Exxon Valdez Oil Spill
Restoration Project Annual Report

Effects of Food Stress on Survival and Reproductive Performance of Seabirds

Restoration Project 99479
Annual Report

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Study History: Food stress can be quantified by measuring base levels of stress hormones such as corticosterone in the blood of seabirds, or the rise in blood levels of corticosterone in response to a standardized stressor: capture, handling and restraint. We applied these techniques to seabirds breeding in Lower Cook Inlet and also used captive birds for controlled experiments. This study uses a unique opportunity for a concurrent field and captive study of the behavioral and physiological consequences of stress in seabirds. Moreover, in coordination with restoration projects 99163 and 99338 it links stress physiology to changes in foraging conditions and demographics, which provides the basis for management of seabird populations in the areas affected by the *Exxon Valdez* oil spill, and it will have broader applications for seabird monitoring programs.

Abstract: We examined the seasonal dynamics of body condition (BC), circulating corticosterone levels (baseline, BL), and the adrenocortical response to acute stress (SR) 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. We tested whether the dynamics of corticosterone levels reflect a seasonal change in bird physiological condition due to reproduction and/or variation in foraging conditions. 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 to those on Gull Island. During the egg-laying and chick-rearing stages, birds had lower SR on Duck Island than on Gull Island. Our 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. We also examined hormonal responses of Black-legged Kittiwake chicks to experimental variations in energy content and nutritional quality (low or high lipid to protein ration, LPR) of their food. Starting at the age of 10 days, chicks were fed either high or low LPR fish at 30, 50, 70 and 100% of *ad libitum* energy intake. After 20 days of treatment, chicks were exposed to a standardized acute handling and restraint stress protocol. We found that food restricted chicks had elevated baseline and acute stress-induced levels of corticosterone compared to chicks fed *ad libitum*. An elevation of circulating levels of corticosterone in energetically stressed individuals was further magnified by low nutritional quality of food. Baseline and acute stress-induced corticosterone levels of chicks were negatively correlated with their fat reserves. We conclude that the physiological condition of Black-legged Kittiwake chicks can be assessed reliably by measuring circulating levels of corticosterone. We discuss short- and long-term effects of elevated corticosterone secretion in food-stressed seabird chicks.

Key Words: Coricosterone, ecology, food-stress, reproduction, survival, seabirds

Project Data: (will be addressed in final report of 2002)

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The annual report consists of two published papers (attached), and also results and preliminary conclusions to date as organized in various manuscripts.

Published papers:

1) Kitaysky A.S., Wingfield J.C. and J.F. Piatt. 1999. Dynamics of food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes. Functional Ecology, 13: 577-584.

    This paper documents initial findings that adult kittiwake body condition declined seasonally, and the decline was more pronounced in birds at the food-poor colony on Chisik Island. Correspondingly, baseline and acute stress-induced levels of corticosterone rose steadily through the reproductive season, and baseline levels were significantly higher in birds on food-poor Chisik Island compared to those at the food-rich colony on Gull Island. Birds breeding at the food-poor colony had suppressed acute stress-response compared to those at the food-rich colony. Our results suggest that, in addition to a seasonal change in bird physiology during reproduction, food availability affects circulating levels of corticosterone and the adrenal response to acute stress. **Conclusion: Baseline and acute-stress induced levels of corticosterone may be useful for monitoring foraging conditions in breeding Black-legged Kittiwakes, but more study is needed to confirm these results and to measure annual variability.**

2) Kitaysky A.S., Piatt, J.F. and J.C. Wingfield. 1999. The adrenocortical stress-response of Black-legged Kittiwake chicks in relation to dietary restrictions. Journal of Comparative Physiology B, 169: 303-310. This study was done in conjunction with Romano et al.'s experimental study of chick growth under differing dietary regimes. We found that food-restricted Black-legged Kittiwake chicks had elevated baseline and acute-stress induced levels of corticosterone compared to chicks fed *ad libitum*. An elevation of circulating levels of corticosterone in energetically stressed individuals was further magnified by low nutritional quality of food (pollock). Baseline and acute stress-induced corticosterone levels of chicks were negatively correlated with their fat reserves. **Conclusion: The physiological condition of Black-legged Kittiwake chicks raised on differing diets and energy intakes can be assessed reliably by measuring circulating levels of corticosterone.**

The following manuscript is submitted and in review:

1. Kitaysky et al. Corticosterone facilitates begging and affects resource allocation in the Black-legged Kittiwake. In review, Behavioral Ecology.
   We found that parents with experimentally elevated levels of corticosterone spent more time away from the nest – perhaps foraging, and less time brooding/guarding chicks than controls. At the same time, experimental parents fed their chicks at similar rates as controls. All experimental and control birds were observed at the colony during four weeks following the experiment. However, about 80% of corticosterone treated individuals failed to return to the nesting colony in the following reproductive season. **Conclusion: During food shortages, parent kittiwakes continue to provide food at chick demands thereby decreasing the probability of their post-breeding survival and increasing the likelihood of chick predation.**

Manuscripts in preparation are:

1. Kitaysky A.S., Piatt, J.F. and J.C. Wingfield. 1999. Functional significance of seasonal elevation of circulating levels of corticosterone in breeding Common Murres. In preparation, Functional Ecology.
   The results of this study were similar to the study of Black-legged Kittiwakes described above, and also resulted from pilot work. In addition, Common Murres responded to an experimental increase of corticosteroid levels by fledging their chicks at younger age compared to controls. **Conclusion: Baseline and acute-stress induced levels of corticosterone may be useful for monitoring foraging conditions in breeding Common Murres, but more study is needed to confirm these results and to measure annual variability.**

2. Kitayksy et al. Endocrine correlates of dietary restrictions in Tufted Puffin chicks. In preparation, Physiological and Biochemical Zoology.
   This study was done in conjunction with Romano et al.'s experimental study of chick growth under differing dietary regimes. We examined plasma levels of corticosterone in captive Tufted puffin chicks exposed to variable rates of daily energy intake. Baseline levels of corticosterone were not significantly different among the treatments. These results are not consistent with the results obtained for Black-legged Kittiwake chicks (see above) exposed to similar dietary restrictions. From other studies, we know that puffin chicks can respond to food deprivation by decreasing their metabolic rates. **Conclusion: The stress-response may be lacking or greatly diminished in puffin chicks, which are adapted to highly variable rates of provisioning. The difference in endocrine responses to food stress between puffins and kittiwakes may be phylogenetically determined and/or reflect a physiological adaptation of young puffins to intermittent type of food provisioning.**

Other manuscripts in preparation are:

Kitaysky A.S., Wingfield, J.C., Piatt, J.F., Kitaiskaia E.V. Effects of stress on cognitive abilities of Black-legged kittiwakes.

