

Dynamics of food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes

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Summary

1. The seasonal dynamics of body condition (BC), circulating corticosterone levels (baseline, BL) and the adrenocortical response to acute stress (SR) were examined in long-lived Black-legged Kittiwakes, *Rissa tridactyla*, breeding at Duck (food-poor colony) and Gull (food-rich colony) Islands in lower Cook Inlet, Alaska. It was tested whether the dynamics of corticosterone levels reflect a seasonal change in bird physiological condition due to reproduction and/or variation in foraging conditions.

2. BC declined seasonally, and the decline was more pronounced in birds at the food-poor colony. BL and SR levels of corticosterone rose steadily through the reproductive season, and BL levels were significantly higher in birds on Duck Island compared with those on Gull Island. During the egg-laying and chick-rearing stages, birds had lower SR on Duck Island than on Gull Island.

3. The results suggest that, in addition to a seasonal change in bird physiology during reproduction, local ecological factors such as food availability affect circulating levels of corticosterone and adrenal response to acute stress.

Key-words: Corticosterone, ecology, reproduction, seabirds, seasonality

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Introduction

Birds respond to stressful events by a rapid increase in secretion of corticosterone. Variations in circulating levels of corticosterone and the adrenocortical response to acute stress are known to correlate with unpredictable environmental events such as food shortages (Wingfield 1994), and predictable life-history events such as wintering, migration and breeding (e.g. Romero, Ramenofsky & Wingfield 1997). Secretion of corticosterone, the primary glucocorticosteroid released by the adrenal glands in birds, regulates body maintenance processes by modifying behaviour of individuals in accordance with ecological and life-history events. In particular, corticosterone can facilitate foraging behaviour and trigger irruptive migration, abandonment of reproduction, and mobilization of stored energy resources to fuel increased locomotory activities (Astheimer, Buttemer & Wingfield 1992; Bray 1993; reviewed in Wingfield, Bruener & Jacobs 1997a; Wingfield *et al.* 1997b). Although these responses can improve survival during food shortages (Astheimer *et al.* 1992), they also may result in reproductive failure (Silverin 1986). Thus, an elevation in corticosterone levels during food shortages can result in a trade-off between body mainte-

nance and reproductive processes. Perhaps to ameliorate this trade-off, birds breeding in high Arctic habitats accumulate large fat reserves and modulate their stress response, which allows them to breed under severe environmental conditions (Wingfield, Suydam & Hunt 1994a). Here we examine seasonal patterns in body condition, baseline corticosterone levels, and adrenal response to acute stress in adult Black-legged Kittiwakes, *Rissa tridactyla*, long-lived pelagic seabirds breeding under variable food regimes in lower Cook Inlet, Alaska.

Seasonal variations in circulating levels of corticosterone and adrenal stress response probably differ between short- and long-lived species of birds (Wingfield, O'Reilly & Astheimer 1995). Short-lived birds are limited to a few reproductive events during their life and each reproductive bout can be crucial in determining fitness of individuals. In contrast, long-lived birds have a long reproductive life and survival of adults during or after each reproductive event can be more important than the success of a current reproduction (Stearns 1992). During food shortages, a trade-off between body maintenance and reproduction should be more apparent in long-lived than in short-lived parent birds. Short-lived birds should show

more suppression of the adrenocortical response to stress while breeding, whereas long-lived bird species should show less suppression (Wingfield *et al.* 1995). However, seasonal dynamics of stress response in long-lived birds are not well studied.

As a group, seabirds have adapted to large variations in food supply (Lack 1968). Pelagic seabirds are long-lived animals that reproduce at low rates, and they have an extended period of chick dependence on food provided by parents. Seabirds can accumulate fat as energy reserves for self-maintenance during reproduction (Drent & Daan 1980). As fat reserves are depleted, breeding seabirds should rely more on amino acid metabolism (mobilized mostly from muscle protein; Cherel, Robin & Le Maho 1988), which is stimulated by corticosterone secretion (Veiga, Roselino & Migliorini 1978). Elevation of circulating levels of corticosterone can also alter behaviour of parent birds, so that they would allocate more resources to self-maintenance than to reproductive efforts (Wingfield & Silverin 1986). A seasonal increase in adrenal stress response is also expected because seabirds must work harder during chick rearing to feed hungry chicks.

Stress in wild birds can be examined by using a capture and handling protocol as a standardized acute stressor (Wingfield 1994). This technique, based on a serial bleeding of birds during a 1-h period after capture and restraint, allows examination of circulating baseline levels of corticosterone and the adrenal capacity for secretion of corticosterone in response to acute stress of captivity (Wingfield, Vleck & Moore 1992).

The main objective of this study was to examine seasonal changes in body condition, circulating levels of corticosterone, and response to acute stress in Black-legged Kittiwakes breeding on two closely situated colonies in the lower Cook Inlet, Alaska. During the breeding season of 1997, kittiwakes nesting on Duck Island experienced chronic food shortages, whereas on Gull Island food resources were abundant.

