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

Frédéric Angelier [a,*], John C. Wingfield [b], Charline Parenteau [a], Marie Pellé [a], Olivier Chastel [a]

[a] Centre d'Etudes Biologiques de Chizé, CNRS-Université de La Rochelle, F-79360 Villiers en Bois, France
[b] Neurobiology, Physiology and Behavior Department, University of CA, Davis, USA

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; Wilcoxen 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

* Corresponding author.
  E-mail address: angelier@cebc.cnrs.fr (F. Angelier).

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 Pétrels, 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
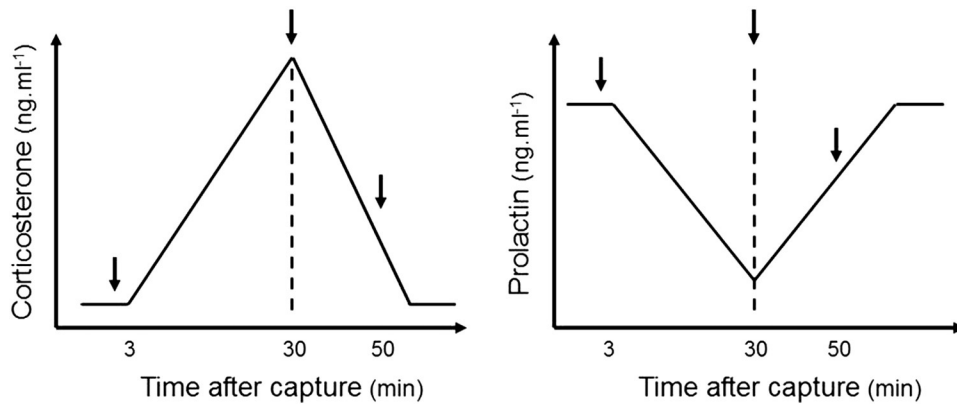
Fig. 1. Scheme of the field protocol that allows us to measure baseline, stress-induced and post-stress hormone levels. The left panel represents the expected changes in corticosterone levels when a stress occurs, and then, stops. The right panel represents the expected changes in prolactin levels when a stress occurs, and then, stops. The dashed lines indicate the time when the stressor stops. The arrows indicate the time of blood sampling.

(thereafter called 'stress induced' sample, Fig. 1). During handling of the adult birds, their eggs were covered with cotton to reduce heat loss. After these blood samples, each bird was put back in its nest. Snow petrels are very tame and resume parental duties as soon as returned to their nest. After this stress protocol, we set up a new protocol to measure the stress recovery: petrels were left undisturbed at their nest for 20 min and were then captured again and blood sampled within 3 min of recapture (thereafter called 'post stress' sample, Fig. 1) to monitor how quickly hormone levels may return to baseline after a stressor. This blood sample was taken before corticosterone and prolactin levels returned to normal, allowing us to effectively monitor the stress recovery (Fig. 1). All birds were weighed to the nearest 2 g using a spring balance and their skull length (head + bill) was measured to the nearest 0.5 mm. Body condition was calculated as the residuals between body mass and skull length (regression: $F_{1,57} = 15.21$, $p < 0.001$, $r = 0.458$). Eleven birds left their nest during the recovery period or were difficult to sample for blood and the last blood sample could not be obtained for these birds so that this last blood sample could be obtained for 48 individuals only. We kept these eleven birds to increase the power of our statistical analyses regarding baseline and stress-induced hormone levels but removing them does not change qualitatively our results. After capture and blood sample, each nest was monitored twice a day until the manipulated petrel was relieved by its mate. We were therefore able to know whether a bird neglected its egg during the incubation bout following capture/restraint stress protocol.

Molecular sexing and hormone assays

Blood samples were centrifuged and plasma was decanted and both plasma and red cells were stored at −20 °C until analyzed at the lab. The sex was determined by polymerase chain reaction (PCR) amplification of part of two highly conserved genes (CHD) genes present on the sex chromosomes at the Centre d'Etudes Biologiques de Chizé (CEBC), as detailed in Weimerskirch et al. (2005). Plasma concentrations of corticosterone and prolactin were determined by radioimmunoassay at the CEBC, as described previously (Angelier et al., 2007a). All samples were run in one assay for both hormones (intra-assay variation, corticosterone: 7.07%, prolactin: 4.77%).