Kitaysky A.S., Kitaiskaia E.V., Wingfield J.C. Dietary restrictions cause a delay in development of hypothalamus-pituitary-adrenal axis in Tufted Puffin chicks.

Kitaysky A.S., Piatt, J.F., Wingfield J.C. Seasonal dynamics of corticosterone and LH in breeding Common Murres in relation to fluctuations in food supply.

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

Functional Ecology (1999) **13**, 577–584

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-μl 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	*n*	Mean	SE	*n*
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 °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 × 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 × reproductive stage interaction term: $F_{2,55} = 5.12$, $P = 0.009$, Fig. 2).
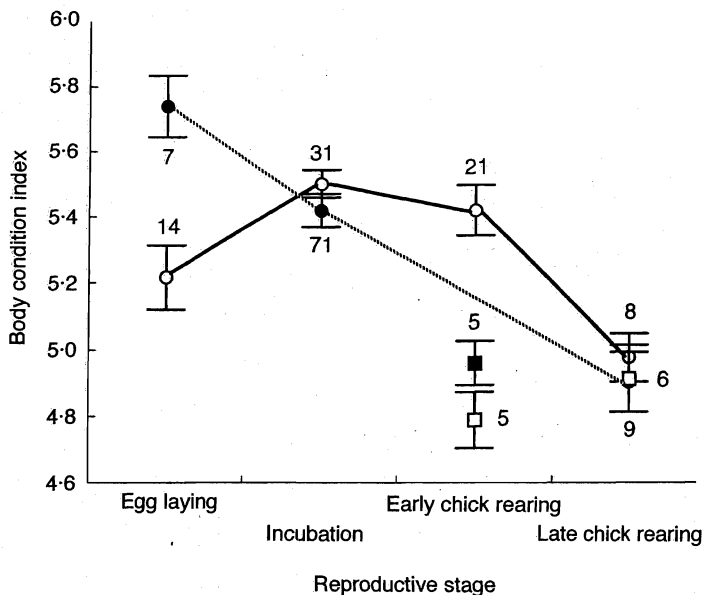

Fig. 1. Seasonal pattern of body condition (means, SE, N) in adult kittiwakes in relation to breeding phenology. Birds breeding under poor foraging conditions on Duck Island in 1997 (●, N = numbers below the symbol) started reproduction at higher body condition, which declined rapidly toward the late 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.
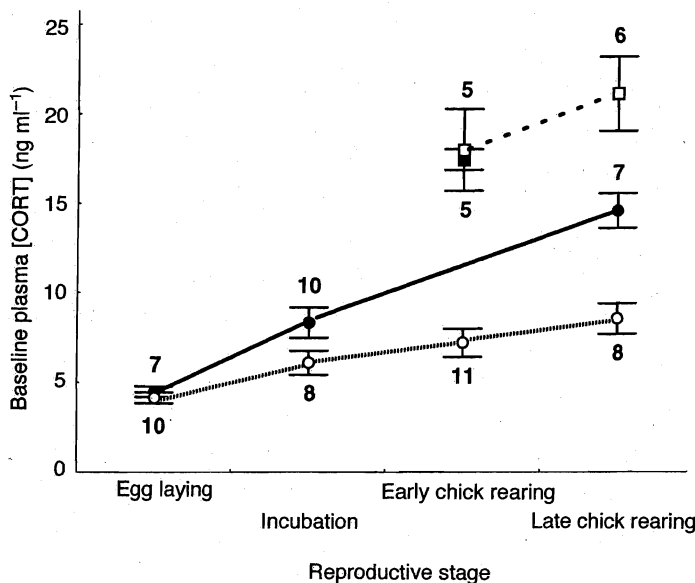

