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Modulation of prolactin but not corticosterone responses to stress in relation to parental effort in a long-lived bird

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Abstract

We tested the hypothesis that parental effort modulates the magnitude of corticosterone and prolactin responses to stress in a long-lived bird, the Black-legged kittiwake (*Rissa tridactyla*). To do so, we compared corticosterone and prolactin responses to capture/restraint stress between chick-rearing birds and failed breeders (no parental effort). We predicted that (1) the increase in plasma corticosterone levels in response to stress should be lower in chick-rearing birds, (2) the decrease in plasma prolactin levels in response to stress should be lower in chick-rearing birds, and (3) as both sexes care for the chick, there should be no sex difference in the hormonal response to stress. Baseline plasma corticosterone and prolactin levels were higher in chick-rearing birds and were not influenced by body condition. Failed breeders were in better condition than chick-rearing individuals. Corticosterone response to stress was unaffected by parental effort as both chick-rearing and failed birds exhibited a robust corticosterone increase. Prolactin response to stress was however clearly influenced by parental effort: chick-rearing birds showed a modest 9% prolactin decrease whereas in failed birds prolactin concentrations fell by 41%. Body condition did not influence hormonal responses to stress. When facing stressful condition, breeding kittiwakes attenuate their prolactin response to stress while enhancing their secretion of corticosterone. Increasing corticosterone secretion triggers foraging efforts and diminishes nest attendance whereas an attenuation of prolactin response to stress maintains parental behavior. We suggest that this hormonal mechanism facilitates a flexible time-budget that has been interpreted as a buffer against environmental variability.
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Introduction

The general reproductive effort model based on the cost of reproduction (Williams, 1966) predicts the existence of an adaptive trade-off that allows reproducing individuals to allocate resources either to current reproductive episodes or to their own survival (i.e., future reproduction) (Stearns, 1992). The study of hormones can offer great insights into the mechanisms mediating life-history trade-offs (Sinervo and Svensson, 1998). For example, plasma levels of the hormone corticosterone rapidly rise in response to stressful conditions (Wingfield and Farner, 1993), and this can

ultimately lead to a cessation of territorial and reproductive behaviors (Silverin, 1986; Wingfield and Silverin, 1986). This adrenocortical response and its behavioral consequences can be considered as adaptive because it may interrupt the current reproductive episode of an individual and promote its survival and future reproduction during stressful periods (Wingfield et al., 1998).

However, in some ecological situations, individuals downregulate their adrenocortical response. In severe environments such as Arctic areas or deserts where periods of extreme weather are commonly encountered, the timeframe during which offspring can be produced is narrow and the chances of successful renesting after failure are low. In this context, several species show a reduced adrenocortical response during the most critical stages of parental care, thus delaying the expression of life-saving behaviors that

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might otherwise result in reproductive failure ("The short season hypothesis", Holberton and Wingfield, 2003; Meddle et al., 2003; Reneerkens et al., 2002; Silverin et al., 1997; Wingfield et al., 1992, 1995). This facultative reduction of the adrenocortical response may also be linked to parental effort itself as suggested by Wingfield et al. (1995). They hypothesized that the magnitude of the adrenocortical response to stress is a function of the degree of parental care provided, with a lower adrenocortical response expected to be observed in the sex that provides most parental care. Likewise, it has been shown that in marine turtles, females involved in parental effort (egg laying) displayed an almost complete suppression of their cortico-sterone response to stress, contrary to males and non-breeding females (Jessop, 2001). Therefore, a reduction of the adrenocortical response to stress might be considered a hormonal tactic by which individuals maximize their current reproductive effort, even though under certain situations this may entail survival costs ("The parental care hypothesis": Jessop, 2001; O'Reilly and Wingfield, 2001; Wingfield and Sapolsky, 2003; Wingfield et al., 1995).

