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SPECIAL FEATURE The physiological ecology of seabirds

Does corticosterone affect diving behaviour of male Adélie Penguins? A preliminary experimental study

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Abstract The amount of energy that organisms can allocate to self-maintenance and/or reproduction largely depends on their foraging strategies. Because of corticosterone (CORT) involvement in the control of energy metabolism, food intake and locomotor activity, recent studies have sought to demonstrate the role of this hormone in foraging decisions and performance. Moreover, considerable recent advances in animal-attached loggers now allow the study of behaviour in free-living animals. In order to assess the effects of CORT administration on the foraging behaviour of free-living Adélie Penguins *Pygoscelis adeliae*, we studied a group with CORT implants and a control group without CORT implants, by attaching time-depth recorders to the two groups and monitoring them throughout up to seven consecutive foraging trips during the guard stage (in Adélie Land, Antarctica). We found that foraging trips duration was similar between both groups. Dive durations, time spent at the bottom phase of dives, and the number of undulations per dive of CORT-implanted birds were all significantly higher than those of controls. However, CORT-implanted birds performed fewer dives overall (ca. 4,400) than controls (ca. 6,250) and spent many (13 and 6 times for penguins #3 and #4, respectively) long periods (>3 h) without diving. The low foraging effort and long resting periods support the view that CORT-implanted birds probably gained less energy than did the control birds. CORT treatment appears then to result in redirecting bird behaviour from costly activity (i.e. reproduction) to a behaviour promoting the preservation of energy reserves. Future studies are therefore needed to assess body condition and reproductive success of CORT-manipulated birds in parallel with the recording of their diving performances.

Key words Bio-logging, Foraging behaviour, Hormone, *Pygoscelis adeliae*, Seabirds

The physiological mechanisms underlying animal behaviour are partly controlled and regulated by neuroendocrine processes (reviewed by Lovejoy 2005). Hormones are chemical messengers released into the blood or the interstitial fluid, through which they can reach most organs within an organism, including the brain. Thanks to the development of hormonal assay techniques, a new discipline: "environmental endocrinology" (history and studies reviewed in Bradshaw 2007), has recently emerged. This approach aims at understanding the link between hormonal levels and behavioural processes in free-living animals; an essential step in better understanding the plasticity of animal strategies to face environmental changes.

One of the most studied groups of hormones in ecophysiology is that of the glucocorticoids (mainly cortisol and corticosterone). Because of their importance in stress mechanisms, these hormones are increasingly used as an index of the condition of individuals and populations in conservation biology (Wikelski & Cooke 2006). They are secreted when the hypothalamo-pituitary-adrenal (HPA) axis is activated in response to energetic needs, which are determined by the ratio between available energy and energetic demand (reviewed by Landys et al. 2006). Thus, the primary glucocorticoid in birds, i.e. corticosterone (CORT), mobilizes energy reserves depending on environmental conditions (e.g. food shortage, environmental perturbation) by adjusting the birds' phys-

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iology and behaviour (Wingfield et al. 1998).

Previous studies have shown the involvement of CORT in foraging-related behaviour, as a promoter of locomotor activity and food intake (Astheimer et al. 1992; Wingfield et al. 1998; Breuner & Wingfield 2000; Pravosudov 2003; Lõhmus et al. 2006). Moreover, Angelier et al. (2007) found that pre-trip CORT levels in Wandering Albatrosses *Diomedea exulans* were not related to the time spent at sea but to the distance travelled per day. The fact that elevated CORT levels could facilitate foraging-related behaviours, has also been highlighted by experimental studies. For instance, an administration of CORT leads adult Black-legged Kittiwakes *Rissa tridactyla* to perform more trips away from the nest than control birds, and as a consequence, the treated birds spent less time guarding/brooding their chicks (Kitaysky et al. 2001). Yet, because CORT-implanted adults did not decrease their provisioning rates, these authors suggested that these frequent trips were due to an increase in the birds' own food requirements. So, foraging strategies to maximize energy intake are an advantage to increase the amount of energy that organisms can allocate simultaneously to self-maintenance and reproduction (Boggs 1992). In this context, examining the role of CORT in foraging activity can help us understand how animals modulate their behaviour in response to energetic demand, especially during the breeding season.

