SHORT NOTE

Food restricted Tufted Puffin (*Fratercula cirrhata*) nestlings increase vocal activity during handling without modulating total or free corticosterone

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Abstract In some species, corticosterone (CORT) appears to play a role in the control of begging behavior. Because of the potentially high costs associated with chronic elevation of CORT, it has also been proposed as a mechanism to ensure begging is an honest signal. We determined the effects of moderate food restriction (50% of high calorie treatment) on vocal behavior during handling, and on baseline levels of both total and 'free' unbound CORT in Tufted Puffin (*Fratercula cirrhata*) nestlings. Chick vocalizations during handling were similar to begging calls, and we assumed they were representative of begging behavior. We also measured total and free CORT in free-living Tufted Puffin chicks to determine if hormone levels in our experiment were comparable to natural levels. We found no effect of caloric restriction on either total or free baseline CORT, yet food-restricted nestlings vocalized more intensely during handling than chicks in the high calorie group. Mean plasma concentrations of total and free CORT in experimentally manipulated birds did not differ from levels in free-living nestlings. These results suggest that CORT does not play a role in modulating begging behavior in this species.

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Introduction

Nest-bound chicks are completely reliant on parental provisioning to acquire nutrients and energy for growth and metabolism. Food-deprived nestlings communicate their need for more food by begging. Although begging is generally regarded as an honest signal of nutritional state (Cotton et al. 1996), the mechanisms responsible for ensuring honesty are unclear. Corticosterone (CORT), a steroid hormone that stimulates mobilization of endogenous energy stores and elicits behavioral changes that promote survival (reviewed in Sapolsky et al. 2000), has been proposed as a potential mechanism to ensure honest begging behavior (Kitaysky et al. 2001; Loiseau et al. 2008).

In many species, food shortage during growth activates the hypothalamus-pituitary-adrenal (HPA) axis resulting in increased circulating levels of CORT (Nunez-de la Mora et al. 1996, Kitaysky et al. 1999, Walker et al. 2005). Total circulating levels of CORT includes CORT bound to binding globulins (CBGs), as well as an unbound fraction (free CORT) which is thought to represent the concentration of hormone available for diffusion into tissues (Breuner and Orchinik 2002; Love et al. 2004). CBG binds CORT specifically and reversibly, and therefore functions to transport this insoluble hormone to target tissues. CBG may also serve to buffer target tissues from negative effects of elevated CORT and to slow metabolic clearance rates (reviewed in Breuner and Orchinik 2002). In Black-legged Kittiwakes (*Rissa tridactyla*) and House Sparrows (*Passer domesticus*), experimental elevation of CORT increases

begging intensity (Kitaysky et al. 2001; Loiseau et al. 2008). For Kittiwakes, this increase ultimately resulted in greater provisioning rates by attending adults (Kitaysky et al. 2001). However, chronic elevation of CORT has a variety of negative effects including muscle wasting, impaired cognitive abilities, and reduced immune function (Saino et al. 2003; Kitaysky et al. 2006; Loiseau et al. 2008). Thus, short term elevation of CORT may benefit nestlings by promoting mobilization of stored energy reserves and inducing parents to increase provisioning whereas the costs of chronic elevation may ensure begging behavior is honest (Kitaysky et al. 2001; Loiseau et al. 2008).

However, in species subjected to extended periods of reduced energy intake, the high costs associated with chronic elevation of CORT may lead to non-responsiveness or suppression of the HPA axis during nutritional restriction. Kitaysky et al. (2005) demonstrated that for Tufted Puffins (*Fratercula cirrhata*), a species in which nestlings routinely experience chronic food shortages, captive chicks respond to severe dietary restriction by decreasing plasma total CORT concentrations. The negative relationship between nutritional state and total CORT presents a potential paradox: CORT is highest in well-fed puffin chicks and in some species CORT is known to invoke begging behavior. This apparent paradox may be resolved in three ways: (1) CORT may inhibit, rather than promote, begging behavior in Tufted Puffins, (2) CBGs may be modulated in response to restriction such that free CORT in Tufted Puffin nestlings is actually negatively correlated with nutritional state, or (3) begging behavior may not be triggered by CORT in this species.

