RESEARCH ARTICLE

Feather corticosterone reveals developmental stress in seabirds

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ABSTRACT

In nest-bound avian offspring, food shortages typically trigger a release of the stress hormone corticosterone (CORT). Recent studies indicate that CORT is passively deposited in the tissue of growing feathers and thus may provide an integrated measure of stress incurred during development in the nest. The current hypothesis predicts that, assuming a constant rate of feather growth, elevated CORT circulating in the blood corresponds to higher levels of CORT in feather tissue, but experimental evidence for nutritionally stressed chicks is lacking. Here, we examined how food limitation affects feather CORT content in the rhinoceros auklet (*Cerorhinca moncerata*). We (i) used captive chicks reared on control versus restricted diets, and (ii) applied this technique to free-living chicks with unknown nutritional histories that fledged at three separate colonies. We found that (i) feather growth was not affected by experimentally induced nutritional stress; (ii) captive chicks raised on a restricted diet had higher levels of CORT in their primary feathers; (iii) feather CORT deposition is a sensitive method of detecting nutritional stress; and (iv) free-living fledglings from the colony with poor reproductive performance had higher CORT in their primary feathers. We conclude that feather CORT is a sensitive integrated measure revealing the temporal dynamics of food limitations experienced by rhinoceros auklet nestlings. The use of feather CORT may be a powerful endocrine tool in ecological and evolutionary studies of bird species with similar preferential allocation of limited resources to feather development.

KEY WORDS: Nutritional stress, Adrenal function, Rhinoceros auklet, Resource allocation

INTRODUCTION

The environmental stressors that animals experience during development have fitness consequences. A disruption in homeostasis in birds triggers release of the stress hormone corticosterone (CORT), which enables an individual to cope with changes in its environment (Schoech et al., 2011). For example, nutritional limitation in nestlings has been shown to increase CORT secretion (Astheimer et al., 1992; Kitaysky et al., 1999; Kitaysky et al., 2001; Pravosudov and Kitaysky, 2006; Herring et al., 2011), which in turn may increase begging behavior (Kitaysky et al., 2001), and result in a stronger adrenocortical response to future stressors (Pravosudov and Kitaysky, 2006; Spencer et al., 2009) (reviewed in Schoech et al., 2011). Short- and long-term exposure to elevated CORT, however, can reduce an individual's quality (Kitaysky et al., 2003;

Dehnhard et al., 2011), lower survival (Kitaysky et al., 2007; Blas et al., 2007; Kitaysky et al., 2010, Satterthwaite et al., 2010; Goutte et al., 2010) and interfere with morphological development (Müller et al., 2009; Honarmand et al., 2012). Because of the short-term benefits and long-term costs of increased CORT secretion, quantifying an individual's exposure to CORT is an informative method of assessing an individual's response to its environment (e.g. Dorresteijn et al., 2012) and may provide insight into the evolution of current life-history strategies (Kitaysky et al., 2003; Satterthwaite et al., 2010; Schoech et al., 2011; Atwell et al., 2012).

Current methods of measuring CORT exposure (such as CORT concentrations in blood and fecal samples) provide a measure of CORT levels experienced by an individual at one point in time (Brewer et al., 2008; Müller et al., 2009; Herring et al., 2011). However, even repeated samples of blood or fecal material may not always capture a complete profile of stress incurred by individuals on the scale of days or weeks. For example, experimental evidence in the red-legged kittiwake (*Rissa brevirostris*) indicates that prolonged periods of food shortage may not always correspond to an increased secretion of baseline plasma CORT (Kitaysky et al., 2001). Recently, several studies have employed a technique that measures the amount of CORT contained in feather tissues, which are grown over a period of days or weeks. Several of these studies indicate that the relatively non-invasive sampling of whole feathers may provide an integrated measure of stress incurred throughout the growth of that feather (Fairhurst et al., 2013), and that feathers can be sectioned to obtain a rough profile of stress experienced during feather growth (Bortolotti et al., 2008; Bortolotti et al., 2009; Lattin et al., 2011). The current 'passive deposition' hypothesis predicts that elevated CORT in blood plasma will correspond to higher levels of CORT in feather tissue because the CORT circulating in the blood is incorporated into the feather tissues as they are being formed (although the mechanisms are still unknown) (Bortolotti et al., 2008).

