Corticosterone and foraging behavior in a diving seabird: The Adélie penguin, *Pygoscelis adeliae*

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Abstract

Because hormones mediate physiological or behavioral responses to intrinsic or extrinsic stimuli, they can help us understand how animals adapt their foraging decisions to energetic demands of reproduction. Thus, the hormone corticosterone deserves specific attention because of its influence on metabolism, food intake and locomotor activities. We examined the relationships between baseline corticosterone levels and foraging behavior or mass gain at sea in a diving seabird, the Adélie penguin, *Pygoscelis adeliae*. Data were obtained from free-ranging penguins during the brooding period (Adélie Land, Antarctica) by using satellite transmitters and time-depth-recorders. The birds were weighed and blood sampled before and after a foraging trip (pre-trip and post-trip corticosterone levels, respectively). Penguins with elevated pre-trip corticosterone levels spent less time at sea and stayed closer to the colony than penguins with low pre-trip corticosterone levels. These short trips were associated with a higher foraging effort in terms of diving activity and a lower mass gain at sea than long trips. According to previous studies conducted on seabird species, these results suggest that penguins with elevated pre-trip corticosterone levels might maximize the rate of energy delivery to the chicks at the expense of their body reserves. Moreover, in all birds, corticosterone levels were lower post-foraging than pre-foraging. This decrease could result from either the restoration of body reserves during the foraging trip or from a break in activity at the end of the foraging trip. This study demonstrates for the first time in a diving predator the close relationships linking foraging behavior and baseline corticosterone levels. We suggest that slight elevations in pre-trip corticosterone levels could play a major role in breeding effort by facilitating foraging activity in breeding seabirds.

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1. Introduction

In animals, the ability of individuals to extract resources from the environment influences the amount of energy that they will be able to expend on fitness-related activities (Boggs, 1992). Specifically, breeding individuals must allocate energy to reproduction, but also to self-maintenance (Stearns, 1992). Unless they have anticipated the high energetic demands of the breeding period by increasing their

body reserve stores prior to reproduction (i.e., capital breeders), they have to increase their energy intake in order to meet these increased energetic demands. Such an increase in energy intake is often achieved by timing breeding to coincide with peak forage availability or peak prey quality (Thomas et al., 2001). In addition, it can also be achieved by an increase in foraging activity. In this case, foraging and life-history theories predict that, during the breeding season, parents investing a large amount of energy in reproduction should forage more intensively (Drent and Daan, 1980; Ydenberg et al., 1994). The ratio of investment in reproduction and self-maintenance should, therefore result, in different foraging decisions (Boggs, 1992). Energy and time allocation decisions and

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foraging behaviors have been shown to depend on three main factors: (1) environmental conditions (Costa et al., 1989; Weimerskirch et al., 2001); (2) parent's energetic state (McNamara and Houston, 1996; Weimerskirch, 1998; Spencer and Bryant, 2002); (3) reproduction requirement (Bolton, 1995; Varpe et al., 2004).

Although the influence of these factors on foraging behaviors has been extensively studied, proximate factors associated with foraging decisions remain unknown. Because hormones mediate physiological or behavioral responses to intrinsic or extrinsic stimuli (Ricklefs and Wikelski, 2002), examining changes in concentrations of hormones that influence foraging decisions can help us understanding how animals modulate their foraging decisions to energetic demands of reproduction. Indeed, some hormones have been demonstrated to govern food intake and appetite in laboratory rodents (i.e., ghrelin, leptin and insulin, Nakazato et al., 2000; Kahler et al., 1998). In addition to these hormones, it is likely that glucocorticoid hormones (cortisol and corticosterone) also play a crucial role in the regulation of foraging decisions because they influence metabolism, food intake and locomotor activity (reviewed in Landys et al., 2006).

In this study, we focused specifically on corticosterone, the primary glucocorticoid hormone in birds, reptiles and rodents. In response to a poor energetic situation, corticosterone secretion increases and elevated corticosterone levels are known to reduce or even to suppress parental behavior (Silverin, 1986). Indeed, corticosterone mediates breeding decisions by modulating the allocation of available resources between body maintenance and reproductive processes (reviewed in Wingfield et al., 1998). Recently, it has been suggested that this effect of corticosterone on parental investment could be mediated through the influence of corticosterone on foraging behavior (Kitaysky et al., 2001; Wingfield and Kitaysky, 2002; Angelier et al., 2007a).

Supporting this theory, laboratory experiments have clearly demonstrated that glucocorticoid levels are involved in the expression of locomotor activity and food intake in rodents, humans and birds (Astheimer et al., 1992; Breuner et al., 1998; reviewed in Dallman et al., 2004; Lõhmus et al., 2006). For instance, adrenalectomy reduces locomotor activity and food intake in rats and exogenous administration of corticosterone restores these behaviors (Leshner, 1971; Dallman et al., 1993; Challet et al., 1995). Corticosterone also plays a major role in lipid (Cherrington, 1999; Landys et al., 2004a) and glucose mobilization (Dallman et al., 1989; Plaschke et al., 1996). In addition, foraging and food intake may also affect corticosterone secretion. For instance, short-term fasting and food supplementation have been shown to, respectively, increase and reduce corticosterone secretion in birds (Lynn et al., 2003; Lanctot et al., 2003; Angelier et al., 2007b). Few studies have been conducted to examine the relationships between foraging behavior, foraging success and baseline corticosterone levels in free-living animals (Angelier et al., 2007a).