In this study, we experimentally altered the nutritional state of free-living Tufted Puffin nestlings by preventing adults from provisioning them and feeding them by hand. Chicks responded to hand provisioning by making repeated "peep-peep" vocalizations, which we assume to be representative of begging behavior (Piat and Kitaysky 2002). This enabled us to examine the relationships between free CORT, total CORT, nutritional state, and begging behavior. We also measured total CORT and free CORT in free-living Tufted Puffins to determine whether hormone levels of manipulated birds were similar to levels in free-living chicks.

Methods

We conducted a feeding experiment with Tufted Puffin nestlings reared in their natural burrows on Cliff Island in Chiniak Bay, Kodiak Island, AK (57°40′N, 152°20W) in 2004. Tufted Puffins are monogamous with both parents caring for a single chick raised in a burrow excavated in the soil. We located 13 free-living puffin nestlings during the early stages of chick-rearing and excavated vertical access holes which were patched with flat rocks to permit later access to the nesting chamber. When chicks were estimated to be approximately 10 days old, based on wingchord measurements, we blocked burrow entrances to prevent adults from provisioning their young and began feeding the chicks one meal per day in the morning. On the first day of the trial, chicks were fed several fish by hand, and the remaining fish were placed on the ground inside their burrows. On all subsequent days, nestlings were fed by placing the entire meal on top of a plastic bag and placing the bag on the floor of the nesting chamber. Nestlings were removed and handled (mass taken) prior to feeding every 2–3 days during the first 9 days of the trial to ensure they were gaining mass. After day 9, chicks were handled and mass was taken using a spring scale (± 2 g) every 4–5 days prior to feeding. We fed nestlings either 120 g/day (high calorie treatment: 650 kJ/day, $n = 6$) or 60 g/day (low calorie treatment: 325 kJ/day, $n = 7$) of Pacific herring (*Clupea pallasi*) plus a multivitamin supplement. Quantities of fish fed were determined based on a previous captive study (Kitaysky et al. 2005). We expected the caloric intake of the high-calorie group to result in rates of mass growth equivalent to maximum levels observed in the wild and low-calorie birds to grow at slightly below the mean growth rate (reviewed in Piatt and Kitaysky 2002).

We drew blood samples from post-absorptive (24 h after last meal) nestlings by puncture of the alar vein with a 24-gauge needle within 3 min of handling after 9, 18, and 27 days on the controlled diet. Nestlings were fed and bled between 1000 and 1200 hours. Total CORT values were not affected by time of bleed within 3 min of handling ($P = 0.33$), therefore we consider samples to be indicative of baseline levels (Romero and Reed 2005). On two occasions, we were unable to obtain a baseline sample from one of the nestlings in the high calorie group. We also collected baseline blood samples from free-living puffin nestlings ($n = 18$) captured in their burrows on Chiniak Island (located 22 km east of Cliff Island) in 2005. All free-living nestlings were bled when their wingchord lengths were between 120 and 130 mm to minimize potential effects of developmental stage on CORT. This wingchord length is comparable to that of high-calorie and low-calorie nestlings sampled on day 27 of the feeding trial (low-calorie: 120.3 ± 4.0 mm SD; high-calorie: 134.5 ± 3.6 mm). Mean mass of free-living nestlings at time of bleeding was 480.0 ± 47.0 g. We sampled only nestlings from burrows that were not connected to other burrows via underground tunnels. Blood was collected in heparinized 250-µl Natelson blood collecting tubes and transferred into 1.5-ml microcentrifuge tubes which were stored on ice for several hours. Blood samples were

centrifuged, separated, and plasma samples stored frozen (−70°C) until laboratory analyses were performed.

After 22 and 27 days of provisioning nestlings by hand, we recorded whether chicks "begged" (repeated "peep-peep" vocalization; Piatt and Kitaysky 2002) continuously, intermittently, or not at all during the first 20 s following removal from their burrows. We measured vocal activity during handling, rather than when food was added to burrows to ensure measures were standardized across all chicks. The proximity of excavation holes to the nesting chamber as well as the length and size of burrows varied widely between individuals. Tufted Puffins are not known to beg in the absence of parents, and so we assume vocal activity during handling was representative of begging behavior in response to hand feeding. Following collection of the final blood sample, we fed all chicks ad libitum until they reached the age and size of wild fledglings, at which point we removed obstructions from the burrow entrance and allowed them to fledge on their own initiative or released them to the water.