This allowed us to examine how corticosterone levels reflect seasonal changes in bird physiology due to reproduction and temporal variability in food supply. In the discussion, we consider the role of corticosterone in regulating the balance between self-maintenance and reproductive effort.

Materials and methods

Gull Island and Duck Island are situated 60 km apart in lower Cook Inlet, Alaska. Continual studies of seabird breeding biology (diets, chick growth, breeding success, foraging behaviour) and food availability have been conducted at both colonies since 1995 (J. F. Piatt *et al.*, unpublished data).

Phenology of the reproductive season, and temperature and weather conditions were similar at both islands in 1997 (J. F. Piatt *et al.*, unpublished data). Independent measures of forage fish abundance, duration of foraging trips of parent kittiwakes and breeding success provided evidence that in 1997, Black-legged Kittiwakes breeding on Duck Island experienced severe food shortages compared to birds breeding on Gull Island (Table 1, J. F. Piatt *et al.*, unpublished data). Breeding birds were captured at their nests by the same method (using a noose pole) and approximately at the same dates in 1997: at egg-laying, 11–12 June on Duck and 15–16 June on Gull; at incubation, 23–24 June on Duck and 22–25 June on Gull; early chick-rearing, 24–25 July on Gull Island and late chick-rearing, on 1 August on Duck and 4 August on Gull Island. In addition, data were collected in 1996 at early chick-rearing on 20 and 24 July on Gull and Duck Islands, respectively; and on 4 August on Gull Island.

Blood samples were collected by puncture of the alar vein and collection of blood in heparinized microhaematocrit capillary 100- μ l tubes. All birds were bled according to the following standardized technique. An initial sample was collected within 3 min of capture, and further samples were taken at

Table 1. Direct and indirect evidence that food was in short supply for Black-legged Kittiwakes breeding on Duck Island compared with Gull Island in 1997 (J. F. Piatt *et al.*, unpublished data)

	Gull Island			Duck Island		
	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>
Beach seines (no. fish set ⁻¹)	317.4	84.4	51*	19.4	6.8	14
Midwater trawls (no. fish km ⁻¹)	525	199	16†	342	193	10
Foraging trip duration (min)	191.7	11.5	74‡	294.1	50.6	8
Breeding success (chicks nest ⁻¹)	0.64	0.11	300‡	0.02	0.01	140
Median hatch date	9 July			6 July		

*No. of seine sets.

†No. of trawl sets.

‡No. of nests.

Foraging trip duration is the mean time between departure and subsequent arrival of a parent (with nest as a sampling unit); breeding success is the number of fledglings per occupied nest.

10, 30, 50 and 70 min. During incubation and early chick-rearing in 1997, only initial samples were collected. Corticosterone levels generally do not start to increase until 3 min after capture (Wingfield, Smith & Farner 1982), and in this study a significant relationship was not found between time after capture and concentration of corticosterone within 0–3 min after capture. In particular, linear regression analyses showed the following results for the effect of time after capture (within 0–3 min interval) on plasma levels of corticosterone in initial blood samples: egg-laying – $R^2 = 0.10$, $F_{1,15} = 1.85$, $P = 0.194$; incubating – $R^2 = 0.02$, $F_{1,16} = 0.36$, $P = 0.555$; early chick-rearing – $R^2 = 0.01$, $F_{1,8} = 0.286$, $P = 0.607$; late chick-rearing – $R^2 = 0.09$, $F_{1,19} = 1.904$, $P = 0.184$. Thus, initial blood samples were considered to reflect baseline levels of corticosterone. After each sample, blood flow was stopped by application of cotton and birds were placed in individual opaque cloth bags. After collection of blood, haematocrit tubes were emptied into 0.5-ml vials, which were stored on ice. Within 12 h, blood samples were centrifuged and plasma collected. Plasma samples were frozen at $-20\text{ }^\circ\text{C}$ and transported to J.C.'s laboratory at the University of Washington for radioimmunoassay analyses (for a detailed description of the analysis see Wingfield & Farner 1975; Wingfield *et al.* 1992).

Captured birds were weighed, measured for wing chord and bill length, and banded with a standard aluminium band and a unique combination of colour bands between subsequent bleeds. After sampling, birds were released at the colony. In most cases kittiwakes resumed their parental duties 1–10 min after they were released. Earlier studies did not find sex-dependent differences in baseline and stress-induced levels of corticosterone in the Black-legged Kittiwake (J. C. Wingfield *et al.*, unpublished data), thus sex of birds was ignored in this study. No birds were sampled more than once during the season, and all collections of blood samples occurred during daylight hours (between 11.00 and 18.00 h).

Corticosterone concentrations were measured in duplicate for each sample after extraction in dichloromethane. Recovery values following extraction ranged from 80 to 90% and were used to adjust assayed concentrations of corticosterone. Intra- and interassay coefficients of variation were 8% and 10.9%, respectively.

