

Corticosterone and time–activity budget: An experiment with Black-legged kittiwakes

Frédéric Angelier^{a,*}, Céline Clément-Chastel^a, Geir Wing Gabrielsen^b, Olivier Chastel^a

^a Centre d'Etudes Biologiques de Chizé, CNRS, F-79360, Villiers en Bois, France

^b Norwegian Polar Research Institute, Polarmiljøseneteret, Tromsø, N-9296 Norway

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Abstract

In vertebrates, the well established increase in plasma corticosterone in response to food shortage is thought to mediate adjustments of foraging behavior and energy allocation to environmental conditions. However, investigating the functional role of corticosterone is often constrained by the difficulty to track time–activity budget of free-ranging animals. To examine how an experimental increase in corticosterone affects the activity budget of male Black-legged kittiwakes (*Rissa tridactyla*), we used miniaturized activity loggers to record flying/foraging, presence on the sea surface and nest attendance. To investigate how corticosterone affects allocation processes between self-foraging and foraging devoted to the brood, we monitored body mass change of males from capture (day 0) to recapture (day 3). Among control birds, males in poor condition at day 0 spent significantly more time flying/foraging and less time attending the nest site than did males in good condition. Corticosterone treatment affected time spent flying/foraging in interaction with body condition at day 0: corticosterone-implanted males in good condition spent more time flying/foraging than control ones; this was not observed in poor condition males. In control birds, change in body mass was negatively correlated with body condition at day 0. This was reinforced by corticosterone treatment and, on average, corticosterone-implanted males gained much more mass than controls. These results suggest that in Black-legged kittiwakes, body condition and corticosterone levels can interact to mediate foraging decisions and possibly energy allocation: when facing stressful environmental conditions, birds in good body condition may afford to increase the time spent foraging probably to maintain brood provisioning, whereas poor body condition birds seemed rather to redirect available energy from reproduction to self-maintenance.

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Introduction

A key concept in life-history theory is that individuals must allocate their energy to competing life-history traits (Stearns, 1992; Roff, 1992). When organisms face adverse environmental conditions and energetic constraints, the competing demands of all the life-history traits cannot be maintained at the maximal level and individuals should adopt an optimal allocation strategy in order to maximize their fitness (McNamara and Buchanan, 2005). This allocation process is primarily influenced by the ability of the individuals to extract resources from the environment because it determines the amount of energy

available to an individual to be expended on fitness-related activities, such as self-maintenance or brood provisioning (Costa, 1991; Boggs, 1992). Because of this connection between foraging activity and energy allocation processes, it is essential to understand how foraging decisions are influenced by environmental conditions and the physiological state of the animal (McNamara and Houston, 1996; Houston and McNamara, 1999).

In this context, endocrine mechanisms deserve specific attention because of their role in mediating interactions between environment, physiology and behavior (Sinervo and Svensson, 1998; Ricklefs and Wikelski, 2002). Focusing on glucocorticosteroid hormones (cortisol and corticosterone) is especially judicious when examining resource allocation processes because these hormones may be involved in breeding and foraging

* Corresponding author. Fax: +33 5 49 09 65 26.

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

decisions (Wingfield et al., 1998; Wingfield and Kitaysky, 2002; Wingfield and Sapolsky, 2003). Corticosterone is the primary mediator of allostasis in birds and increases in corticosterone levels allow to mobilize energy stores and to adjust behavior and physiology appropriately to the conditions encountered (review in McEwen and Wingfield, 2003; Landys et al., 2006).

Although increase in glucocorticosteroid levels beyond a certain threshold is known to suppress parental care (Silverin, 1986; Cherel et al., 1988; Wingfield and Sapolsky, 2003), slight and temporary increases in glucocorticosteroid levels may lead to increases in foraging activities (Astheimer et al., 1992; Challet et al., 1995; Breuner et al., 1998; Koch et al., 2002; Pravosudov, 2003; Landys et al., 2004; Angelier et al., 2007a). Under low food availability, such a response may help to meet the increased energetic demands of reproduction (Kitaysky et al., 2001; Romero, 2002; Moore and Jessop, 2003; Love et al., 2004; Landys et al., 2006).

However, the relationship linking corticosterone and foraging behavior is certainly more complex because foraging behavior is known to be influenced by other components of the individual's physiological state (McNamara and Houston, 1996). For example, several studies have clearly shown that body condition is involved in the regulation of foraging decisions in vertebrates (Weimerskirch, 1998, 1999; Spencer and Bryant, 2002; Gorman and Nager, 2003; Varpe et al., 2004) and therefore, it is likely that the effect of increased corticosterone levels on foraging and allocation processes may interact with body condition (Astheimer et al., 1992; Orchinik, 1998; Landys et al., 2006).

To our knowledge, no study has simultaneously and experimentally investigated the role of corticosterone and body condition on foraging behavior in free-living vertebrates. This certainly results from the difficulty to obtain accurate measurements of foraging behavior and time–activity budget in free-ranging animals. The recent development of electronic miniaturized devices has allowed to obtain detailed information on foraging areas, foraging activity and efficiency for several large-sized bird species (Weimerskirch et al., 2002, 2005a; Pinaud and Weimerskirch, 2002; Shaffer et al., 2003; Phillips et al., 2004, 2005; Angelier et al., 2007a). For flying seabirds, activity loggers are useful tools to measure time allocation because they enable one to distinguish key behaviors such as flying, foraging, resting on the sea surface or guarding the chick at the nest (Benvenuti et al., 2001; Daunt et al., 2002; Tremblay et al., 2003). Studying how corticosterone and body condition correlate with the time budget of each activity should shed some light on the functional role of this hormone as a link between environmental stressors (such as temporary food shortages) and foraging decisions (Kitaysky et al., 1999, 2001; Wingfield and Kitaysky, 2002).