Fig. 2. Seasonal pattern of baseline levels of corticosterone (means, SE, N) in adult kittiwakes in relation to breeding phenology. In 1997, birds breeding at the food-poor colony on Duck Island (●, solid line) had stronger seasonal increase in baseline levels of corticosterone compared with those of 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 × 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 × 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 × 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
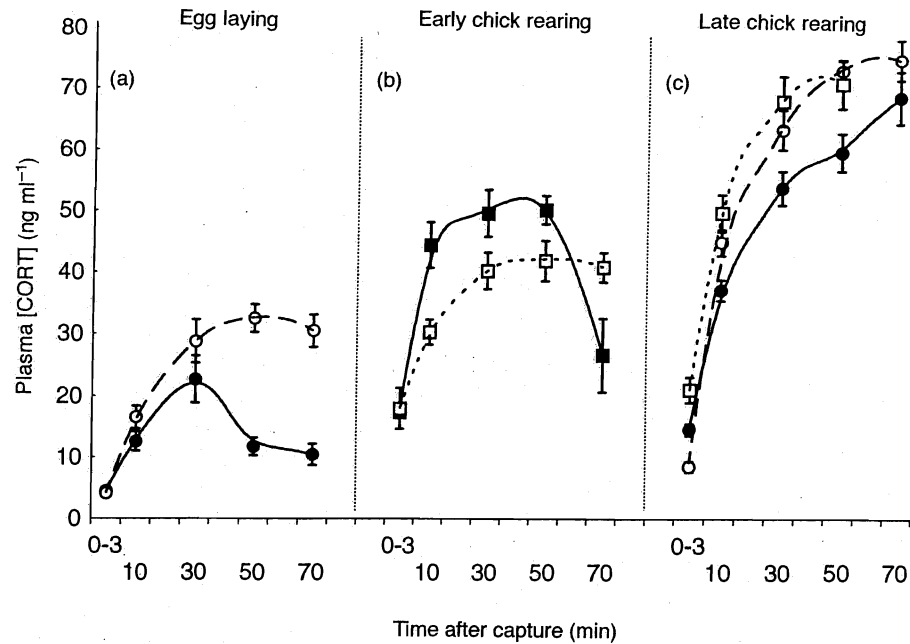
Fig. 3. Seasonal pattern in stress-induced levels of corticosterone (means, SE) in adult kittiwakes in relation to breeding phenology. In 1997 (a and c), birds breeding at the food-poor colony on Duck Island (●, solid line, egg-laying: $N = 7$; late chick-rearing: $N = 7$) had a suppressed response to 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 similar 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
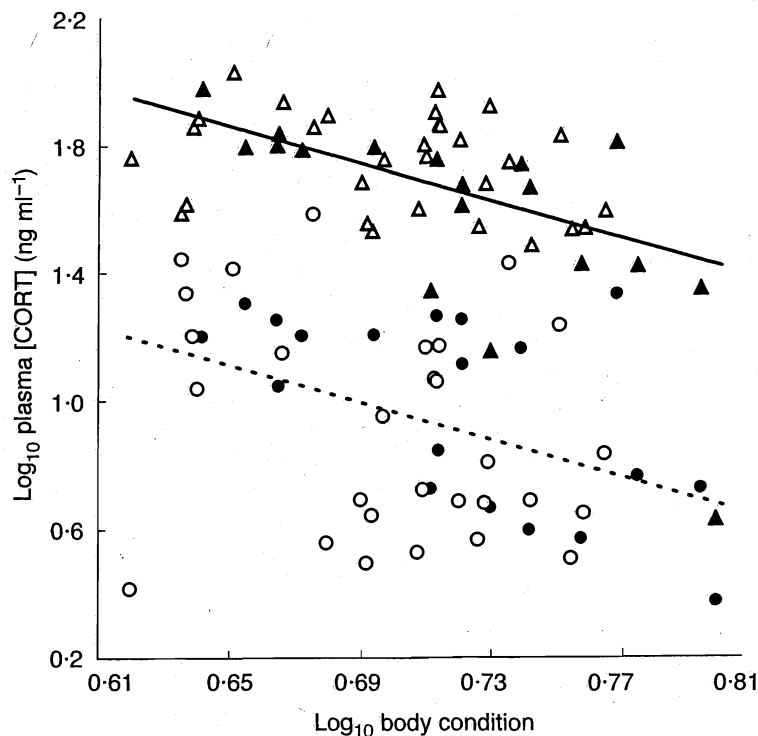

Fig. 4. Body condition of breeding Black-legged Kittiwakes was significantly negatively correlated with their baseline ($\log_{10} BL = 2.98 - 2.87 \times \log_{10} BC$, $r^2 = 0.15$, $P = 0.006$, $n = 48$, dashed line) and stress-induced maximal ($\log_{10} SR = 3.81 - 3.0 \times \log_{10} BC$, $r^2 = 0.29$, $P < 0.001$, $n = 48$, 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.

Acknowledgements

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ORIGINAL PAPER

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The adrenocortical stress-response of Black-legged Kittiwake chicks in relation to dietary restrictions

Abstract In this study we examined hormonal responses of Black-legged Kittiwake (*Rissa tridactyla*) chicks to experimental variations in energy content and nutritional quality (low or high lipid to protein ratio, LPR) of their food. Starting at the age of 10 days, chicks were fed either high or low LPR fish at 30, 50, 70 and 100% of ad libitum energy intake. After 20 days of treatment, chicks were exposed to a standardized acute handling and restraint stress protocol, where a baseline sample was taken immediately after taking a chick from the nest, and three additional blood samples were taken at intervals up to 50 min. Testosterone and corticosterone titres in plasma were measured via radioimmunoassay. We found that baseline testosterone levels were not significantly affected by the experimental treatments. Food-restricted chicks had elevated baseline and acute stress-induced levels of corticosterone compared to chicks fed ad libitum. An elevation of circulating levels of corticosterone in energetically stressed individuals was further magnified by low nutritional quality of food. Baseline and acute stress-induced corticosterone levels of chicks were negatively correlated with their fat reserves. We conclude that the physiological condition of Black-legged Kittiwake chicks can be assessed reliably by measuring circulating levels of corticosterone. We discuss short- and long-term effects of elevated corticosterone secretion in food-stressed nest-bound chicks.

Introduction

Seabirds feed their young with food that varies in its abundance and nutritional quality (Hislop et al. 1991; Hunt et al. 1996a, b; Van Pelt et al. 1997). Furthermore, when parents have a choice, they provision their young with the most energy-rich food [usually due to a high lipid to protein ratio (LPR)] and feed themselves on lower quality food (Bradstreet and Brown 1985; Swihart and Johnson 1986; Piatt 1987; Vermeer et al. 1987). The major factors shaping the decision of birds to provision their young with energy-rich food are thought to be short- and long-term costs and benefits to foraging parents (e.g., Orians and Pearson 1979; Cuthill and Kacelnik 1990). As a short-term benefit, feeding young with energy-rich food maximizes energy delivery per unit of energy spent by parents during foraging (Waite and Ydenberg 1996). As a long-term benefit, the enhanced physiological condition of young reared on energy-rich food might facilitate future survival of those young, thereby increasing reproductive fitness of a 'prudent' parent (Clutton-Brock 1991; Wright et al. 1998). Thus, the sensitivity of chicks to the content of exogenous nutrients can be an important factor influencing parental decisions to feed their young energy-rich food. The functional relationship between the quality of food and the physiological condition of young birds is not well studied (Boag 1987; Johnston 1993). In this paper, we examine whether variations in energy consumption *or* nutritional quality of food (LPR) affects the physiological condition of growing seabird chicks.

The physiological condition of seabird chicks is difficult to assess because they may retard growth processes and decrease metabolic rates in response to dietary restrictions. As a result, they still may fledge successfully

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despite severe food shortages during their development (Cherel et al. 1988; Kitaysky 1996; Øyan and Anker-Nilssen 1996). Controlled experiments have shown that food-related retardation of growth can account for the lower body mass and smaller body size of the young at fledging when compared to the young raised on ad libitum nutritional regimes (Boag 1987; Kitaysky 1996). However, growth rates and body mass of young seabirds at fledging are not reliable predictors of their post-fledging survival (Lloyd 1979; Hedrgren 1981; Harris and Rothery 1985). These traditional methods of assessing physiological condition of chicks provide little insight into the consequences.