Body mass to wing chord, bill and tarsus length ratios are commonly used to assess body conditions in birds (e.g. Chastel, Weimerskirch & Jouventin 1995). However, we found that on both colonies length of wing chord decreased significantly over a 3-month period, mostly because birds were wearing off the tips of their primaries. Bill and tarsus length did not change seasonally. To estimate body condition, a ratio of body mass (g) to (bill length + tarsus length) (mm) was therefore calculated.

Intraseasonal changes of body condition and baseline corticosterone were examined with two-way ANOVA, where colony and reproductive stage were used as factors. Baseline levels of corticosterone were not statistically different between early and late chick rearing, therefore data were combined for statistical purposes. Intercolony comparison of stress response to handling was performed with two-way repeated measures ANOVA, where reproductive stage and colony were used as factors and serial bleeds of the same bird during the stress protocol as repeated measures. Interseasonal comparison of body condition and baseline corticosterone levels was achieved with two-way ANOVA, where year and colony were used as factors. Interseasonal differences of stress response in birds on Gull Island at late chick-rearing were examined with repeated measures ANOVA, with year as factor and serial bleeds as repeated measures. Effects of body condition on baseline levels of corticosterone and stress response to handling (expressed as the maximal level of corticosterone achieved during 70 min of restraint) were examined in all individual birds with complete data on adrenal response to stress by using linear regression analysis.

During statistical analyses initial data were tested for assumptions required by a statistical test according to Sokal & Rohlf (1981). If these data violated assumptions they were \log_{10} -transformed and examined again. All computations were performed using the SYSTAT statistical package (Wilkinson 1992).

Results

INTRASEASONAL EFFECTS

Body condition

In 1997, body condition was not significantly different between birds breeding on Duck and Gull Islands (colony effect: $F_{1,134} = 1.07$, $P = 0.304$, Fig. 1), whereas reproductive stage (compared at egg-laying, incubation and early chick-rearing, Fig. 1) had a significant effect on body condition ($F_{2,134} = 9.34$, $P < 0.001$). Seasonal changes in body conditions were different between kittiwakes breeding on Duck and Gull Islands (Fig. 1). In particular, body condition decreased steadily between egg-laying and late chick-rearing on Duck Island but decreased significantly only between incubation and late chick-rearing on Gull Island (colony \times reproductive stage interaction term: $F_{2,134} = 3.26$, $P = 0.040$, Fig. 1).

Baseline levels of corticosterone

In 1997, baseline levels of corticosterone were significantly elevated in birds breeding on Duck Island compared with those breeding on Gull Island (colony effect: $F_{1,55} = 13.24$, $P = 0.001$, Fig. 2). Baseline corticosterone levels increased seasonally on both colonies (reproductive stage effect: $F_{2,55} = 21.94$, $P < 0.001$, Fig. 2).

However, seasonal increase in baseline levels of corticosterone was significantly stronger among birds on Duck Island than on Gull Island (colony \times reproductive stage interaction term: $F_{2,55} = 5.12$, $P = 0.009$, Fig. 2).

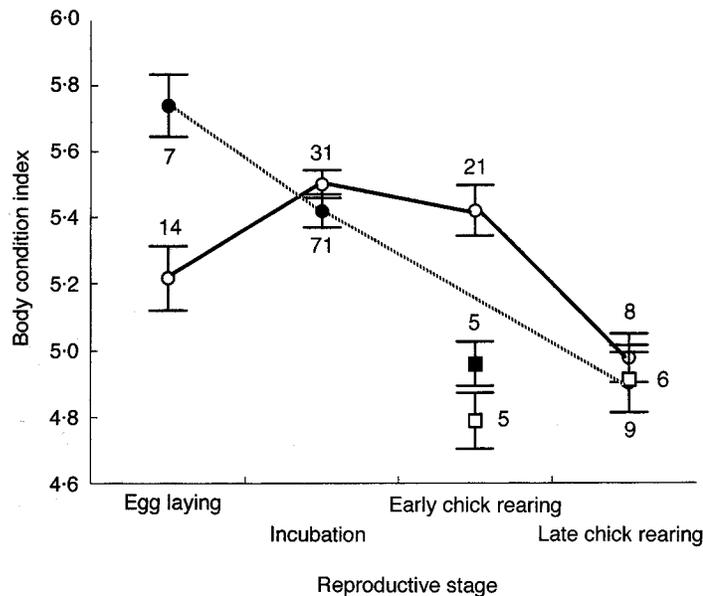


Fig. 1. Seasonal pattern of body condition (means, SE, N) in adult kittiwakes in relation to breeding phenology. Birds breeding under poor foraging conditions on Duck Island in 1997 (●, $N =$ numbers below the symbol) started reproduction at higher body condition, which declined rapidly toward the late stages of the reproductive cycle, whereas body condition declined only at late chick-rearing of kittiwakes breeding under good foraging conditions on Gull Island in 1997 (○, $N =$ numbers above the symbol). In 1996, body condition of chick-rearing kittiwakes was similar among birds breeding on Gull (□, $N =$ numbers to the right of the symbol) and Duck (■, $N =$ number above the symbol) Islands.