Indeed, the study of foraging behavior is often constrained by the difficulty to accurately monitor activity of free-living birds. Although this problem might be solved by the use of miniaturized devices, only few bird species are large enough to be equipped with such devices. In that respect, large seabirds are of special interest and these devices allow determining their at-sea movements and collecting detailed information on their foraging activity (Bost et al., 1997; Charrassin et al., 1998, 2001; Clarke et al., 2006; Weimerskirch et al., 2002, 2007; Phillips et al., 2005; Cotté et al., 2007). During the brooding stage, seabird parents alternate between guarding and feeding the chick at the nest and foraging at sea (Warham, 1990; Williams, 1995). The time spent at sea is constrained by the need to regularly return to the nest to relieve the mate and to feed the young chicks. During this period, parents of some petrel and penguin species adopt a specific strategy by conducting foraging trips of either short or long duration (Chaurand and Weimerskirch, 1994; Weimerskich et al., 1994; Weimerskirch, 1998; Clarke, 2001; Tremblay and Cherel, 2005). Short trips allow parents to increase feeding frequency but have a negative energetic yield: parents increase the energy flow to the chick at the expense of their body reserves during a short trip (Weimerskirch et al., 2003). In contrast, parents restore their body reserves at the expense of provisioning their chicks during a long trip (Weimerskirch, 1998; Clarke, 2001; Weimerskirch et al., 2003). Therefore, the frequency of short trips can mirror parental investment in these species. The decision to do either a short trip or a long trip is associated with body condition: parents always start a long trip when their body mass reaches a low threshold. However, they can start either a short trip or a long trip when their body mass is above this threshold (Weimerskich et al., 1994; Weimerskirch, 1998; Clarke, 2001), suggesting that foraging decisions might be influenced by other mechanisms such as changes in baseline corticosterone levels.

The aim of this paper is to explore the relationships between baseline corticosterone levels, mass gain at sea and foraging behavior in a diving pelagic bird, the Adélie penguin (*Pygoscelis adeliae*), during the breeding period. Specifically, we examine (1) whether baseline corticosterone levels measured prior to a foraging trip (pre-trip corticosterone levels) are correlated with foraging parameters obtained from satellite transmitters or time-depth recorders; and (2) how plasma levels of corticosterone change with a foraging trip (from departure to return at the colony).

According to life-history theory, long-lived species should not jeopardize their survival and future reproduction opportunities when environmental conditions deteriorate (Stearns, 1992). Therefore, they should reduce their parental investment when facing high energetic constraints (Drent and Daan, 1980; Boggs, 1992). This should result in a higher frequency of long trips in petrel and penguin species because long trips are associated with a restoration of parent's body reserves and a reduced chick provisioning in

these species (Weimerskirch, 1998; Clarke, 2001; Weimers-kirch et al., 2003). Because elevated corticosterone levels disrupt parental behavior (Silverin, 1986; Wingfield et al., 1998; state C *sensu* Wingfield and Kitaysky, 2002; Landys et al., 2006) and are associated with energetic constraints (low food availability: Kitaysky et al., 1999, 2007; Jenni-Eiermann et al., 2008; poor body condition: Marra and Holberton, 1998; Kitaysky et al., 1999) and with a reduced breeding success in seabirds (Angelier et al., 2007b; Buck et al., 2007), we predict that (1) penguin parents with elevated pre-trip corticosterone levels will start a long foraging trip whereas parents with low pre-trip corticosterone levels will start a short foraging trip. Specifically, we predict that (2) parents with elevated pre-trip corticosterone levels will spend more time at sea and will forage further from the colony than parents with low pre-trip corticosterone levels. In addition, we will examine whether foraging effort is correlated with pre-trip corticosterone levels. Because corticosterone secretion is known to, respectively, increase and decrease in response to fasting and food consumption (Woodley et al., 2003; Lynn et al., 2003; Angelier et al., 2007b,c), we also predict that (3) corticosterone levels will decrease during a foraging trip and that this decrease will be proportional to mass gain over a foraging trip.

2. Materials and methods

2.1. Study site and birds

The study was carried out at Pointe Géologie (66°40′S, 140°01′E) in Adélie Land, Antarctica, between 4 and 14 January 2005. At this time, Adélie penguins were rearing small chicks less than 10 days old. Both parents alternate foraging trips at sea and brooding periods at the colony. A total of 18 Adélie penguins were captured on two occasions. First, penguins were captured for blood sampling, body measurements and instrument attachment. These measurements were made when they were leaving the colony to forage at sea. Once captured, penguins were individually marked with a letter painted on their chest with a picric acid solution. The path used by penguins to come back to their nest was then observed continuously by three observers until the marked birds returned to their nest. Second, penguins were captured just after their return to the colony when they were walking from the sea to their colony. At this time, we took a blood sample from the birds, removed their equipment and reweighed them.

2.2. Blood sampling, body weight and body measurements

To determine the gender and plasma concentrations of corticosterone, a blood sample (maximum: 0.5 ml) was collected from the tarsus vein with a 1-ml heparinized syringe and 25-gauge needle immediately after each capture (before a foraging trip: pre-trip corticosterone; after a foraging trip: post-trip corticosterone). In 3 birds departing to sea and in 5 birds returning from sea, blood samples were not taken within 3 min of handling, a time recommended by Romero and Reed (2005) to assess baseline corticosterone levels. We, therefore, excluded these 8 corticosterone values from analyses (pre-trip corticosterone: $n = 15$, post-trip corticosterone: $n = 13$). Both pre-trip and post-trip corticosterone levels were available in 10 of the 18 captured penguins, allowing for measurements of individual changes in corticosterone levels during a foraging trip (post-trip corticosterone level—pre-trip corticosterone level). Blood samples were put into ice and centrifuged as soon as possible (maximum time elapsed between blood

sample and centrifugation: 4 h). Blood samples were centrifuged for 10 min, plasma was decanted and then both red cells and plasma were stored at $-20\ °C$ until analyzed.