For each plasma sample, we determined CORT concentration in duplicate following extraction in dichloromethane using direct radioimmunoassay as detailed in Wingfield et al. (1992). We determined recovery values, and used these to adjust final assayed concentrations of CORT. Samples from the feeding trial were all run in a single assay, and samples from free-living birds were run in a second assay. Mean recovery was $89 \pm 3\%$ (SD) and $94 \pm 3\%$ in the first and second assay, respectively. Intra- and inter-assay variation were 3 and 4%, respectively. We determined CBG concentrations as described in Love et al. (2004). We determined optimal incubation time (2 h), final plasma concentration (1:450) and CORT affinity ($K_d = 2.33$; SE = 0.196). Exogenous CORT was stripped from plasma by incubating each 10-μl sample with 20 μl dextran-coated charcoal solution for 20 min at room temperature prior to centrifugation at 4,000g for 10 min at 4°C. We analyzed samples for total binding in triplicate and simultaneously determined non-specific binding in duplicate using unlabeled CORT. We did not have sufficient plasma to determine CBGs for five samples; sample size was between five and six for each group in each time period. Following incubation, we separated bound and free radioligand using rapid vacuum filtration (Brandel Harvester) over glass fiber filters (Whatman GF/B, soaked in 25 mM Tris with 0.3% PEI for 1 h before filtering). All samples from the experimental feeding trial were run in a single assay and samples from free-living birds were run in a separate assay. Inter-assay variation was 12% and intra-assay variation ranged between 6 and 7%. Free CORT was estimated using the equation of Barsano and Baumann (1989).

We performed all statistical analyses using SAS 9.1 (SAS Institute) and present data as means ± SD. Nestling masses were available for all birds only on days 0, 9, 18, and 27 of the experiment, therefore only these masses were used in statistical analysis. Total and free CORT values were log-transformed to meet the assumption of normality. Separate repeated-measures mixed models (PROC MIXED) were used to determine the effects of nutritional regime, age, and their interaction on mass, total CORT, and free CORT. Mixed models permit the inclusion of individuals with missing observations. We tested for differences in vocal activity during handling (intermittent, continuous, or no begging) between low and high calorie groups using a likelihood ratio Chi-square test. We tested for differences in total and free CORT between free-living and experimental nestlings using a Student's t test. For this analysis, we used only CORT values from day 27 of the experiment (total CORT: $n = 13$; free CORT: $n = 11$), when experimental chicks were at a similar developmental stage as free-living chicks, based on wingchord measurements. Because we found no treatment effects on CORT (see "Results"), we pooled experimental birds for this analysis.

Ethical note

Tufted Puffin chicks do not have any post-fledging parental care and fledge without parental assistance. Three of the seven food-restricted chicks and three of the six control chicks did not fledge on their own initiative and remained in the nest until they were much older and much larger than free-living fledglings. The cause of this is unclear but it is possible that a reduction in provisioning by parents induces fledging behavior in wild chicks. We examined six burrows approximately mid-way through chick-rearing in the year following this experiment; three burrows had chicks, one burrow had been excavated such that the chamber could no longer be accessed, and one burrow appeared inactive.

Results

Body mass did not differ between treatment groups prior to the experiment ($t = -0.37$, $P = 0.72$). Food restriction severely decreased rate of mass gain (Fig. 1); mass was significantly affected by age ($F_{3,33} = 601.09$, $P < 0.0001$), treatment ($F_{1,11} = 212.77$, $P < 0.0001$), and the interaction between age and treatment ($F_{3,33} = 109.90$, $P < 0.0001$). At age 37 days, the mean difference in body mass between high and low calorie groups was 227.9 g (95% CI: 205.3, 250.2).