Prolactin is another hormone that may act on parental effort through its role in the initiation and maintenance of avian parental behavior (Buntin, 1996). Plasma prolactin levels rapidly increase during stress in mammals, and this rise in plasma prolactin levels is often considered part of the classical stress response (De Vlaming, 1979). In birds, the effect of stress on plasma prolactin levels is however less clear: a study of four passerines species revealed no increase in plasma prolactin as a result of injection or restraint, suggesting that unlike mammals, prolactin is not released during capture and handling stress (Manney et al., 1999). On the contrary, there is some indications that in birds plasma prolactin levels may actually decrease during stressful events. The stress of injections, handling, and restraint has been shown to decrease plasma prolactin levels in bantam hens (*Gallus domesticus*), Florida scrub-jays (*Aphelocoma coerulescens*), Semipalmated Sandpippers (*Calidris pusilla*), and Turkey (*Meleagris gallopavo*) (Gratto-Trevor et al., 1991; Manney et al., 1999; Opel and Proudman, 1986; Sharp et al., 1989). During stressful events, a decrease in plasma prolactin levels can be considered adaptive because it may disrupt the current parental effort (via nest desertion) of an individual and promote its survival and future reproduction (Delehanty et al., 1997). Alternatively, as for the adrenocortical response, individuals involved in parental effort could decide to attenuate or even suppress their prolactin response to stress. As a consequence, attenuation of the prolactin response could be considered as a hormonal tactic permitting the maintenance of parental care behaviors and maximizing current reproductive efforts during temporary stressful conditions.

In this paper, we examined corticosterone and prolactin response to capture/restraint stress in relation to parental effort in a long-lived bird, the Black-legged kittiwake (*Rissa*

tridactyla). In this species, the first part of the chick-rearing period appears constraining as adults are faced with the trade-off of investing either in the chick's needs of being regularly fed and brooded or of investing in the necessity of spending enough time at sea to restore their own body reserves and find food for the chick (Fyhn et al., 2001; Moe et al., 2002). According to the "the parental care hypoth-esis", a modulation of the corticosterone and prolactin response to stress would mediate this trade-off (Jessop, 2001; O'Reilly and Wingfield, 2001; Wingfield et al., 1995). To test this hypothesis, we compared the cortico-sterone and prolactin response to capture/restraint stress of two categories of birds: (1) individual birds involved in parental effort (rearing a 8–12-day-old chick) and (2) individual birds not engaged in parental effort (failed birds that lost the eggs or newly hatched chick). To study the endocrine response of the two groups, we used a capture, handling, and restraint stress protocol (e.g., Wingfield, 1994). It was predicted that (1) the magnitude of the increase in plasma corticosterone levels (adrenocortical response) in response to stress would be lower in individuals involved in parental effort, (2) the magnitude of the decrease in plasma prolactin levels in response to stress would be lower in individuals involved in parental effort, and (3) as both sexes brood and provision the chick in kittiwakes, there would be no sex difference in the adrenocortical and prolactin response to capture/restraint stress.

Methods

Study area and birds

Black-legged kittiwakes are colonial, pelagic seabirds that breed on cliffs throughout the northern parts of the Pacific and the Atlantic, including the Barents Sea region up to the Svalbard Archipelago. Our study was conducted between 17 and 23 July 2000 on a colony of Black-legged kittiwakes at Kongsfjorden, Svalbard ($78°54'$ N, $12°13'$ E), 7 km east of Ny-Ålesund. In Svalbard, continuous daylight and an average ambient temperature of $4.5°C$ (Bech et al., 2002) characterize the breeding period (May–September).

We studied kittiwakes in a sub-colony of ca. 60 pairs breeding on cliffs at a height of 5–10 m. Most nests were therefore accessible and birds were captured at their nest with a noose on the end of a 5 m fishing rod. In Svalbard, kittiwakes lay two eggs but rear a single chick (Gabrielsen et al., 1987; Moe et al., 2002). In order to compare hormone response to capture/restraint stress in relation to parental effort, we therefore took blood samples both from adults rearing a 8–12-day-old chick (called thereafter chick-rearing birds, $n = 18$, 11 females and 7 males) and from adults that had lost the eggs (called thereafter failed birds, $n = 10$, 6 females, 4 males). Both chick-rearing and failed birds were captured on their nest, failed attending their nest for several weeks after breeding failure (Cadiou et al., 1994). For failed

breeders, the exact timing of egg loss was not precisely known. Both chick-rearing and failed birds, only one bird was captured per nest and the data obtained with males and females were hence considered independent.

