



SHORT COMMUNICATIONS

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CORTICOSTERONE LEVELS IN RELATION TO CHANGE OF MATE IN BLACK-LEGGED KITTIWAKES

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Abstract. In birds, changing mates generally results in decreased breeding success. Although costs and benefits of pair break-up have been well studied, endocrine mechanisms associated with mate change are poorly known. We measured baseline and stress-induced corticosterone levels in relation to mate change in Black-legged Kittiwakes (*Rissa tridactyla*). Baseline corticosterone levels were higher in kittiwakes breeding with a new mate than in kittiwakes that did not change mate. Stress-induced corticosterone levels were not influenced by change of mate. Elevated baseline corticosterone levels in birds breeding with a new mate could result from the social stress associated with pair break-up or mirror a higher energetic demand resulting from a lack of coordination between new pair members. Our results emphasize the usefulness of corticosterone levels in elucidating the effects of mate change on the energetic demands of reproduction in free-living birds.

Key words: Black-legged Kittiwake, corticosterone, mate change, *Rissa tridactyla*, seabird.

Concentración de Corticosterona en Relación con los Cambios de Pareja en *Rissa tridactyla*

Resumen. Los cambios de pareja generalmente inducen una disminución del éxito reproductivo en las aves. Aunque los costos y beneficios de la ruptura de pareja han sido bien estudiados, los mecanismos endocrinos asociados con el cambio de pareja permanecen poco conocidos. En este estudio se midieron las concentraciones de base e inducidas por estrés de la corticosterona en relación con el cambio de pareja en *Rissa tridactyla*. La concentra-

ción basal de corticosterona de los individuos que formaron una nueva pareja fue superior a la de aquellos que mantuvieron la misma pareja del año precedente. La concentración de corticosterona luego de una inducción de estrés no estuvo influenciada por el cambio de pareja. Una elevada concentración de corticosterona en los individuos con nueva pareja podría reflejar el estrés social asociado con la ruptura de la pareja o indicar una fuerte demanda energética inducida por la falta de coordinación entre los miembros de la nueva pareja. Nuestros resultados destacan la importancia de los niveles de concentración de corticosterona para dilucidar las consecuencias del cambio de pareja en las demandas energéticas de la reproducción en las aves que viven en libertad.

In monogamous birds, breeding success is the result of the joint effort of both reproductive partners in incubation duties, brood defense, and provisioning of offspring. Repeated breeding attempts with the same partner could therefore provide important benefits by improving coordination of breeding activities (Choudhury 1995, Ens et al. 1996, Cezilly and Nager 1996). Mortality or dispersal of one member of the pair (Rowley 1983), asynchronous arrivals at the breeding site (González-Solis et al. 1999, Gunnarsson et al. 2004), or dissolution of pair bonds (Choudhury 1995, Ens et al. 1996) may result in new pairings between breeding seasons. Individual breeding success generally decreases in response to mate switches (Coulson 1966, 1972, Clutton-Brock 1988, Black 1996) because new pairs pay the costs of delayed laying resulting from prolonged pair formation and a lack of coordination in parental duties between pair members (Choudhury 1995, Ens et al. 1996).

Although the costs and benefits of mate change have been well studied (Black 1996, McNamara and Forslund 1996), the endocrine changes associated with pair break-up are poorly known, especially in birds (Remage-Healey et al. 2003). Several studies have shown that the presence of a known partner can

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reduce glucocorticosteroid secretion in captive mammals facing a novel environment (reviewed by DeVries 2002, Hennessy et al. 2006). Moreover, an excellent experimental study showed that pair separation and reunion, respectively, enhanced and reduced adrenocortical activity in captive Zebra Finches (*Taeniopygia guttata*; Remage-Healey et al. 2003). To our knowledge, however, no data have been reported on the influence of pair break-up on glucocorticosteroid levels in free-living animals.