The physiological condition of birds can also be measured using well-characterized responses of adreno-cortical hormones to stress (Wingfield et al. 1997a). Food-related stress is usually associated with depleted fat reserves and elevated levels of corticosterone in the circulation of affected animals (Axelrod and Reisine 1984; Cherel et al. 1988, 1992; Wingfield 1994). Elevated plasma corticosterone levels can change metabolic pathways so that nutritionally stressed individuals rely on catabolism of proteins to fuel their activities (Axelrod and Reisine 1984; Cherel et al. 1992). In addition, the pattern and extent of corticosterone secretion following the application of a standardized stressor such as capture, handling and restraint, can also indicate the potential for stress effects (Wingfield 1994).

The relationship between acute stress-induced levels of corticosterone and amounts of endogenous energy resources in nest-bound chicks is not well known. If this relationship is similar to those observed in adults and young independent birds, nest-bound chicks with large fat reserves should have lower baseline levels of corticosterone and recover from induced stress back to the baseline faster compared to nutritionally-stressed chicks with depleted fat reserves (Wingfield 1994; Heath and Dufty 1998; but see Romero et al. 1998).

In this study we examined the relationships among energy intake, diet quality, body composition and standardized acute stress-response (sensu Wingfield et al. 1992) in captive Black-legged Kittiwake (*Rissa tridactyla*) chicks. The effects of energy intake and diet quality on accumulation of fat reserves, growth and development of Black-legged Kittiwake chicks are addressed elsewhere by Romano et al. (personal observations). They found that food-restricted chicks grew at slower rates and accumulated smaller fat reserves compared to chicks fed ad libitum. The major goals of this study were: (1) to test whether the quality or energy content of diet are important in determining the physiological condition of growing chicks, as reflected in their baseline and acute stress-induced levels of corticosterone, and (2) to examine whether the quantities and composition of endogenous energy reserves affect a chick's adrenocortical stress-response. For comparison with a natural system, we also measured adrenocortical response of wild Black-legged Kittiwake chicks exposed to a standardized stressor.

In Black-legged Kittiwakes, a cliff-nesting gull with a maximum brood of three, a hungry chick can improve its chances of survival by begging for food from parents and by eliminating nest-mates (Braun and Hunt 1983). In nest-bound chicks begging and aggressive behaviors might be facilitated by increased concentration of testosterone (Schwabl 1996a). Thus, we also examined plasma levels of testosterone in captive and wild chicks.

Materials and methods

One-week-old free-living Black-legged Kittiwake chicks were taken from their nests, kept in captivity in individual nest boxes, and fed a mixture of forage fish given ad libitum until the experiment. Food was provided in small dishes placed on the bottom of nest boxes. Starting at the age of 10 days post-hatch, either low quality fish, Walleye Pollock, *Theragra chalcogramma* (LPR = 0.299), high quality Pacific Herring, *Clupea harengus* (LPR = 1.47), or Pacific Sandlance, *Ammodytes hexapterus* (LPR = 0.813), were fed to chicks for 20 days (Table 1). The energy content of forage fish was determined via proximate analyses of whole fish (see a description of the method below). In 1996, chicks received either 227 kJ day^{-1} of sandlance, 528 kJ day^{-1} of sandlance, or 373 kJ day^{-1} of pollock. In 1997, the dietary treatments were: (1) in two treatments chicks received 373 kJ day^{-1} of either pollock or herring, and (2) in two treatments chicks received 717 kJ day^{-1} of either pollock or herring. The total amount of food given to the chicks was 100 g (wet mass) day^{-1} for all treatments except for 227 kJ day^{-1} of sandlance (43 g day^{-1}), 373 kJ day^{-1} of herring (52 g day^{-1}), and 717 kJ day^{-1} of pollock (192 g day^{-1}). Daily energy intake of Black-legged Kittiwake chicks fed ad libitum was previously measured at 720 ± 29.3 kJ day^{-1}, $n = 5$ (Kitaysky and Belogubova 1988). Therefore, in this study chick energy intake was reduced to

Table 1 Experimental protocols and body mass attained by chicks at the end of the experiment (M. Romano, D.D. Roby, J.F. Piatt, personal observation). (*LPR* lipid to protein ratio)

Diet composition	LPR	Thiamine	Food intake (wet, g day^{-1})	Energy intake (kJ day^{-1})	Body mass (wet, g)		
					mean	SE	n
Sandlance, captives	0.813	no	43	227	194.6	2.76	7
Sandlance, captives	0.813	no	100	528	363.4	4.34	7
Sandlance, wild	0.813	no	100	545	362.3	5.81	8
Pollock	0.299	no	100	373	258.9	4.47	7
Pollock	0.299	yes	100	373	261.3	2.36	6
Pollock	0.299	yes	192	717	394.3	7.02	6
Herring	1.470	yes	52	373	290.4	4.52	5
Herring	1.470	yes	100	717	408.2	13.3	6

30, 50, 70 and 100% of the ad libitum ration. Because we used pre-frozen fish, in 1997 all chicks received a daily supplement of one-half of a Seatabs vitamin (Pacific Research Labs) in their food, which included 50 mg of thiamine. To control for possible effects of captivity on the stress-response of the experimental birds, free-living kittiwake chicks (alpha-chicks from broods of two that were similar to the experimental birds' ages) were exposed to handling stress, and blood samples were taken as described below. The diet of the wild chicks consisted of mostly sandlance (J.F. Piatt personal observation). Daily energy intake, based on wild chick diet composition and their growth rates, was estimated at 545 kJ day^{-1} (J.F. Piatt personal observation).

A blood sample of undisturbed post-absorptive (after 6–7 h of overnight fast) chicks (at age 7–10 days) was taken at the beginning of the experiment. At the end of the experiment (at age 29–31 days), post-absorptive chicks were exposed to a standardized acute handling and restraint stress protocol, where the first blood sample (baseline) was taken immediately after taking a chick from the nest, and three additional blood samples (acute stress response) were taken at intervals up to 50 min after capture. Blood samples were collected by puncturing the alar vein and collecting blood in 100-μl heparinized hematocrit tubes. All captive (except one individual fed at 717 kJ day^{-1} of herring for which only a baseline sample was collected) and wild chicks were bled between 1000 hours and 1400 hours according to the following standardized technique. A first sample was collected immediately after taking a chick from the nest; further samples were taken at 10, 30 and 50 min. The first blood samples provided baseline levels of steroids. After each sample, blood flow was stopped by the application of cotton, and birds were placed individually into opened plastic buckets. After blood collection, hematocrit tubes were emptied into 0.5-ml vials, which were stored on ice (in the field) or in a refrigerator at 4 °C (in the laboratory). Blood samples were centrifuged and plasma collected within 12 h.