Each bird was weighed to the nearest 50 g using a Salter spring balance (Salter Weightronix Ltd., West Bromwich, UK) before (pre-trip body mass) and after (post-trip body mass) a trip to sea, and mass difference between these measures was used as the index of mass gain at sea (post-trip body mass–pre-trip body mass). We also calculated an index of daily mass gain at sea ((post-trip body mass–pre-trip body mass)/time at sea). All penguins were recaptured before feeding their chicks except one, which was found on its nest. We excluded this one individual from the analyses focused on post-trip body mass or mass gain at sea. Before releasing each penguin, we measured its bill length (from feathers to tip of bill) and flipper length to the nearest 0.5 mm with a caliper (bill) or a rule (flipper). We calculated a measure of body size for each from a factor analysis. Factors were extracted by a principal components analysis performed on the two measurement variables (bill length, flipper length). The first axis accounted for 61.68% of variance and the resulting factor for each individual (PC1) was therefore assumed to represent overall body size. Because we collected two measurements of body mass per individual (pre-trip and post-trip body mass), our data were not independent and we, therefore, calculated two indices of body condition defined as the residuals obtained when pre-trip or post-trip body mass was regressed against the body size factor: (1) pre-trip body condition, $n = 18$, $r = 0.69$, $P = 0.002$; (2) post-trip body condition, $n = 17$, $r = 0.46$, $P = 0.06$.

2.3. At-sea foraging behavior

After the first capture, 18 penguins were equipped with either an Argos satellite platform transmitter terminal (PTT, model Kiwisat 101, Sirtrack, New Zealand, 77 g, $n = 9$) to track their movements at sea or with a time-depth recorder (TDR Mk5, Wildlife Computers, USA, 70 g, $n = 9$) to record diving behavior. Devices were attached on the mid-line of the back and were glued to feathers using a cyanoacrylate adhesive (Loctite 420) and secured by using cable ties. No penguins abandoned their nest after capture, sampling and equipping; all returned from foraging and were seen at their nest later in the breeding season.

The PTTs transmitted a signal every 45 s, and 6–19 geographically accurate locations were provided by Service Argos (CLS Argos, Toulouse, France) for each bird per day (number of locations per bird and per trip, mean = 31 [min = 12; max = 80]). The data were manually filtered according to procedures described in Lescroël and Bost (2005). The Argos system assigned locations to 7 classes on the basis of positional accuracy. The accuracy of locations was classified as follows: Class 3 was accurate to within 150 m, Class 2 to 350 m, Class 1 to 1 km; Classes 0, A and B have no assigned accuracy; and Class Z indicates an invalid location. Class Z locations were discarded from the calculation of foraging parameters. Moreover, locations from classes 0, A and B were filtered so that those that gave transit speeds $\geqslant 2.0\ \mathrm{m\ s^{-1}}$ over an hour or more (i.e., the maximum velocity measured for an extended period, Wilson et al., 1989) were discarded. The remaining class 0, A and B locations were kept as advised by Vincent et al. (2002). We were able to calculate the maximum range from the colony (maximum foraging range) and the daily distance traveled. Time at sea was determined by visual observation of the colony every hour.

Dive parameters were analyzed using dedicated dive analysis software (Multi-Trace, Jensen Software Systems, Germany). We calculated the number of dives, the time spent at the bottom of the dive (i.e., the time spent around the maximum depth, defined by the period spent at a depth equal to at least 90% of the maximum depth), the daily dive rate (i.e., the daily vertical distance traveled per foraging trip). According to the depth resolution, a dive was deemed to occur when the maximum depth was >1 m. The number of dives per hour, the hourly dive rate (i.e., the vertical distance traveled per hour during a foraging trip) and the hourly bottom-time can reflect foraging effort (Chappell et al., 1993; Charrassin et al., 2002). Because these three parameters were highly correlated ($n = 9$, $r > 0.75$, $P < 0.02$), we calculated an index of foraging effort per unit of time from a factor analysis. Factors were extracted by a principal compo-

nents analysis. The first axis accounted for 90.3% of variance and all foraging variables were correlated with the first principal component (PC1). The resulting factor for each individual (PC1) was therefore assumed to represent foraging effort per unit of time. Elevated values of this factor (PC1) mirror a high foraging effort (i.e., a large number of dive per hour, a large hourly dive rate and a large hourly bottom-time).

2.4. Molecular sexing and corticosterone assay

All laboratory analyses were performed at the Centre d'Etudes Biologiques de Chizé (CEBC).

Identification of sexes was performed by molecular sexing as detailed in Weimerskirch et al. (2005). Plasma concentrations of corticosterone were determined by radio-immunoassay following procedures described in Lormée et al. (2003). The minimum detectable corticosterone level was 400 pg/ml. All plasma samples were processed in one assay. The intra-assay variation was 8.5% ($N = 5$ duplicates).

2.5. Statistical analyses

All analyses were performed with SAS statistical software (SAS Institute Inc. v 9.1). Only one partner from each nest was studied so the data obtained from male and female penguins were considered independent samples. Because we found no difference in (1) pre-trip/post-trip body condition, (2) pre-trip/post-trip corticosterone levels and (3) foraging parameters between sexes (see Section 3 and Table 1), we pooled data from males and females in subsequent analyses in order to test our hypotheses with enough statistical power.

First, we tested by using linear regression analysis whether pre-trip and post-trip corticosterone levels were associated with respectively pre-trip and post-trip body condition. Second, we examined by using linear regressions whether foraging parameters (time at sea, daily distance traveled, maximum foraging range and foraging effort index) and 'daily mass gain at sea' can be explained by either pre-trip body condition or pre-trip corticosterone levels. Finally, we used (1) paired Student's t-test to test if corticosterone levels and body mass changed over a foraging trip; (2) linear regressions to test if the change in corticosterone levels over a foraging trip was influenced by pre-trip corticosterone level, and (3) linear regressions to test if the change in corticosterone levels over a foraging trip (in percentage) was influenced by time at sea and mass gain at sea. Significance was set to $P < 0.05$.