Seabirds are considered to be good models for studying foraging strategies because they are central place foragers, i.e. they feed at sea and breed on land. During the breeding season, they perform frequent foraging trips at sea in order to regularly supply their chicks, sharing the task of reproduction with their partners. Consequently, they have to increase their energy expenditure to cope with both the energetic requirements of their chicks and their own self-maintenance. For this reason we investigated the diving behaviour of CORT-implanted Adélie Penguins during the chick-rearing period, using animal-attached time-depth recorders. We expected the overall diving effort of CORT-treated penguins to be greater than that of control individuals.

MATERIALS AND METHODS

The study was conducted on four male Adélie Penguins during the chick-rearing period of the 2008/09 austral summer in Dumont d'Urville, Adélie Land, Antarctica (66°40´S, 140°01´E). During the chick-rearing period, parents alternate foraging trips at sea and nest attendance to brood their chicks. In Dumont D'Urville, Adélie Penguins are known to feed principally on two species of krill (*Euphausia superba* and *E. crystallorophias*) and fish (*Pleuragramma antarcticum*) (Wienecke et al. 2000).

1) Hormonal manipulation and equipment

In mid-November (at the end of the courtship period), observations of the copulation behaviour and cloacal inspection (Beaulieu et al. 2010) allowed us to identify 10 male Adélie Penguins. These birds were captured and marked with Nyanzol-D (a commonly-used marker containing a mix of gum arabic, p-phenylene-diamine, sodium sulfite, ethanol and oxygen peroxide; see Beaulieu et al. 2010 for further details) with numbers being painted on their chests to identify them throughout the study period.

At the end of December (ca. 1 week after hatching), four marked males with small chicks were captured on their nests (penguins #1, #3 and #4 were captured on 29 Dec 2008 and penguin #2 on 2 Jan 2009). We implanted subcutaneous corticosterone pellets (C100, Innovative Research of America, USA) in two of them (CORT group). The skin on the nape of the penguins was disinfected with 70% alcohol and incised for ca. 1.5 cm. One CORT pellet was implanted in the incision, which was then closed with a sterile stitch and sprayed with Alumisol® (healing external suspension). These 100 mg CORT implants were 21-day timed-release pellets from Innovative Research of America (IRA, Sarasota, USA). The two other penguins (control group) underwent the same protocol, but without pellet implantation. In a previous study, conducted on captive male Adélie Penguins, it has been shown that these pellets led to an effective increase, by ca. 5–6 times, of CORT levels within three days, reaching on average about 65 ng/ml at the peak (Spée et al. unpublished data, cf. also Bourgeon & Raclot 2006 in Common Eider Duck *Somateria mollissima*). Values at the peak (range 33.9–78.3 ng/ml) fall within the physiological range of a stressful event for this species (range 9.7–78.7 ng/ml following capture; Cockrem et al. 2009).

The four birds were also instrumented with small time-depth recorders (Cefas G5, Cefas Technology Ltd, UK, 8×31 mm, weight including battery: in air 2.7 g, in water 1.0 g), attached with mastic and strips of waterproof black Tesa® tape (Beiersdorf AG, Hamburg, Germany) (Wilson et al. 1997) along the median line of the penguins' lower back (Bannasch

Table 1. Characteristics of the first seven foraging trips in control and CORT-implanted male Adélie Penguins during the guard stage. Values are presented as mean±SD.

Penguin ID	Control		CORT	
	1	2	3	4
Recording duration (d)	15.7	15.2	21.3	16.7
Mean trip duration (d)	1.10±0.36	1.21±0.30	1.65±1.10	1.10±0.44
Number of dives/trip	924±359	865±222	656±450	610±286
Bout Ending Criterion (s)	171	252	231	171
Number of bouts/trip	15±6	12±8	16±13	13±10
Number of dives/bout	80±129	65±107	39±66	49±73
Time spent diving during a trip (%)	53.9±5.0	55.9±10.1	27.2±19.5	44.5±17.3
Maximum dive depth (m)				
- shallow dives	7±6	6±5	6±5	7±5
- deep dives	48±15	53±14	46±13	51±16
Number of undulations/dive	2.2±1.6	2.7±2.1	2.8±2.4	3.2±2.1

et al. 1994). These loggers recorded depths down to 100 m, every 2 s with 4 cm resolution and an accuracy of 1 m, on an 8MBit flash memory. After instrumenting them, the birds were released near their nests.

