



Regular article

Does short-term fasting lead to stressed-out parents? A study of incubation commitment and the hormonal stress responses and recoveries in snow petrels



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ABSTRACT

The hormonal stress response is flexible and can be modulated by individuals according to its costs and benefits. Therefore, it is predicted that parents in poor body condition should modify their hormonal stress response, and thus, redirect energy allocation processes from parental care to self-maintenance when stressors occur. To test this prediction, most studies on free-living vertebrates have only focused on the stress response while the stress recovery – how quickly hormonal levels return to baseline values – has been neglected. Moreover, most studies have only focused on corticosterone – the primary mediator of allostasis – without paying attention to prolactin despite its major role in mediating parental behaviors. Here, we examined the effect of a short-term fasting event on the corticosterone and prolactin stress responses and recoveries, and we subsequently explored their relationships with parental decision in the snow petrel (*Pagodroma nivea*). By comparing the hormonal profiles of fasting and non-fasting snow petrels, we showed that parents modulate their corticosterone (but not prolactin) stress response according to their energetic status. We also described for the first time the hormonal stress recoveries in wild birds and found that they did not differ between fasting and non-fasting birds. Importantly, egg neglect was negatively correlated with circulating prolactin but not corticosterone levels in this species, demonstrating therefore a complex link between body condition, parental behavior and circulating corticosterone and prolactin levels. We suggest that both corticosterone and prolactin play a major role in the way parents adjust to stressors. This multiple signaling may allow parents to fine-tune their response to stressors, and especially, to activate specific allostasis-related mechanisms in a timely manner.

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Introduction

In a changing world, vertebrates must cope with a novel set of stressors that vary in intensity, frequency, duration and nature (Carey, 2009; Wingfield et al., 2011). In order to better assess the ability of individuals, populations and species to cope with these ongoing changes, it appears essential to focus on the series of physiological and behavioral responses that individuals initiate in response to an environmental challenge (Wingfield, 2008; Wingfield et al., 2011). These so-called stress responses promote immediate survival by restoring homeostasis but, this is generally made at the expense of other life-history components such as growth or reproduction (McEwen and Wingfield, 2003; Romero et al., 2009). Among the multiple stress responses, the hormonal responses are especially crucial to consider because hormones are by nature pleiotropic and act on several physiological and behavioral components (Zera and Harshman, 2001; Ricklefs and Wikelski, 2002; Hau, 2007). As hormonal stress responses govern life-history, a better

understanding of their ecological determinants will help us to assess how different individuals, and species could adjust or not to environmental changes (Angelier and Wingfield, 2013; Cockrem, 2013).

Importantly, there is now a large body of evidence that the hormonal stress response is flexible (Cockrem, 2013) and can be modulated by individuals according to its costs and benefits (Wingfield et al., 1992; Romero, 2002; Angelier and Wingfield, 2013). In 2003, Wingfield and Sapolsky first hypothesized that breeding individuals should down-regulate their stress response when their current reproductive value is high relative to their residual reproductive value in order to optimize fitness. Since this initial paper, several studies have supported this hypothesis (e.g. Lendvai et al., 2007; Schmid et al., 2013). For example, older individuals with fewer future breeding opportunities down-regulate their hormonal stress response (i.e. become more resistant to stress) relative to younger individuals (Heidinger et al., 2006; Angelier et al., 2007a; Goutte et al., 2010; Wilcoxon et al., 2011). Interestingly, it has also been suggested that individuals should modulate their corticosterone stress response according to their body condition (Lynn et al., 2003a). Because most birds live for several years – or at least, breed multiple times during their life – it is predicted that parents in poor body

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condition should redirect energy allocation processes from parental care to self-maintenance in order to optimize their residual reproductive value (Stearns, 1992; McNamara and Houston, 1996). Importantly, this effect should be reinforced when individuals face stressful events because an additional stressor is likely to accentuate the risk of mortality for the individuals that already suffer from a poor condition.

However, body condition is a complex measure to interpret because it varies with numerous factors. Specifically, a low body condition can be the result of an energetic constraint but also the result of an adaptive reduction of body mass (reviewed in Brodin, 2007). This complexity may explain why the relationship between body condition and the hormonal stress responses appears inconsistent (Kitaysky et al., 2010; Fokidis et al., 2011). One elegant way to circumvent this problem is to look at the effect of a short-term fasting event on the hormonal stress response. Parents often need to sustain a period of fasting to provide effective parental care (to incubate the egg, to protect the brood, etc.) and such fasting is associated with a reduction of body reserves. Surprisingly, the influence of a short-term fasting event on the hormonal stress response has rarely been studied (Hood et al., 1998; Fokidis et al., 2011; DuRant et al., 2013a) and most studies have only focused on baseline hormone levels (Lynn et al., 2003b, 2010; Angelier et al., 2007b; Spée et al., 2010). In this study, we specifically aim at investigating how a fasting event can affect the hormonal stress response and the related changes in parental behaviors.