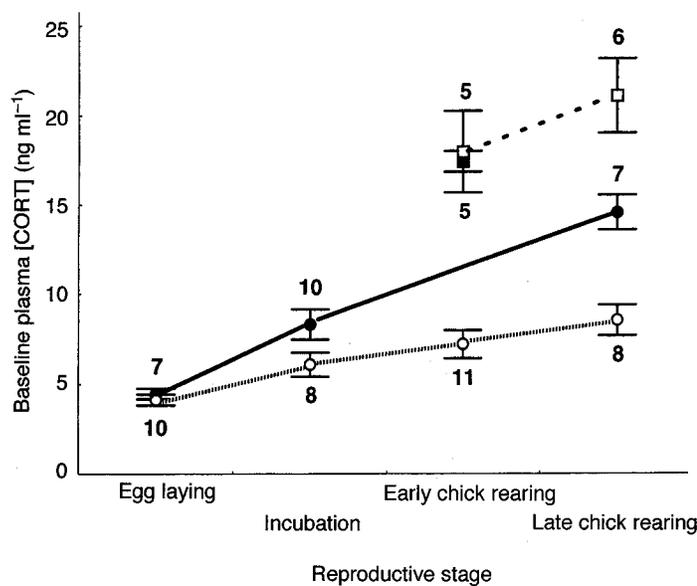


Fig. 2. Seasonal pattern of baseline levels of corticosterone (means, SE, N) in adult kittiwakes in relation to breeding phenology. In 1997, birds breeding at the food-poor colony on Duck Island (●, solid line) had stronger seasonal increase in baseline levels of corticosterone compared with those of birds breeding at the food-rich colony on Gull Island (○, dashed line). In 1996, differences in baseline levels of corticosterone were less pronounced among chick-rearing kittiwakes breeding on Gull (□) and Duck (■) Islands.

Adrenal response to acute stress

At egg-laying and late chick-rearing in 1997, birds responded to acute stress by a significant increase in corticosterone levels (time after capture: repeated-measures ANOVA $F_{4,112} = 109.58$, $P < 0.001$, Fig. 3a). However, stress response was weaker in birds on Duck Island than on Gull Island (time after capture \times colony: $F_{4,112} = 6.64$, $P < 0.001$) (Fig. 3a,c). Although stress response increased seasonally between egg-laying and late chick-rearing stages on both colonies (reproductive stage effect: $F_{1,28} = 209.88$, $P < 0.001$; colony \times breeding stage interaction term: $F_{1,28} = 0.68$, $P = 0.417$), the seasonal increase was weaker in kittiwakes breeding on Duck Island compared with those on Gull Island (colony effect: $F_{1,28} = 14.56$, $P = 0.001$).

At early chick-rearing in 1996, birds responded to handling by a significant increase of corticosterone levels (time after capture: $F_{4,32} = 15.94$, $P < 0.001$, Fig. 3b). Although mean acute stress-induced levels of corticosterone were not significantly different between colonies (colony effect: $F_{1,8} = 0.65$, $P = 0.444$), the rate of increase was different between colonies (colony \times time after capture interaction term: $F_{4,32} = 3.79$, $P = 0.012$). During the first 50 min of handling, adrenal responses of birds were stronger on Duck Island than on Gull Island, but at 70 min corticosterone levels decreased to baseline in Duck Island birds and did not decrease in Gull Island birds (Fig. 3b).

INTERANNUAL COMPARISON

Body condition

On Gull Island, body conditions of kittiwakes at early and late chick-rearing were significantly lower in 1996 than in 1997 (year effect: $F_{1,37} = 6.39$, $P = 0.016$, Fig. 1). However, there was a significant interaction between the reproductive stage and year effects ($F_{1,37} = 5.29$, $P = 0.027$, Fig. 1) because there was a significant decrease in body condition between early and late chick-rearing in 1997 (post-hoc test: $P = 0.019$, Fig. 1) but not in 1996 (post-hoc test: $P = 0.615$, Fig. 1). On Duck Island, body conditions did not differ between early chick-rearing in 1996 and late chick-rearing in 1997 ($t_{12} = 0.272$, $P = 0.790$, Fig. 1).