During the experimental period, visual observations of attendance in the colony were carried out every two to four hours per day. After seven foraging trips (Table 1), the four males were recaptured on their nests, their loggers and Tesa tape were completely removed, and data were downloaded into a computer.

2) Diving data analysis

Only dives >1 m were included in the analyses. A total of 21,380 dives were analysed using IGOR Pro software (Wavemetrics, version 6.1, Portland, USA). Diving parameters considered here were: dive and post-dive durations, maximum depth (MD), descent, bottom and ascent durations, and the number of undulations in the depth profile (see Ropert-Coudert et al. 2007). Parameters were extracted automatically for each dive using a custom-made program in IGOR Pro.

During a trip, Adélie Penguins performed a series of dives in quick succession separated by short surface intervals, referred to as a bout (Watanuki et al. 2001). The bout ending criteria (BEC) was used to determine the end of a dive bout (Gentry & Kooyman 1986). The time spent in the colony (defined by visual observations) between foraging trips was excluded from the analyses and surface intervals >3 hrs were also excluded from the BEC calculation, because birds were probably resting at sea (Watanuki et al. 1997). Briefly, a log survivor curve of surface intervals was plotted for each bird and the break point was calculated using the "segmented" package of R Version 2.11 (R Development Core Team 2005), and was taken as the BEC. Thus, our diving bouts included dives for which post-dive times were <BEC and contained at least four dives. The analyses of post-dive duration only included dives within bouts.

Because the distributions of maximum dive depths were bimodal (Fig. 1), we separated dives into shallow and deep dives. The break point (also defined using the "segmented" R package) was defined at 27 m for both control and treated birds. Thus, all dives> 25 m are considered as deep dives hereafter.

3) Statistical analysis

A Generalized Estimating Equation (GEE) with Gamma distribution was used to compare foraging trip duration between control and experimental groups, including the treatment (control *vs*. CORT), the trip rank and the date of foraging trips as fixed factors and bird identity as a random factor.

Analyses of the number of dives (count data) per trip, per bout and per maximum depth class, between groups for shallow and deep dives, were performed using Generalized Linear Mixed Models (GLMM) with a Poisson distribution. To compare diving parameters between control and experimental groups, Linear Mixed Effects models (LME) were conducted with bird identity as a random factor and the treatment, the MD category and their interaction as fixed factors (all dive parameters are related to MD). All

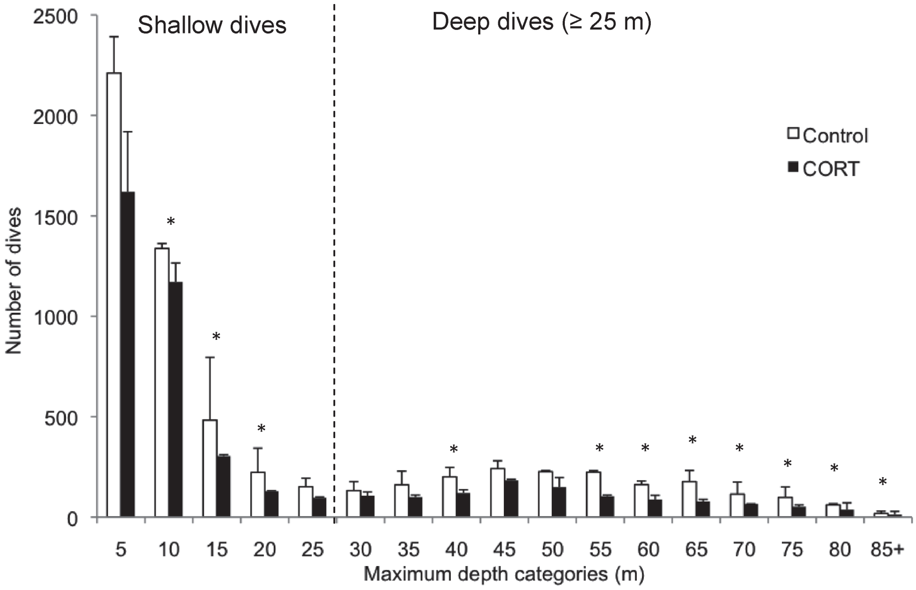

Fig. 1. Distribution of maximum dive depths (>1 m, means±SD) in control and CORT-implanted male Adélie Penguins during the guard stage. * indicates a significant difference between the two treatments for a given depth category.