The potential ecological applications of this technique are broad and already the few published studies that employ it address questions ranging from the impact of the pre-breeding body condition on egg production (Kouwenberg et al., 2013) to the effect environmental enrichment has on the physiological state of captive passerines (Fairhurst et al., 2011). There is evidence, however, that during development variations in resource allocation may produce feather CORT results opposite to those expected from plasma CORT studies (Patterson et al., 2014). Several validation studies have found that feather CORT concentration not only reflects the length of a feather, as originally proposed by Bortolotti et al. (Bortolotti et al., 2008), but also correlates significantly with a feather's mass and growth rate (Lattin et al., 2011; Patterson et al., 2014). There is a need to experimentally validate how feather growth rates and feather CORT respond to natural environmental stressors; otherwise, use of this technique may lead to equivocal interpretations of feather CORT results. To date, only a few studies have assessed the technique of measuring CORT in feather tissues of chicks that have experienced experimentally induced stressful conditions during development (Fairhurst et al., 2012b; Fairhurst et al., 2013).

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We used seabirds as a model system to investigate the use of feather CORT as an indication of a chick's exposure to nutritional stress during development. In seabirds, increased CORT secretion is associated with low food availability (Doody et al., 2008; Kitaysky et al., 2007; Kitaysky et al., 2010; Dorresteijn et al., 2012) and in many species plasma CORT correlates inversely with population parameters such as reproductive success, survival and population trends (Buck et al., 2007; Kitaysky et al., 2007; Kitaysky et al., 2010; Harding et al., 2011; Dorresteijn et al., 2012; Satterthwaite et al., 2012). Chicks experience food limitation when their parents are unable or unwilling to compensate for food shortages (Harding et al., 2009; Fairhurst et al., 2012a; Jacobs et al., 2013), thus presenting a direct physiological response of individuals to changes in their nutritional environment.

We tested the effect of nutritional stress on deposition of CORT in feathers of the rhinoceros auklet, *Cerorhinca monocerata* (Pallas 1811). Experimental and observational studies indicate that in this species chicks preferentially allocate limited resources to wing and feather growth: chicks consistently fledge once attaining a narrow wing length measurement irrespective of body mass (Harfenist, 1995; Deguchi et al., 2004; Takenaka et al., 2005; Sears and Hatch, 2008; Hirose et al., 2012). Experimental evidence also indicates that food-limited rhinoceros auklets have higher plasma CORT concentrations than controls (Sears and Hatch, 2008). Under the passive deposition hypothesis, differences in feather growth rates could interfere with the transfer of CORT from blood to feather tissue (Patterson et al., 2014). Thus, we predict that if feather growth is not affected by food limitation, then feather CORT will be relatively higher in nutritionally stressed chicks. We tested this prediction in the following manner: (1) we compared captive chicks reared on either control or restricted diets to test the relationships among food restriction, baseline plasma CORT and feather CORT; and (2) we measured feather CORT in free-living fledglings sampled on three colonies differing in reproductive performance to determine whether and when wild chicks experienced environmental stress.

RESULTS

Captive chicks

We examined the 1st primary feather of chicks raised on one of two experimental diets: food restricted or control. We found that food restriction had no effect on feather mass, length, growth rate or the age at feather emergence in captive-reared chicks exposed to nutritional stress during development (Table 1). Because feather growth rate was unaffected by food restriction it was not included in our models.