For all variables tested, normality assumptions were checked by plotting the residuals against the predicted value and by running the Shapiro-Wilk test for normality. There were no indications that normality assumptions were violated. When previous inspection suggested that relationships between the dependent and the independent variable were non-linear, the dependent variable was log-transformed (thereafter reported as log-transformed regression) in order to linearize the relationships. For each regression, we examined the influence of each observation on the estimated regression coefficients using Cook's distance and residual analyses. Except in one case (where the outlier was removed from the analysis), no data points were found to be potential outliers (based on residuals analyses; all Cook's distances were <0.75, Cook, 1977). For each significant regression, we reported the r^2.

When several statistical tests are performed, Bonferroni correction is frequently used to reduce the likelihood of committing Type I errors (rejecting H_0 when it is true). However, the use of Bonferroni correction in the field of ecology and behavioral ecology has been criticized for mathematical and logical reasons. Indeed, this procedure dramatically increases the risk of committing Type II errors because they induce a high risk of rejecting a H_0 when it is false (Perneger, 1998; Nakagawa, 2004; Garamszegi, 2006). Recently, reporting effect sizes has been suggested as an appropriate method to report the results without any bias (Nakagawa, 2004; Garamszegi, 2006). Effect size is a standard estimate of the strength and direction of the investigated relationship, which takes differences in sample size into account (Heges and Olkin, 1985). The software Comprehensive Meta Analysis (Biostat 2000) was used to calculate the effect sizes. Indeed, this approach considers the magnitude of an effect on a continuous scale, whereas conventional hypothesis testing based on significance levels tends to treat biological questions as all-or-nothing effects depending on whether P values exceed the limit or not. This approach is now commonly used in ecological studies (Garamszegi et al., 2007; Immler and Birkhead, 2007). Therefore, for each regression and test, we calculated effect sizes and the associated Standard error (Hedges' g, Heges and Olkin, 1985).

3. Results

3.1. Sex, body condition and corticosterone levels

Pre- and post-trip plasma corticosterone levels and pre- and post-trip body condition did not differ between males and females (Table 1). Neither pre-trip nor post-trip corticosterone levels were significantly correlated with body condition (pre-trip: $F_{1,13} = 0.02$, $P = 0.899$, $g = 0.068 \pm 0.544$; post-trip: $F_{1,10} = 0.57$, $P = 0.469$, $g = 0.439 \pm 0.633$). Moreover, baseline pre-trip or post-trip corticosterone levels were not influenced by the time of the day when samples were collected (pre-trip: $F_{1,13} = 0.08$, $P = 0.788$, $g = 0.143 \pm 0.545$; post-trip: $F_{1,11} = 0.41$, $P = 0.540$, $g = 0.357 \pm 0.599$) or by date of sampling (pre-trip: $F_{1,13} = 0.767$, $P = 0.428$, $g = 0.427 \pm 0.557$; post-trip: $F_{1,11} = 0.04$, $P = 0.839$, $g = 0.117 \pm 0.589$).

Table 1
Plasma levels of baseline corticosterone, body condition, foraging success and foraging parameters of male and female Adélie penguins

Parameter	Males	Females	t	P	g
Pre-trip corticosterone (ng ml^{-1})	19.03 ± 2.72 (6)	12.94 ± 1.38 (9)	−2.00	0.09	−0.99 ± 0.56
Post-trip corticosterone (ng ml^{-1})	7.79 ± 0.82 (6)	7.55 ± 1.15 (7)	−0.20	0.85	−0.10 ± 0.52
Pre-trip body condition	0.21 ± 0.39 (9)	−0.43 ± 0.29 (9)	−1.53	0.21	−0.69 ± 0.46
Post-trip body condition	0.30 ± 0.38 (8)	−0.11 ± 0.33 (9)	−0.83	0.42	−0.38 ± 0.47
Foraging success (g)	513.38 ± 110.86 (8)	696.0 ± 110.35 (9)	1.17	0.26	0.54 ± 0.47
Daily foraging success (g day^{-1})	11.63 ± 2.58 (8)	12.95 ± 2.47 (9)	0.37	0.72	0.17 ± 0.46
Time at sea (h)	53.78 ± 10.45 (9)	57.21 ± 6.87 (9)	0.28	0.79	0.13 ± 0.45
Maximal foraging range (km)	65.20 ± 16.46 (5)	94.72 ± 6.44 (4)	1.67	0.15	1.00 ± 0.64
Daily distance traveled (km day^{-1})	3.24 ± 0.45 (5)	3.75 ± 0.40 (4)	0.84	0.43	0.50 ± 0.61
Index of foraging effort	0.18 ± 0.54 (4)	−0.15 ± 0.50 (5)	−0.27	0.80	−0.16 ± 0.60

t-tests were used to test for differences between sexes. Effect sizes were calculated for each test (Hedges' g). All data are presented as means ± SE with sample sizes given in parentheses.

3.2. Pre-trip corticosterone levels and foraging behavior

Time at sea, maximum foraging range, daily distance traveled and the foraging effort index did not significantly vary between males and females (Table 1). Time at sea was positively correlated with maximum range of the foraging trip: short trips were closer to the colony than long trips ($F_{1,7} = 11.14$, $P = 0.012$, $g = 2.261 \pm 1.174$, $r^2 = 0.614$). Time at sea was also negatively correlated with the index of foraging effort as indicated by TDRs data: penguins foraged more actively during short trips than during long trips ($F_{1,7} = 5.62$, $P = 0.050$, $g = -1.589 \pm 0.973$, $r^2 = 0.445$). Moreover, penguins foraging far from the colony had a larger daily mass gain at sea than penguins foraging close to the colony ($F_{1,7} = 8.74$, $P = 0.021$, $g = 1.991 \pm 1.090$, $r^2 = 0.555$).

Pre-trip body condition was not correlated with subsequent time at sea ($F_{1,16} = 0.13$, $P = 0.721$, $g = 0.173 \pm 0.494$), daily distance traveled ($F_{1,7} = 0.67$, $P = 0.443$, $g = 0.546 \pm 0.759$), maximum foraging range ($F_{1,7} = 0.13$, $P = 0.734$, $g = 0.238 \pm 0.732$), the index of foraging effort ($F_{1,7} = 0.51$, $P = 0.500$, $g = 0.478 \pm 0.752$) and daily mass gain at sea ($F_{1,15} < 0.01$, $P = 0.975$, $g = -0.016 \pm 0.507$).