Plasma samples were frozen at −20 °C and transported to J.C. Wingfield's laboratory at the University of Washington for radio-immunoassay analyses (for details see Wingfield and Farner 1975; Wingfield et al. 1992). The concentrations of steroids in plasma samples were measured from 20 μl plasma for corticosterone and 200 μl plasma for testosterone analyses. To determine the plasma concentrations of testosterone, we used only baseline samples of plasma. Steroid concentrations were measured in duplicate for each sample after extraction in 4 ml dichloromethane. Recovery values (ranging from 80% to 90%) following extraction were used to adjust assayed concentrations of steroids. Intra- and inter-assay coefficients of variation were 8% and 11%, respectively.

At age 31 days post-hatch, the experimental birds were anesthetized with di-ethyl ether and killed via cervical dislocation. Carcasses were frozen at −20 °C until they were transported to the D.D. Roby's laboratory at the University of Oregon, Corvallis, where proximate analyses of the whole body were conducted (M. Romano, D.D. Roby and J.F. Fiatt, personal observation). Moisture content was determined by air-drying plucked carcasses to a constant mass at 60 °C in a forced convection oven. Total body lipids were determined by the extraction of aliquots of dried homogenate in a Soxhlet apparatus with petroleum ether as a solvent. We used total body lipids as a measure of endogenous energy reserves (assuming energy equivalent of lipids at 39.4 kJ g^{-1}; Schmidt-Nielsen 1991). We used dry lean body mass as a measure of the accumulation of body tissues during the experiment.

Statistical analyses

The effects of the experimental treatments, daily energy intake, quality of the food, thiamine supplement, and effects of captivity on baseline levels of steroids were examined with independent samples tests (followed by planned comparison Post Hoc tests), where experimental treatments were used as a factor. The effects of the experimental treatments, daily energy intake, thiamine supplement and captivity on acute stress-induced levels of corticosterone were examined with repeated-measures ANOVA, where experimental treatments were used as factors and samples obtained from

the same chick during the acute stress protocol as repeated measures. The effects of chicks' body lipids and lean dry body mass on baseline levels of corticosterone and stress response to handling (expressed as a maximal level of corticosterone achieved during 50 min of restraint) were examined by using stepwise multiple regression analyses.

During statistical analyses, initial data were tested for assumptions required by parametric statistical tests according to Sokal and Rohlf (1981). If these data violated assumptions they were log$_{10}$-transformed and examined again. All computations were performed by using SYSTAT statistical package (Wilkinson 1992). Statistical significance was assumed at $P < 0.05$.

Results

Effects of food-stress on baseline levels of the steroids

Baseline levels of corticosterone were not significantly different among the treatments prior to the experiment ($F_{6,38} = 0.121$, $P = 0.993$; Fig. 1). The experimental treatments had a highly significant effect on baseline levels of corticosterone ($F_{6,38} = 8.551$, $P < 0.001$; Fig. 1).

Baseline levels of corticosterone were significantly elevated among the captive chicks fed 227 kJ day^{-1} of sandlance compared to those of chicks fed 528 kJ day^{-1} of sandlance ($t_{13} = 2.58$, $P = 0.023$; Fig. 1). Baseline levels of corticosterone were not significantly different among the captive chicks fed 528 kJ day^{-1} of sandlance and among the wild chicks fed ca. 545 kJ day^{-1} of sandlance ($t_{14} = 0.28$, $P = 0.787$; Fig. 1).

Baseline levels of corticosterone were significantly elevated among the captive chicks fed 373 kJ day^{-1} of pollock or herring compared to those of the chicks fed 717 kJ day^{-1} of pollock or herring ($F_{1,19} = 27.83$, $P < 0.001$). Baseline levels of corticosterone also depended on the type of prey consumed (diet composi-
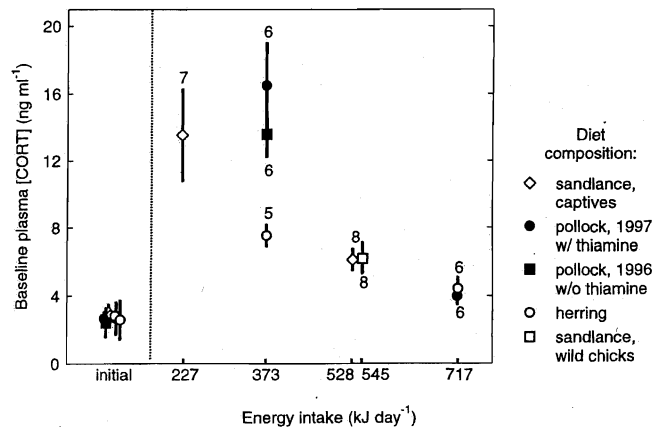

Fig. 1 Baseline levels of corticosterone (means ± SE, n) of 4-week-old Black-legged Kittiwake chicks in relation to daily energy intake (30, 50, 70 and 100% of the ad libitum) and diet composition [lipid to protein ratio (LPR): pollock = 0.299, sandlance = 0.813, herring = 1.47]. All chicks were reared in captivity on the experimentally controlled diets except wild chicks, which were fed by their parents at ca. 545 kJ day^{-1} of sandlance; "initial" represents corticosterone levels of captive chicks prior to the experimental treatments

tion × daily energy intake interaction: $F_{1,19} = 4.67$, $P = 0.044$; Fig. 1). In particular, baseline corticosterone levels were significantly higher among the captive chicks that were fed 373 kJ day^{-1} of pollock (low quality food) compared to those among the chicks fed 373 kJ day^{-1} of herring (high quality food) (Post Hoc test: $P = 0.013$; Fig. 1). However, baseline levels of corticosterone were statistically indistinguishable among the captive chicks that were fed 717 kJ day^{-1} of pollock or herring (Post Hoc test: $P = 0.815$; Fig. 1).

