

## Are stress hormone levels a good proxy of foraging success? An experiment with King Penguins, *Aptenodytes patagonicus*

Frédéric Angelier<sup>1,2,\*</sup>, Mathieu Giraudeau<sup>1,3</sup>, Charles-André Bost<sup>1</sup>, Fabrice Le Bouard<sup>1</sup> and Olivier Chastel<sup>1</sup>

<sup>1</sup>Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, 79360, Villiers en Bois, France, <sup>2</sup>University of California, Department of Neurobiology, Physiology and Behavior, Davis, CA 95616, USA and <sup>3</sup>Laboratoire Evolution et Diversité Biologique, Centre National de la Recherche Scientifique, Université Paul Sabatier, 31062 Toulouse, France

\*Author for correspondence (fangelier@ucdavis.edu)

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### SUMMARY

In seabirds, variations in stress hormone (corticosterone; henceforth CORT) levels have been shown to reflect changing marine conditions and, especially, changes in food availability. However, it remains unclear how CORT levels can be mechanistically affected by these changes at the individual level. Specifically, the influence of food acquisition and foraging success on CORT secretion is poorly understood. In this study, we tested whether food acquisition can reduce baseline CORT levels ('the food intake hypothesis') by experimentally reducing foraging success of King Penguins (*Aptenodytes patagonicus*). Although CORT levels overall decreased during a foraging trip, CORT levels did not differ between experimental birds and controls. These results demonstrate that mass gain at sea is not involved in changes in baseline CORT levels in this species. The overall decrease in CORT levels during a foraging trip could result from CORT-mediated energy regulation ('the energy utilisation hypothesis'). Along with other evidence, we suggest that the influence of foraging success and food intake on CORT levels is complex and that the ecological meaning of baseline CORT levels can definitely vary between species and ecological contexts. Therefore, further studies are needed to better understand (1) how baseline CORT levels are functionally regulated according to energetic status and energetic demands and (2) to what extent CORT can be used to aid in the conservation of seabird populations.

Key words: corticosterone, foraging, food intake, seabird, *Aptenodytes patagonicus*.

### INTRODUCTION

During the last decade, baseline corticosterone levels [CORT, the stress hormone in birds (Wingfield, 1994)] have been considered a reliable indicator of changing environmental, and especially marine, conditions (Kitaysky et al., 1999; Buck et al., 2007; Kitaysky et al., 2007; Brewer et al., 2008; Doody et al., 2008; Jenni-Eiermann et al., 2008; Shultz and Kitaysky, 2008). However, most of these studies were conducted at the population level, and it remains poorly understood how individual CORT levels are affected by marine conditions. Therefore, it is crucial to investigate how marine food availability and its effect on body condition can affect individual CORT secretion in order (1) to better understand the ecological significance of baseline CORT levels and (2) to confirm that CORT is a relevant proxy of marine resources and can be used for the conservation of seabirds (Cockrem, 2006; Wikelski and Cooke, 2006; Kitaysky et al., 2007).

In birds, it is well known that CORT is the primary mediator of allostasis and that CORT secretion is tightly linked to the energetic status of the organism (reviewed by McEwen and Wingfield, 2003). Thus, reduced energy availability activates the Hypothalamo–Pituitary–Adrenal axis and the resulting CORT secretion is thought to adjust physiological and behavioural parameters to the energetic conditions encountered and, therefore, to promote individual energetic balance (reviewed by Landys et al., 2006). Supporting the idea that energetic status influences CORT secretion in wild birds, it has been reported that individuals in poor body condition usually have higher baseline CORT levels than individuals in good body condition (Schoech et al., 1997; Kitaysky et al., 1999; Love et al., 2005; Müller et al., 2006; Williams et al.,

2008). Because of this correlation between body condition and CORT levels, it is likely that the relationship linking food availability and baseline CORT levels in seabirds is functionally regulated by two major energy-related variables: (1) depletion of energy reserves through fasting and (2) energy acquisition through foraging and food intake. Although fasting is well known to result in increased CORT secretion (Cherel et al., 1988; Lynn et al., 2003; Angelier et al., 2007a; Groscolas et al., 2008), the relationship between energy acquisition and CORT secretion remains poorly understood in wild birds. In this study, our objective is to better understand whether and how the ability of wild birds to extract food and energy from the environment can functionally affect their baseline CORT levels.