Compared to penguins with low pre-trip corticosterone levels, penguins with elevated pre-trip corticosterone levels spent less time at sea (log-transformed regression, $F_{1,13} = 7.32$, $P = 0.018$, $g = -1.413 \pm 0.679$, $r^2 = 0.360$, Fig. 1a), traveled a smaller distance per day ($F_{1,5} = 8.76$, $P = 0.031$, $g = -2.240 \pm 1.400$, $r^2 = 0.582$, Fig. 1b) and stayed closer to the colony ($F_{1,5} = 50.09$, $P < 0.001$, $g = -13.480 \pm 6.792$, $r^2 = 0.909$, Fig. 1c). Penguins with elevated pre-trip corticosterone levels tended slightly to have a higher foraging effort index (per unit of time) than penguins with low pre-trip corticosterone levels, but the relationship was not statistically significant ($F_{1,5} = 3.6$, $P = 0.117$, $g = 1.425 \pm 1.103$, $r^2 = 0.313$, Fig. 2a). Penguins with elevated pre-trip corticosterone levels gained less mass per day at sea than penguins with low pre-trip corticosterone levels (log-transformed regression, $F_{1,12} = 6.90$, $P = 0.022$, $g = -1.421 \pm 0.709$, $r^2 = 0.365$, Fig. 2b).

3.3. Influence of foraging on variations in corticosterone levels

At the individual level, body mass increased during a foraging trip (paired Student's t-test, df = 16, $t = 7.70$, $P < 0.001$, $g = 1.868 \pm 0.402$). Concomitantly, corticosterone levels significantly decreased during a foraging trip (paired Student's t-tests, df = 9, $t = -5.16$, $P < 0.001$, $g = 1.632 \pm 0.483$, Fig. 3). The decrease in corticosterone levels was significantly more pronounced in birds with elevated pre-trip corticosterone levels than in birds with low pre-trip corticosterone levels ($F_{1,8} = 13.76$, $P = 0.006$, $g = -2.336 \pm 1.125$, $r^2 = 0.632$, Fig. 4). Moreover, the decrease in corticosterone levels (in percentage) was negatively correlated with mass gain at sea ($F_{1,7} = 7.88$,
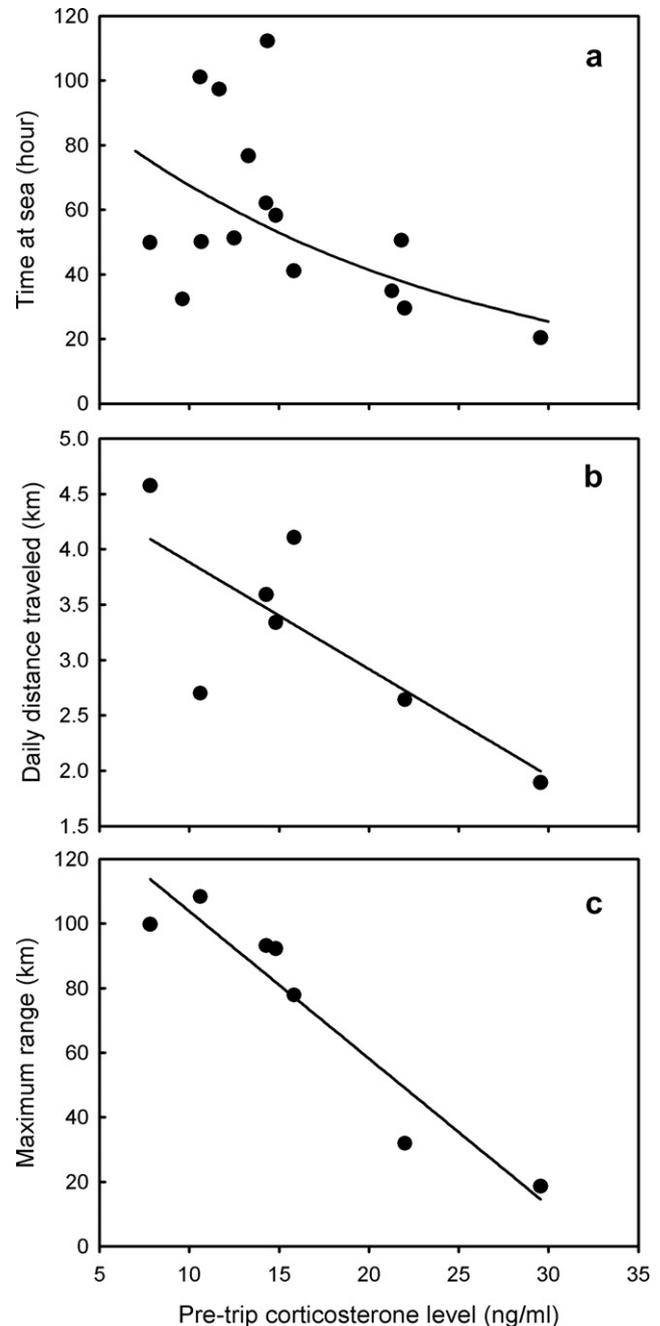

Fig. 1. Relationship between (a) time at sea, $n = 15$, (b) daily distance traveled, $n = 7$, (c) maximum range of the foraging trip, $n = 7$, and pre-trip corticosterone levels of Adélie penguins. In each regression, no bird was considered as an outlier (based on residual and Cook's distance analyses).

$P = 0.026$, $g = -1.891 \pm 1.06$, $r^2 = 0.530$); the more mass a penguin gained at sea, the less its corticosterone level decreased during the foraging trip. The decrease in corticosterone levels (in percentage) was not associated with the time at sea ($F_{1,8} = 0.23$, $P = 0.646$, $g = -0.305 \pm 0.692$).