Statistical analyses

All analyses were performed with SAS statistical software (ver. 9.3; SAS Institute). We used a generalized linear model (GLM) to test whether fasting and non-fasting petrels differed in body condition (dependent variable: body condition, independent factors: sex, fasting and their interaction). To test whether fasting affected baseline hormone levels

(predictions 1a and 1b) and the kinetic of the stress responses (i.e. the change in corticosterone/prolactin levels during the 30 min stress protocol, predictions 2a and 2b), we used a generalized linear mixed effects model (GLMM, normal error distribution) with individual as a random factor (dependent variable: corticosterone or prolactin levels, independent factors: time, sex, fasting and their interaction). To test whether fasting affected the kinetic of the stress recoveries (i.e. the change in corticosterone/prolactin levels during the 20 min stress recovery protocol, prediction 3a and 3b), we also used GLMM (normal error distribution) with individual as a random factor (dependent variable: corticosterone or prolactin levels, independent factors: time, sex, fasting and their interaction). The time factor referred the different time of sampling (baseline and stress-induced when focusing on the stress response, stress-induced and post-stress when focusing on the stress recovery). To test whether the corticosterone and prolactin stress responses and recoveries differed between the birds that neglected their egg and the birds that did not (predictions 4a and 4b), we also include the neglect factor in the previous models (dependent variable: corticosterone/prolactin levels, independent factors: time, sex, fasting, neglect and their interactions). Although it could seem logical to explain neglecting behavior with hormonal levels, we did not build models with neglecting behavior as the dependent variable and hormonal levels, sex, time and fasting as independent variables because this would have led to multi-collinearity problems (hormonal levels are affected by fasting, sex and time), and potentially, to spurious results (see Graham, 2003). For all these models, the best model was selected by backward model selection and the parameter estimates of the selected model were then reported. In addition, Tukey post-hoc tests were used to perform pairwise comparisons and to test whether baseline, stress-induced and post-stress corticosterone and prolactin levels were affected by our factors of interest (i.e. fasting status, sex and neglecting behavior). In addition, we also reported Cohen's effect size (d) for the difference in our variables of interest between groups (fasting vs. non-fasting petrels; neglecting vs. non-neglecting petrels; males vs. females). Finally we also tested whether prolactin levels and corticosterone levels were linked by using GLMs with prolactin levels as the dependent variable and corticosterone levels, sex and their interaction as explanatory variables.

Results

Body condition

Body condition of fasting birds was significantly lower than that of non-fasting birds and fasting birds were by average 45 g lighter than non-fasting birds (GLM, $F_{1,55} = 15.85$, $p < 0.001$, $d = 0.906$). Females had a lower body condition than males (GLM, $F_{1,55} = 14.23$, $p < 0.001$,

d = 0.843) but there was no effect of the sex × fasting interaction on body condition (GLM, $F_{1,56} = 0.01$, p = 0.938).

The hormonal stress responses

Corticosterone levels significantly increased through the stress protocol and we found a significant effect of the fasting status on this increase in corticosterone levels (fasting × time interaction, Table 1A). Thus, corticosterone levels of fasting birds increased faster than those of non-fasting birds (Fig. 2A). However, there was no effect of sex or the sex × fasting status interaction on this increase in corticosterone levels (Table 1A). Specifically, corticosterone levels of fasting birds were higher than those of non-fasting birds (post-hoc, baseline: p = 0.010, d = 0.655; stress-induced: p < 0.001, d = 1.468; Fig. 2A) but they did not differ between sexes (post-hoc, baseline: p = 0.700, d = 0.170, stress-induced: p = 0.559, d = 0.035; Fig. 2A).

Prolactin levels significantly decreased through the stress protocol and there was a significant effect of sex on this decrease in prolactin levels (sex × time interaction, Table 1B), demonstrating that the kinetic of the prolactin stress response differed between males and females (Fig. 3A). However, we did not find any effect of the fasting status or

the sex × fasting status interaction on the kinetic of the prolactin stress response (Table 1B). Specifically, prolactin levels of females were higher than those of males (post-hoc, baseline: p < 0.001 d = 2.362; stress-induced: p < 0.001, d = 2.381; Fig. 3A) but they did not differ between fasting and non-fasting petrels (post-hoc, baseline: p = 0.651, d = 0.003; stress-induced: p = 0.653, d = 0.040; Fig. 3A).

The hormonal stress recoveries

Following the stress protocol, corticosterone levels significantly decreased from 30 to 50 min when the birds were left undisturbed at their nest (Table 2A; Fig. 2B). However, there was no effect of sex, the fasting status or their interaction on this decrease in corticosterone levels (Table 2A). Specifically, post-stress corticosterone levels of fasting birds were significantly higher than those of non-fasting birds (post-hoc, p = 0.004, d = 0.924; Fig. 2B) but they did not differ between males and females (post-hoc, p = 0.910, d = 0.033; Fig. 2B).

