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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.

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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

despite severe food shortages during their development (Cherel et al. 1988; Kitaysky 1996; θyan 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 radioimmunoassay 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-
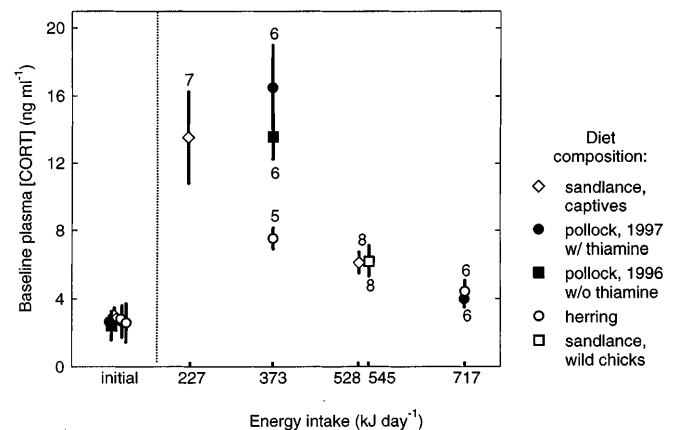

Fig. 1 Baseline levels of corticosterone (means ± SE, n) of 4-week-old Black-legged Kittiwake chicks in relation to daily energy intake (30, 50, 70 and 100% of the ad libitum) and diet composition [lipid to protein ratio (LPR): pollock = 0.299, sandlance = 0.813, herring = 1.47]. All chicks were reared 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
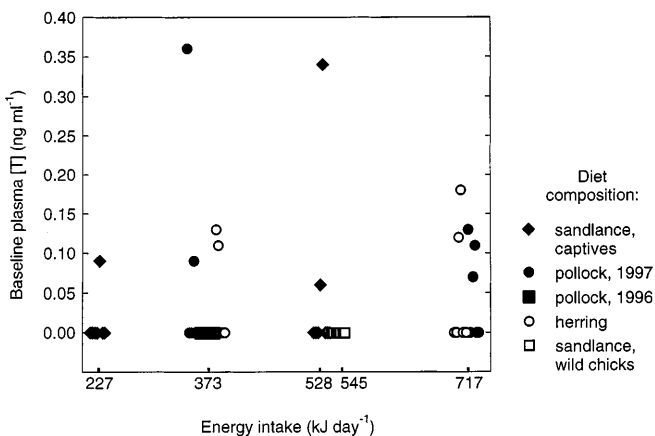

Fig. 3 Adrenal response to a standardized handling and restraint stressor in 4-week-old Black-legged Kittiwake chicks fed sandlance, LPR = 0.813, (means ± SE, sample sizes are as shown in Fig. 1)

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
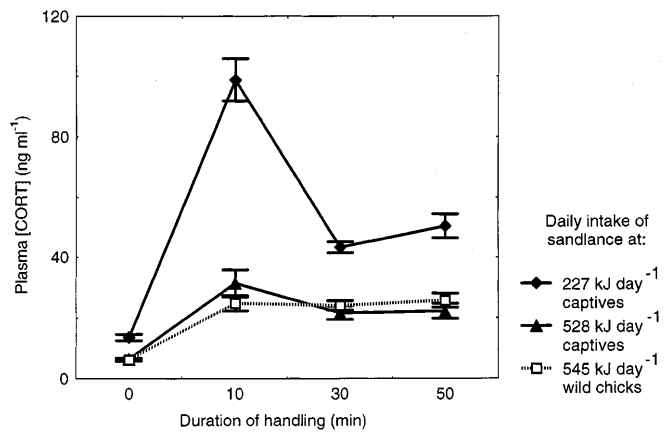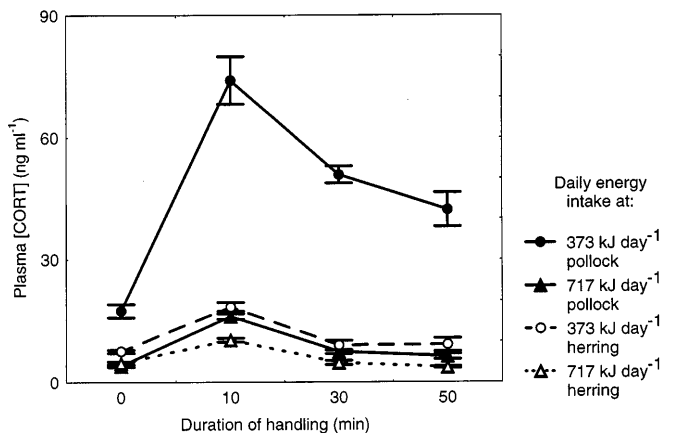