In this study, we investigated time–activity budget and mass change of a seabird, the Black-legged kittiwake (*Rissa tridactyla*), in response to experimentally increased corticosterone levels during the chick rearing period. This period is very energetically demanding because parents must feed the chicks frequently and share the energy extracted from the sea between self-provisioning (foraging devoted to self-maintenance) and brood provisioning (foraging devoted to the brood). Moreover, parents have to stay on the nest as much as possible in order to guard and protect the

chicks against predators (Bech et al., 2002; Fyhn et al., 2001; Moe et al., 2002).

Our first aim was to examine how corticosterone manipulation affects the way kittiwakes partition their time between flying/foraging, resting on the sea surface and guarding the brood at the nest by using activity recorders (Daunt et al., 2002). According to a correlative study conducted on free-living seabird (Angelier et al., 2007a) and to studies on captive birds (Breuner et al., 1998; Koch et al., 2002; Landys et al., 2004), we predict that manipulating corticosterone levels in free-living kittiwake parents will affect the time devoted to locomotor and foraging behaviors. Specifically, we predict that corticosterone-implanted birds will spend more time flying and foraging than control sham-implanted birds. Because body condition is known to be involved in the regulation of foraging decisions in seabirds (review in Weimerskirch, 1999) and that corticosterone is known to be context/state-dependent (Orchinik, 1998; Landys et al., 2006), we also predict that the influence of corticosterone manipulation on time allocation might be further modulated by parent's body condition.

The second aim of this study was to test whether corticosterone also acts on how kittiwake parents allocate energy between self-maintenance and brood provisioning. To assess this latter point, we monitored changes in adult body mass over a three-day period. Indeed, kittiwakes are known to experience a reduction in body condition during chick rearing as a result of intense chick provisioning and reduced opportunity for self-foraging (Bech et al., 2002; Fyhn et al., 2001; Moe et al., 2002). Since corticosterone is suspected to stimulate self-foraging (Silverin, 1986; Wingfield and Silverin, 1986), we predict that body condition will improve among corticosterone-implanted birds. Moreover, since parent's body condition plays a central role in energy allocation (Weimerskirch, 1999), it is likely that as for activity budget the influence of corticosterone manipulation on energy allocation might be further modulated by parent's body condition.

Methods

Study area and birds

Our study was conducted between 23 July and 7 August 2005 with a colony of Black-legged kittiwakes at Kongsfjorden, Svalbard (78°54'N, 12°13'E), 7 km east of Ny-Ålesund, Norway. Black-legged kittiwakes are colonial seabirds that breed on cliffs throughout the northern parts of the Pacific and Atlantic, including the Barents Sea region up to the Svalbard Archipelago. We studied kittiwakes in two plots (plot D and E) of ca. 60 pairs breeding on cliffs at a height of 5–10 m during the mid-chick rearing period (15–20 days old chicks). These two plots are 100 m apart. Nest contents were checked regularly using a mirror at the end of a 4 m fishing rod. Specifically, we were able to determine the number of chicks present in the nest. First, we studied the influence of corticosterone on time–activity budget in the E plot. Second, we examined the influence of corticosterone on energy allocation processes in the D and E plots (i.e., body mass change of the parent over a three-day period). The influence of corticosterone on time–activity budget and energy allocation processes was studied at the same time and on the same birds in the E plot. Regarding the energy allocation processes, we studied some birds of the D plot at the same time to increase the sample size. Finally, we tested the effect of subcutaneous corticosterone implantation on circulating corticosterone levels in the D plot. Because males and females might respond differently to increased corticosterone levels, we focused our study on males only. Males are larger than females in Black-legged kittiwakes (Moe et al., 2002; Chastel et al., unpublished data, body mass, mean ± SE, female: 382.75 ± 4.77, male: 428.33 ± 4.75) and therefore were

more likely to bear the activity logger with less adverse effect. Although females expend slightly more energy than males during the chick rearing period (Fyhn et al., 2001; Jodice et al., 2006), chick rearing roles were almost similar between males and females in kittiwakes (Moe et al., 2002). Birds were individually marked with white PVC plastic bands engraved with a three-digit code and fixed to the bird's tarsus, allowing identification from a distance and their sex was already known by molecular sexing method carried out previously at the Centre d'Etudes Biologiques de Chizé (CEBC) as detailed in Weimerskirch et al. (2005b).

Experimental design

1—Manipulating corticosterone levels

In the D and E plots, at day 0, 41 male parents were captured at their nest with a noose on the end of a 5 m fishing rod. Immediately after capture, a blood sample was collected within 3 min to determine baseline corticosterone levels. In 4 birds blood sampling was difficult and handling time exceeded the one recommended by Romero and Reed (2005) to assess baseline corticosterone levels. Therefore, baseline corticosterone levels were only known for 37 birds. Blood samples were collected from the alar vein with a 1 ml heparinized syringe and a 25 gauge needle (maximum amount of blood collected: 0.5 ml). Immediately after this blood sample, we implanted the 41 male parents subcutaneously (between shoulders) with two 25-mm silastic tubes (internal diameter 1.47 mm, external diameter 1.96 mm, Dow Corning, Michigan) either filled with crystallized corticosterone (C2505, Sigma Chemical Co., St. Louis, USA, $n=20$ corticosterone-implanted birds) or empty ($n=21$ control birds). The implants site was disinfected with povidone iodine and then glued. To facilitate corticosterone diffusion, we cut both ends of each tube just prior to implantation. Our aim was that corticosterone levels increase rapidly and are elevated at the time we recorded time–activity budget of implanted birds, i.e., 1 day after implantation. This hormonal manipulation has been shown to be effective to increase corticosterone levels in many bird species including chick rearing kittiwakes (Kitaysky et al., 2001).