Baseline levels

Baseline levels of corticosterone at chick-rearing (early and late chick-rearing were combined for statistical purposes) were significantly different between colonies ($F_{1,38} = 4.62$, $P = 0.038$) and years ($F_{1,38} = 12.56$, $P = 0.001$), yet interannually variations were different between the colonies (colony-year interaction term: $F_{1,38} = 4.65$, $P = 0.038$) (Fig. 2). In particular, interseasonal differences in baseline levels

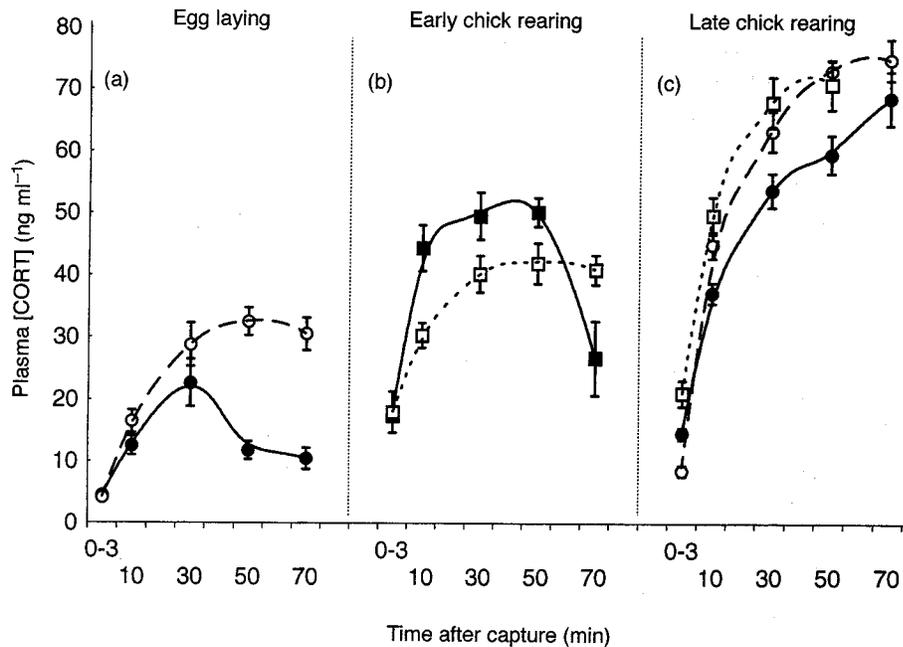


Fig. 3. Seasonal pattern in stress-induced levels of corticosterone (means, SE) in adult kittiwakes in relation to breeding phenology. In 1997 (a and c), birds breeding at the food-poor colony on Duck Island (●, solid line, egg-laying: $N = 7$; late chick-rearing: $N = 7$) had a suppressed response to a standardized stressor compared with birds breeding at the food-rich colony on Gull Island (○, dashed line, egg-laying: $N = 10$; late chick-rearing: $N = 8$). During early chick-rearing in 1996 (b), however, stress-induced levels of corticosterone were significantly higher between 10 and 50 min after capture in birds sampled on Duck Island (■, $N = 5$) than those on Gull Island (□, $N = 5$). During late chick-rearing, stress-induced response of birds breeding on Gull I. was similar between 1996 and 1997 (c, in 1996 $N = 6$, □, dotted line).

of corticosterone were not significant on Duck Island (post-hoc test: $P = 0.413$, Fig. 2), whereas on Gull Island corticosterone levels at chick-rearing were higher in 1996 than in 1997 (post-hoc test: $P < 0.001$, Fig. 2).

Adrenal response to acute stress

During late chick-rearing stage, kittiwakes breeding on Gull Island had similar responses to handling during 50 min after capture (time after capture effect: $F_{3,36} = 110.77$, $P < 0.001$, time after capture–colony interaction term: $F_{3,36} = 1.53$, $P = 0.223$) between 1996 and 1997 (year effect: $F_{1,12} = 0.87$, $P = 0.369$) (Fig. 3c).

EFFECTS OF BODY CONDITION ON BASELINE AND MAXIMAL STRESS LEVELS OF CORTICOSTERONE

On an individual basis, body condition had a significant negative effect on both baseline ($F_{1,46} = 8.19$, $P = 0.006$, Fig. 4) and maximal stress-induced ($F_{1,46} = 18.95$, $P < 0.001$) levels of corticosterone.

Discussion

In this study we assessed temporal variations in body condition, baseline circulating levels of corticosterone and adrenocortical response to a standardized acute stressor (capture, handling and restraint) in long-lived

Black-legged Kittiwakes breeding under poor and good foraging conditions. As the breeding season progressed, body condition of parent kittiwakes declined, baseline levels of corticosterone increased, and birds became more susceptible to acute stress in both populations. The results of this study support the hypothesis that long-lived birds maintain a robust stress response during breeding probably to ensure their postbreeding survival and the possibility of successful reproduction in the future (Wingfield *et al.* 1995). This contrasts with the response of relatively short-lived passerines that first enhance stress response during early nesting (Romero *et al.* 1997) then suppress it during the parental phase of breeding (Astheimer, Buttemer & Wingfield 1994; Wingfield *et al.* 1995).

Strong intraseasonal and intercolony effects on baseline and acute stress-induced levels of corticosterone were also found. On both colonies, birds in the egg-laying stage had a weaker stress response compared with birds sampled at more advanced stages of their reproductive cycle. Furthermore, kittiwakes on Duck Island had higher energy reserves (as indicated by their body condition during the egg-laying stage) but suppressed their response to acute stress compared to birds on Gull Island (Fig. 3a). Similar increases in body mass and fat deposition, and suppressed stress responses were observed by Wingfield *et al.* (1994a, 1994b, 1995) in several species of passerines breeding under severe environmental conditions compared to their con-specifics breeding in less severe environ-

ments. These authors suggested that large energy reserves and suppressed stress response allow birds to cope with severe climate conditions during the breeding season (Wingfield *et al.* 1994a, 1994b).