Corticosterone, the primary glucocorticosteroid in birds, plays some role in the coping mechanisms associated with the daily and seasonal demands of the predictable life-history cycle (Romero 2002, Landys et al. 2006). This hormone is suspected to facilitate foraging activity, food intake behavior (Astheimer et al. 1992, Landys et al. 2006, Angelier, Shaffer et al. 2007) and mobilization of stored energy resources (Gray et al. 1990, Sapolsky et al. 2000). For instance, corticosterone secretion increases during reproduction and these moderately above-baseline corticosterone levels are positively correlated with energetic demands of reproduction (Romero 2002, Love et al. 2004, Landys et al. 2006). Moreover, baseline levels of corticosterone increase slightly in response to environmental constraints such as decreased food availability (Kitaysky et al. 1999, Angelier, Shaffer et al. 2007), fasting (Cherel et al. 1988, Lynn et al. 2003), and poor body condition (Marra and Holberton 1998, Kitaysky et al. 1999, Kitaysky, Kitaikaia et al. 2001, Love et al. 2005). Baseline corticosterone levels could therefore provide some information on the energetic demands of reproduction (Love et al. 2004, Landys et al. 2006) and the ability of individuals to cope with environmental constraints (Kitaysky et al. 1999).

Baseline and stress-induced concentrations of corticosterone have completely different physiological and behavioral effects because they act through different receptors (Romero 2004). Unpredictable stressors activate the hypothalamo-pituitary-adrenal axis, resulting in marked elevation of plasma corticosterone levels well above baseline levels ("the stress response"; Selye 1956). Stress-related corticosterone levels promote an emergency life history stage and trigger behavioral and physiological processes that enhance survival by suppressing costly breeding activities such as parental care (Silverin 1986, Wingfield et al. 1998). Because elevated corticosterone levels consequently are beneficial to the survival of parents but detrimental to their reproductive success, the extent to which the stress response is modulated by breeding individuals could mirror their breeding investment when they are facing unpredictable stressors. Stress-induced levels of corticosterone resulting from a standardized capture and restraint protocol have therefore been suggested as an indicator of breeding investment in birds (Wingfield et al. 1995, O'Reilly and Wingfield 2001, Holberton and Wingfield 2003, Wilson and Holberton 2004). Focusing on stress-induced corticosterone levels is thus relevant to understanding how parents modulate their breeding investment in response to unpredictable stressors which can threaten their survival.

Here, we report the first data on baseline and stress-induced corticosterone levels in relation to mate change in a free-living bird, the Black-legged Kittiwake (*Rissa tridactyla*). Kittiwakes are a relevant biological model to study the influence of mate change on corticosterone levels because they are long-lived, have a high rate of pair fidelity, and experience higher breeding success with a known partner (Coulson 1966, 1972).

METHODS

We studied Black-legged Kittiwakes in a colony at Kongsfjorden, Svalbard, Norway (78°54'N, 12°13'E) during the breeding seasons of 2003–2005. Birds were individually marked with white PVC plastic bands engraved with a three-digit code, allowing identification of breeding pairs at the beginning of each breeding season. Several observations were made throughout each breeding season to check that pairs were correctly identified. We were therefore able to establish whether a bird bred with the same mate as in the previous year or with a new mate in 2004 and 2005 ("pair status" variable, 2004: $n = 17$ pairs, 2005: $n = 15$ pairs). Because not all nests were monitored in 2003, we were unable to test whether all males monitored in 2005 were with the same long-term mate from 2003. Breeding success (number of chicks fledged) of each nest was determined at the end of each breeding season.

Birds were captured at their nests with a noose on the end of a 5 m fishing rod during the mid-chick-rearing period (14 July–7 August). All birds captured in 2004 ($n = 26$) were bled according to the standardized technique of Wingfield (1994): immediately after capture, an initial blood sample (maximum amount of blood: 300 μ l) was collected from the alar vein into a heparinized tube to measure baseline corticosterone levels, and a second sample (maximum amount of blood: 100 μ l) was taken 30 min after capture to measure stress-induced corticosterone levels. In 2005, blood was sampled only once immediately after capture ($n = 9$). Thus, we were able to determine both baseline and stress-induced corticosterone levels in 2004, but only baseline corticosterone levels in 2005. All initial blood samples were collected within 5 min of capture (mean time: 3 min). Because there was no significant relationship between handling time and measured corticosterone levels in the first sample in both years ($P > 0.15$), initial blood samples were considered to reflect baseline levels of corticosterone (Wingfield et al. 1982).