Fig. 4 Adrenal response to a standardized handling and restraint stressor in 4-week-old captive Black-legged Kittiwake chicks fed pollock (LPR = 0.299) and herring (LPR = 0.813) in 1997 (means ± SE, sample sizes are as shown in Fig. 1, except for the herring 717 kJ day^{-1} treatment where $n = 5$)

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
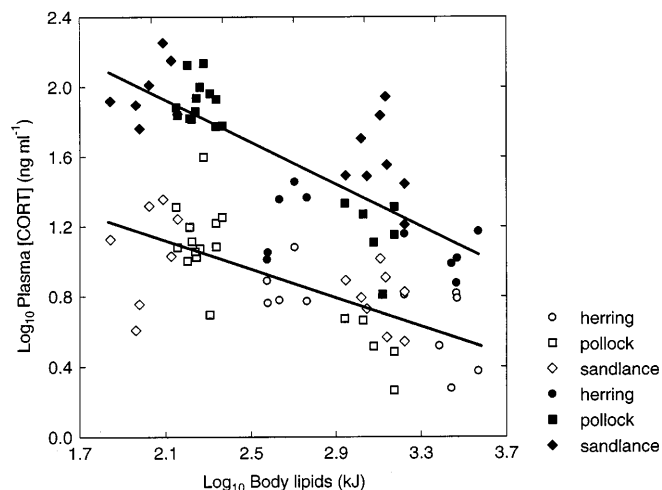

Fig. 6 The relationship between body mass and body H_2O in captive 4-week-old Black-legged Kittiwake chicks

Fig. 5 The relationships between body lipids and baseline (*open symbols*, Log_{10} [CORT] = 1.972 − 0.407 · 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 · Log_{10} body lipids, $r^2 = 0.60$, $P < 0.001$, $n = 44$) of corticosterone in captive 4-week-old Black-legged Kittiwake chicks
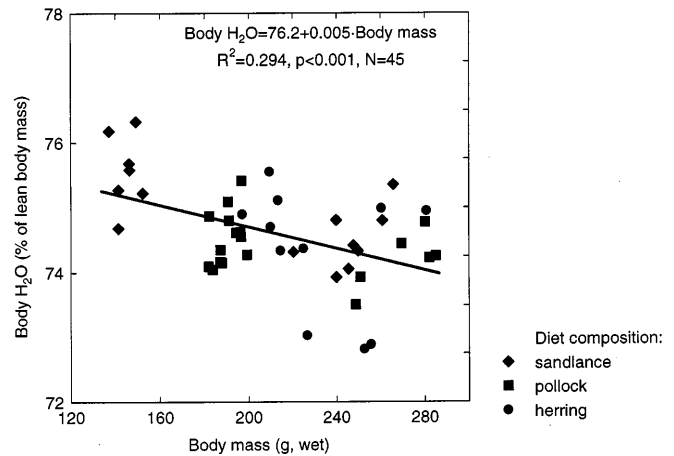
variations in energy content and quality of their food. We found that nutritionally stressed chicks had elevated baseline and acute stress-induced levels of corticosterone compared to chicks fed ad libitum. An elevation of circulating levels of corticosterone in energetically stressed individuals was 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

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.