Total baseline CORT values were not significantly affected by nutritional restriction ($F_{1,11} = 0.39$, $P = 0.55$)
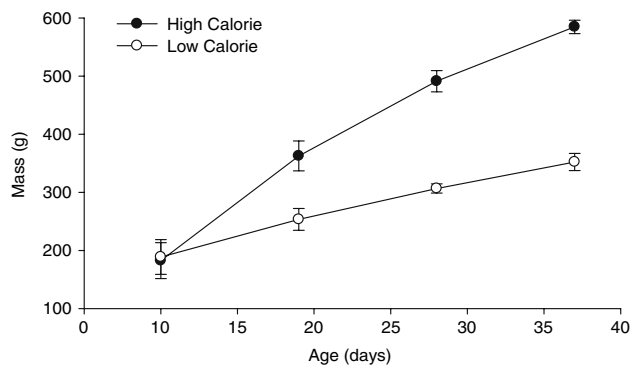
Fig. 1 Changes in mass (mean ± SD) in Tufted Puffins (*Fratercula cirrhata*) with age for high (650 kJ per day, *filled circles*, n = 6) and low calorie diet (325 kJ per day, *open circles*, n = 7)
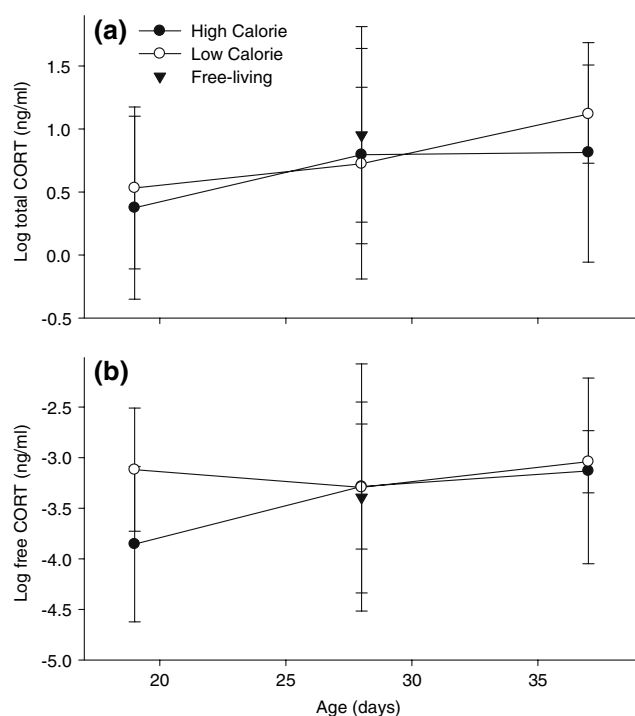

Fig. 2 Changes in the values of baseline **a** total CORT and **b** free CORT (mean ± SD) in Tufted Puffins with age for high (650 kJ per day, *filled circles*, n = 5–6 per time period) and low calorie diet (325 kJ per day, *open circles*, n = 5–7 per time period). Total and free CORT were not significantly affected by age (P > 0.15 for both) or treatment (P > 0.33 for both). Baseline total CORT and free CORT in 27-day-old experimental chicks were not significantly different from levels in free-living Tufted Puffin chicks (*filled triangles*, n = 18, P > 0.4 for both)

baseline CORT in free-living Tufted Puffin chicks was 3.8 ± 3.7 and 0.06 ± 0.08 ng/ml, respectively. These levels were not significantly different from ~ 37-day-old nestlings in the experimental feeding trial (total CORT: $t = 0.09$, $P = 0.9$; free CORT: $t = 0.93$, $P = 0.4$).

Food-restricted nestlings were significantly more likely to vocalize when removed from their nests compared to chicks on the high calorie diet (22 and 27 days post-restriction: $\chi^2 = 12.20$ and 14.13, $P < 0.001$). At 22 days post-restriction, six of the seven food-restricted nestlings vocalized continuously for >20 s when removed from their burrows and one of the seven did not beg. In contrast, none of the six chicks from the high calorie group vocalized when removed from their burrows after 22 days on the controlled diet. After 27 days on the controlled diet, six of the seven food-restricted nestlings vocalized continuously whereas one of the seven food-restricted nestlings and two of the six nestlings from the high calorie group vocalized intermittently during the first 20 s of handling. The remaining four nestlings from the high calorie group did not make any begging vocalizations when removed from their burrow.

Discussion

We found that food-restricted nestlings did not have elevated baseline levels of either total CORT or free CORT compared to chicks fed a high calorie diet. Nevertheless, begging behavior appears to be honest in this species with most food-deprived birds vocalizing intensely during handling. These results suggest that in nestlings with an HPA axis that is uncoupled from nutritional stress; CORT is not responsible for triggering begging behavior.