Following the stress protocol, prolactin levels slightly and significantly decrease from 30 to 50 min when the birds were left undisturbed at their nest (Table 2B; Fig. 3B). Moreover, there was a significant effect of fasting on this decrease (sex × time interaction, Table 2B), demonstrating that

Table 1

General linear mixed models to test the influence of time (baseline vs. stress-induced), fasting (fasting vs. non-fasting), sex (males vs. females), neglecting behavior (birds that neglected their egg vs. birds that did not) and their interactions on the (A) corticosterone and (B) prolactin stress responses. Parameter estimates are provided for the best models.

A

Dependent variable	Independent variable	df	F	p-Value
Corticosterone levels	Time	1,57	1142.1	<0.001
n = 59	Fasting	1,57	31.2	<0.001
	Sex	1,57	0.4	0.548
	Neglect	1,57	0.1	0.717
	Time × fasting	1,57	25.7	<0.001
	Time × sex	1,56	<0.1	0.917
	Time × neglect	1,55	<0.1	0.849
	Fasting × sex	1,57	1.3	0.253
	Fasting × neglect	1,57	0.7	0.389
	Sex × neglect	1,57	0.3	0.554
	Time × fasting × sex	1,54	3.6	0.061
	Time × fasting × neglect	1,53	0.2	0.675
	Time × sex × neglect	1,52	<0.1	0.858
	Fasting × sex × neglect	1,54	0.4	0.548

Parameter	Estimate	Standard error	t	p-Value
Intercept	3.74	1.1	3.4	0.001
Stress-induced	28.09	1.35	20.9	<0.001
Fasting	2.12	1.6	1.3	0.191
Stress-induced × fasting	9.91	1.96	5.1	<0.001

B

Dependent variable	Independent variable	df	F	p-Value
Prolactin levels	Time	1,57	284.9	<0.001
n = 59	Fasting	1,57	0.3	0.566
	Sex	1,57	111.4	<0.001
	Neglect	1,57	12.7	<0.001
	Time × fasting	1,55	<0.1	0.764
	Time × sex	1,57	7.0	0.011
	Time × neglect	1,56	0.2	0.683
	Fasting × sex	1,56	0.1	0.711
	Fasting × neglect	1,56	0.1	0.701
	Sex × neglect	1,55	<0.1	0.949
	Time × fasting × sex	1,54	2.7	0.108
	Time × fasting × neglect	1,53	1.9	0.179
	Time × sex × neglect	1,52	0.2	0.698
	Fasting × sex × neglect	1,53	0.2	0.666

Parameter	Estimate	Standard error	t	p-Value
Intercept	152.53	6.40	23.8	<0.001
Stress-induced	−49.53	4.44	−11.2	<0.001
Female	89.03	8.33	10.7	<0.001
Neglecting	−26.75	7.52	−3.6	<0.001
Stress-induced × female	−18.38	6.96	−2.6	0.011
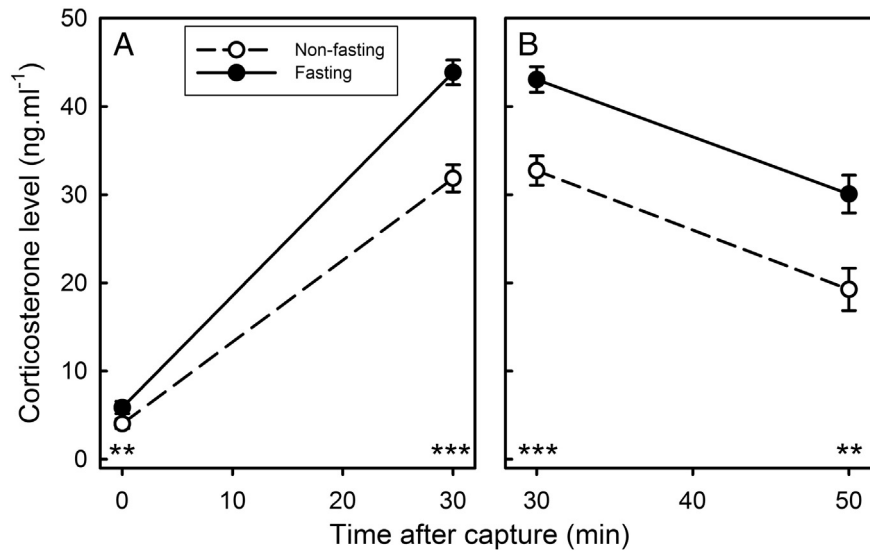
Fig. 2. Influence of a four-days fasting event on (A) the corticosterone stress response (non-fasting birds, n = 31; fasting birds, n = 28), and (B) the corticosterone stress recovery in incubating snow petrels (non-fasting birds, n = 27; fasting birds, n = 21). Stars and 'n.s.' respectively indicate significant and no significant differences in baseline, stress-induced, and post-stress corticosterone levels between fasting and non-fasting petrels (*: p < 0.05, **: p < 0.01, ***: p < 0.001). Data are expresses ad means +/− standard errors.

fasting birds showed a slightly more important decrease in prolactin levels than non-fasting birds (Fig. 3B). However, there was no effect of sex on this change in prolactin levels (Table 2B). Specifically, post-stress prolactin levels of females were significantly higher than those of males (post-hoc, p < 0.001, d = 2.949; Fig. 3B) but they did not differ between fasting and non-fasting petrels (post-hoc, p = 0.346, d = 0.175; Fig. 3B).