4. Discussion

In this study, we showed for the first time that baseline corticosterone levels can be correlated with foraging behav-
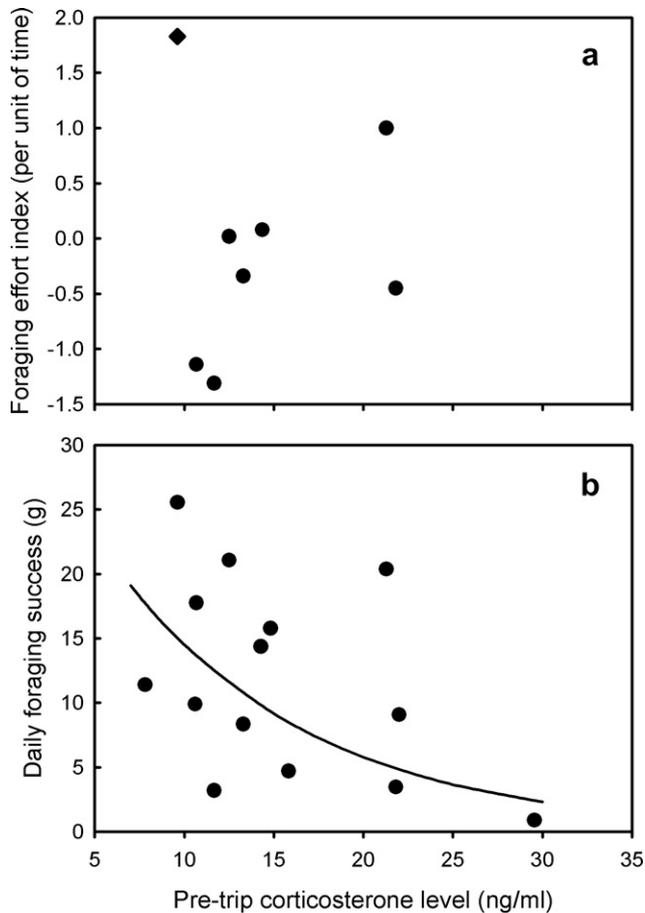
Fig. 2. Relationship between (a) foraging effort index, $n = 8$, (b) daily foraging success, $n = 14$, and pre-trip corticosterone levels of Adélie penguins. The diamond represents a bird that was considered a statistical outlier (based on residuals analysis).
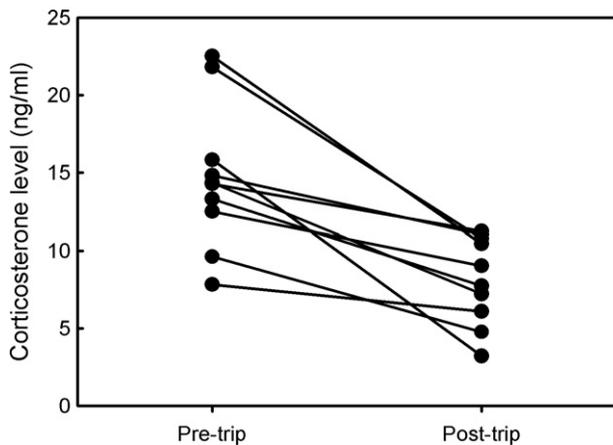

Fig. 3. Individual changes in corticosterone levels during a foraging trip in Adélie penguins.

iors in a diving seabird species. We found that Adélie penguins with elevated pre-trip corticosterone levels spent less time at sea and stayed closer to the colony than penguins with low pre-trip corticosterone levels. These short trips were associated with a higher foraging effort in terms of
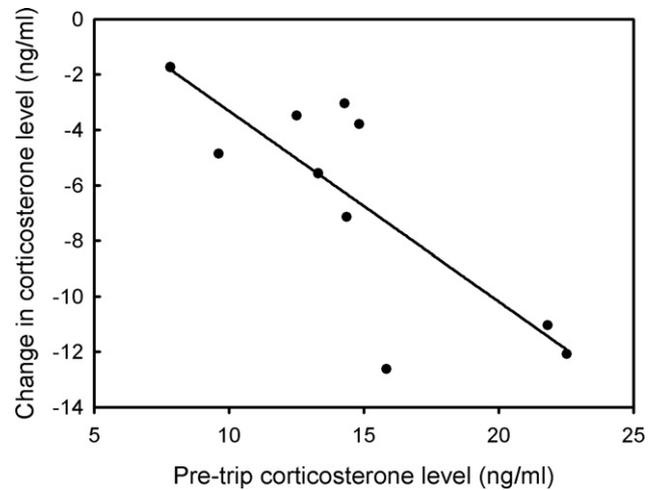

Fig. 4. Relationship between the change in corticosterone level during a foraging trip (post-trip corticosterone level–pre-trip corticosterone level) and pre-trip corticosterone levels of Adélie penguins.

diving activity and a lower mass gain at sea than long trips. Moreover, we also showed that pre-trip corticosterone levels were higher than post-trip corticosterone levels.

4.1. Corticosterone and foraging behavior

In our study, there seems to be a clear distinction between short and long trips: short trips were located in the vicinity of the colony (maximum range below 30 km), whereas long trips were associated with a large foraging range (70–110 km from the colony). As previously reported in procellariiformes (Chaurand and Weimerskirch, 1994; Weimerskirch, 1998; Weimerskirch et al., 2003), we found that penguins forage either actively during short trips that are close to the colony or less actively during long trips that are further away from the colony (Clarke, 2001; Clarke et al., 2006). Indeed, penguins dove more often, spent more time at the bottom of the dive and traveled more vertical distance per unit of time during a short trip than during a long trip. Examination of the stomach contents has clearly shown that Adélie penguins did not fish the same prey species during short and long trips (Bost et al., unpublished data). This suggests that prey community may differ between locations. Alternatively, penguins could search for different species when they conduct either a short trip or a long trip. We found that daily mass gain at sea was low during short trips in comparison to long trips. According to several studies conducted on petrel species, this result suggests that short trips probably allow maximizing rate of energy delivery to the chicks, whereas long trips certainly allow maximizing energy efficiency (Weimerskirch et al., 2003). Therefore, penguin parents probably alternate between short foraging trips for which they feed the chick and long foraging trips to restore their own body reserves. Supporting this theory, the chick growth rate is positively affected by feeding frequency in Adélie penguins during the chick-rearing period (Takahashi et al., 2003; Watanuki

et al., 2004), probably because frequent feedings equate to a large volume of food given to the chick per unit of time.