References

Astheimer LB, Buttemer WA, Wingfield JC (1992) Interactions of corticosterone with feeding, activity and metabolism in passerine birds. Ornis Scand 23: 355–365

Axelrod J, Reisine TD (1984) Stress hormones: their interaction and regulation. Science 224: 452–459

Bentley PJ (1998) Comparative vertebrate endocrinology. 3rd edn. Cambridge University Press, Cambridge

Boag PT (1987) Effects of nestling diet on growth and adult size of zebra finches (*Poephilla guttata*). Auk 104: 413–441

Bradstreet MSW, Brown RGB (1985) Feeding ecology of the Atlantic Alcidae. In: Nettleship DN, Birkhead TR (eds) The Atlantic Alcidae. Harcourt Brace Jovanovich, Toronto, pp 264–318

Braun BM, Hunt GL (1983) Brood reduction in Black-legged Kittiwakes. Auk 100: 469–476

Bray MM (1993) Effect of ACTH and glucocorticoids on lipid metaboilism in the Japanese quail, *Coturnix coturnix japonica*. Comp Biochem Physiol A 105: 689–696

Cherel Y, Robin J-P, Le Maho Y (1988) Physiology and biochemistry of long-term fasting in birds. Can J Zool 66: 159–166

Cherel Y, Robin J-P, Heitz A, Calgary C, Le Maho Y (1992) Relationships between lipid availability and protein utilization duriong prolonged fasting. J Comp Physiol B 162: 305–313

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton, New Jersey

Cuthill IC, Kacelnik A (1990) Central place foraging: a re-appraisal of the "loading effect". Anim Behav 40: 1087–1101

Dufty AM Jr, Belthoff JR (1997) Corticosterone and the stress response in young western screech-owls: effects of captivity, gender, and activity period. Physiol Zool 70: 143–149

Freeman BM, Maning CC, Flack IH (1981) The effects of restricted feeding on adrenal cortical activity in the immature domestic fowl. Brit J Poult Sci 22: 295–303

Geraci JR (1972) Experimental thiamine deficiency in captive harp seals, *Phoca groenlandica*, induced by eating herring, *Clupea harengus*, and smelt, *Osmerus mordax*. Can J Zool 50: 170–195

Grossman R, Kisliuk S, Xu B, Muhlbauer E (1995) The hypothalamo-neurohypophyseal system in birds. Adv Exp Med Biol 395: 657–666

Harris MP, Rothery P (1985) The post-fledging survival of young puffins, *Fratercula arctica*, in relation to hatching date and growth. Ibis 121: 356–361

Heath JA, Dufty AM Jr (1998) Body condition and the adrenal stress response in captive American kestrel juveniles. Physiol Zool 71: 67–73

Hedrgren S (1981) Effects of fledging weight and time of fledging on survival of guillemots in relation to hatching date and growth. Ibis 134: 335–339

Hislop JPG, Harris MP, Smith JGM (1991) Variation in the caloric value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. J Zool (Lond) 224: 501–517

Holmes WN, Cronshow J, Redondo JL (1990) The ontogeny of adrenal steroidogenic function in the Mallard Duck (*Anas platyrhynchos*). In: Wada M, Ishii S, Scanes CG (eds) Endocrinology of birds: molecular to behavioral. Japan Sci Soc Press, Tokyo/Springer, Berlin Heidelberg New York, pp 143–158

Hunt GL, Decker MB, Kitaysky AS (1996a) Fluctuations in the Bering Sea ecosystem as reflected in the reproductive ecology and diets of kittiwakes on the Pribilof Islands, 1975 to 1990. In: Greenstreet SPR, Tasker ML (eds) Aquatic predators and their prey. Blackwell Scientific, Oxford, pp 142–153

Hunt GL, Kitaysky AS, Decker MB, Dragoo DE, Springer AM (1996b) Changes in the distribution and size of juvenile walley pollock, *Theragra chalcogramma*, as indicated by seabird diets at the Pribilof Islands and by the bottom trawl suveys in the Eastern Bering Sea, 1975 to 1993. NOAA Tech Pub NMFS 126: 125–139

Johnston RD (1993) Effects of diet quality on the nestling growth of a wild insectivorous passerine, the house martin *Delichon urbi*ca. J Funct Ecol 7: 255–266

Kitaysky AS (1996) Behavioral, physiological and reproductive responses of alcids (Alcidae) to variation in food availability. PhD Thesis, University of California, Irvine