Empirical evidence suggests that individual CORT levels could be reduced in response to food intake and foraging success, and it has recently been reported that baseline CORT levels decrease during foraging in wild vertebrates (Woodley et al., 2003; Cockrem et al., 2006; Angelier et al., 2007b; Angelier et al., 2008). However, the functional cause of this decrease remains unclear because food supplementation experiments have demonstrated that an increase in food availability or food intake is not always related to a reduction in CORT levels in wild birds (Lanctot et al., 2003; Schoech et al., 2004; Schoech et al., 2007; Bridge et al., 2009). Therefore, empirical and experimental studies suggest that the link between food availability, food intake and CORT levels is complex (Angelier et al., 2008; Schoech et al., 2009), and decreases in individual CORT levels during a foraging trip may, potentially, be related to other intrinsic and environmental factors [such as disturbance, social interaction or endogenous hormonal cycles (Breuner et al., 1999; Creel, 2001; Müller et al., 2006)] which vary over a foraging trip.

For instance, it has been suggested that changes in CORT levels over a foraging trip may result from an endogenous circadian cycle in CORT secretion related to scheduled foraging events but independent of fasting, food intake or status of body reserves [wild marine iguanas (Woodley et al., 2003); rodents and humans (reviewed by Dallman et al., 2004)].

In this study, we aimed to understand how food abundance could affect baseline CORT levels, and our main goal was, specifically, to experimentally test the 'food intake hypothesis' (Angelier et al., 2008). According to this hypothesis, the magnitude of the decrease in CORT levels during a foraging trip would be positively correlated with food intake and, therefore, foraging success. Thus, we experimentally handicapped foraging King Penguins (*Aptenodytes patagonicus* Miller 1778) by fitting them with external devices in order to reduce their foraging success. Then, we examined the effects of our manipulation on CORT levels. Chick-rearing King Penguins are an appropriate species on which to test the 'food intake hypothesis' because they alternate episodes of fasting on the nest with episodes of foraging at sea [~9 days each (Charassin et al., 1998; Koudil et al., 2000; Bost et al., 2002)]. Therefore, it is easy to monitor the influence of food acquisition on CORT levels in this species by sampling the same individual before and after a foraging trip (pre-trip and post-trip CORT levels). We predict that (1) pre-trip CORT levels will be higher than post-trip CORT levels, as previously reported in seabird species (Cockrem et al., 2006; Angelier et al., 2007b; Angelier et al., 2008) and that (2) handicapped birds will have higher post-trip CORT levels than controls if CORT secretion is functionally governed by food acquisition ('the food intake hypothesis').

## MATERIALS AND METHODS

### Study area and species

The study was carried out at a king penguin colony at Ratmanoff, Kerguelen Island (49°11'S, 70°33'E), Southern Indian Ocean, during two subsequent austral summers (2004 and 2005). King penguins are pelagic diving seabirds that breed in dense colonies in sub-Antarctic areas. Penguins reproducing on Kerguelen Island forage for extended periods (~16 days during the incubation period, ~9 days during the brooding period) and far from the colony with a mean foraging range of 260 km [range: 129–400 km (Koudil et al., 2000; Bost et al., 2002)].

We studied king penguin parents during the brooding period when chicks were 2–3 weeks old (2004: 5–28 February; 2005: 7–28 February). During this period, both penguin parents alternate foraging trips at sea and brooding at the colony in order to feed and warm their chicks. Thus, parents alternate between a period of fasting at the nest and a period of feeding at sea (Bost et al., 1997; Charrassin et al., 1998).

This study was approved by the ethic committee of the French Polar Institute Paul Emile Victor (IPEV) and the Terres Australes et Antarctiques Françaises (TAAF).

### Capture, blood sampling and handicapping manipulation

A total of 58 King Penguins were captured on two occasions (2004:  $N=24$ ; 2005:  $N=34$ ). Penguins were captured when leaving the colony to forage at sea and a blood sample (~500 µl) was immediately taken from the flipper vein to measure pre-trip baseline CORT levels. Penguins were sampled during the day (range: 7:00–19:00 h) and we did not find any effect of the timing of sampling on pre-trip or post-trip CORT levels ( $P>0.50$ , in both cases). Body measurements (flipper length, bill length) and body mass (pre-trip body mass) were recorded just after blood sampling.