Feathers were segmented prior to analysis to measure CORT concentration during early (feather tip to 20 mm), middle (21–40 mm) and late (41 mm to feather base) development. Feather CORT concentrations were higher in food-restricted chicks than in controls (treatment effect: $F_{1,11}$=14.69, P=0.0028; Fig. 1A). We
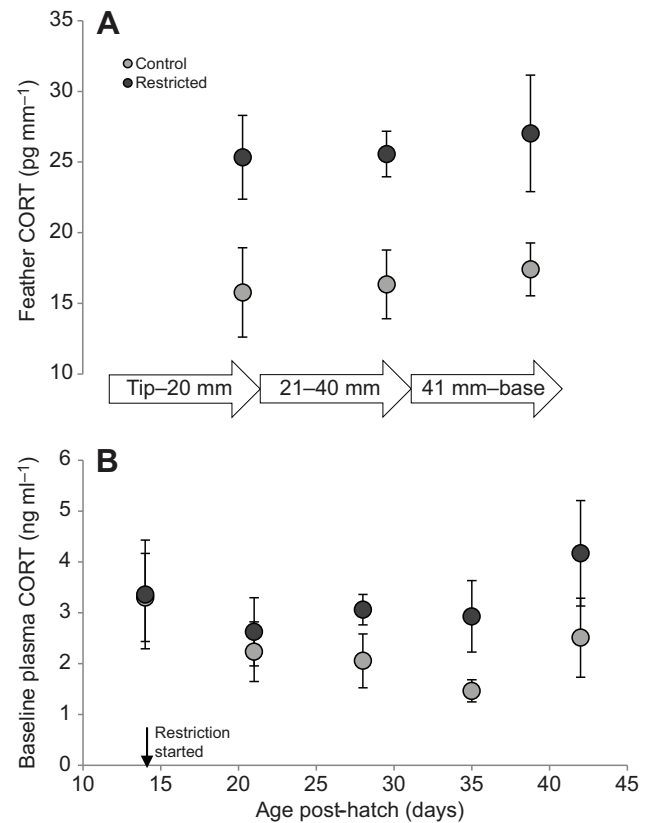
Fig. 1. Food limitation results in higher feather corticosterone (CORT) concentrations. (A) Mean (±s.e.m.) feather CORT concentration (controlled for the mass of the feather segment) in the first primary feather (grown between ~11 and 42 days post-hatch) of control (N=6) and restricted (N=6) rhinoceros auklet chicks, shown by feather segment (growth period indicated by arrows). (B) Mean (±s.e.m.) baseline plasma CORT concentrations (measured weekly between 14 and 42 days post-hatch) of control (N=6) and restricted (N=6) rhinoceros auklet chicks were not significantly different (mixed model; effect of treatment: $F_{1,10}$=2.17, P=0.17, effect of age: $F_{1,46}$=0.009, P=0.92; interaction between treatment and age: $F_{1,46}$=2.04, P=0.16). Plasma CORT values are for 12 of the 26 chicks included in results reported previously (see Sears and Hatch, 2008).

observed a trend for feather CORT to increase from tip to base in both treatments (effect of segment: $F_{2,23}$=3.4, P=0.051). None of the interaction terms were significant (all P>0.22).

On an individual basis, we paired feather segments (feather tip to 20 mm, 21–40 mm, and 41 mm to base of feather) to baseline plasma CORT samples using growth rate measurements (see Materials and methods). We found that baseline plasma CORT (ng ml^{-1}) was not a significant predictor of CORT concentrations in feather tissues (Fig. 2).

Table 1. Parameters of feather growth and development were not significantly different between rhinoceros auklet chicks raised on control and restricted diets

| Feather parameters	Control	Restricted	ANOVA	
			$F_{1,11}$	P
Mass (g)	0.029±0.002	0.03±0.001	0	0.99
Length (mm)	59.69±1.27	59.21±1.15	0.167	0.69
Growth rate (mm day^{-1})	2.22±0.02	2.18±0.04	1.163	0.3
Age at primary emergence (days)	11.61±0.24	11.56±0.26	0.03	0.87