Egg neglect

The kinetics of the corticosterone stress response did not differ between the birds that neglected their eggs and the birds that did not (Table 1A; Fig. 4A). Specifically, there was no difference in baseline corticosterone levels between the birds that neglected their eggs and the birds that did not (post-hoc, p = 0.778, d = 0.074; Fig. 4A). Moreover, stress-induced corticosterone levels did not differ between the birds that neglected their eggs and the birds that did not (post-hoc, p = 0.744, d = 0.005; Fig. 4A). The kinetics of the prolactin stress response did not differ between the birds that neglected their eggs

and the birds that did not (Table 1B). Females had higher prolactin levels than males, and in addition, prolactin levels significantly differed between the birds that neglected their eggs and the birds that did not (Table 1B). Specifically, baseline and stress-induced prolactin levels of the birds that neglected their eggs were lower than those of the birds that did not neglect their egg (post-hoc, baseline: p = 0.009, d = 0.0727, stress-induced: p = 0.004, d = 0.813; Fig. 5A).

The kinetics of the corticosterone stress recovery did not differ between the birds that neglected their eggs and the birds that did not (Table 2A). Fasting birds had higher corticosterone levels than non-fasting birds but corticosterone levels did not significantly differ between and the birds that neglected their egg and the birds that did not (Table 2A). Specifically, post-stress corticosterone levels of the birds that neglected their egg did not differ from those of the birds that did not neglect their egg (post-hoc, p = 0.161, d = 0.503, Fig. 4B). The kinetics of the prolactin stress recovery did not differ between the birds that neglected their eggs and the birds that did not (Table 2B). Females had higher prolactin levels than males, and in addition, prolactin levels
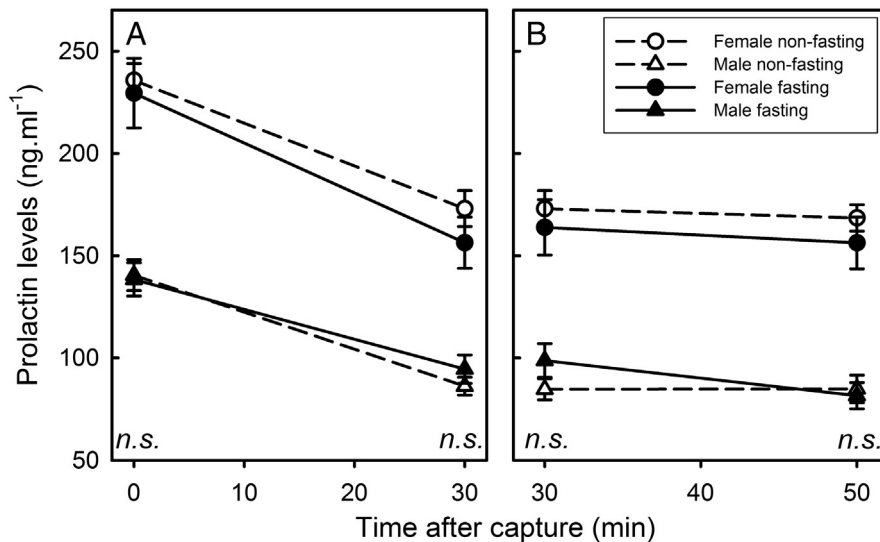
Fig. 3. Influence of a four-days fasting event on (A) the prolactin stress response (non-fasting birds, n = 31; fasting birds, n = 28), and (B) the prolactin stress recovery in incubating snow petrels (non-fasting birds, n = 27; fasting birds, n = 21). Stars and 'n.s.' respectively indicate significant and no significant differences in baseline, stress-induced, and post-stress prolactin levels between fasting and non-fasting petrels (*: p < 0.05, **: p < 0.01, ***: p < 0.001). Data are expresses ad means +/− standard errors.

Table 2
General linear mixed models to test the influence of time (stress-induced vs. post-stress), fasting (fasting vs. non-fasting), sex (males vs. females), neglecting behavior (birds that neglected their egg vs. birds that did not) and their interactions on the (A) corticosterone and (B) prolactin stress recoveries. Parameter estimates are provided for the best models.