parameters that were not normally distributed were log or square-root transformed.

Statistical analyses were performed using R with "nlme" and "lme4" packages, except for the GEE that was conducted with SPSS 16.0 (SPSS Inc., Chicago, IL, USA). The significant threshold was set at $p<0.05$ and results are presented as means±SD, unless stated otherwise.

RESULTS

1) Time budget and number of dives

Foraging trip durations were similar in both groups (GEE: Wald $\chi^2=1.71$, $P=0.19$), trips lasting on average 1.26±0.64 days (Table 1). Neither the trip rank (GEE: Wald $\chi^2=0.01$, $P=0.92$) nor the date of foraging trips (GEE: Wald $\chi^2=0.46$, $P=0.50$) had an effect on the trip duration. However, one CORT-implanted penguin (#3) performed three trips that were unusually long (>2.5 days, trips 1, 5 and 7) compared with other birds.

The number of dives per trip was significantly lower for CORT-implanted birds than for controls (z-value=−11.7, $P<0.001$, Table 1). The trip rank ($P<0.001$) and the interaction treatment x trip rank ($P<0.001$) were both significant but did not show any clear trends. In addition, the total number of dives of CORT-implanted birds (4,592 and 4,267 for penguins #3 & #4, respectively) was markedly lower than the controls (6,468 and 6,053 for penguins #1 & #2, respectively), for both shallow (z-value=−5.7, $P<0.001$) and deep (z-value=−2.6, $P<0.01$) dives (Fig. 1). The MD ($P<0.05$) and the interaction MD x treatment ($P<0.05$) both affected the number of dives.

The percentage of time spent diving during a trip did not differ significantly between the groups (t-value=−2.18, $P=0.16$), but intra-individual variation was high in CORT-implanted birds (Table 1), ranging, for example, between 3.7 and 51.4% in penguin #3. CORT-implanted birds performed exceptionally small numbers of dives per trip in several instances (as low as 77 and 139 for birds #3 and #4, respectively, Fig. 2). In comparison, the lowest number of dives during a trip by control birds was >500. Moreover, control birds never spent more than three hours without diving during a trip, whereas this occurred 13 times for penguin #3 (max time without diving=13.5 h) and six times for penguin #4 (max time without diving=7.4 h, Fig. 2).

2) Diving pattern

For control and treated birds, 70% and 75% of all dives were shallow (i.e. <25m), respectively. The mean maximum depth for shallow (t-value=0.19, $P=0.62$) and deep dives (t-value=−0.58, $P=0.62$) did not differ between the groups (Table 1). The ten deep-