Blood sampling

All birds were bled according to the following standardized technique (Wingfield, 1994): immediately after capture, an initial blood sample (maximum: 300 μl) was collected from the alar vein with a 1 ml heparinized syringe and a 25 gauge needle, and furthers samples (maximum: 100 μl) were taken at 15, 30, and 60 min. To check for possible effect of handling time during initial bleeding on hormone levels, we measured the time elapsed between the capture and the end of the initial blood sampling (minimum: 2 min, maximum: 5 min and 30 s).

After each blood sample, birds were kept in an individual opaque cloth bag. Blood samples were put into ice and centrifuged as soon as possible; plasma (for corticosterone and prolactin assay) and red blood cells (for sexing, Fridolfsson and Ellegren, 1999) were subsequently stored at −20°C. All birds were weighed to the nearest 2 g using a Pesola and their skull length (head + bill) was measured to the nearest 0.5 mm (Moe et al., 2002). Body condition was then expressed as the residual mass from a linear regression relating body mass to skull length ($r^2 = 0.42$, $n = 28$, $P < 0.001$). Defined as such, body condition is calculated as a size-corrected body mass and is expressed in units gram. Birds were dyed on their head and breast to avoid double catching and then released in the colony. All birds returned to their nest 2–20 min after the last blood sample.

Hormone assays

Plasma concentrations of corticosterone were determined by radioimmunoassay at the CEBC as previously described (Lormée et al., 2003). Minimal detectable corticosterone levels were 400 pg/ml. The intra-assay variation was 8.5%. There was no significant relationship between handling time and corticosterone levels measured during the initial bleeding (chick-rearing birds: $r = 0.06$, $P = 0.80$, $n = 18$; failed birds: $r = 0.42$, $P = 0.22$, $n = 10$). Thus, initial blood samples were considered to reflect baseline levels of corticosterone (Wingfield et al., 1982; Kitaysky et al., 1999; Lormée et al., 2003). To check for diel variation, we plotted corticosterone values from the first bleeding against time of the day when the initial sample was collected. No significant relation was found (chick-rearing birds: $r = 0.12$, $P = 0.61$, $n = 18$; failed birds: $r = 0.29$, $P = 0.41$, $n = 10$).

Plasma concentrations of prolactin were determined by and heterologous radioimmunoassay (RIA) at the CEBC (Cherel et al., 1994). Pooled plasma samples of kittiwakes produced a dose response curve that paralleled chicken prolactin standard curves ("AFP 4444B", source: Dr. Parlow, N.H.P.P. Harbor-UCLA Medical Center, Torrance,

California, USA, Fig. 1). Parallelism between the kittiwake and chicken curve indicates that the concentration-dependent binding dynamics of the kittiwake prolactin with the antibody is similar to that of the chicken prolactin with the antibody and that this RIA can be used to assess relative levels of plasma prolactin in the Black-legged kittiwake. Only one assay was performed, the intra-assay coefficient of variation being 7.3% ($n = 4$ duplicates). There was no significant relationship between handling time and plasma prolactin levels measured during the initial bleeding (chick-rearing birds: $r = 0.03$, $P = 0.91$, $n = 18$; failed birds: $r = 0.24$, $P = 0.51$, $n = 10$). Thus, initial blood samples were considered to reflect baseline plasma levels of prolactin. To check for diel variation, we plotted plasma prolactin values from the first bleeding against time of the day when the initial sample was collected. No significant relation was found (chick-rearing birds: $r = −0.06$, $P = 0.82$, $n = 18$; failed birds: $r = −0.46$, $P = 0.18$, $n = 10$).

Statistics

We first analyzed the baseline plasma corticosterone and prolactin data with 2 factor ANOVAs with sex and parental effort (adults rearing chicks or failed breeder) as factors. We examined the corticosterone and prolactin responses to capture/restraint stress with two-factor repeated measures ANCOVAs with sex and parental effort as the factors and body condition as the covariate. Relationships between baseline- and stress-induced corticosterone and prolactin levels (measured after 60 min of capture and restraint) were examined using Pearson correlations. In the statistical analysis, initial data were tested for assumptions required by a statistical test according to Sokal and Rohlf (1981). If these data violated assumptions, they were $\log_{10}$ transformed and examined again. Statistical analyses were
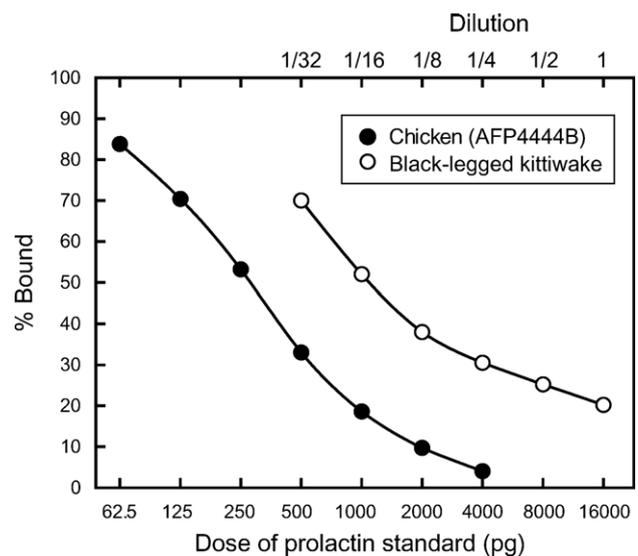