Data are means ± s.e.m. with corresponding statistical parameters.
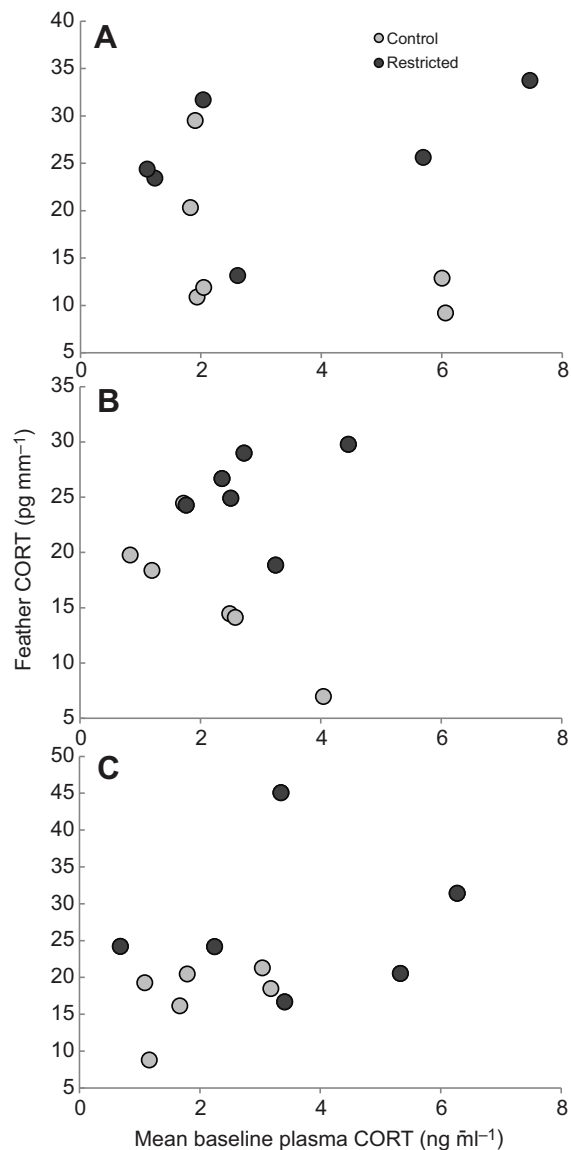
Fig. 2. Baseline plasma CORT is not significantly correlated with feather CORT concentrations. Feather CORT concentrations (controlled for the mass of the feather segment) are reported for (A) the first segment (tip to 20 mm) paired with baseline plasma CORT collected on day 14 ($F_{1,10}=0.002$, $P=0.96$, $R^2<0.001$), (B) the second segment (21–40 mm) paired with the mean concentration of baseline plasma CORT collected on days 21 and 28 ($F_{1,10}=0.04$, $P=0.84$, $R^2=0.004$), and (C) the third segment (41 mm to base) paired with the mean concentration of baseline plasma CORT collected on days 35 and 42 ($F_{1,10}=1.77$, $P=0.21$, $R^2=0.15$). Captive rhinoceros auklet chicks are coded by treatment for illustrative purposes only: control $N=6$, restricted $N=6$.

Free-living chicks

We then applied this technique to feathers collected in 2012 from fledglings on three geographically distinct colonies that differed in diet composition, oceanographic conditions and reproductive performance: Teuri Island in Japan, and St Lazaria Island and Middleton Island in Alaska. Measures of reproductive success were collected on each island as part of ongoing monitoring studies. Fledging success in 2012, determined as the number of chicks fledged/number chicks hatched, was low on Teuri Island: 31% ($N=41$ monitored nests). Both St Lazaria Island and Middleton Island had reproductive success comparable to the long-term
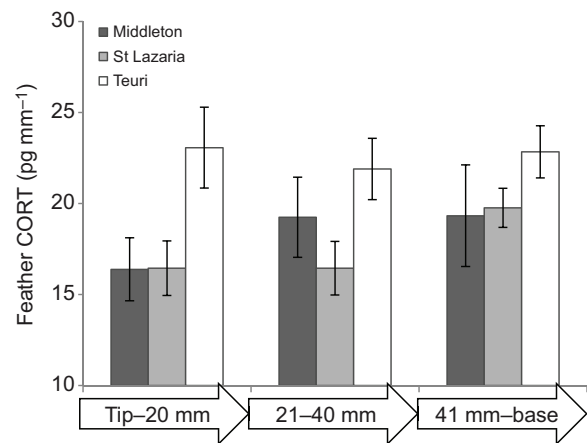
Fig. 3. Feather CORT concentrations of free-living rhinoceros auklet chicks. Reported are mean (±s.e.m.) feather CORT concentrations (controlled for the mass of the feather segment) in three different segments (from tip, grown first, to the base, grown last as indicated by the arrows) of the first primary feather tissues.

average recorded for both colonies (St Lazaria Island: 67%, $N=148$; Middleton Island: 67.3%, $N=52$).

We found that free-living chicks from different colonies had similar feather mass (fixed effect ANOVA; colony effect: $F_{2,32}=1.895$, $P=0.167$). Feather length, measured after removal from fledglings, was not significantly different across colonies (colony effect: $F_{2,32}=3.066$, $P=0.061$). We found that feather CORT concentrations were affected by colony (mixed model; colony effect: $F_{2,32}=5.94$, $P=0.006$; Fig. 3) and that there were temporal differences in CORT concentration (mixed model; feather segment effect: $F_{2,65}=16.97$, $P<0.0001$). None of the interaction terms were significant (all $P>0.07$).