All birds were then weighed to the nearest 2 g using a Pesola spring balance and their skull length (head+bill) was measured to the nearest 0.5 mm with a sliding caliper (Moe et al., 2002). If a bird was feeding its chick at the designated time of capture, we delayed capture until the parent had delivered the meal. As kittiwakes spontaneously regurgitate the food destined for the chicks when captured, we were able to accurately measure the parents' body mass (and not their body mass+the mass of the meal) even in cases where chick feeding had not yet been completed at capture. We are confident that birds regurgitated most of their stomach content when captured: after regurgitation body condition of birds returning from sea did not significantly differ from body condition of birds that have already fed their chicks (Chastel et al., unpublished results). We used body mass and the skull length to calculate an index of body condition. Because residuals from an ordinary least squares linear regression of body mass against body size can lead to spurious results (Green, 2001), we calculated residual indices of condition by using the residuals from a reduced major axis regression of body mass against skull length (Green, 2001).

2—Recording foraging behavior

Immediately after the implantation, 21 of the 41 male parents (10 with corticosterone filled implants and 11 with empty implants) were equipped with activity loggers (Actiwatch®, Cambridge, UK, dimensions: radius 11 mm, height 9 mm; mass 4 g, 0.9 to 1.1% male kittiwake body mass). Activity is measured by means of a piezo-electric accelerometer that is set up to record the integration of intensity, amount and duration of movement in all directions. The corresponding voltage produced is converted and stored as an activity count in the memory unit of the device. Consequently, this activity count is an integration of all voltage spikes over the time recording interval. The device was attached to feathers on the back with white adhesive tape (Tesa tape) commonly used to attach devices in seabirds (e.g. Angelier et al., 2007a). We are confident that there were no deleterious effects of the activity loggers on the behavior of these birds since the logger's weight was only 1% of the mass of the birds, which is far below the limit considered as acceptable for flying birds (Kenward, 2001). Furthermore, Daunt et al. (2002) used larger loggers in their study without detecting any behavioral differences between equipped and non-equipped kittiwakes. Although time–activity budget was computed with little validation,

activity loggers clearly allow distinguishing the main activities of Black-legged kittiwakes (Daunt et al., 2002). As detailed by Daunt et al. (2002), three categories of signals can be identified: (1) very weak, scarce, low intensity signals that correspond to periods when the bird is attending the brood at the nest; (2) weak frequent signals of relatively low intensity that correspond to periods when the bird is present on the sea surface; (3) frequent signals of high intensity corresponding to flight and foraging (Fig. 1). In this study we were not able to discern traveling flight from foraging flight (Daunt et al., 2002) because in 2005, kittiwakes breeding in Kongsfjorden did not seem to forage in one bout in a specific area but foraged opportunistically while traveling (unpublished data). To calculate the time–activity budget of each bird ($n=21$), we therefore considered time spent on the nest, time spent flying/foraging and time spent on sea surface. Of course, these three components of time–activity budget are closely linked because a bird that spends most of its time on the nest cannot spend much time foraging. Activity bouts were extracted from raw data by using an algorithm. Specifically, the activity profile of each bird was examined in order to select the critical values that determined break points. Because of slight variations in the fixing position of the device between individuals, these critical values can vary from an individual to another and they are needed to be individually determined.

The activity loggers had a recording interval of 5 s and signals were recorded during 45 h and 29 min. They were programmed to start recording signals on day 1 (1 day after implantation), at the time corticosterone was effectively increased. Equipped birds were marked with a spot painted on their head in order to facilitate individual determination. They were then opportunistically and frequently observed flying and resting at the sea surface during the recording period. Each bird was at least observed flying/resting at the sea surface twice over the study period. All these observations were made from land in the immediate vicinity of the colony. Moreover, visual observations of nests were made twice a day in order to validate the interpretation of logger signals. In all cases, visual observations of nests and equipped birds confirmed our interpretation of the loggers' signals. Theoretically, kittiwakes could loaf at the colony without protecting and brooding their chicks. However, the percentage of time devoted to this activity is known to be very low in Black-legged kittiwakes (Jodice et al., 2003). In our study, no kittiwake parents were observed loafing in the colony for a prolonged time. After deploying the activity logger, birds were released at the colony. Three days after treatment (day 3), 32 of the 41 birds (including all the equipped birds, $n=21$) were recaptured at their nest and bled for baseline corticosterone levels. Their activity logger was removed and they were then weighed following the same procedure as on day 0. Birds were then released and activity data were downloaded onto a laptop.

Because we regularly checked the number of chicks present in each nest, we were able to know which parents lost a chick over the 3 days of the study period. However, we were unable to monitor chick's growth and chick's body mass

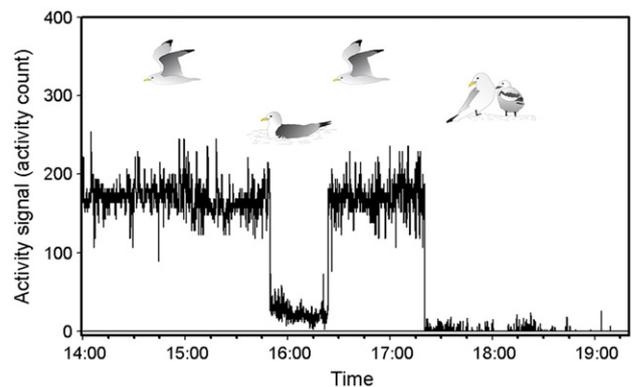


Fig. 1. Example of activity data recorded by an activity logger attached to a male kittiwake parent during the chick rearing period. Activity signal was recorded between 14:00 and 19:20 on 1 August. Scarce, low intensity signals correspond to periods when the bird is attending the brood at the nest; frequent signals of relatively low intensity correspond to periods when the bird is resting on the sea surface; frequent signals of high intensity correspond to periods when the bird is flying and foraging.