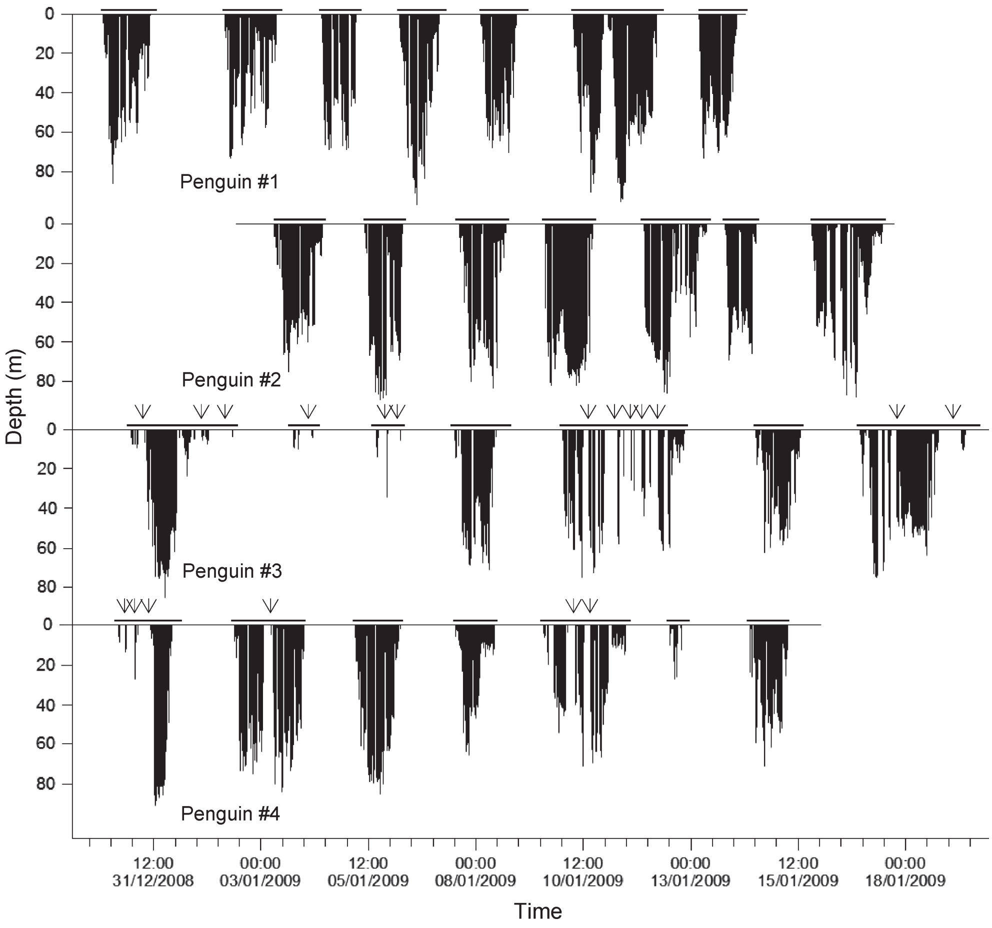

Fig. 2. Dive profiles throughout seven foraging trips in control (#1 and #2) and CORT-implanted (#3 and #4) male Adélie Penguins during the guard stage. Horizontal lines and arrows represent foraging trip duration and long periods without diving (>3 h), respectively.

est dives were all performed by control penguin #1.

As expected, the maximum depth had an effect on all dive parameters ($P<0.001$ in all tests), while the treatment alone did not ($P>0.05$ in all tests). However, the interactions (MD x treatment) on dive duration ($P<0.05$, Fig. 3a), bottom duration ($P<0.05$, Fig. 3b), the number of undulations per dive in the depth profile ($P<0.05$, Fig. 3c) and the post-dive time ($P<0.05$, Fig. 3d), were all significant. Thus, for some maximum depth categories, these parameters were significantly higher for CORT-implanted birds than for controls. However, despite an increase in the number of undulations per dive, the total number of undulations performed by CORT-implanted birds (12,943 and 13,696 for penguins #3 & #4, respectively) was lower than that of controls (14,252 and 16,353 for penguins #1 & #2, respectively).

DISCUSSION

The present study is the first, to our knowledge, to assess the effects of CORT administration on the diving behaviour of wild animals. Interestingly, CORT administration had opposite effects at different scales, apparently decreasing the diving effort at the scale of the trip while simultaneously increasing it at the scale of the dive. Because physiological and behavioural adjustments, which take place at the foraging trip level, do not necessarily account for the dive scale, foraging decisions are scale-dependent. As an illustration of this, Adélie Penguins - at least in some colonies – seem to accumulate more body reserves when engaged in longer trips (Watanuki et al. 2002). This led to the idea that parents could maintain their own body condition by regulating the accumulation of body tissue during foraging trips, but would change food provisioning with respect to variable foraging-