Plasma (for corticosterone assay) and red blood cells (for sexing) were stored separately at -20°C . We weighed all birds to the nearest 2 g using a Pesola spring scale and measured skull length (head + bill) to the nearest 0.5 mm (Moe et al. 2002). As male and female kittiwakes differ in size, body condition was calculated separately for each sex. Body condition was expressed as the residual mass from a linear regression relating body mass to skull length as detailed in Chastel et al. (2005). The sex of each bird was determined with molecular methods as described in Weimerskirch et al. (2005). Plasma concentrations of corticosterone were determined by radioimmuno-

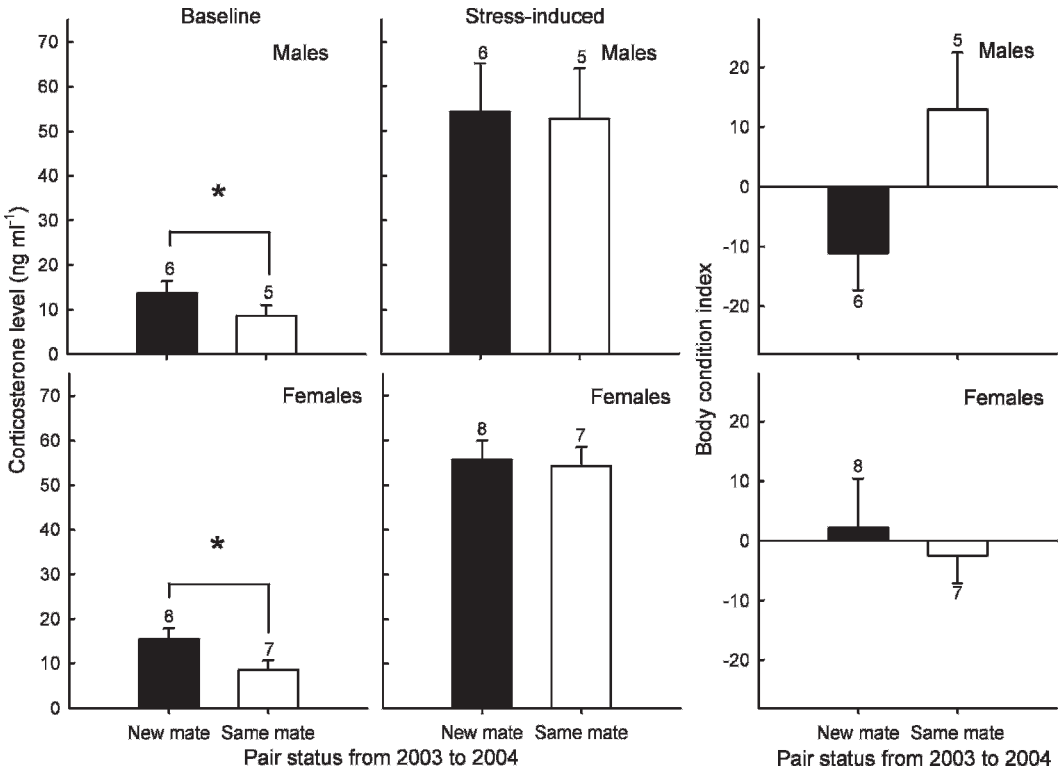


FIGURE 1. Influence of pair status (new mate or same mate as in the previous year) on baseline and stress-induced corticosterone levels (ng ml^{-1}) and body condition of male and female Black-legged Kittiwakes captured and sampled during the chick-rearing period of 2004 (black bars: new mate in 2004; white bars: same mate in 2003 and 2004). Black-legged Kittiwakes that changed mates from the 2003 to 2004 breeding seasons had significantly higher baseline corticosterone levels than kittiwakes that remained with the same mate between years. In contrast, stress-induced corticosterone levels were unaffected by mate change. Body condition was not significantly affected by mate change. Body condition was expressed as the residual mass from a linear regression relating body mass to skull length following Chastel et al. (2005). An asterisk indicates a significant effect of pair status on corticosterone levels ($P < 0.05$). Error bars indicate SE.

assay following Lormée et al. (2003). All samples were run in one assay and the intra-assay coefficient of variation was 9.1%.