A

Dependent variable	Independent variable	df	F	p-Value
Corticosterone levels	Time	1,47	75.5	<0.001
n = 48	Fasting	1,47	18.8	<0.001
	Sex	1,46	0.1	0.729
	Neglect	1,47	0.7	0.391
	Time × fasting	1,45	0.1	0.754
	Time × sex	1,44	<0.1	0.876
	Time × neglect	1,46	2.8	0.099
	Fasting × sex	1,46	0.2	0.638
	Fasting × neglect	1,46	0.9	0.344
	Sex × neglect	1,44	<0.1	0.933
	Time × fasting × sex	1,42	0.4	0.505
	Time × fasting × neglect	1,41	0.5	0.496
	Time × sex × neglect	1,43	0.7	0.415
	Fasting × sex × neglect	1,44	0.8	0.368

Parameter	Estimate	Standard error	t	p-Value
Intercept	32.70	1.76	18.59	<0.001
Post-stress	−13.12	1.51	−8.7	<0.001
Fasting	10.43	2.41	4.34	<0.001

B

Dependent variable	Independent variable	df	F	p-value
Prolactin levels	Time	1,46	7.8	0.008
n = 48	Fasting	1,46	0.8	0.369
	Sex	1,46	130.3	<0.001
	Neglect	1,46	9.9	0.003
	Time × fasting	1,46	4.5	0.040
	Time × sex	1,45	<0.1	0.922
	Time × neglect	1,44	<0.1	0.818
	Fasting × sex	1,46	0.2	0.631
	Fasting × neglect	1,46	1.7	0.204
	Sex × neglect	1,46	1.0	0.333
	Time × fasting × sex	1,42	0.8	0.382
	Time × fasting × neglect	1,43	0.9	0.349
	Time × sex × neglect	1,41	<0.1	0.764
	Fasting × sex × neglect	1,44	0.9	0.344

Parameter	Estimate	Standard error	t	p-Value
Intercept	99.44	6.58	15.12	< 0.001
Post-stress	−1.93	3.79	−0.51	0.612
Fasting	−0.12	7.38	−0.02	0.987
Female	76.39	6.69	11.42	<0.001
Neglecting	−23.14	7.36	−3.14	0.003
Post-stress × fasting	−12.12	5.73	−2.12	0.040

significantly differed between the birds that neglected their eggs and the birds that did not (Table 2B). Specifically, post-stress prolactin levels of the birds that neglected their egg were lower than those of the birds that did not neglect their egg (post-hoc, p = 0.029, d = 0.668, Fig. 5B).

Correlations between corticosterone and prolactin levels

Baseline prolactin levels were affected by sex and females had higher prolactin levels than males (GLM, $F_{1,55}$ = 31.52, p < 0.001). Moreover, baseline prolactin levels were negatively correlated with baseline corticosterone levels (GLM, $F_{1,55}$ = 4.03, p = 0.045) although there was no significant influence of the interaction between sex and baseline corticosterone levels on baseline prolactin levels (GLM, $F_{1,55}$ = 0.13, p = 0.722). However, stress-induced prolactin levels were not correlated with stress-induced corticosterone levels (GLM, stress-induced corticosterone levels: $F_{1,55}$ = 0.13, p = 0.715; sex: $F_{1,55}$ = 13.9, p < 0.001; interaction: $F_{1,55}$ = 1.81, p = 0.184). Similarly, post-stress prolactin levels were not correlated with post-stress corticosterone levels (GLM, stress-induced corticosterone levels: $F_{1,44}$ = 0.75, p = 0.390; sex: $F_{1,44}$ = 24.11, p < 0.001; interaction: $F_{1,44}$ = 0.08, p = 0.779).

Discussion

In this study, we demonstrated for the first time a complex link between body condition, stress and circulating corticosterone and prolactin levels. By comparing the hormonal profiles of fasting and non-fasting snow petrels, we found evidence that incubating individuals modulate their corticosterone (but not prolactin) stress response according to their energetic status. We also described for the first time the corticosterone and prolactin stress recoveries in wild birds and found that they did not dramatically differ between fasting and non-fasting birds. Importantly, our study also shows that egg neglect is tightly linked to circulating prolactin but not corticosterone levels in this species. Taken together, these results suggest that corticosterone and prolactin play major but different roles in the ability of parent birds to cope with stressors.