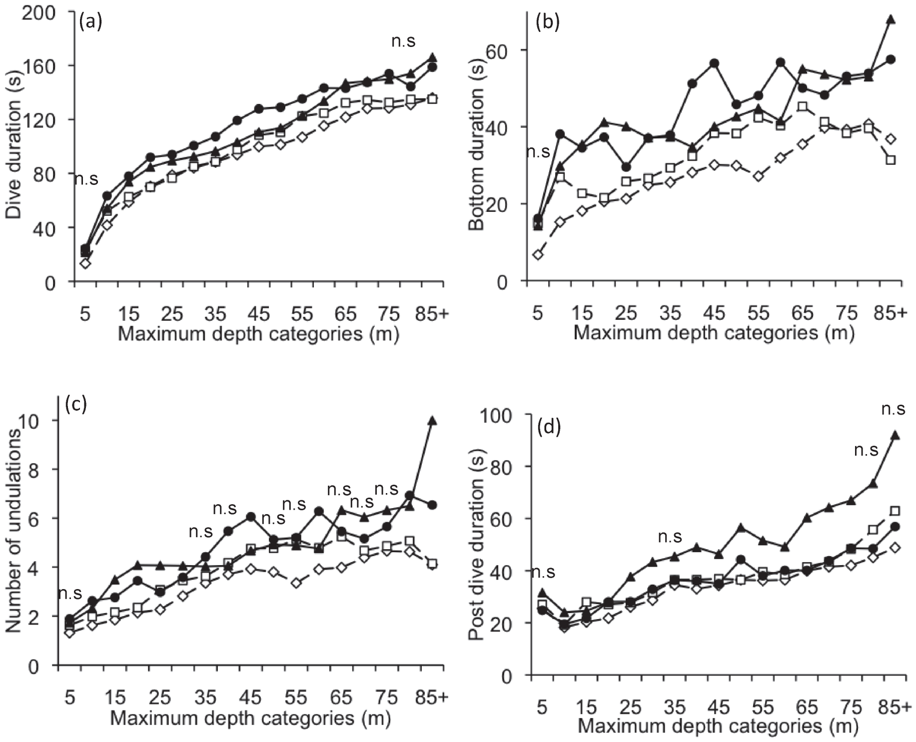

Fig. 3. Relationships between the maximum depths and (a) the mean dive duration, (b) the mean bottom phase duration, (c) the mean number of undulations in a depth profile (see text for details), and (d) the mean post-dive time in control (open symbols) and CORT-implanted (closed symbols) male Adélie Penguins during the guard stage. The absence of symbols indicates a significant difference between the two treatments for a given depth category, and n.s. indicates a non-significant difference.

trip duration.

At the level of a trip, decisions can be adjusted partly in advance, according to for example adult body condition (Kato et al. 2008) or the amount of food required for the chicks. However, the dive scale is a more proximal one, where decisions must be taken almost immediately, in response to immediate prey availability or individual diving capacity (Wilson 2003). Below we discuss the discrepancy in the results of corticosterone administration at these two different scales.

1) At the foraging trip scale

Mean foraging trip durations of Adélie Penguins (on average 1.26±0.64 days) in our study are similar to those reported in another experiment conducted at the same location during the same stage but over different years (1.01±0.02 (S.E.) days in 2006–2007, 1.24±0.04 (S.E.) days in 2007–2008; Beaulieu et al. 2010), and did not differ between groups. However, CORT-implanted birds dived less than controls, some trips having exceptionally small numbers of dives. The absence of a significant difference between the groups in terms of the percentage of time spent diving during a trip can be attributed to the small number of individuals and the high intra-individual variability observed in CORT-implanted birds. Indeed, for several parameters (e.g. percentage of time spent diving, post-dive time, and resting time), we showed that CORT-implanted penguins #3 and #4 exhibited individually different behaviours. This can be attributed to 1) intrinsic characteristics of each individual (e.g. body condition and age), 2) a different response to CORT implantation or 3) the interaction of both factors. Very long intervals of time without diving (i.e.> 3 h) were observed repeatedly during foraging trips for CORT-implanted birds (Fig. 2). We propose that long surface intervals, such as those observed in our study, could correspond to protracted travel times towards or between food patches. This recalls the findings of Angelier et al. (2007) who showed that Wandering Albatrosses with elevated pre-trip CORT levels engaged in long-distant trips (Angelier et al. 2007). Alternatively, exceptionally long periods without diving may represent time spent resting outside the colony, either on land or on sea-ice (Watanuki et al. 1997). The use of GPS could allow us to test this hypothesis in future studies. Finally, as suggested by Ropert-Coudert et al. (2004) for the Cape Gannet *Morus capensis*, protracted resting periods may allow birds to digest a portion of their food in order to restore their own reserves. In our case, the latter hypothesis appears to be the most plausible one, but requires further confirmation. Such an increase in protracted resting periods could allow CORT-implanted birds to promote self-maintenance at the expense of the food supply for their chicks.