Fig. 1. Dose response curve for prolactin of chicken and Black-legged kittiwakes. Prolactin standard is expressed in pg/tube.

performed using SYSTAT 7.0 (Wilkinson, 1997). Data are presented as means $\pm$ 1 standard error of means (SEM).

Results

Baseline hormone levels and body condition

Baseline corticosterone levels (range: 1.94–20.35 ng/ml for chick-rearing birds; 1.39–10.51 ng/ml for failed birds) did not differ between sexes. On the other hand, parental effort had a significant effect on baseline corticosterone levels ($F(1,24) = 7.29$, $P = 0.012$); chick-rearing birds had higher corticosterone titers than failed breeders (Fig. 2).
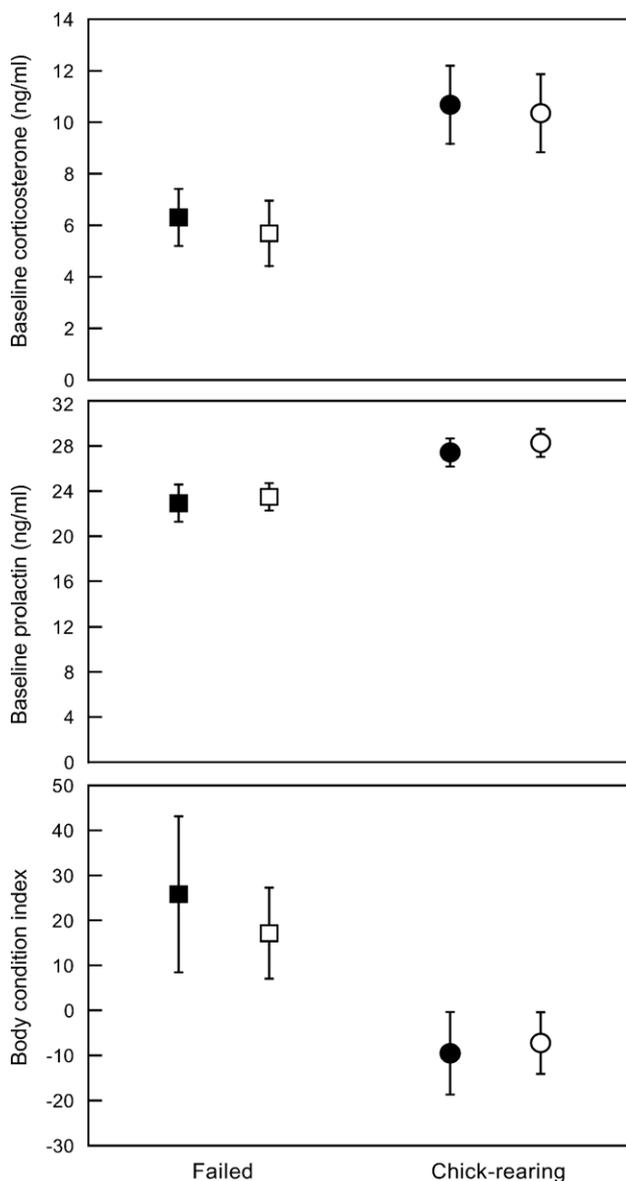

Fig. 2. Baseline corticosterone and prolactin levels and body condition index of failed (squares, 6 females, 4 males) and chick-rearing (dots, 11 females and 7 males) Black-legged kittiwakes. Open symbols denote females and filled ones males. Data are expressed as mean $\pm$ SEM.

