatching date of the chicks. Thirteen days after hatching (once all chicks were thermally independent), we returned to 54 nests to capture and measure the chick (tarsus length and body mass with a calliper (±0.1 mm) and a scale (±5 g), respectively). We noted if one of the parents was present in the nest or not (i.e. visiting the nest to feed its chick). Forty-four chicks were alone at the nest (thereafter, 'alone chicks') while 10 chicks were visited by one of their parents (thereafter, 'attended chick'). During the approach to the nest, we noted whether the chick showed a defensive spitting behavior or not (1: yes or 0: no). In case of predator attack (or human disturbance), snow petrel chicks regurgitate stomach oil to repel the predator (Imber, 1976).

We calculated the body condition of each chick by using the scaled mass index (SMI). This method consisted to standardize the individual body mass with respect to a body size indicator so as to take account of scaling relationships (see Peig and Green, 2009 for details). For all these chicks, we were not able to monitor food delivery and the timing of the last meal because parents stay only for a few hours at the nest. Our body condition index is therefore representative of the combined mass of the chick and its stomach content (which may vary depending on the delivery of the last meal). We also measured the corticosterone stress response of each chick by using a well-established protocol, validated for snow petrels (Angelier et al., 2007). Briefly, we collected two blood samples (~150 μL) from the alar vein with a 25-gauge needle and heparinized microcapillary tubes. The first one was collected within 3 min after initial disturbance and was considered as representative of baseline corticosterone levels, and the second one was collected 30 min after a standardized stress restraint protocol and represented stress-induced corticosterone levels.

2.2. Laboratory analyses

All blood samples were centrifugated (7 min at 1844 g) and plasma and red blood cells were stored at −20 °C until subsequent analyses at the CEBC-CNRS. Plasma corticosterone concentration was determined by radioimmunoassay as described previously in Angelier et al. (2007). All samples were run in four assays, the intra-CV assay was 6.91% and the inter-CV assay was 13.78%. The sex of each chick was determined by molecular sexing (see Dupont et al., 2020). Our dataset includes 44 alone chicks (19 males and 25 females) and 10 attended chicks (4 males and 6 females).

2.3. Statistical analyses

To test the impact of the parental presence on our variables of interest, we ran 4 Linear models where dependent variables were: i) body condition, ii) baseline CORT levels, iii) stress-induced CORT levels, iv) defensive behavior; and the independent variables were: 1) parental presence, 2) sex and 3) their interaction. Because offspring body condition was affected by parental presence due to parents feeding their chick (see Results), we could not include both variables as independent variables in the models. Therefore, we ran 3 other Linear models to specifically test the influence of offspring body condition on our variables of interest for alone chicks and attended chicks (dependent variables: i) baseline CORT levels, ii) stress-induced CORT levels, iii) defensive behavior; independent variable: 1) body condition). Because of the practical difficulty to sample attended chicks, we only had access to 10 attended chicks, which may limit our statistical power for this specific category of chicks. Normal distributions and identity link functions were used for all models, except when the defensive behavior was the dependent variable (binomial distribution, logit link function). We conducted a sensitivity analysis and reported the effect sizes (Hedges' g) for all comparisons (Lenhard and Lenhard, 2016). Model selections were performed using a backwards stepwise approach.

2.4. Ethic statements

Licenses and permissions were granted by the Ethic Committee of Institut Polaire Francais (IPEV) and by the Préfet of Terres australes et

antarctiques francaises (TAAF) after advices from the Comité de l'Environnement Polaire (CEP).

3. Results

3.1. Influence of parental attendance on body condition, defensive behavior, and stress physiology

The body condition of attended chicks was significantly higher than that of alone chicks (Table 1A; Fig. 1A). Male chicks were also in better body condition compared to female chicks (Table 1A).

Attended chicks showed significantly less defensive behavior (i.e., regurgitation) compared to alone chicks (Table 1; Fig. 1B) and defensive behavior was not affected by the sex of the offspring (Table 1).

Baseline CORT levels were marginally but non significantly lower for the attended chicks compared to the alone chicks (Table 1A; Fig. 1C). Baseline CORT levels were not affected by the sex of the offspring (Table 1A). Stress-induced CORT levels were significantly lower for the attended chicks compared to the alone chicks (Table 1A; Fig. 1D). Male chicks also had lower stress-induced CORT levels compared to female chicks (Table 1A). In all models, interaction terms were non-significant (all P-value >0.306).

Table 1
(A) Influence of the parental presence (attended and alone chicks), sex (male and female) and their interaction on morphometric, physiological and behavioral variables in snow petrel chicks; (B) Influence of the chick's body condition on physiological and behavioral variables in snow petrel chicks for each category of chicks ('alone' and 'attended').