STATISTICAL ANALYSES

We used a chi-squared test to test the influence of pair status on breeding success in each year. Because we sometimes sampled both individuals of a breeding pair, female and male data were not independent. Thus, we analyzed data from females and males separately. First, we tested for an effect of pair status on body condition by using ANOVA with pair status as the factor. Second, we tested for an effect of pair status and body condition on baseline corticosterone level by using GLMs with pair status as the factor and body condition as the covariate. In addition, we used Kruskal-Wallis tests to examine whether baseline corticosterone levels varied between birds that bred successfully and birds that failed to fledge chicks. Third, we examined the influence of pair status and body condition on: (1) corticosterone

response to capture-restraint stress by using repeated measures GLMs with pair status as the factor and body condition as the covariate; and (2) stress-induced levels of corticosterone by using GLMs with pair status as the factor and body condition as the covariate. Finally, we examined how baseline corticosterone levels varied from 2004 to 2005 in relation to pair status by using a repeated ANOVA with pair status as the factor. All analyses were performed using SAS version 8.02 (SAS Institute 1999).

RESULTS

Of the 26 birds sampled in 2004 (11 males, 15 females), 14 changed mates from 2003 to 2004 (six males, eight females). Among the nine birds sampled in 2005 (all males), two changed mates from 2004 to 2005. Body condition was not significantly lower in kittiwakes breeding with a new mate in 2004 or 2005 (ANOVAs, 2004, males: $F_{1,9} = 4.6$, $P = 0.06$, females: $F_{1,13} = 0.2$, $P = 0.64$; 2005, males: $F_{1,7} = 0.1$, $P = 0.83$, females: no data; Fig. 1). Birds

TABLE 1. Relationship between pair status (new mate or same mate as in the previous year) and breeding success in Black-legged Kittiwakes (*Rissa tridactyla*), 2003–2005. Data are expressed as mean ± SE (*n*), with *n* = number of pairs.

| Year | Breeding success (number of fledglings) | | χ^2 (df) | <i>P</i> | Year | Breeding success (number of fledglings) | | χ^2 (df) | <i>P</i> |
|------|--|---------------------|---------------|----------|------|--|---------------------|---------------|----------|
| | Same mate in 2003 and 2004 | New mate in 2004 | | | | Same mate in 2004 and 2005 | New mate in 2005 | | |
| 2003 | 0.3 ± 0.2 (7) | 0.2 ± 0.1 (10) | 1.1 (1) | 0.28 | 2004 | 1.3 ± 0.2 (7) | 0.9 ± 0.2 (8) | 3.0 (2) | 0.22 |
| 2004 | 1.4 ± 0.2 (7) | 0.8 ± 0.2 (10) | 6.2 (2) | 0.04 | 2005 | 1.6 ± 0.3 (7) | 1.3 ± 0.3 (8) | 3.6 (2) | 0.16 |

breeding with a new mate in 2004 had lower breeding success than birds breeding with the same mate in 2003 and 2004, whereas breeding success was similar between these two groups in 2003 (Table 1). Pair status did not influence breeding success in 2005 (Table 1).

In 2004, baseline corticosterone levels were higher (6 ng ml⁻¹ on average) in females and males breeding with a new mate and were slightly correlated with body condition (GLM, females: pair status, $F_{1,12} = 7.0$, $P = 0.02$, body condition: $F_{1,12} = 4.6$, $P = 0.05$, $r^2 = 0.46$; males: pair status, $F_{1,8} = 7.7$, $P = 0.02$, body condition: $F_{1,8} = 6.1$, $P = 0.04$, $r^2 = 0.52$; Fig. 1). In 2004, baseline corticosterone levels of males that lost their broods were elevated compared to those of males that fledged chicks (Kruskal-Wallis test, $n = 11$, $U = 18.0$, $P = 0.03$). This difference was not found for females (Kruskal-Wallis test, $n = 15$, $U = 12.0$, $P = 0.86$). In 2005, baseline corticosterone levels were higher in males breeding with a new mate but were not influenced by body condition (GLM, pair status: $F_{1,6} = 53.5$, $P < 0.01$; body condition: $F_{1,6} = 1.0$, $P = 0.34$, $r^2 = 0.90$). In 2005, only one sampled male failed to fledge chicks. Kittiwakes responded to capture-restraint stress with a significant increase in corticosterone secretion (repeated GLM, $P < 0.01$ in both sexes). This increase was not affected by pair status or body condition (repeated GLM, males and females: pair status, $P > 0.30$; body condition, $P > 0.40$). Stress-induced corticosterone levels also were not influenced by pair status or body condition (GLM, males and females: pair status, $P > 0.70$, body condition, $P > 0.20$; Fig. 1).