Presence of thiamine supplements did not affect corticosterone levels. In particular, baseline levels of corticosterone were not significantly different among the captive chicks fed 373 kJ day^{-1} of pollock with (in 1997) and without (in 1996) thiamine supplement ($t_{11} = 0.952$, $P = 0.362$; Fig. 1).

The experimental treatments did not affect baseline levels of testosterone (Kruskal-Wallis test: $H = 8.66$, $df = 7$, $P = 0.278$; Fig 2). Regardless of the experimental treatment, plasma levels of testosterone were low in most of the captive and in all of the wild chicks (Fig. 2).

Acute stress-induced levels of corticosterone

All captive and free-living chicks responded to an acute standardized stressor by a rapid increase in secretion of corticosterone (Figs. 3, 4).

Acute stress-induced levels of corticosterone were significantly higher among the captive chicks fed 227 kJ day^{-1} of sandlance compared to those among the chicks fed 528 kJ day^{-1} of sandlance (Fig. 3; daily energy intake effect: $F_{1,13} = 34.16$, $P < 0.001$; acute stress effect: $F_{3,39} = 12.1$, $P < 0.001$). The adrenal responses

Fig. 3 Adrenal response to a standardized handling and restraint stressor in 4-week-old Black-legged Kittiwake chicks fed sandlance, LPR = 0.813, (means ± SE, sample sizes are as shown in Fig. 1)

were statistically indistinguishable among the captive chicks fed 528 kJ day^{-1} of sandlance and the wild chicks fed ca. 545 kJ day^{-1} of sandlance (Fig. 3; daily energy intake effect: $F_{1,14} = 0.71$, $P = 0.414$; acute stress effect: $F_{3,42} = 12.42$, $P < 0.001$).

The quality of food and daily energy intake significantly affected adrenal responses of the captive chicks fed 373 kJ day^{-1} of pollock or herring compared to those of chicks fed 717 kJ day^{-1} of pollock or herring (quality of food effect: $F_{1,18} = 31.53$, $P < 0.001$; daily energy intake effect: $F_{1,18} = 47.0$, $P < 0.001$; Fig. 4). However, there was a significant interaction between quality of food and daily energy intake ($F_{1,18} = 11.92$, $P = 0.003$; Fig. 4). Chicks in all the treatments responded to a standardized stressor by an increased secretion of corticosterone (acute stress effect: $F_{3,54} = 19.71$, $P < 0.001$), but the adrenal response of the chicks fed with pollock (poor quality food) was higher compared to that of chicks fed with herring (high quality
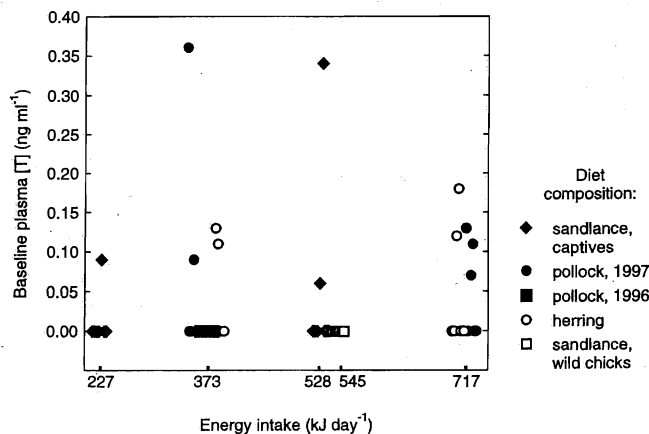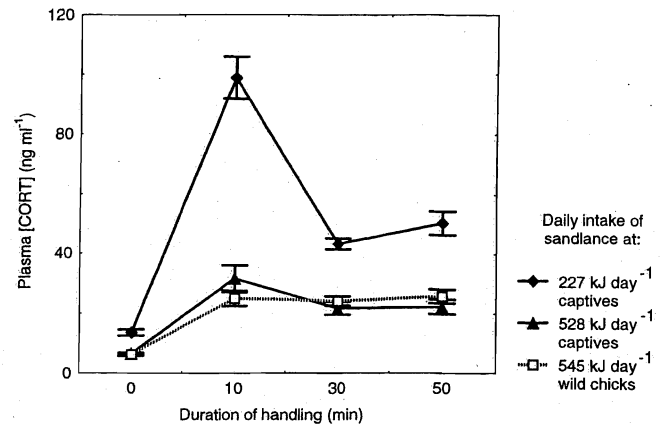

Fig. 2 Baseline levels of testosterone of 4-week-old Black-legged Kittiwake chicks in relation to daily energy intake (30, 50, 70 and 100% of the ad libitum) and diet composition (LPR: pollock = 0.299, sandlance = 0.813, herring = 1.47). All chicks were reared in captivity on the experimentally controlled diets except wild chicks, which were fed by their parents at ca. 545 kJ day^{-1} of sandlance. All individual data points are presented; overlapping values have been jittered for illustrative purposes; sample sizes are as shown in Fig. 1
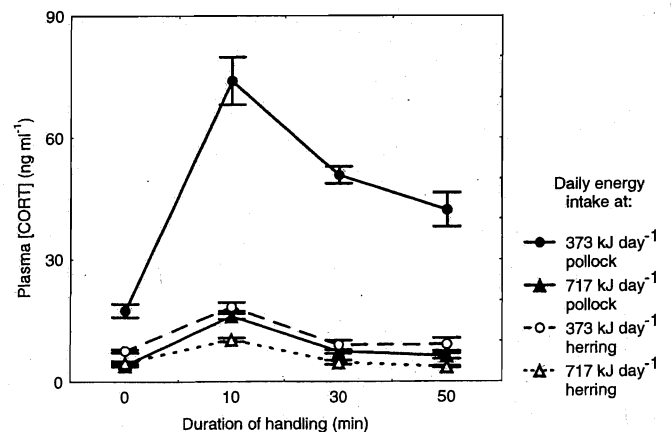

Fig. 4 Adrenal response to a standardized handling and restraint stressor in 4-week-old captive Black-legged Kittiwake chicks fed pollock (LPR = 0.299) and herring (LPR = 0.813) in 1997 (means ± SE, sample sizes are as shown in Fig. 1, except for the herring 717 kJ day^{-1} treatment where $n = 5$)

food) (quality of food × acute stress, interaction term: $F_{3,54} = 3.154$, $P = 0.032$; Fig. 4).