The hormonal response to a stressor can be defined by three successive phases (Romero, 2004; Wingfield, 2013; Angelier and Wingfield, 2013): (i) an initial phase when the stressor has not occurred yet is characterized by baseline hormonal levels; (ii) a second phase when the stressor has been perceived (hereafter called “the stress response”), when hormonal values change rapidly to reach stress-induced levels; (iii) a final phase when the organism does not have to cope with the stressor anymore (hereafter called “stress recovery”), and hormone levels return to baseline. To date, most studies on free-living vertebrates have only focused on baseline and stress-induced hormonal levels and the stress recovery – how quickly hormonal levels return to baseline values – has been neglected. However, hormone action on behavior and physiology certainly depends on the duration of tissue or cell exposure to stress-induced levels and, therefore, assessing this hormonal stress recovery is probably as critical as assessing the hormonal stress response itself (Romero, 2004; Wingfield, 2013).

In addition, most studies have only focused on glucocorticoids (i.e. the main mediator of the stress response in vertebrates): elevated glucocorticoid secretion increases rapidly in response to stress and in birds elevated corticosterone levels are usually associated with reduced parental investment and with brood desertion (reviewed in Wingfield et al., 1998; Wingfield, 2003; Romero et al., 2009). However, much less attention has been paid to another hormone, prolactin, despite its potential role in mediating behavioral and physiological responses to stress in parent birds (Angelier and Chastel, 2009): prolactin levels decrease in response to stress and low prolactin levels are associated with reduced parental care (Angelier et al., 2009a, 2009b; Spée et al., 2011; Thierry et al., 2013a). Therefore, studying concomitantly these two hormones may be crucial to obtain a comprehensive picture of the modulation of the stress response in relation with environmental factors in parent birds (Angelier et al., 2013).

In this study, we investigated for the first time the effects of a short-term fasting event on (1) the hormonal (both corticosterone and prolactin) stress response and recovery, and (2) their relationship with parental decisions in an Antarctic seabird, the snow petrel (*Pagodroma nivea*). This species is suitable for investigating these questions because incubating snow petrels lose a significant portion of their body mass during an incubation shift, but also because, as many birds, they frequently show spontaneous egg neglect which delays hatching and lowers the probability of chick survival (Angelier et al., 2007a, 2007b; Moe et al., 2007; Ardia et al., 2009; reviewed in Durant et al., 2013b). Life-history theory predicts that birds with a poor body condition may

be more prone to reduce parental investment than those with a good body condition (Stearns, 1992; McNamara and Houston, 1996). Because elevated corticosterone levels and low prolactin levels are often linked with a reduced parental investment (Wingfield et al., 1998; Angelier and Chastel, 2009; Angelier et al., 2007a, 2009a; Spée et al., 2011; Ouyang et al., 2012; Thierry et al., 2013a, 2013b), we predicted that fasting birds should respectively have higher baseline corticosterone (prediction 1a) and lower baseline prolactin levels (prediction 1b) than non-fasting birds. In addition, this negative influence of fasting on parental investment should be reinforced when an additional stressor occurs. Therefore, we predicted that fasting birds should respectively show a stronger stress response (i.e., a greater increase in corticosterone levels, prediction 2a; a greater decrease in prolactin levels, prediction 2b) and a slower stress recovery (i.e., a slower decrease in corticosterone levels at the end of the stressor, prediction 3a; a slower increase in prolactin levels at the end of the stressor, prediction 3b) than non-fasting birds. Accordingly, we also predicted that egg neglect will be related to hormonal stress responses and recoveries. Specifically, we predict that the birds that neglect their egg will have overall higher corticosterone levels (prediction 4a) and lower prolactin levels (prediction 4b) than the birds that do not neglect their egg.

Materials and methods

Study site and species

Snow petrels are seabirds that reproduce exclusively on the Antarctic continent. They are characterized by a slow pace of life with delayed sexual maturity, low fecundity and high annual survival probability. Incubating snow petrels were studied in 2010 (January 8–21) on Ile des Pétrils, Pointe Géologie Archipelago, Terre Adélie (66°40'S, 140°01'E), Antarctica. In snow petrels, the incubation period lasts for about 45 d, during which males and females alternate incubation spells lasting 5–9 d. 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 (Barbraud and Weimerskirch, 2001).

Fasting protocol

We first selected 75 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 without disturbing them during the period of the study. Then, we checked every nest twice a day to monitor the presence and absence of both partners (marked and unmarked). We monitored the return from the sea of these petrels from January 8 to January 21. Among these 75 petrels, 29 petrels were caught and blood sampled just after their return from the sea (hereafter called “non-fasting birds”) and 30 petrels were caught and blood sampled after 4 d of fast on the nest (hereafter called “fasting birds”). Only one bird was captured per nest so that male and female data can be considered independently.

Blood sampling and stress protocol

Birds were captured by hand at their nest and all birds were bled according to the standardized capture/restraint stress protocol described by Wingfield et al. (1992). Immediately after capture (i.e. within 3 min), an initial blood sample (300 µl) was collected from the alar vein with a 1-mL heparinized syringe and a 25-gauge needle. These initial blood samples were considered to reflect baseline levels of corticosterone and prolactin (thereafter called ‘baseline’ sample, Fig. 1). After collection of the initial blood samples birds were placed into cloth bags, and a subsequent sample (300 µl) was collected 30 min after capture at a time when corticosterone levels have reached their maximum

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