Although baseline corticosterone levels measured during the chick-rearing period did not vary from 2004 to 2005 (year of sampling, $F_{1,7} = 1.4$, $P = 0.27$), variation in baseline corticosterone levels from 2004 to 2005 was strongly influenced by pair status (pair status × year of sampling: $F_{1,7} = 26.8$, $P < 0.01$). Baseline corticosterone levels were lower in 2005 than in 2004 among birds breeding with the same mate in 2004 and 2005, whereas baseline corticosterone levels were higher in 2005 than in 2004 among the two birds breeding with a new mate in 2005 (Fig. 2).

DISCUSSION

In our study, many Black-legged Kittiwake pairs split up between the 2003 and 2004 breeding seasons, whereas most pairs were maintained from 2004 to 2005. In Kongsfjorden, breeding success was much

better in 2004 than in 2003 because of greater food availability and food quality in 2004 (BM et al., unpubl. data). Because breeding failure can induce the decision to change mate, the low breeding success of 2003 could explain the large number of new pairs in 2004 (Coulson 1966, 1972, Choudhury 1995). Moreover, poor environmental conditions in 2003 could have resulted in higher mortality rates in kittiwakes in the subsequent year, resulting in the necessity of finding a replacement partner for many birds in 2004.

We found a strong effect of pair status on baseline corticosterone levels and breeding success. By monitoring breeding success between 2003 and 2005, we were able to confirm that breeding with a new mate can negatively influence breeding success in kittiwakes as previously suggested by Coulson (1966, 1972). Moreover, we obtained blood samples from nine males in both 2004 and 2005, allowing us to observe changes in corticosterone secretion in relation to mate change from one breeding season to

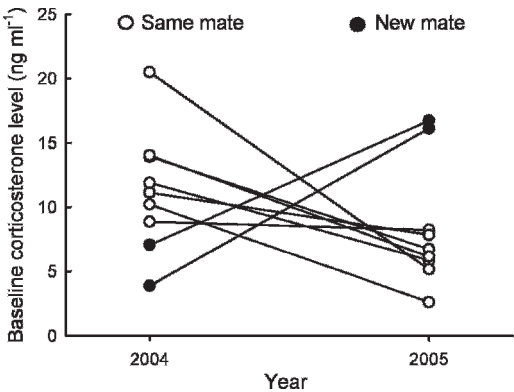


FIGURE 2. Influence of pair status on variation in baseline corticosterone levels (ng ml⁻¹) from 2004 to 2005 in male Black-legged Kittiwakes captured and sampled during the chick-rearing period (black dots: new mate in 2005, white dots: same mate in 2004 and 2005). Baseline corticosterone levels of Black-legged Kittiwakes that changed mates between the 2004 and 2005 breeding seasons were higher in the 2005 breeding season with a new mate, whereas corticosterone levels were lower in 2005 for kittiwakes that remained with the same mate in both years.

the next. Baseline corticosterone levels of these nine males were lower in 2005 than in 2004 among birds breeding with the same mate in both years, whereas they were higher among birds breeding with a new mate in 2005, confirming that experience with a mate influenced corticosterone secretion.