A. Dependent variable	Independent variables	df	F-value/ χ^2	P-value	Hedges' g
1. Body condition	Parental presence	1, 51	18.6	<0.001	1.388
	Sex of the offspring	1, 51	11.1	0.002	0.781
	Interaction	1, 50	<0.001	0.955	–
2. Baseline CORT levels	Parental presence	1, 52	3.04	0.087	−0.618
	Sex of the offspring	1, 51	<0.01	0.973	0.021
	Interaction	1, 50	0.003	0.852	–
3. Stress-induced CORT levels	Parental presence	1, 51	10.5	0.002	−1.10
	Sex of the offspring	1, 51	4.06	0.049	−0.499
	Interaction	1, 50	<0.001	0.924	–
4. Defensive behavior	Parental presence	1, 52	11.5	<0.001	−1.60
	Sex of the offspring	1, 51	0.72	0.396	0.221
	Interaction	1, 50	1.05	0.306	–

B. Dependent variable	Independent variable	df	F-value/ χ^2	P-value
1. Baseline CORT levels of attended chick	Body condition	1, 8	0.91	0.367
2. Baseline CORT levels of alone chick	Body condition	1, 42	5.66	0.022
3. Stress-induced CORT levels of attended chicks	Body condition	1, 8	0.26	0.627
4. Stress-induced CORT levels of alone chicks	Body condition	1, 42	29.10	< 0.001
5. Defensive behavior of attended chicks	Body condition	1, 8	0.78	0.377
6. Defensive behavior of alone chicks	Body condition	1, 42	0.48	0.489

3.2. Influence of body condition on defensive behavior, and stress physiology

Both baseline and stress-induced CORT levels were significantly and negatively associated with body condition for alone chicks (Table 1B; Fig. 1E; F). However, this relationship was not apparent for the attended chicks (Table 1B; Fig. 1E; Fig. 1F). Defensive behavior was not linked with body condition both for alone chicks and attended chicks (Table 1B).

4. Discussion

In this study, we demonstrated in a wild bird species that parental presence had a significant impact on stress sensitivity in developing chicks. Attended chicks had lower stress-induced corticosterone levels and a lower probability to show defensive behavior compared to the alone chicks. These results support the idea that the presence of a parent in the nest can reduce the stress of the chick when a perturbation occurs. This reduced corticosterone stress response certainly results from satiety and increased body reserves (Astheimer et al., 1992; Angelier et al., 2015; Krause et al., 2017; Cornelius et al., 2018), but it might also partly result from the presence of the parent (protection against predators and inclement weather, and psychosocial comfort, Enríquez et al., 2011).

Firstly, it is very likely that the reduced stress sensitivity of attended chicks is related to their good nutritional status (Angelier et al., 2015; Krause et al., 2017; Cornelius et al., 2018) and to the recent delivery of a meal (Astheimer et al., 1992). In seabirds, baseline corticosterone levels and the corticosterone stress response are reduced when chicks are in good body condition (e.g., Kitaysky et al., 2001) and several studies have demonstrated in birds that corticosterone levels drop in response to satiety or meal delivery (Astheimer et al., 1992). In our study, attended chicks likely recently received a meal from their parents and they were consequently heavier and in better condition compared to alone chicks, although we cannot disentangle the mass of the undigested meal from the mass linked to body reserves. This certainly explains their lower corticosterone levels, and supporting this idea, we found that corticosterone levels were negatively correlated with body condition in snow petrel chicks. However, we must also emphasize that our sample size was rather limited for the attended group because of the practical difficulty to control the nest at the time of parental visit. Therefore, we may have lacked statistical power for some tests, especially those linking body condition and physiological or behavioral variables (Table 1B).

This reduced stress sensitivity in attended chicks may also result from the reduction of nest predation risk. Logically, nest predation is reduced when a parent is present at the nest because parents can often defend efficiently their progeny against predators. Accordingly, most nest predation actually occurs when the chick or the egg is left alone in snow petrels (Barbraud, 1999) because the main predator of this species (the south polar skua, *Catharacta maccormicki*) generally avoids attacking adults in their nest (Warham, 1990). In addition, this reduced stress sensitivity in attended chicks could also result from the protection that parents provide against inclement weather (e.g. snowfall, cold temperatures). In snow petrels, inclement weather can have huge detrimental effects on developing chicks (Dupont et al., 2020), and parental presence at the nest may attenuate its impact on chicks through heat transfer and protection (Tveraa et al., 1998). The behavioral and hormonal stress responses may help chicks surviving when stressors occur (predation, inclement weather, Gormally and Romero, 2020). However, these stress responses also come at a cost because they require resources that cannot be invested into growth and development anymore (Angelier and Wingfield, 2013). By protecting chicks against stressors, parental presence seems to allow developing offspring to downregulate their stress responses and probably to avoid the energetic costs of defensive behavior (Caro, 2005), and those associated with elevated corticosterone levels (e.g. growth and cognitive impairments; Nowicki et al., 2002; Kitaysky et al., 2003; Wada and Breuner, 2008). Finally, this