We showed for the first time that corticosterone levels are associated with specific foraging strategies in diving seabirds. Thus, we found that variations in baseline pre-trip corticosterone levels were strongly correlated with foraging behaviors. However, contrary to our predictions, penguins with elevated pre-trip corticosterone levels spent less time at sea, stayed closer to the colony and traveled a smaller distance per day than penguins with low pre-trip corticosterone levels. Does this result suggest that moderately elevated corticosterone levels could be associated with a low locomotor activity? It is unlikely because several studies have found that a moderate increase in circulating corticosterone levels stimulate locomotor activity in birds (Breuner et al., 1998; Breuner and Wingfield, 2000; Lõhmus et al., 2006; Angelier et al., 2007c). In diving seabirds, locomotor activity is difficult to monitor because it depends on the distance traveled at sea, but also on diving behavior (i.e., vertical distance). Thus, penguins with elevated pre-trip corticosterone levels may have searching for food very actively during these short trips despite a low traveling distance. Supporting this interpretation, we found that foraging effort was especially high during short trips, which were also associated with elevated pre-trip corticosterone levels. Although this last result suggests that elevated pre-trip corticosterone levels might be associated with a high foraging effort, we found no significant correlation between foraging effort index and pre-trip corticosterone levels (note however that our sample size was quite low). Although we have shown that corticosterone and foraging behavior are closely associated in diving seabirds, our study left this foraging effort topic open to debate and future studies should experimentally test the influence of corticosterone on foraging effort in diving seabirds.

Because elevated corticosterone levels redirect energy allocation from parental cares to self-maintenance (reviewed in Wingfield et al., 1998), we had predicted that elevated pre-trip corticosterone should be associated with a low parental investment decision, and, therefore, with the occurrence of long trips. How can we explain that elevated corticosterone levels were associated with active short trips? It has recently been suggested that corticosterone can have different action according to the energetic status of the individual (Landys et al., 2006; Angelier et al., 2007a). If the energetic demand exceeds the immediate ability of animals to cope, elevated corticosterone levels result in a reduced parental investment (state C *sensu* Wingfield and Kitaysky, 2002; Landys et al., 2006). If not, corticosterone action maintains systems within a heightened operating range to support increased energetic demands (state B *sensu* Wingfield and Kitaysky, 2002; Landys et al., 2006). In our study, corticosterone levels were not correlated with body condition, suggesting that penguin parents were not energetically constrained (Cherel et al., 1988). Therefore, in our case, elevated cor-

ticosterone levels may support the increased energetic demands of the early chick-rearing period by stimulating foraging activity. It suggests that moderately elevated corticosterone may be an inherent and necessary part of successful reproduction, as previously suggested in several studies (Moore and Jessop, 2003; Love et al., 2004; Landys et al., 2006). Indeed, elevated baseline corticosterone levels may prepare the organism for energy-demanding activity ("the energy mobilization hypothesis", Romero, 2002). Accordingly, corticosterone levels peak prior to foraging activity in laboratory species, humans and in several free-living vertebrates (la Fleur et al., 1999; Woodley et al., 2003; Dallman et al., 2004; Angelier et al., 2007c) and elevated corticosterone levels stimulate physiological mechanisms that permit the mobilization of energy from body reserves (reviewed in Landys et al., 2006). For instance, Landys-Ciannelli et al. (2002) showed that corticosterone levels increase in Bar-Tailed Godwit, *Limosa lapponica*, in preparation for migratory flight. Similarly, Landys et al. (2004b) showed that corticosterone secretion and the concomitant utilization of lipid reserves increase at the onset of the migratory activity in the white-crowned sparrow, *Zonotrichia leucophrys*. Therefore, elevated pre-trip corticosterone levels may help parents to prepare for the impending energetic demands of energetically costly short trips.

In addition to this preparative effect of corticosterone on foraging behavior, corticosterone might also trigger the decision to engage in the energetically expensive short trip. Corticosterone is involved in locomotor activity in laboratory rats (Challet et al., 1995). Similarly, moderate elevations of corticosterone increase activity in passerine bird species (Breuner et al., 1998; Breuner and Wingfield, 2000; Lõhmus et al., 2006). Corticosterone is also known to enhance food intake and to influence food preference in rats and humans (reviewed in Dallman et al., 2004; la Fleur, 2006). For instance, fat intake was increased following exogenous administration of low doses of corticosterone to adrenalectomized rats (la Fleur et al., 2004). All these results suggest that variations in baseline pre-trip corticosterone levels could mediate foraging behavior and foraging strategy in free-living animals.

Alternatively, we can raise the hypothesis that penguins with elevated pre-trip corticosterone levels were birds of poor quality, less experienced or younger birds that foraged close to the colony, whereas penguins with low pre-trip corticosterone levels were birds of high quality, older or more experienced birds that foraged far from the colony. However, this interpretation is unlikely because we found no relationship between pre-trip body condition (a proxy of individual quality in seabirds, Chastel et al., 1995; Takahashi et al., 2003), time spent foraging and foraging behaviors. Moreover, short trips and high feeding frequency are beneficial for the growth of the brood in the Adélie penguin (Takahashi et al., 2003; Watanuki et al., 2004) and therefore appear necessary for successfully rearing chicks.