2) At the dive scale

CORT treatment decreased the number of dives but paradoxically it affected positively other diving parameters (dive duration, bottom phase duration, number of undulation per dive). Several explanations can be proposed to explain such behaviour. First, the enhancement of the dive-scale effort could be viewed as a partial compensation of the decrease in the trip-scale effort. Corticosterone would drive the bird away from its reproductive duties but in the present case it proceeds from an experimentally-induced behaviour. We cannot overlook the fact that, here, the birds were already engaged in reproduction at the time of the experiment, and, as such, had already been provisioning their chicks before the corticosterone started to affect their physiological status and foraging performances. The hormone is thus operating in a non-prepared environment and we do not know whether other hormones secreted during reproduction are counteracting CORT effects or not. Prolactin, for example, is known to be present at high concentrations in Adélie Penguins during the guard stage (Vleck et al. 1999) and is involved in mediating the trade-off between parental effort and self-maintenance (Chastel et al. 2005; Angelier et al. 2009). Secondly, an elevated hunting effort (e.g. an elevated number of undulations) could also indicate a lower capture success displayed by CORT-implanted birds, which then would lead to a higher number of capture attempts. Future studies to assess the number of prey captured, for instance via the use of jaw movement recorders (Wilson et al. 2002) and/or accelerometers (Ropert-Coudert et al. 2006), are needed to examine more precisely the effects of CORT on diving efficiency.

3) Overall foraging efficiency

Finally, at the global scale of the study period, the enhancement of the dive-scale effort did not inverse the trend of an overall lower foraging effort in CORT-implanted birds. Indeed, the total number of undulations per bird remained low (ca. 13,319 for CORT *vs.* ca. 15,302 for controls), leading us to suspect a low number of prey were captured by treated birds (the use of undulations as an index of prey capture has been discussed in Ropert-Coudert et al. 2001 and Bost et al. 2007). Interestingly, our results are not consistent with the correlative study of Angelier et al. (2008), who found that Adélie Penguins with elevated pre-trip CORT levels performed shorter trips closer to the colony and travelled a smaller distance per day than penguins with low pre-trip CORT levels. Because birds with relatively elevated pre-trip CORT levels tended to have a higher foraging effort index (assessed by time-depth recorders), Angelier et al. (2008) suggested that naturally high CORT levels might be associated with high foraging effort. In our study, CORT administration clearly had the opposite effect, significantly reducing diving effort. These different effects of CORT on behaviour may be explained by the range of CORT levels that are probably not comparable between Angelier et al. (2008) and our study. Even though each bird's pre-trip CORT levels were not assessed in our study, we can hypothesise that elevated CORT levels probably redirected energy allocation from reproduction towards self-maintenance. Two recent studies support this view. Spée et al. (2010) showed that a high corticosteronemia is a major contributor to nest abandonment by male Adélie Penguins that go to feed at sea when the incubation fast threatens their own survival. Moreover, Cottin et al. (unpublished data) showed that CORT treatment of male Adélie Penguins during the guard stage led to an increase in chick mortality. In order to learn if CORT administration may redirect energy allocation towards self-maintenance at the expense of reproduction, future studies need to assess body condition and reproductive success of hormonally manipulated birds in parallel with the recording of their diving behaviour.

Despite the limitation of the current study, due to the small number of individuals, we believe our preliminary results can contribute to a better understanding of how CORT affects foraging decisions. The association between bio-logging and hormonal manipulation approaches appears particularly promising in the study of physiological mechanisms underlying the behaviour of free-living animals.

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