Kitaysky AS, Belogubova EG (1988) Chick growth energetics in the Black-Legged Kittiwake (*Rissa tridactyla*). In: Andreev AV, Kondratyev AY (eds) Studies and protection of birds in northern ecosystems.Vladivostok: Far-Eastern Branch, USSR Academy of Sciencies, pp 68–76

Lloyd CS (1979) Factors affecting breeding of razorbills *Alca torda* on Skokholm. Ibis 121: 165–176

Nunez-de la Mora A, Drummond H, Wingfield JC (1996) Hormonal correlates of dominance and starvation-induced aggression in chicks of the Blue-footed Booby. Ethology 102: 748–761

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds) Analyses of ecological systems. Ohio State University Press, Ohio, pp 154–177

θyan HS, Anker-Nilssen T (1996) Allocation of growth in food-stressed Atlantic puffin chicks. Auk 113: 830–841

Piatt JF (1987) Behavioural ecology of common murre and Atlantic puffin predation on capelin: implications for population biology. PhD Thesis, Memorial University of Newfoundland

Romero ML, Soma KK, Wingfield JC (1998) The hypothalamus and adrenal regulate modulation of corticosterone release in redpolls (Carduelis flammea – an arctic-breeding song bird). Gen Comp Endocrinol 109: 347–355

Sapolsky RM (1992) Neuroendocrinology of the stress-response. In: Becker JB, Breedlove SM, Crews D (eds) Behavioral endocrinology. A Bradford book, MIT, pp 287–324

Sapolsky RM, Krey LC, McEwen BS (1986) The neuroendocrinology of stress and aging: the glucocorticosteroid cascade hypothesis. Endocr Rev 7: 284–301

Schmidt-Nielsen K (1991) Animal Physiology: Adaptation and Environment. 5th ed., Cambridge University Press, Cambridge, England

Schwabl H (1996a) Maternal testosterone in the avian egg enhaces postnatal growth. Comp Biochem Physiol A114(3): 271–276

Schwabl H (1996b) Environment modifies the testosterone levels of a female bird and its eggs. J Exp Zool 276: 157–163

Sokal RR, Rohlf FJ (1981) Biometry. Freeman, San Francisco

Swihart RK, Johnson SG (1986) Foraging decisions of American robins: somatic and reproductive tradeoffs. Behav Ecol Sociobiol 19: 275–282

Van Pelt TI, Piatt JF, Lance BK, Roby DD (1997) Proximate composition and energy density of some North Pacific forage fish. Comp Biochem Physiol 118: 1393–1398

Vermeer K, Sealy SG, Sanger GA (1987) Feeding ecology of the Alcidae in the eastern North Pacific Ocean. In: Croxall JP (ed) Seabirds: feeding ecology and role in marine ecosystems. Cambridge University Press, pp 189–228

Waite TA, Ydenberg RC (1996) Foraging currencies and the load-size decision of scatter-hoarding grey jays. Anim Behav 51: 903–916

Wilkinson L (1992) Systat for Windows. SYSTAT, Evanston

Wingfield JC (1994) Modulation of the adrenocortical response to stress in birds. In: Davey KG, Peter RE, Tobe SS (eds) Perspectives in comparative endocrinology. National Research Council of Canada, Ottawa, pp 520–528

Wingfield JC, Farner DS (1975) The determination of five steroids in avian plasma by radioimmunoassay and competitive protein binding. Steroids 26: 311–327

Wingfield JC, Vleck CM, Moore MC (1992) Seasonal changes of the adrenocortical response to stress in birds of Sonoran Desert. J Exp Zool 264: 419–428

Wingfield JC, Bruener C, Jacobs J (1997a) Corticosterone and behavioral responses to unpredictable events. In: Harvey S, Etches RJ (eds) Perspectives in avian endocrinology. Journal of Endocrinology, Bristol, pp 267–278

Wingfield JC, Hunt K, Bruener C, Dunlap K, Fowler GS, Freed L, Lapson J (1997b) Environmental stress, field endocrinology, and conservation biology. In: Clemmons JR, Buchhols R (eds) Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge, pp 95–131

Wright J, Both C, Cotton PA, Bryant D (1998) Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. J Anim Ecol 67: 620–634