There was no between-factor interaction (sex $\times$ parental effort).

Baseline plasma prolactin levels (range: 20.59–33.10 ng/ml for chick-rearing birds; 19.31–27.21 for failed birds) did not differ between sexes. On the other hand, parental effort had a significant effect on baseline plasma prolactin levels ($F(2,24) = 19.88$, $P < 0.001$); chick-rearing birds had slightly but significantly higher plasma prolactin titers than failed birds (Fig. 2). There was no between-factor interaction (sex $\times$ parental effort). Baseline plasma prolactin levels were not correlated with baseline corticosterone levels in chick-rearing and failed birds.

Body condition did not differ between males and females, but failed breeders were significantly in better condition than adults rearing a chick ($F(2,24) = 8.57$, $P = 0.007$, Fig. 2). There was no between-factor interaction (sex $\times$ parental effort). Body condition was neither correlated with baseline corticosterone levels nor with baseline plasma prolactin levels in chick-rearing and failed birds.

Hormones response to stress

Birds responded to acute stress by a rapid and significant response of the adrenocortical system to the stress of being captured and held (time after capture, $F(3,69) = 110.97$, $P < 0.0001$, Fig. 3). This acute stress response was unaffected by parental effort or by body condition. On the other hand, males showed a slightly but significantly stronger response to stress than females (sex, $F(1,23) = 4.75$, $P = 0.04$; sex $\times$ time after capture, $F(3,69) = 2.90$, $P = 0.044$, Fig. 4). Maximum corticosterone levels were significantly higher in males ($F(1,26) = 5.030$, $P = 0.034$) and this difference was already apparent 15 min after capture ($F(1,26) = 5.22$, $P = 0.031$).

Birds responded to acute stress of being captured and held by a significant decrease of plasma prolactin titers (time after capture, $F(3,63) = 14.65$, $P < 0.0001$, Fig. 3). This prolactin response to stress was slightly although not significantly more pronounced in males (Fig. 4; sex, $F(1,21) = 3.95$, $P = 0.06$), but was not influenced by body condition. The magnitude of the prolactin response to stress was however clearly influenced by parental effort (parental effort, $F(1,21) = 35.82$, $P < 0.001$; parental effort $\times$ time after capture, $F(3,63) = 2.86$, $P = 0.04$, Fig. 4). In chick-rearing birds, there was a slight but significant increase in plasma prolactin levels 15 min after capture ($F(1,15) = 4.53$, $P = 0.05$). Thereafter, plasma prolactin levels slightly declined, resulting in a modest 9% decrease in prolactin levels, after 60 min of capture and restraint. In failed birds, the effect of stress was much more pronounced and prolactin levels decreased by 41% after 60 min of capture and restraint (Fig. 3). In failed birds, there was a significant and negative relationship between stress-induced corticosterone levels and stress-induced prolactin levels ($r = -0.71$, $P = 0.02$, $n = 10$, Fig. 4). This was not observed in chick-rearing birds (Fig. 4).