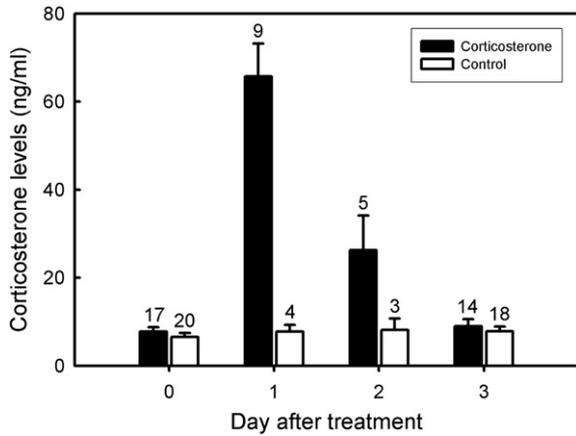


Fig. 2. Effect of corticosterone and empty implants on baseline plasma levels of corticosterone 1, 2 and 3 days after implantation in male Black-legged kittiwakes during the chick rearing period (mean±SE). Numbers above bars denote sample sizes.

because the nests cannot be reached easily in these colonies and we would have disturbed the behavioral recording of the parents.

3—Measuring the effect of corticosterone implants on plasma levels of corticosterone

To confirm that the corticosterone implants led to an increase in circulating corticosterone levels of parents on day 1 and day 2 (1 and 2 days after implantation), we captured and collected blood samples from 20 birds in the D plot. Ten kittiwakes were implanted with corticosterone implants and ten with empty implants. Among these 20 birds, 13 birds were recaptured at day 1 and 8 birds were recaptured at day 2. To measure the effect of implants on corticosterone levels on day 3, we used all the birds, which were blood sampled within 3 min at day 3 (D and E plots, n=32). The study was approved by the Governor of Svalbard and by the French Committee for Animal Research (Animal experiment permit n° 79-2 to O. Chastel).

Corticosterone assay

After blood sampling, the samples were put into ice and centrifuged at the end of the day. Plasma was subsequently stored at -20 °C. Plasma concentrations of corticosterone were determined by radioimmunoassay at the CEBC as previously described (Lormée et al., 2003). All samples were run in one assay; the coefficient of intra-assay variation was assessed using several reference plasmas within the assay. Minimal detectable corticosterone level was 0.5 ng/ml. The intra-assay coefficient of variation was 7.7% (n=5 duplicates).

Statistical analyses

All analyses were performed with SAS statistical software (SAS Institute Inc, 2000). We used generalized linear models (GLM) and maximum likelihood techniques to find the most likely model given the data (Hilborn and Mangel, 1997; Burnham and Anderson, 2002). Significance of independent variables was determined by a likelihood ratio-test that is asymptotically χ^2 distributed (Hilborn and Mangel, 1997). This statistical technique has been widely used in previous studies (Biro et al., 2003; Mitchell et al., 2004; Eeva and Lehikoinen, 2004).

We first used GLMs with normal errors and an identity link function (Proc GENMOD, type 3 analyses) to test for an effect of treatment, body condition at day 0 and their interaction on (1) the percentage of time spent on the nest, (2) the percentage of time spent flying/foraging and (3) the percentage of time spent resting on the sea surface. The time–activity budget was computed by using the whole recording time (45 h and 29 min).

Because we found a significant effect of the interaction between body condition at day 0 and treatment on time–activity budget (see Results), we split our data set in order to separate males in poor body condition (body condition index <0) and males in good body condition (body condition index >0). We then

tested an effect of treatment on the percentage of time spent on the nest and on the percentage of time spent flying/foraging within these two groups by using ANOVAs (dependent variable: time spent on the nest or time spent flying/foraging; factors: treatment).

Second, we used GLMs with normal errors and an identity link function (Proc GENMOD, type 3 analyses) to test for an effect of treatment, body condition at day 0 and their interaction on (4) the change in body mass from day 0 to day 3 (body mass at day 3 – body mass at day 0). Because the change in body mass from day 0 to day 3 was not linked to our individual body size index, i.e., skull length ($F_{1,30}=0.814$, $p=0.374$), correcting the change in body mass from day 0 to day 3 by skull length was not necessary and could even have generated spurious results (Green, 2001).

Finally, we fitted a GLM with binomial errors and a logit link function (Proc GENMOD, type 3 analysis) to test an effect of treatment, body condition at day 0 and their interaction on (5) the probability of losing a chick during the study period.

The goodness of fit tests revealed that all the models fitted the data satisfactorily (χ^2 tests, $p>0.25$) and examination of diagnostics (e.g. deviance/df ratios) indicated that the data met assumptions of these analyses (deviance/df were comprised between 1 and 1.25). In each case, we assessed evidence about specific hypotheses, so we did not adjust significance criteria with the Bonferroni method (Perneger, 1998).

To examine the effect of corticosterone implants on circulating corticosterone levels, we used a generalized linear mixed model (GLMM). Because male kittiwakes were sampled several times, we included bird identity as a random factor. We tested an effect of treatment (corticosterone, control), day of sample (day 0, day 1, day 2 and day 3) and their interaction on baseline corticosterone levels.