Effects of CORT on begging behavior appear to be species-specific and may depend on the adrenocortical response to food deprivation. Nutritional restriction causes increases in CORT secretion, which in turn increases begging in Kittiwakes (Kitaysky et al. 2001, 2003) and House Sparrows (Loiseau et al. 2008). In contrast, exogenous CORT had no effect on begging by Blue-footed Booby (*Sula nebouxii*) nestlings (Vallarino et al. 2006) even though total CORT levels of chicks in this species rise during food deprivation (Nunez-de la Mora et al. 1996). However, Vallarino et al. (2006) were unable to verify whether CORT implants actually increased plasma CORT concentrations in their study.

The effect of food restriction on HPA activity in Tufted Puffins apparently depends on the degree of restriction, with moderate restriction having no effect (this study) and severe restriction having suppressive effects (Kitaysky et al. 2005). In our study, levels of total and free CORT in free-living Tufted Puffins were no different from levels observed in manipulated birds. Baseline total CORT levels

or age ($F_{2,22} = 2.02$, $P = 0.16$; Fig. 2a). Similar to total CORT, free CORT was not significantly affected by food restriction ($F_{1,10} = 1.03$, $P = 0.33$) or age ($F_{2,19} = 0.84$, $P = 0.45$; Fig. 2b). Mean values of total CORT and free CORT across treatment groups and ages were 2.6 ± 1.7 and 0.05 ± 0.03 ng/ml, respectively. Total and free

of free-living Tufted Puffin chicks in our study were also comparable to levels in captive-reared chicks, but lower than levels reported for free-living chicks, in the study of Kitaysky et al. (2005). Wild chicks sampled by Kitaysky et al. were older and it is possible their CORT concentrations were elevated because chicks were approaching fledging age (e.g., Quillfeldt et al. 2007).

An important consideration when manipulating energy intake of growing chicks is determining whether experimental procedures effectively mimic natural conditions. In Tufted Puffins, chick provisioning and nestling growth rates are highly variable (Piatt and Kitaysky 2002), and nestlings are adapted to adjust metabolic rates to food provisioning (Kitaysky 1999). In our study, mass gain of nestlings during the "linear growth phase" (age 10–30 days; Gjerdrum 2001) in high and low-calorie groups was 17.15 and 6.55 g/day, respectively. Piatt and Kitaysky (2002) review 49 colony years of nestling growth data and report an overall mean growth rate of 10.9 g/day $\pm$ 4.7 SD (range −0.6 to 19 g/day). Thus, growth rates of food-restricted birds in our experiments were less than 1 SD below the overall mean and well within the range reported for wild birds. Growth rates of the high-calorie group approached the maximum level observed in the wild. However, we only provided chicks with one large meal per day, whereas in the wild they are fed, on average, two meals per day from each parent (Piatt and Kitaysky 2002). Kitaysky et al. (2005) found that altering rates of meal delivery had no effect on CORT levels in captive chicks, although effects on begging behavior, if any, are unknown.

In the wild, Tufted Puffin nestlings make repeated "peep-peep" begging vocalizations when adults enter the burrow with food (Piatt and Kitaysky 2002; C.T.W., personal observation), although variability in begging behavior and its relation to nutritional status has not been studied in free-living Tufted Puffins. Gjerdrum (2004) found that Tufted Puffin parents reduced feeding rates in response to supplemental provisioning of their chicks, suggesting they have some means of gauging nestling hunger status. Presumably, Tufted Puffin parents are able to perceive the nutritional status of their chicks through the intensity of their begging during feeding. Atlantic Puffin (*Fratercula arctica*) parents, for example, increased provisioning in response to play-back of recorded begging calls (Harris 1983). Differences in vocalizations during handling were extreme in our study; most nestlings on a high calorie diet made no vocalizations whereas all food-restricted chicks did. However, we prevented nestlings from interacting with their parents and therefore our results should be treated with some caution. Further study is required to determine how the changes in behavior measured in our experiment (vocalizations during handling) translate into differences in the solicitation of food from adult puffins.