DISCUSSION

We used captive seabird chicks to test whether nutritional stress is reflected in an increased deposition of CORT in feather tissues. We then applied this technique to free-living chicks with unknown nutritional histories to determine whether and when individuals experienced environmental stress during their development. Feather growth did not differ significantly between treatments, ruling out effects of varying feather growth rates on feather CORT deposition. In all of our analyses we controlled for mass of the feather, thus eliminating any potential confounding effects feather mass had on CORT concentrations (Patterson et al., 2014). Feather CORT was higher in experimental chicks experiencing chronic nutritional limitation and higher in wild chicks fledged from a colony with low breeding performance.

In general, our results provide limited support for the passive deposition hypothesis (Figs 1, 2). Sears and Hatch found a muted, but statistically significant, difference in the adrenocortical response of rhinoceros auklet chicks exposed to nutritional stress: food-limited chicks had a higher secretion of baseline CORT than controls (Sears and Hatch, 2008). In this study we sampled 12 ($N=6$ individuals per control and restricted diet treatments, respectively) chicks that had been killed at the conclusion of their study (other individuals were donated to a zoo for permanent housing and breeding programs). In this subset, using data previously reported by Sears and Hatch (Sears and Hatch, 2008), baseline plasma CORT concentrations were not different between treatments (Fig. 1B) and at the individual level there was no statistically significant

relationship between baseline plasma and feather CORT concentrations (Fig. 2). The weak relationship between baseline plasma CORT and feather CORT may be due to either the relatively weak adrenocortical response of rhinoceros auklet chicks to food stress (Sears and Hatch, 2008) or to a diurnal cycle in baseline CORT secretion (Chung et al., 2011).

Furthermore, it is not unusual for baseline plasma CORT to be highly variable, and when sample sizes are relatively small, this variability may decrease the explanatory power of independent variables. An experimental study of red-legged kittiwakes found substantial inter-individual variation in baseline plasma CORT during prolonged food restriction (Kitaysky et al., 2001); and a long-term study of free-living black-legged kittiwake (*Rissa tridactyla*) chicks found that intra-annual variability in baseline plasma CORT obscured inter-annual patterns in chick physiological status (Brewer et al., 2008). Previous studies have also found baseline plasma CORT to be a non-significant correlate with feather CORT, which was instead significantly positively correlated with stress-induced CORT (Bortolotti et al., 2008; Patterson et al., 2014). Feather CORT may, therefore, be a more robust method of detecting exposure to environmental stressors that vary in duration and intensity (see also Fairhurst et al., 2013). Like measuring the stress-induced CORT response (Kitaysky et al., 2007; Kitaysky et al., 2010), feather CORT might provide a more long-term continuous measure of an individual's exposure to elevated corticosterone, but would do so in a fraction of the handling time, under less duress to individuals and would not have the ability to 'reset' when conditions improved.

It is also possible that baseline plasma CORT and feather CORT concentrations are composed of different components of the total CORT in circulation. The free-hormone hypothesis states that biological responses are regulated by the portion of CORT that is freely circulating in the bloodstream, and that the proportion bound to the corticosteroid-binding globulin is biologically inactive (Breuner et al., 2013). Sears and Hatch measured total CORT, which quantifies both free and bound steroids (Sears and Hatch, 2008). It may be that only free CORT is deposited in feather tissues. Nevertheless, in contrast to the lack of a strong relationship with baseline plasma CORT results, and despite a reduced sample size [this study: *N*=12, versus Sears and Hatch (Sears and Hatch, 2008): *N*=26], we found a very strong signal of food restriction in feather CORT concentrations (Fig. 1A).

We then applied this technique to free-living chicks to determine whether feather CORT could detect exposure to environmental stress during their development in the nest. We found that feather CORT revealed whether and when chicks experienced elevated CORT levels. Feather CORT co-varied with reproductive success at the colony level, and intra-feather variation in deposition suggested that CORT was higher during some windows of development than others. For example, chicks from Teuri Island had higher concentrations of CORT in the first grown portion of their feathers and experienced overall higher stress than chicks on St Lazaria Island (Fig. 3). While direct causes may vary, elevated CORT is an indicator of environmental stress (such as food shortage, inclement weather, disease, inter-sibling aggression and predation), and indicates that perhaps poor early chick-rearing conditions contributed to the overall low fledging success on Teuri Island compared with St Lazaria Island and Middleton Island, where reproductive success was relatively high. Rhinoceros auklets raise a single chick in a subterranean burrow (Gaston and Dechesne, 1996) so their offspring are well protected and have little opportunity to experience environmental stress other than lack of food. It is,

therefore, most likely that the early-season elevation in feather CORT concentrations we found in the free-living chicks was primarily due to food shortage.