Discussion

Baseline hormone levels and body condition in relation to parental effort

Baseline corticosterone levels were significantly higher in kittiwakes engaged in parental effort (chick-rearing) than in failed breeders (no parental effort). Kittiwakes loose a significant part of their body mass during the chick-rearing period (Golet and Irons, 1999; Kitaysky et al., 1999; Moe et al., 2002), and a rise in baseline corticosterone levels often mirrors a worsening of adult body condition (Kitaysky et al., 1999). In our study, there was however no significant relationship between baseline corticosterone levels and body condition at the individual level, suggesting that both failed breeders and chick-rearing birds did not have depleted protein resources (Le Ninan et al., 1988). Corticosterone is known to trigger foraging efforts (Astheimer et al., 1992; Wingfield and Silverin, 1986; Wingfield et al., 1998). The higher baseline corticosterone levels found in chick-rearing kittiwakes reflect the increased likelihood of higher foraging activity in parents that search for food both for the chicks and themselves (Kitaysky et al., 2001).
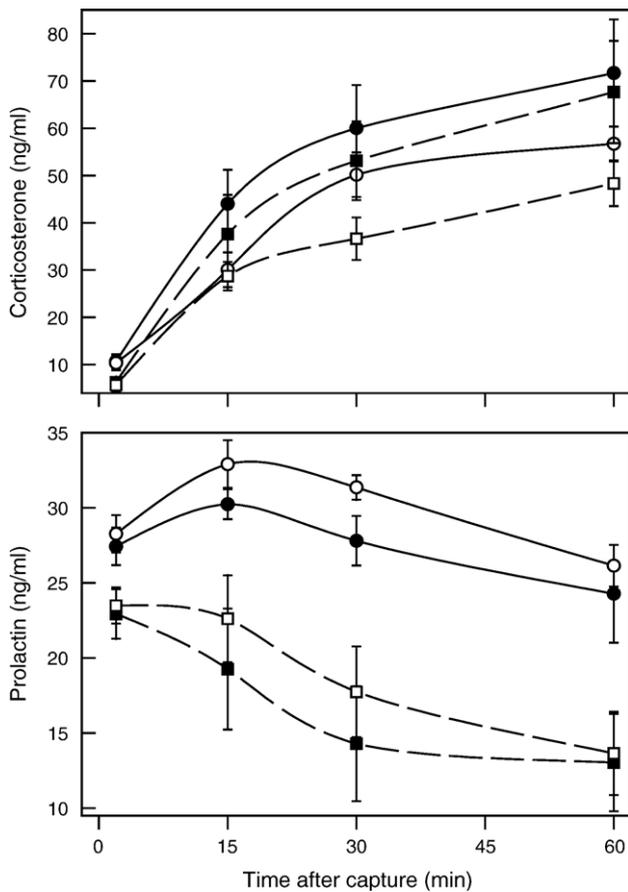

Fig. 3. Corticosterone and prolactin response to capture/handling stress of failed (squares, 6 females, 4 males) and chick-rearing (dots, 11 females and 7 males) Black-legged kittiwakes. Open symbols denote females and filled ones males. Data are expressed as mean ± SEM.
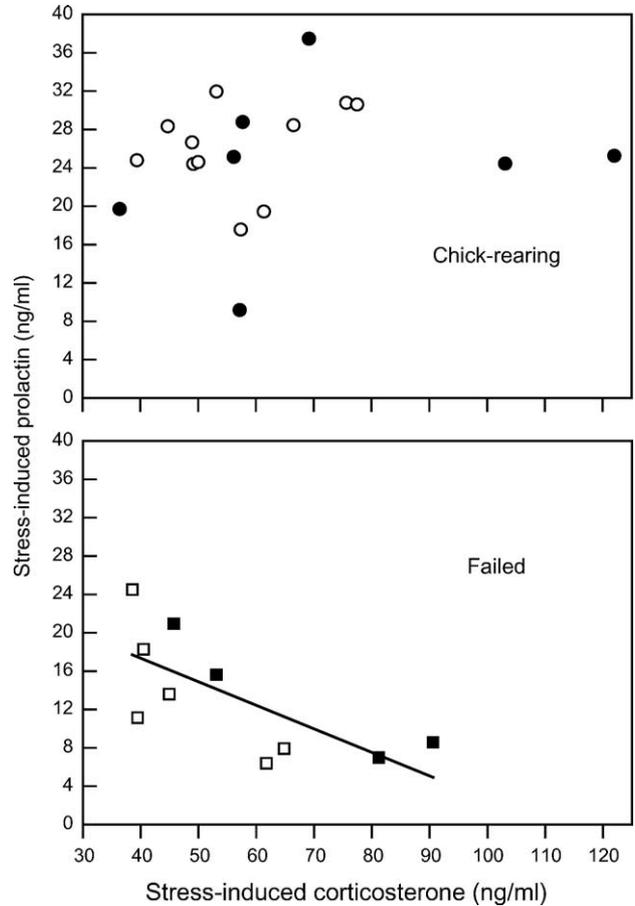

Fig. 4. Relationship between stress-induced corticosterone levels and capture/handling stress-induced prolactin levels (measured after 60 min of capture and restraint) in failed (squares, 6 females, 4 males) and chick-rearing (dots, 11 females and 7 males) Black-legged kittiwakes. Open symbols denote females and filled ones males.