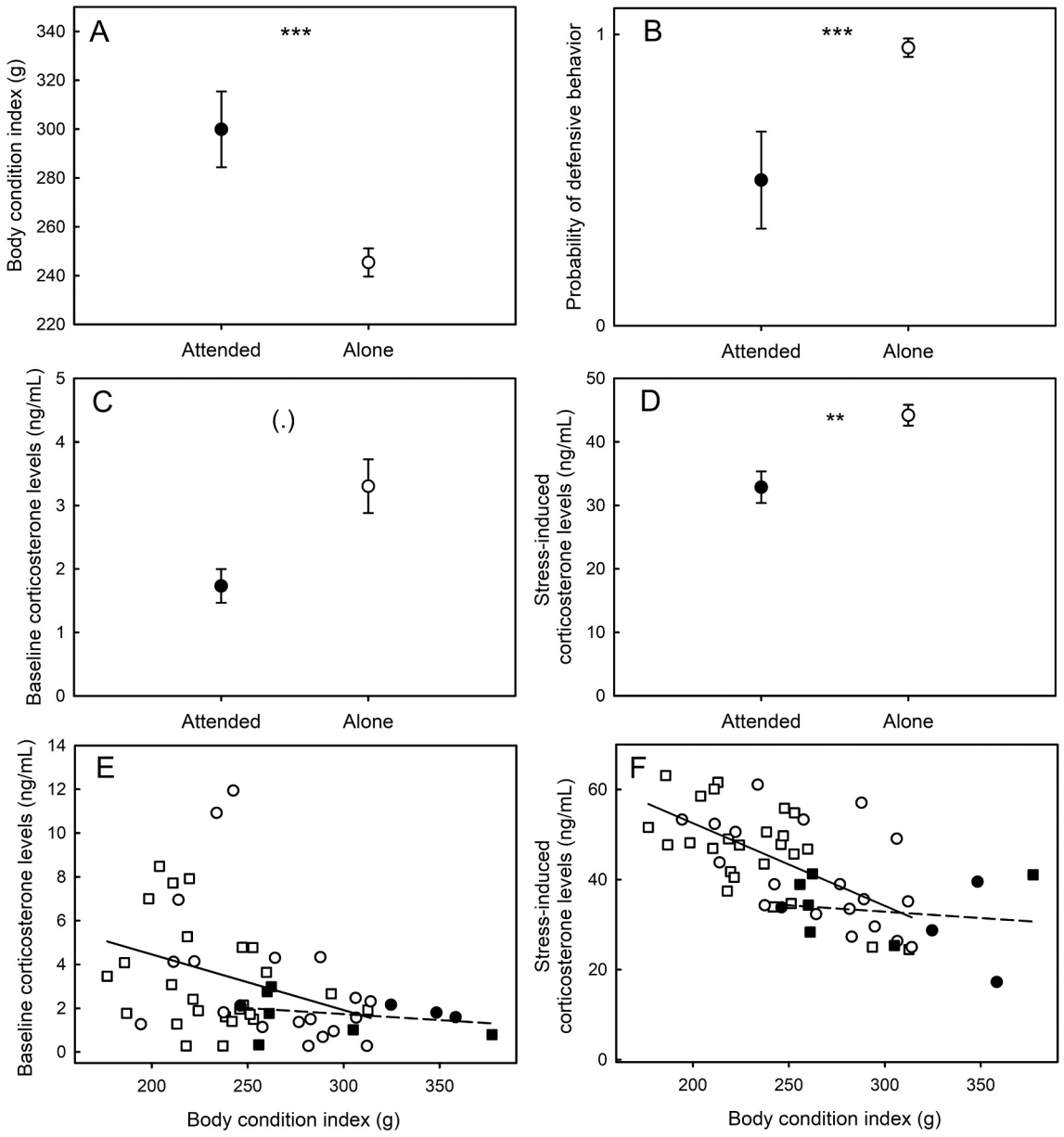

Fig. 1. Parental presence effect on body condition index (A), probability of defensive behavior (B), baseline corticosterone levels (C) and stress-induced corticosterone levels (D) in 13-days old chicks snow petrel (mean ± SE). Relationship between baseline (E) or stress-induced corticosterone levels (F) and body condition index in alone chicks (solid line) and attended chicks (dashed line). Filled symbols denote alone chicks (N = 44) and open ones denote attended chicks (N = 10). Circles represent male chicks (N = 25 and N = 4 for alone and attended males respectively) and squares represent female chicks (N = 19 and N = 6 for alone and attended females respectively). ***: P-value <0.001; **: P-value <0.01; (.): P-value <0.1.

reduced stress sensitivity may also result from the beneficial psychosocial effect of parental presence for the progeny. The parent-young bond can create a psychosocial comfort for the offspring that could in turn reduce its stress sensitivity, as previously shown in domestic animals (Enríquez et al., 2011).

In conclusion, the nutritional hypothesis is the most likely explanation of reduced corticosterone levels in attended chicks. However, it does not seem to explain their reduced behavioral stress sensitivity because the probability to show a defensive behavior was unrelated to body condition. Therefore, nutritional state and satiety certainly affect the physiological and behavioral stress sensitivity of snow petrel chicks. Although it is difficult to disentangle the relative importance of nutritional status and psychosocial comfort in such field studies, our results suggest that this effect may also be reinforced by other psychosocial factors.

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