Results

Effect of corticosterone implants on circulating corticosterone levels

The treatment, the day of sampling and their interaction have a significant effect on baseline corticosterone levels (GLMM, treatment: $F_{1,43}=56.68$, $p<0.001$, day of sampling:

Table 1

Generalized linear models (GLM) to test the influence of increased corticosterone levels and body condition at first capture (day 0) on the percentage of time spent flying/foraging (model A), the percentage of time spent on the nest (model B), the percentage of time spent on water (model C), the change in body mass from day 0 to day 3 (model D) and the probability of losing the chicks (model E)

Model	Dependent variable	Independent variables	df	χ^2	p
A	Time spent flying/foraging (%) (n=21)	Treatment	1	0.73	0.393
		Body condition	1	12.75	<0.001
		Body condition × treatment	1	5.97	0.015
B	Time spent on the nest (%) (n=21)	Treatment	1	0.21	0.644
		Body condition	1	5.92	0.015
		Body condition × treatment	1	4.88	0.027
C	Time spent resting on water (%) (n=21)	Treatment	1	1.97	0.161
		Body condition	1	0.71	0.399
		Body condition × treatment	1	0.12	0.726
D	Change in body mass from day 0 to day 3 (g) (n=32)	Treatment	1	4.62	0.031
		Body condition	1	10.68	0.001
		Body condition × treatment	1	0.03	0.863
E	Probability of losing a chick (n=41)	Treatment	1	2.37	0.124
		Body condition	1	2.21	0.137
		Body condition × treatment	1	2.47	0.116

Significant variables were indicated in bold.

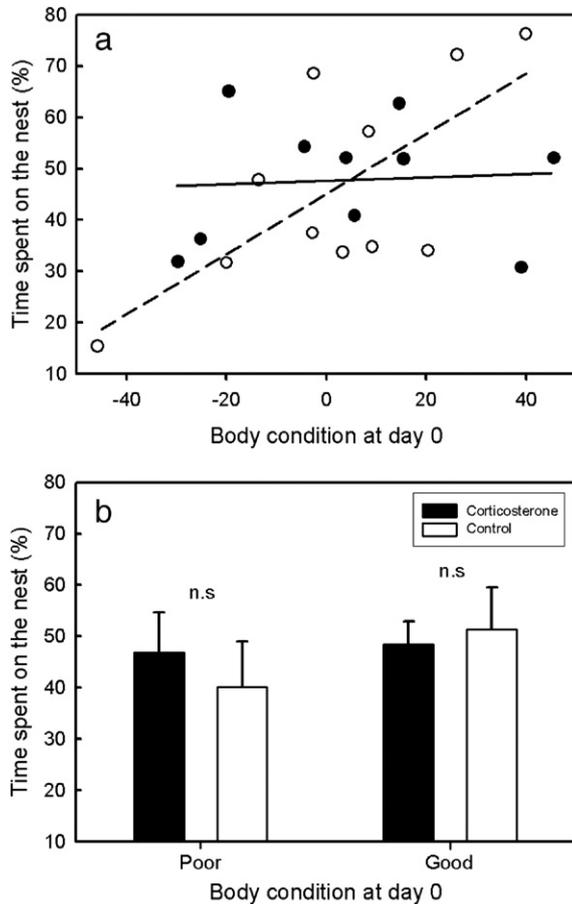


Fig. 3. (a) Effect of increased corticosterone levels and body condition at first capture (day 0) on the percentage of time spent guarding the chick at the nest. Filled symbols and solid line denote corticosterone-implanted kittiwakes whereas open symbols and dashed line denote control kittiwakes. The results were still almost significant when we removed the control bird in very poor body condition (interaction 'treatment \times body condition at day 0', $p=0.056$). Note that this point is not considered as an outlier (based on residual analysis). (b) Influence of the experimental treatment on the percentage of time spent guarding the chick among birds in poor or good body condition. n.s. indicates no significant difference between corticosterone-treated and control birds.

$F_{3,43}=38.86$, $p<0.001$, interaction: $F_{3,43}=37.81$, $p<0.001$). Specifically, baseline corticosterone levels did not vary between corticosterone-implanted and control birds at day 0 (Fig. 2). Corticosterone implantation resulted in a significant increase in baseline plasma corticosterone level on day 1 and day 2, whereas such an increase was not found in control birds (Fig. 2). At day 3, corticosterone levels returned to the values observed prior to treatment in corticosterone-implanted birds and were similar to those of control birds (Fig. 2). Baseline corticosterone levels at day 3 did not differ significantly between each plot (D and E) in both experimental groups (Student's tests; corticosterone-implanted birds: $t=-0.52$, $df=12$, $p=0.616$; control: $t=1.05$, $df=16$, $p=0.311$).

At day 0, both groups (corticosterone-implanted birds and controls) were similar in body condition ($t=0.06$, $df=39$, $p=0.949$), baseline corticosterone levels ($t=1.17$, $df=35$, $p=0.249$), date of treatment ($t=0.62$, $df=39$, $p=0.567$), and

brood size ($\chi^2=0.59$, $df=1$, $p=0.444$). Moreover, at day 0, birds from the D and the E plots did not differ significantly in body condition ($t=-0.44$, $df=39$, $p=0.663$), baseline corticosterone levels ($t=-1.58$, $df=35$, $p=0.123$), date of treatment ($t=-0.32$, $df=39$, $p=0.754$), and brood size ($\chi^2=0.79$, $df=1$, $p=0.375$).

Effects of corticosterone implants on activity-budget

Body condition at day 0 had a positive and significant effect on the percentage of time spent on the nest and a negative and significant effect on the percentage of time spent flying/foraging (GLMs; time spent on the nest: Table 1, model A, Fig. 3a; time spent flying/foraging: Table 1, model B, Fig. 4a). Although corticosterone treatment alone had no significant effect on activity budget (GLMs; time spent on the nest: Table 1, model A; time spent flying/foraging: Table 1, model B), there was a