Impact of fasting on hormonal profiles

We found that fasting birds were in poorer body condition than non-fasting individuals. To date, many studies have investigated the impact of extreme fasting events on hormonal profiles (Cherel et al., 1988;
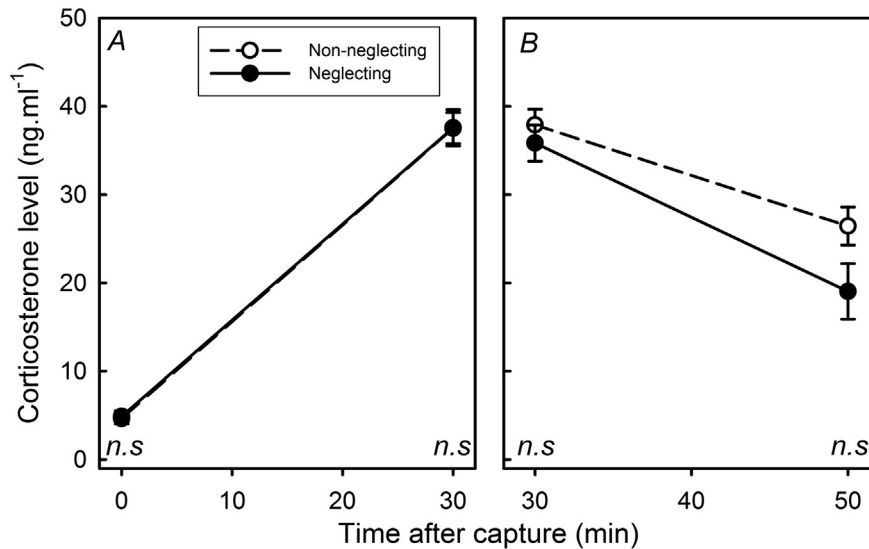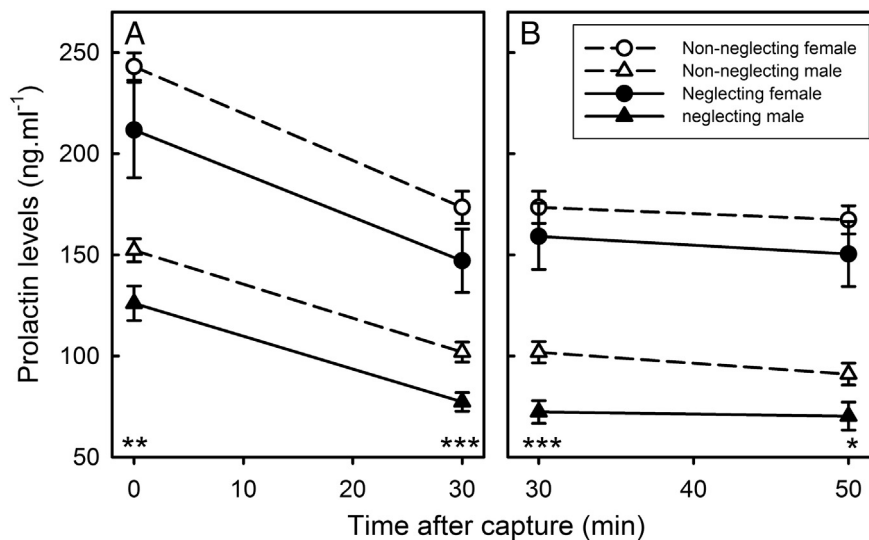
Fig. 4. Difference in hormonal profiles (A: corticosterone stress response; B: corticosterone stress recovery) between the petrels that neglected their egg (A, n = 25; B, n = 15) and the birds that did not (A, n = 34; B, n = 33). Stars and 'n.s.' respectively indicate significant and no significant differences in baseline, stress-induced, and post-stress corticosterone levels between fasting and non-fasting petrels (*: p < 0.05, **: p < 0.01, ***: p < 0.001). Data are expresses ad means +/− standard errors.

Cockrem et al., 2006; Groscolas et al., 2008; Spée et al., 2010) and much less attention has been paid to short-term fasting events (Hood et al., 1998; Lynn et al., 2003b, 2010; Fokidis et al., 2011, 2012; DuRant et al., 2013a). Moreover, several studies on this topic were conducted with captive individuals, and thus, could not fully disentangle the effects of captivity and changes in body condition on the hormonal stress responses (Lynn et al., 2003b, 2010; Fokidis et al., 2011, 2012). Here, we took advantage of a peculiarity of seabirds' reproduction: contrary to many bird species, several seabird species have to fast for several days on their nest to incubate their egg while their partner is foraging at sea. This specificity allowed us to test the effect of an ecologically relevant change in body mass on endocrine stress responses.