Birds were then randomly assigned to either the experimental handicap group (hereafter, 'experimental birds'; 2004:  $N=4$ ; 2005:  $N=13$ ) or to the control group (hereafter, 'control birds'; 2004:  $N=20$ ; 2005:  $N=21$ ). Experimental birds were then equipped with either an externally attached Argos satellite platform transmitter signal (PTT, model Kiwisat 101, Sirtrack, Havelock, New Zealand; dimensions: 130×28×14 mm; weight: 77 g) or a time-depth recorder (TDR, Mk6 Wildlife computers, Redmond, WA, USA; dimensions: 70×38×51 mm; weight: 125 g) that aimed to record their foraging behaviour at sea (Koudil et al., 2000; Bost et al., 2002; Charrassin et al., 2004). These loggers were attached on the mid-line of the bird's back, glued to the feathers using a cyanoacrylate adhesive (Loctite 420, Avon, OH, USA) and secured by cable ties. Both of these devices are known to similarly constrain penguins in terms of a lower foraging success (Wilson et al., 1986; Ropert Coudert et al., 2000; Ropert Coudert et al., 2007) (and Bost et al., unpublished data). Controls were not equipped with these handicapping devices but were handled for the same amount of time as experimental birds. Penguins were individually marked with a letter painted on their chest with a picric acid solution and they were then released in the vicinity of their colony. The path used by the penguins to return from the sea to their nests in the colony was then observed continuously from dawn to dusk, and marked penguins were intercepted/captured and sampled for measurement of post-trip baseline CORT levels and body mass (post-trip body mass). Penguin parents usually come back directly from sea to the colony to feed their chick and relieve their partner. Thus, we were able to monitor the duration of the foraging trips (hereafter, 'time at sea') and the change in their body mass over a foraging trip (hereafter, 'mass gain at sea').

We calculated an index of body size from a factor analysis. Factors were extracted by a Principal Component Analysis performed on the measurement variables (bill length, flipper length). The first axis accounted for 70.21% of variance, and the resulting factor for each individual (PC1) was therefore assumed to represent overall body size. Body condition was then defined as the residuals obtained when body mass was regressed against body size (Green, 2001).

### Blood sampling and corticosterone assay

All the birds were bled within three minutes (Romero and Reed, 2005). In some penguins, blood sampling was difficult and we did not get blood to assess baseline CORT levels (final sample size, pre-trip:  $N=50$ , post-trip:  $N=41$ ; 34 penguins were successfully sampled on both pre-trip and post-trip occasions). The samples were then put into ice and centrifuged within a few minutes (10,000 g). Plasma was separated and subsequently stored at -20°C. All laboratory analyses were performed at the Centre d'Etudes Biologiques de Chizé (CEBC), Villiers en Bois, France. Identification of sexes was performed by molecular method, and plasma concentrations of CORT were determined by radioimmunoassay as previously detailed by Lormée et al. (Lormée et al., 2003) and Weimerskirch et al. (Weimerskirch et al., 2005). All samples were run in a single assay. The minimum detectable CORT level was 400 pg ml<sup>-1</sup>, and the intra-assay variation was 10.4% ( $N=4$  duplicates).

### Statistical analyses

All analyses were performed with SAS statistical software (SAS Institute v. 9.1, Chicago, IL, USA). Only one parent from each nest was studied so the data obtained from male and female penguins were considered independent samples. Because our variables of