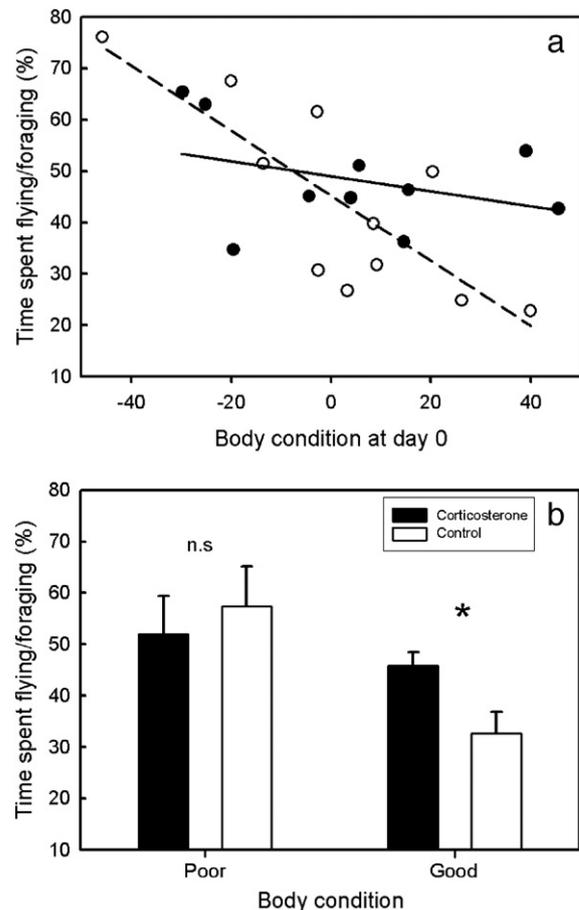


Fig. 4. (a) Effect of increased corticosterone levels and body condition at first capture (day 0) on the percentage of time spent flying/foraging. Filled symbols and solid line denote corticosterone-implanted kittiwakes whereas open symbols and dashed line denote control kittiwakes. The results were still almost significant when we removed the control bird in very poor body condition (interaction 'treatment \times body condition at day 0', $p=0.092$). Note that this point is not considered as an outlier (based on residual analysis). (b) Influence of the experimental treatment on the percentage of time spent flying/foraging among birds in poor or good body condition. n.s. and * respectively indicate no significant difference or significant difference ($p<0.05$) between corticosterone-treated and control birds.

significant influence of the interaction between body condition at day 0 and treatment on activity budget (GLMs; time spent on the nest: Table 1, model A, Fig. 3a; time spent flying/foraging: Table 1, model B, Fig. 4a). The interaction between body condition at day 0 and treatment was significant because, in both cases, the effect of body condition was highly significant in control animals, whereas this effect was removed in corticosterone-treated animals (Figs. 3a and 4a).

Specifically, among males in good body condition, corticosterone-implanted birds spent significantly a higher proportion of their time flying/foraging than control parents (ANOVA, $F_{1,10}=7.09$, $p=0.024$; Fig. 4b), but there was no difference in the percentage of time spent on the nest between the two groups (ANOVA, $F_{1,10}=0.10$, $p=0.755$; Fig. 3b). Among males in poor body condition, corticosterone-implanted parents spent as much time flying/foraging and on the nest as control parents (time on the nest: $F_{1,7}=0.31$, $p=0.597$, Fig. 3b; time spent foraging: $F_{1,7}=0.24$, $p=0.637$, Fig. 4b).

Body condition at day 0, treatment and their interaction had no significant effect on the time spent resting on the sea surface (Table 1, model C).

Effects of corticosterone implants on change in body mass and breeding success

Corticosterone treatment had a significant effect on change in body mass from day 0 to day 3 (GLM; Table 1, model D; Fig. 5a, b): Corticosterone-implanted birds gained much more mass than controls. In addition, change in body mass from day 0 to day 3 was negatively correlated with body condition at day 0 (GLM; Table 1, model D; Fig. 5b). There was no significant interaction between treatment and body condition at day 0 (GLM; Table 1, model D; Fig. 5a).

The probability of losing a chick over the 3-day period was not affected by treatment or body condition at day 0 (GLM; Table 1, model E). There was no significant effect of the interaction between treatment and body condition at day 0 (GLM; Table 1, model E).

Discussion

Experimental manipulation of corticosterone levels

By using the same dose as Kitaysky et al. (2001) used for the same species, we temporarily increased baseline levels of corticosterone by an average of about 30 ng/ml during the study period (from day 1 to 3), a similar level to that observed in kittiwake parents when food shortages and stressful events occur (Kitaysky et al., 1999, 2001; Buck et al., 2007; Chastel et al., unpublished data). Therefore, corticosterone levels were increased within a physiological range (corticosterone levels measured during several breeding seasons, mean±SE [min, max]; baseline: 10.50 ± 0.61 [10.49, 30.00], stress-induced: 54.87 ± 1.85 [19.52, 100.94]; Chastel et al., 2005, unpublished results). In Svalbard, kittiwakes rely on ephemeral food supply which may substantially vary in abundance from one day to the other and we are confident that a short-term corticosterone increase as achieved by the hormone implants does mimic a short-term food shortage (Kitaysky et al., 2001), as kittiwakes often experience during the breeding season.

Corticosterone and activity budget

By using miniaturized activity loggers, we showed that body condition and corticosterone levels significantly affected time–activity budgets in a free-living seabird. First, as reported in many other seabirds (review in Weimerskirch, 1999), we found a strong effect of body condition on time–activity budget: control kittiwake parents in poor body condition spent more time flying/foraging and less time at the nest than control parents in good body condition. Birds in poor body condition may then be inexperienced/poor foragers (Weimerskirch, 1992; Chastel et al., 1995; Blums et al., 2005) which probably have to allocate more time flying/foraging than good condition ones in order to extract food from the environment (Weimerskirch, 1990; Daunt et al., 2006; Lewis et al., 2006). On the other hand, birds in good body condition, being better foragers, may afford to spend less time flying/foraging.