In our study, plasma prolactin levels of chick-rearing birds were significantly higher than those of failed birds. This probably mirrors the parental commitment of chick-rearing kittiwakes which have to brood their youngs almost continuously during the first part of the chick-rearing period to protect them from cold or predator (Fyhn et al., 2001; Moe et al., 2002), a behavior that requires elevated plasma prolactin levels (Lormée et al., 2000; Sharp et al., 1988). Furthermore, elevated prolactin levels are known to trigger hyperphagia in birds (Koch et al., 2002). The higher plasma prolactin levels found in chick-rearing birds probably reflect their higher provisioning effort as they have to collect food both for the chicks and themselves. Despite being no longer engaged in parental effort, failed breeders exhibited plasma prolactin levels that were only 15% lower than levels observed in chick-rearing birds. Plasma prolactin levels in failed breeders were two times higher than levels observed in immature kittiwakes (12 ng/ml, $n = 3$, Chastel et al., unpublished data). Thus, as penguins (Lormée et al., 1999; Vleck et al., 2000), reproductive failure in kittiwakes does not seem to result in the same abrupt cessation of prolactin secretion that was found in other seabird species (Hall,

1986; Chastel and Lormée, 2002). Kittiwakes attend either their own nest or another nest site (squatting behavior) for several weeks after the breeding failure has occurred (Cadiou et al., 1994). It is therefore possible that such a behavior requires the maintenance of elevated plasma prolactin levels.

Hormones response to stress in relation to parental effort

Contrary to our first prediction, the magnitude of the adrenocortical response to capture/restraint stress was unaffected by parental effort as kittiwakes engaged in chick-rearing activities showed a robust 6-fold increase in corticosterone levels as did failed breeders. This result is in agreement with those found in another seabird, the Blue footed booby (*Sula nebouxii*), and which show that corticosterone response to stress was similar in breeding and non-breeding individuals (Wingfield et al., 1999). Our results might be explained by the life-history traits of the Black-legged kittiwake, which is a long-lived bird with a deferred maturity (see Golet et al., 1998 for a review). For species with a potentially long life span, the parent's lifetime reproductive interest should be to minimize the risk of mortality due to breeding to a greater extend than short-lived species (Weimerskirch, 1992). Accordingly, long-lived birds should maintain a robust stress response during breeding to ensure their post-breeding survival and the possibilities of successful future reproduction (Kitaysky et al., 1999; Wingfield et al., 1995). This is supported by data showing that in seabirds, the sensitivity of the hypothalamo–pituitary–adrenal axis increases as parental investment increases. In kittiwakes breeding in the north Pacific, the magnitude of the adrenocortical response rises steadily through the breeding cycle and peaks during the rearing of large chicks (Kitaysky et al., 1999), which corresponds to the period when parents are working the most intensely (Fyhn et al., 2001) and are in poorest condition (Kitaysky et al., 1999; Moe et al., 2002). Similarly, the strength of the adrenocortical response to handling and restraint increased throughout incubation in the Magellanic penguin (*Spheniscus magellanicus*) (Hood et al., 1998).

Male kittiwakes showed a slightly but significantly higher adrenocortical response to stress than females, independently of parental effort. In the Black-legged kittiwake, male failed breeders are more prone to squat on nests containing chicks than females (Cadiou et al., 1994) and they are also more involved in the defense of their nest against squatters (Jodice et al., 2002). The slightly more pronounced sensitivity of males to stress might be related either to the stress of challenging nest site holders or to the stress of defending the nest site against prospecting birds. This interpretation is supported by observations made on Nazca boobies (*Sula granti*) where non-breeding birds visiting unattended chicks showed an elevation of corticosterone levels (Tarlow et al., 2003).

The data presented here bring new evidence that unlike mammals, for which prolactin is released during stress (De Vlaming, 1979), birds show a decrease in circulating prolactin when exposed to acute stress (Gratto-Trevor et al., 1991; Manney et al., 1999; Sharp et al., 1989). This corroborates the findings of Delehanty et al. (1997) who showed that in a year of severe environmental stress (drought and extremely high temperatures), incubating male Wilson's phalaropes (*Phalaropus tricolor*) had lower plasma prolactin levels than in other years.