interest don't differ between sexes (Cherel et al., 1988; Bost et al., 1997; Bost et al., 2002; Charassin et al., 1998), we pooled data from both sexes in order to test our hypotheses with enough statistical power. First, we checked that pre-trip body condition did not differ between experimental birds and controls by using a Student's *t*-test. Second, we tested by using General Linear Model (GLM) whether mass gain at sea and time at sea were affected by year of sampling ('year' factor, 2004 vs 2005), handicap manipulation ('handicap' factor, experimental birds vs controls) and their interaction ('year × handicap'). Because preliminary analysis showed that mass gain at sea and time at sea may be correlated with pre-trip body mass, we also added this variable as a covariate in these models ('pre-trip body mass' variable). In addition, we used Student's *t*-tests to check that TDRs and Argos devices have the same effect on our variable of interests (i.e. time at sea and mass gain at sea). Third, we examined by using General Linear Mixed Models (GLMM) whether baseline CORT levels varied according to time of sampling ('time' factor, pre-trip vs post-trip), year of sampling ('year' factor), body condition ('body condition' variable), handicap manipulation ('handicap' factor) and their interactions. Bird identity was included as a random factor. Finally, we examined by using GLM whether the change in CORT level (pre-trip CORT level – post-trip CORT level) was affected by our handicap experiment ('handicap' factor) or year of sampling ('year' factor). Because preliminary data inspection suggested that change in CORT levels over a foraging trip might be correlated with pre-trip CORT levels, we included this variable in the GLM ('pre-trip CORT' variable). There were no indications that normality assumptions were violated for any of the variables tested.

## RESULTS

Pre-trip body condition did not differ between control and experimental birds (Student's *t*-test, d.f.=48,  $t=-0.39$ ,  $P=0.698$ ). There was a highly significant effect of our handicap manipulation on mass gain at sea: experimental penguins gained significantly less

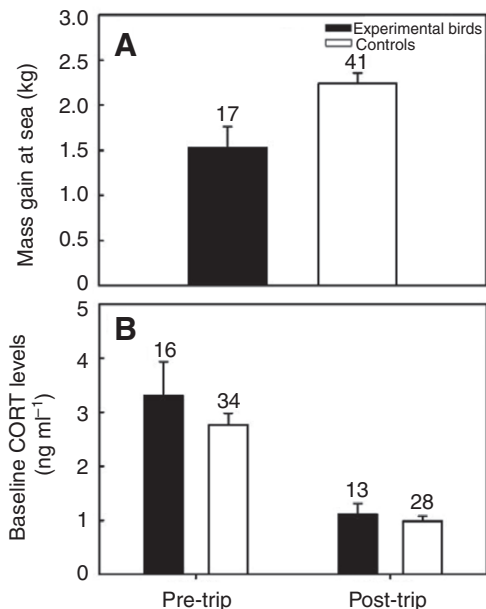


Fig. 1. Effect of the handicap experiment on (A) mass gain at sea and (B) baseline corticosterone (CORT) levels (pre-trip and post-trip) in breeding King Penguins. Data are expressed as means + s.e.m. Numbers above bars denote sample size.

mass at sea than controls (GLM,  $F_{1,55}=12.04$ ,  $P=0.001$ ) (Fig. 1A). Moreover, mass gain was negatively correlated with pre-trip body mass (GLM,  $F_{1,55}=13.06$ ,  $P=0.001$ ). Mass gain at sea did not differ between years (GLM, year:  $F_{1,54}=1.46$ ,  $P=0.231$ ). The 'year × handicap' interaction was not significant (GLM,  $F_{1,53}=0.10$ ,  $P=0.758$ ), demonstrating that the effect of our handicapping experiment on mass gain at sea did not vary between years. The handicap manipulation, the year of sampling and their interaction had no significant effect on the time spent at sea by penguin parents (GLM, handicap:  $F_{1,55}=0.39$ ,  $P=0.532$ ; year:  $F_{1,54}=0.14$ ,  $P=0.707$ ; interaction:  $F_{1,53}=0.02$ ,  $P=0.886$ ). In addition, time at sea was not correlated with pre-trip body mass (GLM,  $F_{1,56}=0.56$ ,  $P=0.457$ ). Mass gain at sea and time at sea did not differ between Argos-equipped birds and TDR-equipped birds (Student's *t*-tests,  $P>0.450$  in both cases).