In both captive and free-living chicks we observed temporal changes in feather CORT concentrations (Figs 1, 3). In captive chicks there was an increasing trend in feather CORT concentrations as chicks approached fledging age. An increase in the adrenocortical function towards the end of development has been observed across avian species and is largely attributed to an upregulation of the hypothalamus–pituitary–adrenal axis in anticipation of coping with the initial stress of being independent (Corbel and Groscolas, 2008; Kozlowski et al., 2010; Wada et al., 2009; Rivers et al., 2012). While the observed increase in feather CORT concentrations over time may be due to ontogenetic processes, we cannot discount the possibility that captive chicks may have become mildly nutritionally stressed near the end of their development. In the wild, as chicks near fledging age, adult auklets have been observed to decrease their chick provisioning efforts (Bertram et al., 1991; Bertram et al., 1996), which may explain the late season increase in feather CORT concentration of free-living chicks on the Alaskan colonies (Fig. 3). In captive chicks, daily rations were determined based on the low and high levels of daily food intake recorded in wild chicks (Bertram et al., 1991) and did not change during chick development. Because of their static diets, all captive individuals could have experienced food limitations prior to fledging. Because of a potential interplay of pre-fledging physiology, parental decisions and changes in environmental conditions, it is difficult (and beyond the scope of our current study) to determine causal factors that explain the trends we observed in feather CORT concentrations over time. Most notable is that we were able to observe these changes in CORT secretion over time by using the continuous record of CORT deposited into growing feather tissues.

We conclude that rhinoceros auklets, seabirds that preferentially allocate limited resources to wing and feather growth and retain an adrenocortical response to food limitation during development, deposit higher concentrations of CORT in growing feather tissue in response to nutritional stress. We also found that feather CORT can detect food limitation in rhinoceros auklet chicks when baseline plasma CORT does not. Our results demonstrate that feather CORT can be used to make spatial and temporal comparisons of environmental conditions and reveal specific periods, and durations, of stress experienced by seabird chicks during their development. This relatively non-invasive technique, when applied appropriately, could provide important physiological information to evolutionary and ecological studies of free-living seabirds.

MATERIALS AND METHODS
Captive chicks

All handling of free-living birds was conducted under the approval of the University of Alaska Fairbanks Animal Care and Use Committee protocol no. 251294-9 and sampling occurred under US Fish and Wildlife Service collection permit MB072512-1 and Alaska Department of Fish and Game permit 12-046. Importation of feathers from Japan was approved by the US Department of Agriculture (permit 115130).

We used captive-reared fledglings exposed to nutritional stress during their development (see Sears and Hatch, 2008). These birds were fed the same fish diet (the silverside, *Menidia menidia*) given *ad libitum* until 14 days post-hatch, and either control (up to 75 g day^{-1}, *N*=6) or restricted (up to 40 g day^{-1}, *N*=6) diets thereafter. Birds were killed at 56 days post-hatch and have been stored frozen at −80°C since 2006 [see Bortolotti et al. (Bortolotti et al., 2009) for details of sampling 'old' feathers, which suggests CORT is stable in feather tissue and its concentration is unaffected by long-term storage]. All chick measurements, blood collection and plasma CORT

analysis were completed as part of previously reported work (Sears and Hatch, 2008). Briefly, feather growth rates were calculated from measurements of the 10th primary taken every 7 days from the time the feather burst through its sheath to day 42 post-hatch when feathers reached their full length. Age at primary emergence was back-calculated using the length of the primary at day 14 and the growth rate for the individual feather (average age at primary emergence was 11.57 days, feathers stopped growing between measurements taken at 42 and 49 days post-hatch and average growth rate was 2.2 mm day^{-1}). Blood samples (100–200 μl) of post-absorptive chicks (after overnight fasting) were collected weekly starting at age 7 days, from the alar vein within 3 min of handling to obtain a baseline measure of circulating CORT (Sears and Hatch, 2008). Plasma CORT concentrations were determined by extracting hormones with dicholoromethane followed by a standard radioimmunoassay (Wingfield and Farner, 1975) with a 3% intra-assay variation and recovery values of 85–99% (Sears and Hatch, 2008).