The high variability in growth rates observed in wild populations suggests that Tufted Puffin parents are often unable or unwilling to respond to chick begging. Kitaysky et al. (2005) propose that uncoupling HPA activity from nutritional state in Tufted Puffin chicks is adaptive because it allows slow-growing nestlings to avoid the deleterious effects associated with chronic elevation of CORT. Growing chicks may be particularly susceptible to chronic elevation of CORT as the rate of protein synthesis in skeletal muscle is significantly reduced in the presence of CORT (Klasing et al. 1987) and elevated CORT during development in chicks can impair their ability to associate food distribution with visual cues later in life (Kitaysky et al. 2003,2006). If long-term elevation of CORT is costly, then why do Tufted Puffin chicks not increase CORT in anticipation of a feeding event, as Thin-billed Prion (*Pachyptila belcheri*) chicks apparently do (Quillfeldt et al. 2007), or in response to the presence of an adult? Although, feeding rates of Tufted Puffins peak during the morning, chicks are fed throughout the day (Piatt and Kitaysky 2002) and timing of provisioning is likely not predictable enough for an anticipatory increase to be effective. Furthermore, adult Tufted Puffins often remain in the burrow for less time than the several minutes required to increase circulating levels of CORT following activation of the HPA axis. Thus, CORT levels would increase after the adult has already left the burrow and modulation of the HPA axis in response to adult presence would therefore not be a useful mechanism to increase begging.

It is possible that begging behavior is less costly in species where nestlings routinely encounter prolonged food deprivation. However, this can only be determined once the trigger(s) for begging behavior and the costs associated with these triggers are known. Although CORT is apparently not responsible for modulating begging behavior in Tufted Puffins, begging is likely regulated by other endocrine systems. The effects of yolk androgen levels on begging behavior is well established in several passerine species (Schwabl 1996; Eising and Groothuis 2003). Additionally, elevated levels of endogenous testosterone are positively correlated with begging intensity in Pied Flycatchers (*Ficedula hypoleuca*; Goodship and Buchannan 2005) and in Thin-billed Prions (Quillfeldt et al. 2006), but testosterone implants suppress begging behavior in Black-headed Gulls (*Larus ridibundus*; Groothuis and Ros 2005). However, total androgen levels were below the minimum detectable level of 0.05 ng/ml in free-living and captive >14 days post-hatch Tufted Puffin nestlings sampled in a prior study (Kitaysky, unpublished data). Further study is therefore needed to elucidate the hormone(s) responsible for triggering begging behavior in Tufted Puffins, as well as the mechanism(s) responsible for ensuring this behavior is honest.

Zusammenfassung

Unterernährte Nestlinge des Gelbschopflunds (*Fratercula cirrhata*) steigern ihre Rufaktivität ohne Veränderung der Kortikosteron-Konzentration

Bei einigen Vogelarten scheint Kortikosteron eine Rolle bei der Kontrolle des Bettelverhaltens zu spielen. Aufgrund der möglicherweise hohen Kosten einer chronischen Erhöhung von Kortikosteron wurde dieses Hormon auch als Mechanismus angesehen, das Betteln als ehrliches Signal zu sichern. Wir untersuchten die Effekte einer moderaten Nahrungsverknappung (50% der Energiezufuhr) auf Rufverhalten und Kortikosteron- Basiswerte bei Nestlingen des Gelbschopflunds (Fratercula cerrhata). Wenn die Küken gegriffen wurden, waren ihre Lautäußerungen den Bettellauten ähnlich und werden als repräsentativ für Bettelverhalten angesehen. Daneben wurden gesamtes und freies Kortikosteron auch in unbehandelten Gelbschopflund-Küken gemessen, um zu ermitteln, ob die Hormonwerte unter experimentellen und natürlichen Bedingungen vergleichbar waren. Wir fanden keine Effekte der Nahrungslimitierung, weder auf die gesamten noch freien Kortikosteron-Basiswerte, obwohl die unterversorgten Nestlinge intensiver riefen als unbehandelte Küken. Die mittleren Plasmakonzentrationen von gesamtem und freiem Kortikosteron unterschieden sich nicht zwischen behandelten und wildlebenden Nestlingen. Die Ergebnisse legen nahe, dass Kortikosteron keine Rolle bei der Steuerung des Bettelverhaltens dieser Vogelart spielt.

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