Pre-trip CORT levels were significantly higher than post-trip CORT levels (Table 1A; Fig. 1B). CORT levels did not vary between years of sampling, and the 'time × year' interaction was not significant, demonstrating that year of sampling had no significant effect on either pre-trip or post-trip CORT levels (Table 1A). CORT levels were not affected by our handicap experiment, and the 'time × handicap' interaction was not significant, demonstrating that our handicap experiment had no significant effect on either pre-trip or post-trip CORT levels (Table 1A; Fig. 1B). In other words, pre-trip and post-trip CORT levels did not differ between experimental penguins and controls. Moreover, body condition did not significantly explain variations in either pre-trip or post-trip CORT levels (Table 1A). Analyses of individual changes in CORT levels showed that, overall, CORT levels decreased over a foraging trip (Fig. 2), but this decrease did not vary between years of sampling and was not affected by our handicap experiment (Table 1B; Fig. 2). Moreover, this decrease was positively correlated with pre-trip CORT levels.

## DISCUSSION

Our handicap experiment appropriately affected the ability of penguins to extract resources from the environment because it reduced mass gain to values experienced by individuals during poor environmental conditions (Bost et al., 1997). Interestingly, and according to previous studies, our experimental manipulation did not affect the duration of the foraging trip (Kooyman et al., 1992; Ropert-Coudert et al., 2000). Therefore, we are confident that we did not affect the parental investment of experimental penguins because the duration of the foraging trip is a good proxy of this life-history component in penguins (Charrassin et al., 1998; Ropert-Coudert et al., 2004). Moreover, we are confident that our experiment did not affect prey preference because King Penguins only rely on myctophid fishes during this period (Cherel and Ridoux, 1992). In King Penguins, the main effects of the loggers are reductions in the frequency of deep dives and increases in the duration of recovery between two deep dives (Ropert-Coudert et al., 2000). This reduced diving activity of experimental birds certainly allows them to compensate for the increased energetic costs of diving with a logger (Ropert-Coudert et al., 2000) but, at the same time, dramatically reduces food intake, which occurs mainly during deep dives (Charrassin et al., 2001). Therefore, we believe that the primary effect of our experiment was to reduce the ability of experimental penguins to acquire resources even though the loggers may have also slightly increased their overall energy expenditure.

Our handicap experiment did not affect baseline CORT levels, and, contrary to the 'food intake hypothesis', the magnitude of the

Table 1. Models to test the influence of time of sampling, year of sampling, body condition and handicap experiment on (A) baseline corticosterone (CORT) levels (bird identity was included as a random factor) and (B) change in CORT level over a foraging trip

Dependent variable	Independent variables and factors	d.f.	F	P
A Baseline CORT levels (ng ml <sup>-1</sup> )	<b>'Time' (pre-trip vs post-trip)</b>	<b>1,32</b>	<b>39.20</b>	<b>&lt;0.001</b>
	'Year' (2004 vs 2005)	1,32	3.71	0.063
	'Handicap' (experimental vs control)	1,31	0.41	0.528
	'Body condition'	1,30	<0.01	0.960
	'Time × year' interaction	1,31	1.78	0.192
	'Time × condition' interaction	1,29	0.49	0.489
	'Time × handicap' interaction	1,28	0.12	0.732
B Change in CORT level over a foraging trip (ng ml <sup>-1</sup> )	<b>Pre-trip CORT levels</b>	<b>1,32</b>	<b>348.11</b>	<b>&lt;0.001</b>
	'Year' (2004 vs 2005)	1,31	0.24	0.628
	'Handicap' (experimental vs control)	1,30	0.04	0.846

The best models were selected by using a step-down approach starting from the most global model (models were simplified by eliminating independent variables with  $P \geq 0.15$ ). Significant variables are indicated in bold type.

decrease in CORT levels during a foraging trip was not correlated with food intake. Moreover, neither pre-trip nor post-trip CORT levels were correlated with body condition, suggesting that energy availability did not affect baseline CORT levels in our study. Although such an absence of a relationship between body condition and CORT levels may appear astonishing, it has already been reported in many vertebrates that rely on a large amount of fat reserves (Hector and Harvey, 1986; Cherel et al., 1988; Romero and Wikelski, 2001; Groscolas et al., 2008). In these species, CORT levels appear to increase only after the individual reaches a very poor body condition associated with protein catabolism and the exhaustion of lipid reserves [Phase III (Cherel et al., 1988)]. For instance, King Penguins do not show any increase in baseline CORT levels over a fasting episode of several weeks (Cherel et al., 1988; Groscolas et al., 2008). All together, these results do not support 'the food intake hypothesis' but rather suggest that variations in baseline CORT levels over a foraging trip are independent of food

acquisition and restoration of body reserves in breeding King Penguins.