Second, the experimental increase in corticosterone levels removed the effect of body condition since we found no effect of

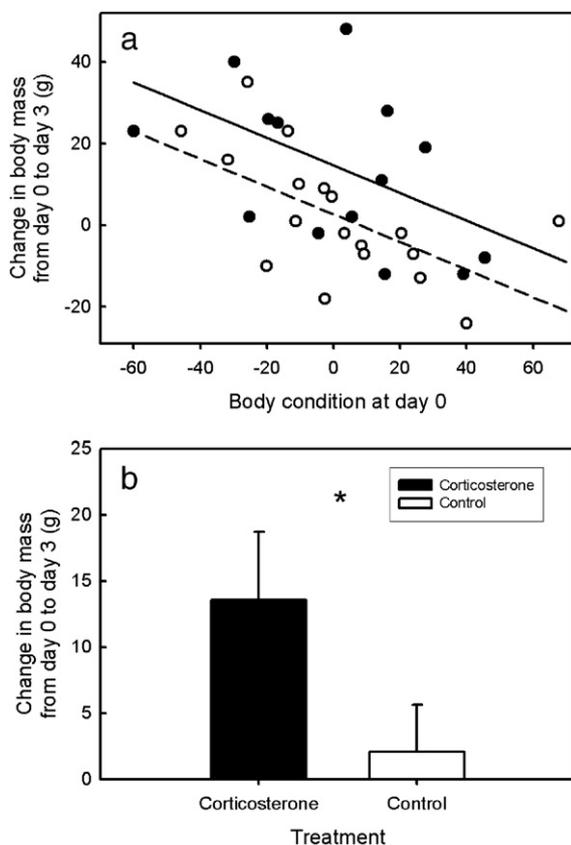


Fig. 5. (a) Effect of increased corticosterone levels on change in body mass from day 0 to day 3 in kittiwake parents during the chick rearing period (Mean±SE). * indicates a significant difference between corticosterone-treated and control birds ($p<0.05$). (b) Additive effects of increased corticosterone levels and body condition at first capture, i.e., day 0, on change in body mass from day 0 to day 3. Filled symbols and solid line denote corticosterone-implanted kittiwakes whereas open symbols and dashed line denote control kittiwakes. These two figures were two representations of the same data.

body condition on time–activity budget within the corticosterone-treated group (the slope of the regression lines did not significantly differ from 0). However, (1) among males in good condition, corticosterone-implanted birds spent more time flying/foraging than controls, (2) among males in poor condition, corticosterone-implanted males spent as much time flying/foraging as controls.

These findings support the more general idea that the influence of corticosterone on foraging behavior could be context-dependent (Astheimer et al., 1992; Orchinik, 1998; Landys et al., 2006). At the proximate level, the interaction between body condition and corticosterone treatment on time–activity budget could result from interactions between multiple physiological mechanisms (review in Romero, 2004; Landys et al., 2006). First, corticosteroid-binding globulin (CBG) binds corticosterone in the plasma and regulates therefore the active unbound proportion of corticosterone, which is available for the tissues (Breuner and Orchinik, 2002). Moreover, CBG may also enhance binding of corticosterone to the receptor and, therefore, affect the biological effect of increased corticosterone levels (Breuner and Orchinik, 2002). Body condition may have affected CBG levels in our study since Lynn et al. (2003) showed that CBG levels decreased in white-crowned sparrows when individuals were fasting. Second, the levels of intracellular and membrane receptors for corticosterone might also be influenced by nutritional state (i.e., body condition) and may, therefore, play an important role in regulating the target cell sensitivity and consequently the behavioral and physiological responses to increased corticosterone levels (Breuner and Orchinik, 2001; Landys et al., 2004, 2006; Romero, 2004). Few data exist on the effect of body condition on CBG levels and intracellular and membrane receptors for corticosterone in free-living birds (but see Lynn et al., 2003) and our results underline the need to describe these levels in order to fully understand how corticosterone mediates foraging decisions in birds.

At the ultimate level, why only good condition birds did increase their time spent flying/foraging in response to increased corticosterone levels? In seabirds, modulation of a flexible time budget has been interpreted as a buffer against environmental variability (Burger and Piatt, 1990; Hamer et al., 1993). During a food shortage episode, the concomitant elevation of corticosterone levels (Kitaysky et al., 1999, 2001) may then facilitate the modification of this flexible time budget. Having a buffer of time, birds in good condition may then afford to slightly increase their time spent flying/foraging to meet the energy requirements of the brood.

Because Black-legged kittiwakes are relatively long-lived, they should not compromise their survival (Goodman, 1974; Drent and Daan, 1980), we would have predicted parents in poor condition to further increase the time devoted to flying/foraging in order to maintain their body condition when facing poor environmental conditions. However, we found that corticosterone-treated kittiwakes in poor body condition did not significantly modify their time–activity budget. Spending already much time flying/foraging, birds in poor condition may probably be unable to further increase this type of activity without suffering long-term fitness costs: males in poor condition may of course

lose the chicks but also ownership of the nest site. In kittiwakes, the ability of breeders to keep the same nest and the same mate from one breeding season to another appears essential since it positively affects breeding success (Coulson and Thomas, 1985; Naves et al., 2007; Angelier et al., 2007b). Because nest sites can be prospected and appropriated by non-breeding birds (especially in nests where parent spends much time foraging; Cadiou et al., 1994), breeders in poor condition may need to maintain a minimum percentage of their time to guard the nest, explaining therefore at the ultimate level that time spent flying/foraging did not vary in response to increased corticosterone levels.

We found no influence of corticosterone treatment or body condition on the time spent resting on water. In the present study the percentage of time spent on water was very low in all birds, certainly because of the elevated metabolic costs associated with resting on cold water (Humphreys et al., 2007).