According to our prediction, baseline corticosterone levels of fasting petrels were higher than those of non-fasting petrels (prediction 1a), supporting therefore the idea that baseline corticosterone levels increase when body condition decreases (Lynn et al., 2003b, 2010; Jenni-Eiermann et al., 2008; Kitaysky et al., 2007, 2010; Fokidis et al., 2011). Since corticosterone is one of the main mediators of allostasis

(McEwen and Wingfield, 2003; Romero et al., 2009), these results suggests that fasting birds mobilize more energy than non-fasting birds. Although the increase in corticosterone levels in response to the standardized stressor was greater for fasting birds relative to non-fasting birds (prediction 2a), the corticosterone stress recovery did not differ between these two groups (prediction 3a). Because fasting individuals reached higher stress-induced corticosterone levels than non-fasting individuals, this means that corticosterone levels of fasting individuals were overall elevated for a longer period than those of non-fasting individuals. These results show that the combination of depleted energy reserves and a stressful event results in an important activation of the HPA axis. From a physiological point of view, these results make sense since a temporary elevation of corticosterone levels is known to activate several physiological and behavioral adjustments that aim at restoring homeostasis (Wingfield et al., 1998; Wingfield, 2003; McEwen and Wingfield, 2003; Romero et al., 2009). Indeed, corticosterone is known to activate several metabolic pathways (lipid and protein catabolism, and gluconeogenesis that lead to increased

Fig. 5. Difference in hormonal profiles (A: prolactin stress response, B: prolactin stress recovery) between the petrels that neglected their egg (A, n = 25; B, n = 15) and the birds that did not (A, n = 34; B, n = 33). Stars and 'n.s.' respectively indicate significant and no significant differences in baseline, stress-induced, and post-stress corticosterone levels between fasting and non-fasting petrels (*: p < 0.05, **: p < 0.01, ***: p < 0.001). Data are expresses ad means +/− standard errors.

circulating glucose levels) (Sapolsky et al., 2000; Landys et al., 2006; Davies et al., 2013). In addition, corticosterone is known to affect foraging activity (Angelier et al., 2007c; Fokidis et al., 2011; Crossin et al., 2012; Cottin et al., 2014), which can lead to an improved food intake, and thus, to an increased energy availability (Wingfield and Silverin, 1986; Angelier et al., 2007d; Crossin et al., 2012). Therefore, elevated baseline, stress-induced and post-stress corticosterone concentrations may be a way to prepare the organism for subsequent energy-demanding activities as suggested recently by Love et al. (2014).

However and despite a weak negative correlation between baseline prolactin and corticosterone levels, baseline prolactin levels did not differ between fasting and non-fasting petrels (prediction 1b). This demonstrates that prolactin does not change dramatically when body condition decreases in incubating birds. Accordingly, prolactin levels are rarely correlated with body condition in birds except when parents are energetically constrained and reach poor body condition (Cherel et al., 1994; Criscuolo et al., 2002; Angelier et al., 2007b; Groscolas et al., 2008; Spée et al., 2010). Contrary to non-fasting birds, fasting birds had been in contact with their egg for four days. Therefore, similar prolactin levels between fasting and non-fasting birds also demonstrate that baseline prolactin levels do not primarily depend on visual or contact stimuli from the egg in this species (but see Hall, 1987; Sharp et al., 1998). Prolactin levels of females were higher than those of males. The origin of this difference is not very well understood but may result from sex-differences in other endocrine pathways that interact with prolactin (Vleck, 1998).

Although we found that prolactin levels decrease in response to stress in all individuals, this decrease did not significantly vary between fasting and non-fasting individuals (prediction 2b). This shows that the prolactin stress response does not primarily depend on the energetic status of incubating parents. Supporting this result, the prolactin stress response has, to our knowledge, never been found to be modulated according to body condition in birds (Angelier et al., 2013). Since slight variations in prolactin levels are thought to influence parental behaviors (Angelier and Chastel, 2009; Thierry et al., 2013a; but see Williams, 2012), our findings suggest that individuals do not reduce their parental commitment during a short-term fasting event. However, it is important to note that snow petrels have a large amount of body reserves and are adapted to such fasting events. Therefore, we cannot exclude that a longer fast may have impacted the prolactin stress response. Importantly, we showed for the first time that the prolactin stress recovery is very slow in snow petrel parents because prolactin levels did not increase while the birds were returned at their nest for 20 min.

Overall, corticosterone and prolactin have quite different kinetics in response to stress and this logically results in the absence of correlation between corticosterone and prolactin levels (stress-induced and post-stress levels). Corticosterone levels increase greatly and rapidly in response to a stressor, but also return quite rapidly to baseline once the stressor ends (Fig. 2 and 4). In contrast, prolactin levels change more slowly than corticosterone levels in response to a stressor and they require quite a long time to return to baseline levels when the stressor ends (Fig. 3 and 5). The combination of an elevation of corticosterone levels and a reduction of prolactin levels in response to a stressor may be a way to prepare the organism to an upcoming energetic challenge. The increase in corticosterone levels may increase the energy input through metabolic changes (Sapolsky et al., 2000; Romero, 2004; Landys et al., 2006) whereas the decrease in prolactin levels may reduce the amount of energy allocated to parental activities (Angelier and Chastel, 2009; Angelier et al., 2009a; Thierry et al., 2013a). Interestingly, this suggests that both of these hormones may play a major role in the way parents adjust to stressors (Angelier and Chastel, 2009; Angelier et al., 2013). This complexity and multiple signaling may allow fine-tuning the response of parents to stressor, and especially, to differentially activate specific allostasis-related mechanisms in a timely manner (i.e., metabolism, foraging behavior and parental behavior).