Although our handicap experiment did not affect CORT levels, we found that pre-trip CORT levels were significantly higher than post-trip ones. Interestingly, we found that foraging is associated with slight modulations of baseline CORT levels in breeding penguins because both pre-trip and post-trip CORT levels are very low – much lower than stress-induced CORT levels (Cherel et al., 1988; Groscolas et al., 2008). Therefore, our study confirms the following general pattern in seabirds: baseline CORT levels decrease overall during a foraging trip in seabirds (Cockrem et al., 2006; Angelier et al., 2007b; Angelier et al., 2008). How could we explain this decrease because the food intake hypothesis is not supported by our results?

First, CORT levels could be modulated according to the energetic needs of penguin parents ['the energy utilisation hypothesis' (Angelier et al., 2008)]: pre-trip CORT levels may be high in anticipation of the elevated energy needs of foraging (Froget et al., 2004; Halsey et al., 2007), and, accordingly, post-trip CORT levels may be low in anticipation of the low energy needs of guarding/brooding the chick at the nest (Fahlman et al., 2005). Supporting this interpretation, slight increases in baseline CORT levels in wild vertebrates have been correlated with energy-demanding activities such as preparation for foraging activity or migratory flight (Landys-Ciannelli et al., 2002; Woodley et al., 2003; Landys et al., 2004; Angelier et al., 2007b) and intense brood provisioning (Love et al., 2004). Interestingly, these slight increases in CORT levels have been reported independently of variations in body condition, supporting the interpretation that modulation of CORT levels can be independent of the status of energetic reserves in specific cases of energy-demanding activities.

Second, elevated pre-trip CORT levels could result from social factors ('the social interaction hypothesis'). King penguins defend small territories in dense colonies, and parents have to cross many territories and face many aggressive interactions when leaving their nest to embark on a foraging trip (Cote, 2000; Viera et al., 2008). These displays are potentially stressful and might result in elevated pre-trip CORT levels. On the contrary, parents caught while returning from a foraging trip had not faced any aggressive interactions because they had not yet entered the colony at this time. This might explain their low post-trip CORT levels. However, 'the social interaction hypothesis' is unlikely because high pre-trip CORT levels have also been reported in Wandering Albatrosses, *Diomedea exulans* (Angelier et al., 2007b), which breed in loose colonies and do not face aggressive interactions when leaving their nest.

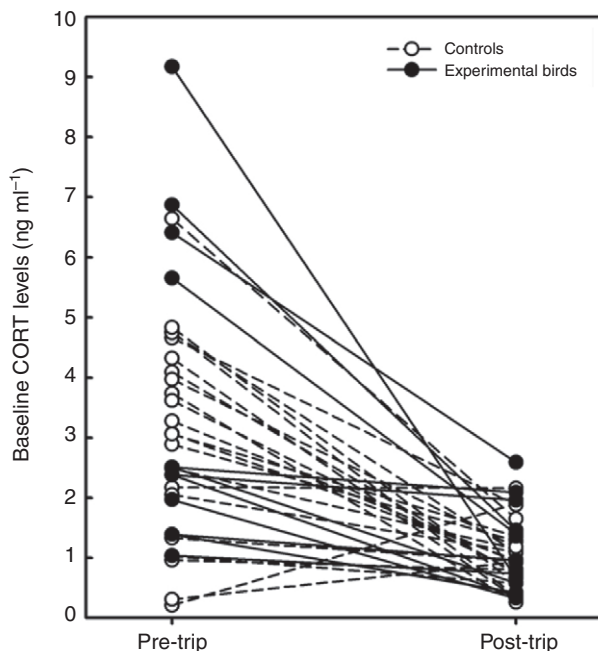


Fig. 2. Individual changes in baseline corticosterone (CORT) levels in breeding King Penguins in relation to the handicap experiment.