Corticosterone, activity budget and resource allocation

Adult kittiwakes are known to lose body mass during chick rearing as a result of intense chick provisioning and reduced opportunity for self-foraging (Moe et al., 2002; Fyhn et al., 2001; Chastel et al., 2005). Our results clearly showed that this mass change greatly differed according to body condition at day 0: over the three-day period of this study, good condition males lost mass whereas poor condition ones gained mass. Interestingly, this effect was reinforced by corticosterone treatment and, on average, corticosterone-treated males gained much more mass than control ones, suggesting a stimulating effect of corticosterone on food intake (review in Dallman et al., 2004; La Fleur, 2006).

However, our study showed that the effect of increased corticosterone levels on time spent flying/foraging differed according to the energetic status of the individual (measured by body condition at day 0): specifically, males in good body condition increased their time spent flying/foraging in response to increased corticosterone levels, whereas males in poor body condition did not. Because corticosterone-treated males in poor body condition gained much more mass than control ones, this result strongly suggests that corticosterone-treated males in poor condition increased the amount of energy allocated to self-maintenance at the expense of brood provisioning rate. In our study, we found no effect of experimentally increased corticosterone levels on breeding success (measured by the probability of losing a chick over the three-day period). Moreover, we were not able to monitor the change in body condition of chicks over the study period. Therefore, it is also possible that the corticosterone treatment increased food acquisition to an extent that both male parents and chicks gained weight. However, this second interpretation is unlikely because elevated corticosterone levels are well-known to suppress reproductive and parental behaviors (review in Wingfield et al., 1998; Wingfield and Sapolsky, 2003). For instance, an experimental increase in corticosterone levels has been reported to reduce brood provisioning (Silverin, 1986) and to stimulate fat accumulation in parent pied flycatchers, *Ficedula hypoleuca* (Wingfield and Silverin, 1986).

On the other hand, corticosterone-implanted males in good condition spent more time flying/foraging but still gained slightly

more mass than controls. Due to increased time spent flying/foraging, corticosterone-implanted males in good body condition probably extracted more resources from the environment than controls. They could, therefore, slightly improve their body condition (this study) while probably maintaining their chick provisioning rates (Kitaysky et al., 2001), although we did not monitor chick growth in the present study. Thus, in case of poor food situation (during which corticosterone levels increase, Kitaysky et al., 1999, 2001; Buck et al., 2007; Angelier et al., 2007a), male kittiwakes, as relatively long-lived birds, probably balance energy allocation between offspring provisioning and self-maintenance according to their own condition.

In our study, all manipulated birds were seen at the nest during and after the study period and no corticosterone-implanted males definitively abandon their chicks and their nest (“leave-it” strategy, Wingfield and Kitaysky, 2002) as it has been observed in passerine species (Silverin, 1986). This result suggests that male kittiwakes probably tried to ride out the stressful factor by improving their body reserves when facing a food shortage (“take-it” strategy, Wingfield and Kitaysky, 2002). However, such an improvement of body reserves seems to be achieved by different behavioral mechanisms depending on parent’s body condition. When birds are in poor body condition, this improvement is probably achieved by a re-allocation of the energy available from brood provisioning to self-maintenance. On the other hand, when birds are in good body condition, this improvement is achieved through increased time spent flying/foraging, probably at the expense of nest attendance (Kitaysky et al., 2001). This “take-it” strategy could be more adaptive than the “leave-it” strategy in high arctic kittiwakes for two reasons. First, because male kittiwakes did not abandon the nest site, they can defend it against prospecting kittiwakes and therefore avoid the fitness costs of losing their nest site (Cadiou et al., 1994). Second, they did not abandon the brood and can potentially resume their parental duties if environmental conditions recover. This could be highly adaptive since high-arctic kittiwakes have a narrow temporal window to breed and cannot lay a second clutch if they lose their chicks.

Although the “take-it” strategy may maximize the fitness of parents when food shortage occurs, food shortage still entails fitness costs for the chicks. First, a decreased provisioning rate negatively affects chick’s growth, cognitive ability and survival (Kitaysky et al., 2000, 2001, 2003, 2006; Nowicki et al., 2002; Buchanan et al., 2003; Pravosudov, 2003, 2005). Second, a decreasing nest attendance incurred by increasing time spent flying/foraging (Kitaysky et al., 2001) certainly reduces the survival of the chicks as they are left alone and may be more vulnerable to predation (Moe et al., 2002). However, we found no influence of body condition and corticosterone treatment on the probability of losing a chick over the study period. Indeed, the study period lasted 3 days and it could be a too short period to find a significant effect of treatment or body condition on the probability of losing a chick.

Conclusion

Corticosterone has been regarded as a mechanistic link between foraging conditions and reproductive decisions and an

increase in corticosterone secretion is thought to facilitate the mobilization of energy stores and to adjust behavior and physiology in ways appropriate to the conditions at hand (Kitaysky et al., 1999, 2001; Wingfield and Kitaysky, 2002; Lanctot et al., 2003; Buck et al., 2007). Our study further showed with mounting evidence a context-dependent effect of corticosterone (Orchinik, 1998; Landys et al., 2006). Specifically, body condition and corticosterone levels can interact to modulate foraging decisions and possibly energy allocation. This finding supports the general view that the physiological state (corticosterone levels: Angelier et al., 2007a, and body reserves: Chaurand and Weimerskirch, 1994; Spencer and Bryant, 2002) can modulate reproductive decisions (McNamara and Houston, 1996). For a better understanding of the interactions between corticosterone physiology, body condition, foraging behavior and resource allocation, future studies should include measurements of the energetic costs of foraging decisions (Shaffer et al., 2003; Jodice et al., 2003) together with fine-scale measurements of foraging movements and foraging success at sea (Weimerskirch et al., 2002, 2005a). Interactions between corticosterone levels and other endocrine mechanisms should also be considered. One such hormone could be prolactin because of its major role in parental behavior (review in Buntin, 1996) and its state-dependent sensitivity to stress (Chastel et al., 2005).

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