In our study, climate conditions were similar between the colonies, but Black-legged Kittiwakes breeding on Duck Island foraged at greater distances from the colony and on less abundant food resources than birds on Gull Island (Table 1, J. F. Piatt *et al.*, unpublished data). Accumulation of large fat deposits may provide Duck Island birds with energy reserves to fuel their activities at the colony and subsequent long foraging trips during the egg-laying stage. During chick-rearing, however, parent kittiwakes must deliver large food loads to their young, thereby increasing wing-loading and energy expenditure in flying (Pennycuick 1987). Furthermore, Black-legged Kittiwakes usually increase the frequency of foraging trips as energy demands of their chicks increase with age (Roberts & Hatch 1993). These factors presumably prevented parent kittiwakes on Duck Island from accumulating fat deposits during the chick-rearing stage. As fat reserves declined, the elevation in circulating levels of corticosterone may have been related to mobilization of proteins for gluconeogenesis (Adams 1968; Veiga *et al.* 1978). In contrast, the body condition of kittiwakes at Gull Island remained simi-

lar between egg-laying and early chick-rearing, and decreased significantly only between early and late chick-rearing in 1997. Baseline levels of corticosterone increased slightly from egg-laying to chick-rearing. In 1996, however, body conditions and baseline corticosterone levels in Gull Island kittiwakes were similar to those observed on Duck Island in both 1996 and 1997.

The comparison of acute stress-induced levels of corticosterone between kittiwakes nesting on Duck and Gull Island colonies provided evidence that breeding long-lived birds can suppress their stress response during chronic food shortages. Although commonly observed in short-lived birds, the suppression of stress response during food shortages in Black-legged Kittiwakes seems to contradict a major prediction of life-history theory on reproductive strategies. In particular, one would expect that long-lived birds should cease any activities that might reduce future survival, including reproduction, if they experience stressful ecological conditions such as prolonged food shortages. How can the results of our study explain this discrepancy? First, we need to establish whether the differences in stress response observed in this study have an ecological rather than a colony-specific basis. The data collected during the breeding season in 1997 show that kittiwakes nesting on Duck Island *always* had a suppressed stress response to handling and a stronger seasonal increase of baseline levels of corticosterone compared with birds on Gull Island. Although low abundance of forage fish, long duration of foraging trips of parent kittiwakes and almost complete breeding failure suggest severe food shortages for kittiwakes on Duck Island in 1997 (Table 1), it is possible that baseline and acute stress-induced levels of corticosterone were colony-specific traits. However, in 1996, birds sampled at the early chick-rearing stage on Duck Island had higher acute stress levels of corticosterone between 10 and 50 min after capture than those of birds sampled on Gull Island (Fig. 3b). In addition, baseline levels of corticosterone at chick-rearing were significantly elevated in kittiwakes breeding on Gull Island in 1996 compared with 1997 (Fig. 2), probably because food was less abundant in 1996 than in 1997 (J. F. Piatt *et al.*, unpublished data). These results give us confidence that the observed intercolony differences in stress response to handling and baseline levels of corticosterone have an ecological basis and indeed reflect food shortages on Duck Island in 1997.

Suppression of the adrenocortical response to stress during poor feeding conditions may prevent fast depletion of limited protein resources (Le Ninan *et al.* 1988). It was found that baseline and acute stress-induced levels of corticosterone were negatively correlated with body condition suggesting that potential for metabolic stress increased as the body condition of breeding kittiwakes decreased. Interestingly, acute stress-induced levels of corticosterone were almost