Third, one must keep in mind that our experiment probably reduced the foraging effort of penguins by limiting their number of deep dives (Ropert-Coudert et al., 2000). Therefore, the lower mass gain at sea of experimental birds may result from a lower foraging effort and not from a lower foraging efficiency. In this case, experimental birds may have been as effective in catching prey as controls, and they may have perceived the same environment in terms of food availability and ease of catching prey, which might explain why they did not differ in their post-trip CORT levels. However, this interpretation is unlikely because it would imply that CORT secretion is not related to food intake or foraging success but rather to the perception of overall food availability.

Finally, baseline CORT levels of penguin parents typically only increase if their own homeostasis is threatened and not when the threat is to the homeostasis of their chick (Cockrem et al., 2006; Müller et al., 2007). Therefore, we may have found no effect of foraging success on CORT levels because baseline CORT levels are only modulated according to the energy allocated to self maintenance rather than to the overall mass gain at sea (which includes both the change in the parent's body reserves and the stomach contents destined to feed the chick). However, this last point is not supported by our data or by the literature because CORT levels do not seem to be associated with the status of the parent's energetic reserves in King Penguins. Thus, we did not report any correlation between pre-trip body condition (i.e. when the parent's stomach was empty) and baseline pre-trip CORT levels. Similarly, it has been reported that CORT levels do not vary with body condition in King Penguins unless they reach a certain low threshold in mass [ $\sim 9$  kg (Cherel et al., 1988; Groscolas et al., 2008)], which is far from being the case in our study (minimum post-trip body mass = 11.2 kg).

Many studies have found that, in seabirds, baseline CORT levels can mirror marine conditions (Kitaysky et al., 1999; Kitaysky et al., 2006; Buck et al., 2007) and it is obvious that CORT should be monitored when investigating the influence of environmental changes on seabird populations (Kitaysky et al., 2007). In the present study, the two years did not really differ in terms of prey availability and oceanic conditions (Bost et al., unpublished data) and we did not report any difference in CORT levels. However, our results also demonstrate that the functional meaning of elevated baseline CORT levels is not straightforward in seabirds. Interestingly, this complexity is supported by several studies, which have examined how foraging success or food availability can affect CORT levels. For instance, food supplementation reduces CORT secretion in the Florida scrub-jay (*Aphelocoma coerulescens*) under resource-limited conditions but not under resource-abundant conditions (Schoech et al., 2004; Schoech et al., 2007). Similarly, food supplementation does not reduce baseline CORT levels in black-legged kittiwakes, *Rissa tridactyla* (Lanctot et al., 2003), although low food availability has been associated with elevated baseline CORT levels in this species (Kitaysky et al., 1999). Moreover, foraging success and CORT levels are negatively correlated in Wandering Albatrosses (Angelier et al., 2007b) but not in Adélie penguins, *Pygoscelis adeliae* (Angelier et al., 2008). All these results convincingly suggest that, in birds, the influence of foraging success and food intake on CORT levels depend on ecological and energetic contexts (Schoech et al., 2009).

To conclude, we showed that baseline CORT levels appear independent of energy acquisition in breeding King Penguins that are above a threshold in body condition (Cherel et al., 1988). Baseline CORT levels may rather be modulated according to foraging activity [*'the energy utilisation hypothesis'* (Angelier et

al., 2008)]. It is obvious that baseline CORT levels are relevant to mirror changing marine conditions (Kitaysky et al., 2006; Buck et al., 2007; Kitaysky et al., 2007; Shultz and Kitaysky, 2008). Thus, at the population level, the average CORT level over a given period can mirror a negative energetic balance resulting from low food abundance (Kitaysky et al., 1999; Buck et al., 2007; Kitaysky et al., 2007; Jenni-Eiermann et al., 2008), poor prey quality (Kitaysky et al., 2006), poor weather conditions (Wingfield et al., 1983; Romero et al., 2000; Jenni-Eiermann et al., 2008) or disturbance and stress (Müller et al., 2006; Walker et al., 2006; Thiel et al., 2008). However, at the individual level, the ecological meaning of CORT levels is complex and may vary between species and energetic situations (Angelier et al., 2007b; Angelier et al., 2008) (and this study). Therefore, further studies are needed to better understand how baseline CORT levels are individually regulated according to energetic status and energetic demands in seabirds. This functional step is crucial in determining to what extent CORT can be useful for conservation of seabird populations (Cockrem, 2006; Wikelski and Cooke, 2006).

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