Acute stress-induced levels of corticosterone were not significantly different among the captive chicks fed at 373 kJ day^{-1} of pollock with (in 1998) or without (in 1997) thiamine supplement (thiamine supplement effect: $F_{1,11} = 0.001$, $P = 0.970$; acute stress effect: $F_{3,33} = 13.74$, $P < 0.001$; thiamine supplement × acute stress interaction term: $F_{3,33} = 0.33$, $P = 0.804$).

Body composition and circulating levels of corticosterone

Among the captive chicks, the baseline and maximal acute stress-induced levels of corticosterone were significantly negatively correlated with endogenous energy reserves stored as body lipids (partial correlation coefficient (PC) = -0.407, $F_{1,43} = 39.71$, $P < 0.001$ and PC = -0.606, $F_{1,42} = 62.12$, $P < 0.001$ for the baseline and maximal levels, respectively; Fig. 5). Dry lean body mass was not significantly correlated either with baseline levels (PC = 0.045, $F_{1,43} = 0.086$, $P = 0.770$) or maximal acute stress-induced levels of corticosterone (PC = -0.03, $F_{1,43} = 0.038$, $P = 0.847$).

Food restricted chicks had lower body mass compared to chicks fed ad libitum (Table 1). However, they also retained more body water compared to ad libitum-fed individuals (Fig. 6).

Discussion

In this study we examined hormonal responses of nest-bound Black-legged Kittiwake chicks to experimental
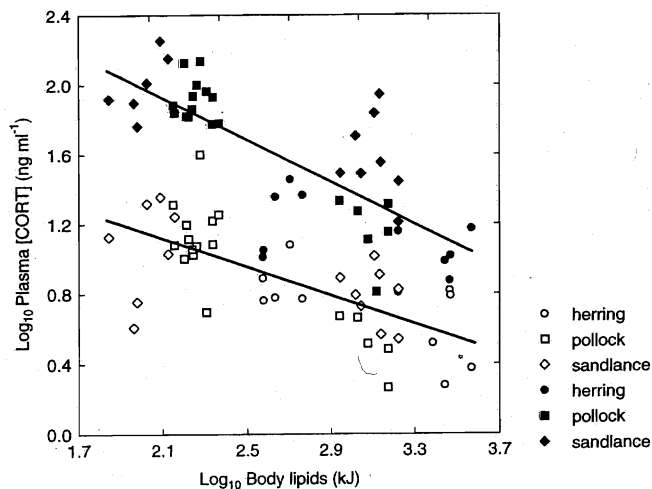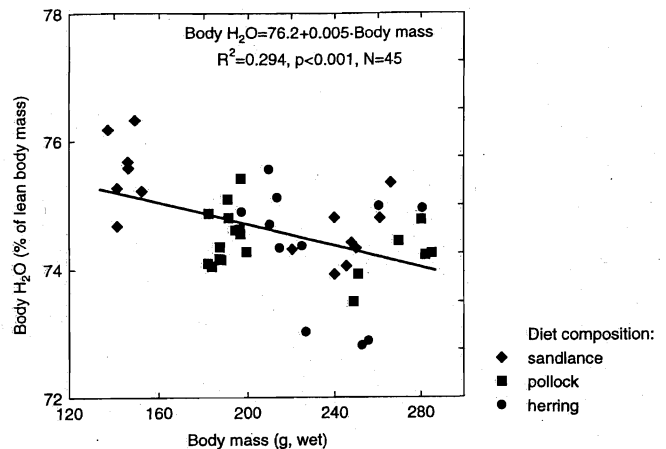

Fig. 6 The relationship between body mass and body H$_2$O in captive 4-week-old Black-legged Kittiwake chicks

variations in energy content and quality of their food. We found that nutritionally stressed chicks had elevated baseline and acute stress-induced levels of corticosterone compared to chicks fed ad libitum. An elevation of circulating levels of corticosterone in energetically stressed individuals was further magnified by the low nutritional quality (LPR) of their food. In particular, diets that were iso-caloric but different in nutritional quality and given to chicks at 50% of ad libitum energy intake, resulted in higher baseline and acute stress-induced levels of corticosterone among chicks raised on the low quality food (low LPR) compared to those among chicks raised on the high quality food (high LPR). Finally, we have shown that baseline and acute stress-induced corticosterone levels of chicks were negatively correlated with endogenous lipid reserves of these chicks rather than with their growth rates (as reflected in lean dry body mass of chicks). Variation in the proportion of high- and low-quality prey species in the diet of Black-legged Kittiwakes is frequently observed in natural situations (e.g., Hunt et al. 1996a, b). In contrast, substantial decreases in chick growth rates are observed only during severe food shortages (A.S. Kitaysky, G.L. Hunt, B. Flint, M. Rubega and M.B. Decker, personal observation; J.F. Piatt personal observation). We conclude that the physiological condition of Black-legged Kittiwake chicks can be assessed reliably from circulating levels of corticosterone.

To the best of our knowledge, this paper represents the first experimental demonstration of the adrenal response of nest-bound (semi-precocial) chicks to a standardized acute stressor in relation to dietary restrictions. Among birds that have precocial young, such as the domestic fowl (*Gallus domesticus*) and the mallard (*Anas platyrhynchos*), the baseline plasma concentration of corticosterone in chicks fed ad libitum does not change significantly during the first 4 weeks after hatching (reviewed in Holmes et al. 1990). Freeman and co-authors (1981) found that reducing food intake to 75% of ad libitum causes an increase in plasma corticosterone

Fig. 5 The relationships between body lipids and baseline (*open symbols*, Log$_{10}$ [CORT] = $1.972 - 0.407 \cdot$ Log$_{10}$ body lipids, $r^2 = 0.48$, $P < 0.001$, $n = 45$) and acute-stress induced maximal levels (*solid symbols*, Log$_{10}$ [CORT] = $3.201 - 0.606 \cdot$ Log$_{10}$ body lipids, $r^2 = 0.60$, $P < 0.001$, $n = 44$) of corticosterone in captive 4-week-old Black-legged Kittiwake chicks

concentration after 1 week of restriction in domestic fowl chicks. In mallard chicks fed ad libitum, a restraint for 30 min caused a significant increase in corticosterone concentration and the adrenal stress response was stronger in the chicks during first 2 days post-hatch than between 3 weeks and 4 weeks of post-hatch (Holmes et al. 1990). Similarly, we did not find a significant change in baseline levels of corticosterone among Black-legged Kittiwake chicks fed ad libitum between 2 weeks and 4 weeks of postnatal life (Fig. 1). Black-legged Kittiwake chicks responded to a standardized stressor by increasing the secretion of corticosterone, which was significantly correlated with their nutritional state (e.g., body lipids). Although adrenal responsiveness of precocial and semi-precocial chicks to environmental stressors appear to be similar, the behavioral effects of increased secretion of corticosterone might be different between self-feeding chicks (precocial) and chicks provisioned by parents (semi-precocial; see below).