High baseline corticosterone levels among birds breeding with a new mate did not result from poor body condition because we found no significant relationship between pair status and individual body condition. Mammals increase blood cortisol levels in response to separation from a mate or established partner (reviewed by DeVries 2002, Hennessy et al. 2006), thus social stress associated with pair break-up may be the functional cause of elevated corticosterone levels in kittiwakes breeding with a new mate. In support of this hypothesis, temporary mate separation resulted in increased corticosterone secretion in Zebra Finches (*Taeniopygia guttata*). The corticosterone levels of finches returned to baseline levels upon reunion with the pair mate but not upon pairing with a new partner (Remage-Healey et al. 2003). Thus, high corticosterone levels among birds breeding with a new mate may reflect a cognitive state of anxiety, which might result from a lack of coordination and familiarity between partners. Individual quality could also contribute to the high corticosterone levels found in new pairs if poor-quality birds change mate often and have high corticosterone levels. However, this interpretation is unlikely because we were able to demonstrate an effect of pair status on changes in baseline corticosterone levels from 2004 to 2005 by sampling the same individuals in both years.

In addition to this potential effect of social context on baseline corticosterone levels, the lack of coordination of parental duties between new pair members might also explain the elevated baseline corticosterone levels observed in birds breeding with a new mate. A lack of coordination during the chick-rearing period might result in increased energetic demands for new pairs (Black 1996), and energetic demands are known to be positively correlated with baseline corticosterone levels in vertebrates (Romero 2002, Love et al. 2004, Landys et al. 2006). At the functional level, elevated corticosterone levels can promote foraging activity in birds (Astheimer et al. 1992, Kitaysky et al. 2001, Angelier, Shaffer et al. 2007) and moderately elevated corticosterone levels in birds breeding with a new mate might be necessary to compensate for the lack of coordination between new pair members and therefore to meet the high energetic demands of the chick-rearing period (Golet and Irons 1999, Bech et al. 2002, Moe et al. 2002). Corticosterone can promote foraging activity at the expense of guarding the brood in Black-legged Kittiwakes (Kitaysky et al. 2001). Because parents from new pairs have elevated corticosterone levels, their chicks are likely to be left alone more often, thus becoming more vulnerable to predation or inclement weather (Kitaysky et al. 2001). This may explain the low breeding success of new kittiwake pairs (Coulson 1966, 1972, this study). Moreover, increased foraging activity associated with elevated corticosterone levels could be directed toward self-maintenance at the expense of brood provisioning (Silverin 1986), which

could explain why elevated corticosterone levels are associated with breeding failure in seabird species (Angelier, Weimerskirch, et al. 2007, this study).

We found no influence of pair status on the magnitude of the induced stress response; birds in both new and established pairs showed a strong six-fold increase in corticosterone levels. Because Black-legged Kittiwakes are long-lived birds and have a high residual reproductive value, they should behave as prudent parents and minimize the risk of mortality due to breeding independently of pair status, especially when unpredictable stressors occur (Drent and Daan 1980, Weimerskirch 1999). In accordance with this theory, we demonstrated that the sensitivity of the hypothalamo-pituitary-adrenal axis to unpredictable stressors is not affected by pair status in kittiwakes during the chick-rearing period. This result suggests that: (1) unpredictable stressors trigger an emergency stress response independently of pair status, and (2) chick-rearing kittiwakes do not modulate their breeding investment according to their pair status when they face unpredictable stressors (Wingfield et al. 1995, O'Reilly and Wingfield 2001, Holberton and Wingfield 2003, Wilson and Holberton 2004). However, birds breeding with a new mate may lower their breeding investment by endocrine mechanisms other than the corticosterone response to stress. Prolactin is a hormone involved in expression of parental behavior (reviewed by Buntin 1996) and prolactin levels decrease in response to stress in birds (Delehanty et al. 1997, Chastel et al. 2005). The magnitude of the decrease in plasma prolactin levels resulting from capture-restraint stress can be interpreted as an index of parental effort or breeding investment (Chastel et al. 2005). Interestingly, Chastel et al. (2005) showed that prolactin, but not corticosterone, response to stress was influenced by breeding activity in kittiwakes, supporting the idea that kittiwakes breeding with a new mate may reduce their parental investment through prolactin secretion (Chastel et al. 2005, O'Dwyer et al. 2006).

This is the first study to show that the hypothalamo-pituitary-adrenal axis is influenced by mate change from one breeding season to the next in a long-lived seabird. Future studies are needed to describe the influence of mate change on baseline and stress-induced corticosterone and prolactin levels in other bird species. Understanding how corticosterone and prolactin secretion are regulated in relation to mate change should help to shed light on the role of pair break-up on breeding investment in species with varied life-history strategies.

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