Free-living chicks
In 2012, free-living chicks were captured in the act of fledging (age unknown, range 42–58 days) (Gaston and Dechesne, 1996) on three colonies (Teuri Island, Japan, 44°25′N, 141°18′E, N=15 individuals; Middleton Island Alaska, 59°26′N, 146°19′W, N=7; St Lazaria Island, Alaska, 56°59′N, 135°42′W, N=13).

These three colonies encompass a broad range of environmental conditions typically experienced by breeding rhinoceros auklets. Teuri Island birds depend heavily upon lipid-rich Japanese anchovy (*Engraulis japonicus*), whose availability is affected on an inter-annual basis by a summer shift in ocean currents (Watanuki et al., 2009). Diets of breeding birds at Alaskan colonies consist of the Pacific sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*) and/or greenling (*Hexagrammos decagrammus*) and change on an inter- and intra-annual basis (Thayer et al., 2008). St Lazaria Island birds breed in a shallow continental shelf environment while Middleton Island birds have access to a more pelagic habitat. Typically, years that are food-rich for the Alaskan colonies are less so for the Japan colony (Thayer et al., 2008). Thus, we expected that auklets breeding at these three colonies in a given year would experience contrasting foraging conditions.

Feather collection and analysis
For both captive and free-living fledglings the 1st primary from the right wing was clipped at the base. After washing with distilled water and air-drying, the calamus was removed and feathers were weighed to the nearest 0.0001 g and measured to the nearest 0.5 mm. The entire feather was then divided into three 20 mm segments. Each segment was weighed to the nearest 0.0001 g and analyzed for CORT content separately. Feather segments were prepared according to Bortolotti et al. (Bortolotti et al., 2008) followed by a radioimmunoassay (Wingfield and Farner, 1975) using Sigma-Aldrich antibody (C 8784, St Louis, MO, USA), intra-assay CV<2%. The Sigma-Aldrich antibody patterns of specific binding were parallel between dilution of feather CORT extract and standard CORT (Sigma-Aldrich H4001). To control for loss of CORT during the extraction process, 2000 cpm of H^3-labeled CORT (PerkinElmer NET399, Boston, MA, USA) was added to each sample and final feather CORT titers were adjusted for % recovery (mean 97%, range 80.2–100%). Assay results were normalized by converting to units of pg mm^{-1} (Bortolotti et al., 2008).

Statistical analysis
Statistical analysis was conducted in R (R Development Team version 3.0.0). All dependent variables met assumptions of normality and homogeneity of variance. We used ANOVA to compare feather mass, length, growth rate and age at emergence between treatments and among colonies. Sex (N=4 males, N=8 females) did not account for a significant amount of variation in any of the measured parameters in the experimental chicks, so it was excluded from further analyses. We used linear mixed models ('lme' function in R) to test the effect of feather segment (captive and free-living), dietary treatment (captive chicks only) and colony (free-living chicks only) on feather CORT concentrations. We included chick identity as a random factor. For all models we first tested the interactions among the fixed factors and feather mass, and removed non-significant interaction terms from final models.

Feather CORT concentrations (pg mm^{-1}) were significantly [mixed model; effect of feather segment mass (g): $F_{1,87}$=20.76, P<0.0001] and positively (parameter estimate: 392.6±260.8) correlated with the mass of feather segments in both captive and wild individuals (there was no significant interaction between feather origin, i.e. captive versus wild, and segment mass: $F_{4,87}$=0.62, P=0.65). Thus, feather mass was included as a continuous predictor in all statistical analyses and in all figures we report mass-specific feather CORT concentrations, which are the detrended values using residuals calculated from the best fit linear model for feather mass (g) and feather CORT concentrations (pg mm^{-1}).

In captive chicks, we tested the relationship between baseline plasma CORT (ng ml^{-1}) and feather CORT (pg mm^{-1}) using general linear models with baseline plasma CORT as a continuous predictor. Feather segments were matched to weekly plasma CORT samples by using the mean growth rate (2.2 mm day^{-1}) and day of emergence (11 days post-hatch) for the primaries of all captive-reared chicks. Thus, we determined that the first 20 mm of each feather (tip to 20 mm) corresponded to plasma CORT on day 14, that the 21–40 mm feather segment corresponded to the average of plasma CORT concentrations measured on days 21 and 28, and that the 41 mm to base feather segment corresponded to the average of plasma CORT concentrations measured on days 35 and 42 post-hatch.

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