It is possible that the variations in adrenal response of Black-legged Kittiwake chicks observed in this study resulted from conditions of captivity, rather than a functional response to variations in energy content and quality of food. However, baseline and acute stress-induced levels were identical among free-living and captive chicks that were fed at similar rates of energy intake and with food of similar nutritional quality. In addition, captive chicks in all treatments were subject to similar controlled conditions. The only differences between them being the energy content and nutritional quality of their food. Other studies of adrenal response in young birds to a standardized acute stressor did not indicate a habituation of those birds to frequent handling (Freeman et al. 1981; Dufty and Belthoff 1997; Heath and Dufty 1998).

In birds, corticosterone is also involved in osmoregulatory processes (Holmes et al. 1990; Bentley 1998). Black-legged Kittiwake chicks fed the reduced amounts of food consequently received reduced amounts of water and those chicks may have been dehydrated by the end of the experiment. Salt loading might result in an increase in baseline and acute-stress induced levels of corticosterone in chicks (Holmes et al. 1990). However, we did not find any indication of dehydration among the chicks fed restricted amounts of food. Although these chicks had lower body mass (Table 1) they also retained more body water compared to ad libitum-fed individuals (Fig. 6). Thus, it is not likely that the variations in corticosterone secretions resulted from neuroendocrine regulation of body fluids in the experimental Black-legged Kittiwake chicks.

Because we fed chicks pre-frozen fish, they could have developed a thiamine deficiency (Geraci 1972). However, the thiamine supplement did not have a significant effect on circulating levels of corticosterone and we therefore conclude that feeding chicks with previously frozen fish did not affect their adrenocortical activity.

Thus, it is reasonable to conclude that the results of this study demonstrate differences in the functional responses of Black-legged Kittiwake chicks to variations in energetic content and nutritional quality of their food.

In the Black-legged Kittiwake, nest-bound chicks appeared to have two behavioral options to improve their nutritional state during food shortages (Braun and Hunt 1983). First, chicks can modify provisioning behavior of their parents by begging more frequently. Second, chicks can increase energy intake by eliminating their siblings. Recent studies have shown that increased concentrations of testosterone in the yolks might facilitate future aggressive and begging behaviors of chicks hatched from those eggs (Schwabl 1996a, b). However, it is possible that yolk testosterone has a developmental effect on chick growth and metabolic rate (Schwabl 1996a), rather than a regulatory effect on begging behavior. For example, Nunez-de la Mora and co-authors (1996) did not find a correlation between testosterone levels and a dominance status in chicks of the Blue-footed Booby (*Sula nebouxii*) exposed to short-term (2 days) food deprivation. In fact, testosterone concentrations were not detected in Blue-footed Booby chicks in this study at all. Similary, we did not find a significant relationship between nutritional status and testosterone concentrations in captive Black-legged Kittiwake chicks exposed to the long-term nutritional limitations at 30, 50 and 70% of ad libitum food intake. Our results showed that Black-legged Kittiwake chicks are capable of testosterone secretion, but this was not correlated with their nutritional state (Fig. 2). Thus, seabird chicks did not respond to either short-term (Nunez-de la Mora et al. 1996) or long-term (this study) food stress by increasing secretion of testosterone. Sibling aggression in nest may thus be independent of circulating testosterone, but a possible developmental effect of testosterone in yolk may still apply.

Alternatively, nest-bound seabird chicks increase secretion of corticosterone in response to a depletion of endogenous energy reserves, and this might be proportionally related to the begging rate of chicks. Nunez-de la Mora and co-authors (1996) found that in the Blue-footed Booby, baseline corticosterone levels were twice as high in beta-chicks than in alpha-chicks after 2 days of food deprivation. Corticosterone levels returned to normal after the chicks resumed feeding. Because beta-chicks are likely to have smaller energy reserves than alpha-chicks, we expect that they would respond to fasting with a stronger increase in baseline levels of corticosterone. The results of our study support this hypothesis: corticosterone secretion increases log-linearly with depletion of endogenous energy reserves (Fig. 5). In a recent experimental study (A.S. Kitaysky, J.C. Wingfield, J.F. Piatt, personal observation), we showed that an elevated concentration of corticosterone increases begging behavior in free-living Black-legged Kittiwake chicks and that parents respond to the change in their chicks' begging by providing more food. Therefore, we conclude that Black-legged Kittiwake chicks first respond to food deprivation by an increase in

corticosterone secretion, which is inversely related to energy reserves. An increase in corticosterone secretion is then followed by an increase in begging rate and, finally, followed by an increase in food provisioning of those chicks by parents. The results of this study also suggest that if food is in shortage, feeding a chick with prey that is high in fat content would decrease a corticosterone secretion of that chick and would decrease its begging rate.

Short-term increases in corticosterone secretion might improve survival of adult animals during stressful conditions by facilitating foraging behavior, dispersal, and mobilization of stored energy resources to fuel increased locomotory activities (Astheimer et al. 1992; Bray 1993; Wingfield et al. 1997b). In contrast, chronic elevation of corticosterone is known to suppress memory and immune systems, promote wasting of muscle tissue, and cause neuronal cell death (Sapolsky et al. 1986, Sapolsky 1992; also reviewed in Wingfield 1994). If chronically elevated, corticosterone may cause similar deleterious effects in juveniles as in adults. In many species of seabirds, offsprings are independent of their parents after fledging and they must quickly learn to forage after leaving the nest. Impaired learning ability of chicks reared on a poor quality diet might therefore affect post-fledging survival of those chicks. Our study suggests that the energetic content *and* nutritional quality of food fed to chicks are both determinants of physiological stress in chicks. The long-term effects of chronically increased levels of corticosterone on learning, memory, and survival of young birds deserve futher investigation.

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