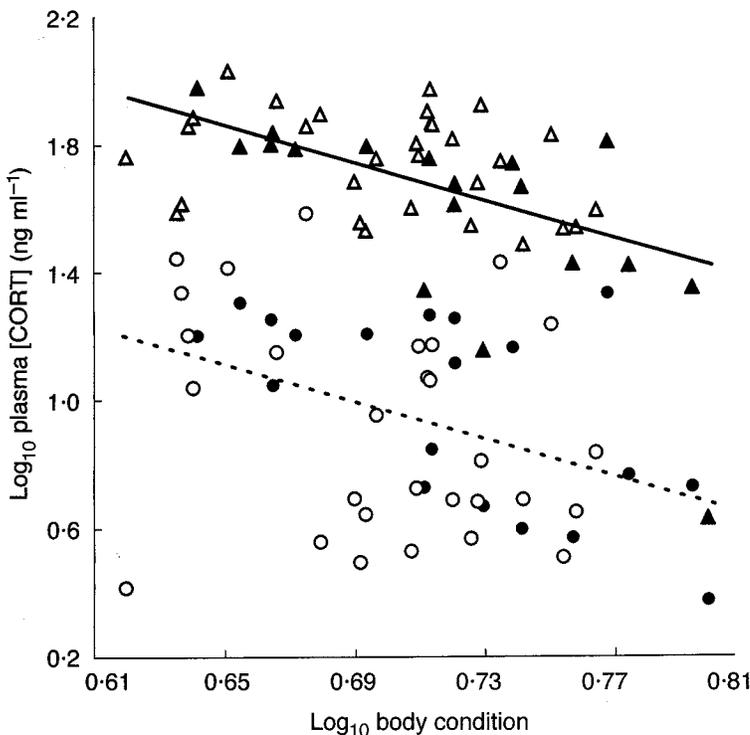


Fig. 4. Body condition of breeding Black-legged Kittiwakes was significantly negatively correlated with their baseline ($\log_{10}BL = 2.98 - 2.87 \times \log_{10} BC$, $r^2 = 0.15$, $P = 0.006$, $n = 48$, dashed line) and stress-induced maximal ($\log_{10}SR = 3.81 - 3.0 \times \log_{10} BC$, $r^2 = 0.29$, $P < 0.001$, $n = 48$, solid line) levels of corticosterone. Circles represent baseline levels of corticosterone: ● Duck Island, ○ Gull Island. Triangles represent stress-induced maximal levels of corticosterone: ▲ Duck Island, △ Gull Island.

identical on Gull Island in 1996 and 1997 at chick-rearing (Fig. 3c) and possibly represent the maximal capacity of adrenal response that breeding kittiwakes can achieve during the reproductive season. Any further increase in stress levels of corticosterone might trigger abandonment of reproduction, as has been observed in other species of birds (Silverin 1986). Thus, suppression of adrenal responsiveness to stress may prevent abandonment of reproductive effort during chronic food shortages. A suppressed stress response was found among animals reproducing under severe environmental conditions of Arctic (Astheimer, Buttemer & Wingfield 1995) and desert environments (Wingfield *et al.* 1992), where the potential for disruption of breeding is great. This may also be important at some colonies of seabirds in Alaska, where chronic food shortages and limited breeding success of Black-legged Kittiwakes have been observed during the past 25 years (Hatch *et al.* 1993).

Although the modulation of stress response might facilitate successful reproduction during food shortages, it may impair postbreeding survival of parent kittiwakes. Recent studies have shown that kittiwakes invest a significant effort in reproduction under poor foraging conditions (A. S. Kitaysky *et al.*, unpublished data), which in turn affects their postbreeding survival (Golet, Irons & Estes 1998). On the other hand, poor feeding conditions usually result in an increase in adult kittiwake foraging trip duration, which ultimately increases the amount of time that chicks spend in the nest alone (Roberts & Hatch 1993; A. S. Kitaysky, unpublished data) – making them more vulnerable to predation. Thus, predation may terminate stressful reproductive efforts and thereby facilitate survival of parent birds and increase their chances of successful reproduction in the future.

In conclusion, as expected for long-lived animals, Black-legged Kittiwakes maintain a stress response during reproduction. Seasonal increases in adrenal responsiveness to acute stress coincide with seasonal declines in endogenous energy resources of breeding birds. Perhaps, if physiological conditions of breeding kittiwakes approached levels of metabolic stress, elevation in corticosterone levels even further would modify their behaviour and parents might cease any unnecessary activities, including reproduction. Before reaching this point, however, a suppression of stress response during food shortages would offer some evolutionary advantages, such as successful breeding, over abandonment of reproduction. This would fit the general prediction of the life-history hypothesis on a trade-off between body maintenance and reproductive processes in long-lived animals. However, an experimental examination of the functional role of corticosterone in regulation of parental effort in long-lived birds is needed.

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References

- Adams, B.M. (1968) Effects of cortisol on growth and uric acid excretion in the chick. *Journal of Endocrinology* **40**, 145–151.
- Astheimer, L.B., Buttemer, W.A. & Wingfield, J.C. (1992) Interactions of corticosterone with feeding, activity and metabolism in passerine birds. *Ornis Scandinavica* **23**, 355–365.
- Astheimer, L.B., Buttemer, W.A. & Wingfield, J.C. (1994) Gender and seasonal differences in the adrenocortical response to ACTH challenge in an Arctic passerine, *Zonotrichia leucophrys gambelii*. *General and Comparative Endocrinology* **94**, 33–43.
- Astheimer, L.B., Buttemer, W.A. & Wingfield, J.C. (1995) Seasonal and acute changes in adrenocortical responsiveness in an Arctic-breeding bird. *Hormones and Behavior* **29**, 442–457.
- Bray, M.M. (1993) Effect of ACTH and glucocorticoids on lipid metabolism in the Japanese quail, *Coturnix coturnix japonica*. *Comparative Physiology and Biochemistry A* **105**, 689–696.
- Chastel, O., Weimerskirch, H. & Jouventin, P. (1995) Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* **76**, 2240–2246.
- Cherel, Y., Robin, J.-P. & Le Maho, Y. (1988) Physiology and biochemistry of long-term fasting in birds. *Canadian Journal of Zoology* **66**, 159–166.
- Drent, R.H. & Daan, S. (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**, 225–252.
- Golet, G.H., Irons, D.B. & Estes, J.A. (1998) Chick rearing costs in kittiwakes. *Journal of Animal Ecology* **67**, 827–841.
- Hatch, S.A., Byrd, G.V., Irons, D.B. & Hunt, G.L. (1993) Status and ecology of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. *The Status, Ecology, and Conservation of Marine Birds of the North Pacific* (eds K. Vermeer, K. T. Briggs, K. H. Morgan & D. Siegel-Causey), pp. 140–153. Canadian Wildlife Service Special Publication, Ottawa.
- Lack, D. (1968) *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- Le Ninan, F., Cherel, Y., Sardet, C. & Le Maho, Y. (1988) Plasma hormone levels in relation to lipid and protein metabolism during prolonged fasting in King penguin chicks. *General and Comparative Endocrinology* **71**, 331–337.