4.2. Influence of devices on foraging behavior

It is well known that transmitters and devices can affect behavior, survival and reproductive success in flying sea-birds (Hamel et al., 2004; Whidden et al., 2007). Similarly, non-streamlined devices may significantly affect diving behavior and breeding success in some species (Ropert-Coudert et al., 2000; Wilson et al., 2004). In previous studies conducted on Adélie penguins, Rodary et al. (2000) and Ballard et al. (2001) found that trip duration and breeding success did not vary between birds carrying devices (the same TDRs, Mk5, Wildlife Computers, Rodary et al., 2000; or slightly lighter ones, Mk7, Wildlife Computers, Ballard et al., 2001) and control birds. Similarly, Tremblay and Cherel (2005) used the same TDRs (Mk5, Wildlife Computers) in a smaller species, the Rockhopper penguin (*Eudyptes chrysocome filholi*) and they found no detrimental effect of these devices on foraging trip duration. Moreover, these devices are small, streamlined, and are less than 1% of the cross-sectional area of Adélie penguins. Therefore, we believe that the instruments did not affect our results.

4.3. Change in corticosterone levels during a foraging trip

According to our predictions, we found that baseline corticosterone levels decreased during a foraging trip and that this decrease is paralleled by a concomitant increase in body mass. These results might suggest that food intake and restoration of body reserves could be one of the functional mechanisms influencing corticosterone secretion in this pelagic diving seabird. Supporting this argument, baseline corticosterone levels decreased during a foraging trip in a flying seabird, the wandering albatross, *Diomedea exulans* (Angelier et al., 2007c) and during feeding bouts in marine iguanas, *Amblyrhyncus cristatus* (Woodley et al., 2003). Contrary to our prediction, we did not find that the decrease in corticosterone levels over a foraging trip was positively correlated with mass gain over a foraging trip. The finding could result from our inability to separate the parent's body condition and the mass of its stomach contents: we did not measure stomach contents in this study and Adélie penguins feeding chicks at the colony are known to store food in their stomach (up to 650 g). On the one hand, the decrease in corticosterone levels over a foraging trip may not result from an improvement of penguin parent's body condition: previous studies have reported that corticosterone secretion is not affected by fasting or variations in body mass when Adélie penguins are above a mass threshold of 2.5 kg as in our study (Vleck and Vleck, 2002; Cockrem et al., 2006). On the other hand, the decrease in corticosterone levels over a foraging trip might result from an increase in satiation. However, it is unlikely because the results of a recent study suggest that satiation does not affect corticosterone levels in seabirds: corticosterone levels are low when birds are fed with a high-quality diet, whereas they remain elevated when birds

are fed with a similar quantity of poor quality diet (Kitaysky et al., 2006).

Alternatively, energy utilization may modulate corticosterone secretion and explain the decrease in corticosterone levels over a foraging trip. Thus, pre-trip corticosterone levels may be high in anticipation of the energy needs of foraging, whereas post-trip corticosterone levels may be low in anticipation of the low energy needs of guarding the chicks at the nest. Indeed, the mobilization of energy required to forage could necessitate moderately elevated pre-trip corticosterone levels because corticosterone enhances lipid catabolism and gluconeogenesis (Dallman et al., 1989; Plaschke et al., 1996; Cherrington, 1999; Landys et al., 2004a). On the contrary, guarding the chicks at the nest is not energetically costly (Chappell et al., 1993) and low post-trip corticosterone levels could be sufficient to mobilize energy required for guarding the chicks at the nest. Therefore, the decrease in corticosterone levels over a foraging trip could not result from an improvement of parent's body condition but rather from the break in foraging activity and energy mobilization.

The functional cause of the negative relationship between mass gain at sea and the decrease in corticosterone levels over a foraging trip remains unclear and deserves further examination. We found that penguins with elevated pre-trip corticosterone levels had a low daily mass gain at sea and a large decrease in corticosterone levels over their foraging trip. Therefore, the association between a low mass gain at sea and a large decrease in corticosterone levels could result from these two correlations without any functional effect of mass gain on corticosterone secretion. In addition, we can notice that the decrease in corticosterone levels over a foraging trip varies between individuals. Because corticosterone levels are not associated with body condition, it suggests that some other factors determine this variability. Indeed, pre-trip and post-trip corticosterone levels are probably affected by many environmental factors such as weather (Smith et al., 1994), predator attacks (Cockrem and Silverin, 2002a) or disturbance (Ellenberg et al., 2007) and this could explain the inter-individual variability in the decrease in corticosterone levels over a foraging trip (Cockrem and Silverin, 2002b).

Finally, we can also raise the hypothesis that low post-trip corticosterone levels may result from a habituation to handling because penguins have already been captured few days before. However, it is unlikely because Vleck et al. (2000) found that handling Adélie penguins at intervals of several days during the breeding season did not produce a decrease in baseline corticosterone levels.

5. Conclusion

This study is the first to show that foraging behavior is closely associated with corticosterone levels in a diving seabird. Corticosterone levels were found to decrease during foraging trips in all birds. Moreover, elevated pre-trip corticosterone levels were linked with short and energetically

costly trips (high foraging effort), whereas low pre-trip corticosterone levels were linked with long foraging trips. These results suggest that corticosterone may either stimulate foraging activity or prepare the organism to the increased energetic demands of foraging through its action on energy mobilization. To disentangle these two hypotheses, future studies should simultaneously manipulate pre-trip corticosterone levels (Astheimer et al., 1992; Kitaysky et al., 2003; Bonier et al., 2007), accurately quantify energy expenditure (Weimerskirch et al., 2003), and measure the mass of food in the stomach of parents. Such a study would give insight into how weight gain is parsed between body tissues and stomach contents in post-foraging birds and how corticosterone is related to weight gain in the tissue and stomach contents.

Acknowledgments

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