Egg neglect

According to our prediction, we found that egg neglect was tightly correlated to the prolactin stress profile (prediction 4b). Specifically, birds with low baseline, stress-induced and post-stress prolactin concentrations were more likely to neglect their egg than birds with high prolactin concentrations. This result is supported by recent studies that reported a functional link between parental behavior and prolactin levels (Angelier et al., 2007c, 2009a, 2009b; Groscolas et al., 2008; Spée et al., 2010). For example, Thierry et al. (2013a) found that experimentally decreased prolactin levels reduced parental commitment in incubating Adélie penguins (Pygoscelis adeliae). Interestingly, our study also suggests that egg neglect does not seem to predominantly be determined by the rate of change in prolactin levels during the stressor (i.e., the stress response) or after the stressor (i.e., the stress recovery) but rather by absolute prolactin levels. Indeed, the rate of prolactin decrease in response to an acute stressor did not differ between the birds that neglected their egg and the birds that did not, and similarly, the prolactin stress recovery did not significantly vary between these two categories of birds. Of course, this does not mean that the stress-related decrease in prolactin levels does not mediate egg neglect because egg neglect probably happens only when a stressor occurs and prolactin levels fall below a low threshold level (Angelier and Chastel, 2009; Spée et al., 2010). However, prolactin levels will obviously be more likely to fall below this threshold value when a stressor occurs if baseline prolactin levels are already low. Similarly and for the same reasons, the duration of egg neglect may depend on the prolactin stress recovery because the return to the nest is likely to happen when prolactin levels return above the prolactin threshold value. We were not able to measure the duration of egg neglect in our study but supporting this interpretation, the latency to resume parental duties after a stressor was negatively linked to circulating prolactin levels in black-legged kittiwakes, Rissa tridactyla (Angelier et al., 2009a).

Surprisingly, we found that baseline, stress-induced and post-stress corticosterone levels were independent of egg neglect in snow petrels. However, an experimental increase in corticosterone levels is associated with reduced parental investment and nest desertion in wild birds (Silverin, 1986; Angelier et al., 2007d; Spée et al., 2011; Thierry et al., 2013b, 2013c). A recent study even found that elevated stress-induced corticosterone levels were associated with an increased probability of nest desertion in the great tit, Parus major (Ouyang et al., 2012). Corticosterone levels are known to increase through fasting (Lynn et al., 2003b, 2010; Fokidis et al., 2011) and egg neglect may be determined by corticosterone levels and the corticosterone stress response at the time of egg neglect, rather than corticosterone levels at the time of sampling. This could explain the absence of relationship between corticosterone levels and egg neglect in our study. However, our study also confirms that the influence of corticosterone on parental behavior is not equivocal since some studies found that moderately elevated baseline corticosterone levels are associated with reduced reproductive performances (Angelier et al., 2007b; Kitaysky et al., 2007; Bonier et al., 2009; Spée et al., 2010) whereas other studies found that moderately elevated baseline corticosterone levels can be correlated with increased parental activities and improved reproductive performances (Love et al., 2004, 2014; Bonier et al., 2009; Ouyang et al., 2011, 2013; Crossin et al., 2012). This suggests that the influence of corticosterone on parental behavior may depend on the energetic or environmental context (Angelier et al., 2007d; Bonier et al., 2009).

All these studies strongly suggest that the influence of corticosterone on parental behavior is context-dependent (Bonier et al., 2009). Here, we additionally suggest that the influence of corticosterone on parental behavior might indeed depend on prolactin levels. The primary function of corticosterone is to restore homeostasis and energetic balance by triggering physiological and metabolic changes that increase the amount of available energy to the organism (Sapolsky et al., 2000; Romero, 2004; Landys et al., 2006). Prolactin might then determine

how this energy is allocated regarding parental care. Thus, the decision to reduce parental care may be governed by a concomitant increase and decrease in corticosterone and prolactin levels respectively. An elevation of corticosterone levels may trigger nest desertion only when prolactin levels are low whereas such an elevation of corticosterone levels may instead trigger an increase in the amount of energy allocated to parental care when prolactin levels are high. Further studies with simultaneous experimental manipulations of both corticosterone and prolactin levels are now required to better understanding not only how these two hormones interact to affect parental behavior, but also their relative influence on reproductive success.

Acknowledgments

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