- Pennycuik, C.J. (1987) Flight of seabirds. *Seabirds: Feeding Ecology and Role in Marine Ecosystems* (ed. J. P. Croxall), pp. 43–62. Cambridge University Press, Cambridge.
- Roberts, B.D. & Hatch, S.A. (1993) Behavioral ecology of Black-legged Kittiwakes during chick-rearing in a failing colony. *Condor* **95**, 330–342.
- Romero, L.M., Ramenofsky, M. & Wingfield, J.C. (1997) Season and migration alters the corticosterone response to capture and handling in an Arctic migrant, the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *Comparative Biochemistry and Physiology C* **116** (2), 171–177.
- Silverin, B. (1986) Corticosterone binding proteins and behavioral effects of high plasma levels of corticosterone during the breeding period in the pied flycatcher. *General and Comparative Endocrinology* **64**, 67–74.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. W.H. Freeman, San Francisco.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Veiga, J.A.S., Roselino, E.S. & Migliorini, R.H. (1978) Fasting, adrenalectomy, and gluconeogenesis in the chicken and a carnivorous bird. *American Journal of Physiology* **234**, R115–R121.
- Wilkinson, L. (1992) *Systat for Windows*. SYSTAT Inc. Evanston, Illinois.
- Wingfield, J.C. (1994) Modulation of the adrenocortical response to stress in birds. *Perspectives in Comparative Endocrinology* (eds K. G. Davey, R. E. Peter & S. S. Tobe), pp. 520–528. National Research Council of Canada, Ottawa.
- Wingfield, J.C. & Farner, D.S. (1975) The determination of five steroids in avian plasma by radioimmunoassay and competitive protein binding. *Steroids* **26**, 311–327.
- Wingfield, J.C. & Silverin, B. (1986) Effects of corticosterone on territorial behavior of free-living male song sparrows, *Melospiza melodia*. *Hormones and Behavior* **20**, 405–417.
- Wingfield, J.C., Smith, J.P. & Farner, D.C. (1982) Endocrine responses of white-crowned sparrows to environmental stress. *Condor* **84**, 399–409.
- Wingfield, J.C., Vleck, C.M. & Moore, M.C. (1992) Seasonal changes of the adrenocortical response to stress in birds of Sonoran Desert. *Journal of Experimental Zoology* **264**, 419–428.
- Wingfield, J.C., Suydam, R. & Hunt, K. (1994a) The adrenocortical responses to stress in snow bunting (*Plectrophenax nivalis*) and Lapland longspurs (*Calcarius lapponicus*) at Barrow, Alaska. *Comparative Biochemistry and Physiology B* **108**, 299–306.
- Wingfield, J.C., Deviche, P., Sharbaugh, S., Astheimer, L.B., Holberton, R., Suydam, R. & Hunt, K. (1994b) Seasonal changes of the adrenocortical responses to stress in Redpolls, *Acanthis flammea*, in Alaska. *Journal of Experimental Zoology* **270**, 372–380.
- Wingfield, J.C., O'Reilly, K.M. & Astheimer, L.B. (1995) Modulation of the adrenocortical responses to acute stress in Arctic birds: a possible ecological basis. *American Zoologist* **35**, 285–294.
- Wingfield, J.C., Bruener, C. & Jacobs, J. (1997a) Corticosterone and behavioral responses to unpredictable events. *Perspectives in Avian Endocrinology* (eds S. Harvey & R. J. Etches), pp. 267–278. Society for Endocrinology, Bristol.
- Wingfield, J.C., Hunt, K., Bruener, C., Dunlap, K., Fowler, G.S., Freed, L. & Lapson, J. (1997b) Environmental stress, field endocrinology, and conservation biology. *Behavioral Approaches to Conservation in the Wild* (eds J. R. Clemmons & R. Buchholz), pp. 95–131. Cambridge University Press, Cambridge.

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