In accordance with our second prediction, the magnitude of this decrease was clearly influenced by parental effort, since kittiwakes rearing a chick only showed a modest decrease in plasma prolactin levels whereas in birds with no parental duties (failed breeders), plasma prolactin concentrations fall to levels observed in immature kittiwakes (12 ng/ml, $N = 3$, Chastel et al., unpublished data). Therefore, as observed for the adrenocortical response, individuals can decide to attenuate their prolactin response to stress to maintain investment in parental care and maximize their current reproductive effort during temporary stressful conditions. In kittiwakes rearing chicks, plasma levels of prolactin even slightly increased during the first 15 min of restraint, a pattern that resembles those found in mammals (De Vlaming, 1979).

When facing temporary stressful conditions, chick-rearing kittiwakes attenuate their prolactin response to stress while enhancing their secretion of corticosterone. Because high corticosterone levels are known to activate emergency behaviors associated with the ending of the current reproductive effort (Wingfield et al., 1998), our first interpretation was that the Black-legged kittiwake, as a long-lived bird, should enhance the adrenocortical response during stressful conditions to avoid any risk for post-breeding survival and future reproductive opportunities (Kitaysky et al., 1999). According to this interpretation, plasma prolactin titers should return to basal levels and parental care should cease. The relative insensitivity to stress of prolactin secretion in chick-rearing birds may provide another explanation. As pelagic seabirds, Black-legged kittiwakes exploit distant food resources (Daunt et al., 2002) and during stressful environmental conditions, such as temporary food shortage, an enhancement of corticosterone secretion would trigger foraging efforts in parents (Kitaysky et al., 2001). As a consequence, nest attendance will diminish, but due to a concomitant attenuation of the prolactin response to stress parental behavior would be maintained. In the Black-legged kittiwake, nest attendance during early chick rearing is normally 100% but can drop sharply during years of food shortage (Fyhn et al., 2001; Hamer et al., 1993; Roberts and Hatch, 1993). We suggest that this hormonal mechanism facilitates a flexible time-budget that has been interpreted as a buffer against environmental variability (Hamer et al., 1993).

On the other hand, in failed breeders, plasma prolactin levels return to basal ones as a result of capture and restraint. The standardized capture/restraint stress protocol (Wing-

field, 1994) requires repeated blood sampling and therefore loss in blood volume (a maximum of 600 μl in our study). One way in which an individual can retain/restore blood is to dilute the blood via interstitial fluid from surrounding tissues and this may result in hemodilution (Sturkie, 1986) and lower measured plasma prolactin. One may conclude that failed breeders did not reduce their prolactin output, but rather did not increased their prolactin output in response to capture/restraint, contrary to chick-rearing birds. There was however a significant negative relationship between stress-induced corticosterone levels and stress-induced prolactin levels in failed birds. Although mechanisms linking cortico-sterone release and decrease in plasma prolactin levels are unclear, this correlation suggests that the more failed breeders are stressed, the more their plasma prolactin levels decrease.

Being disengaged from all parental duties, failed breeders probably have no direct fitness interests in keeping elevated plasma prolactin levels during stressful situations. The stress-induced return to basal plasma prolactin levels could lead to the desertion of the nest site and possibly of the breeding colony, whereas the concomitant increase in corticosterone levels could trigger locomotor activities and dispersal (Astheimer et al., 1992; Belthoff and Dufty, 1998). Breeding dispersal and prospection of other colonies after failure is common in kittiwakes (Cadiou et al., 1994; Danchin et al., 1998) and could be related to hormonal changes occurring during stressful events.

In conclusion, prolactin but not corticosterone responses to stress differed in relation to parental effort in the Black-legged kittiwake. Because birds engaged in parental effort were able to attenuate their prolactin response to stress, prolactin may show potential for mediating some life-history trade-offs as does the extensively studied corticosterone (Wingfield and Sapolsky, 2003). In our study, both the adrenocortical and the prolactin responses to capture/restraint stress were independent of body condition, whereas Kitaysky et al. (1999) reported that for kittiwakes breeding in the Pacific, stress-induced corticosterone levels were negatively correlated with body condition. Pelagic seabirds forage far from their breeding site and year-to-year variations in food availability affect their body reserves. Because prolactin secretion in some pelagic seabird is dependant on threshold levels of body mass (Cherel et al., 1994), future studies should focus on prolactin response to stress in situations of contrasted food supply. At the moment, few data exist on the effects of stress on avian prolactin secretion. Our results underline the need to describe the prolactin response to stress in birds in relation to different lifestyles and life-history traits.

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