

# Corticosterone in thin-billed prion *Pachyptila belcheri* chicks: diel rhythm, timing of fledging and nutritional stress

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**Abstract** Glucocorticosteroids (GCs) of the hypothalam–pituitary–adrenal axis play a role in association with both stressful events and daily life processes. However, relatively little is known about the role of GCs in relation to daily and seasonal life processes in animals in the wild. In this paper, we present data on basal levels of plasma corticosterone CORT in chicks of a pelagic seabird, the thin-billed prion, *Pachyptila belcheri*, during two predictable changes in demands, the daily activity pattern and the preparation for fledging. By comparing chicks fed recently with unfed chicks, we test how GC levels are modified according to nutritional condition. In accordance with their nocturnal feeding rhythm, chicks had a clear daily rhythm with increased CORT secretion at night, but CORT levels during the active phase were also highly elevated in unfed chicks compared with fed chicks. Close to fledging, chicks rapidly increased basal CORT levels, and again unfed chicks had higher levels than fed chicks, although the age effect here was stronger than the effect of recent feeding. The present data thus support the hypothesis that GC levels are adjusted to life stages with predictable changes in demands, but food availability and/or internal energy stores also affect the level to which GCs increase.

**Keywords** Procellariiformes · Seabirds · Day–night cycle · Dispersal · Hormonal regulation

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## Introduction

The life of most animals consists of stages of different energetic demand. For example, seasonally distinct times such as reproduction and migration may be demanding life history stages, but even short cycles such as the daily activity cycle have more and less demanding phases. However, energetically demanding phases are part of the annual or daily routine and can be anticipated.

However, animals also experience less predictable handicaps, such as diseases and parasite load, and unpredictable environmental events that can lead to stress, such as sudden food shortage experienced during adverse weather. Superimposed on the normal annual or daily cycles, such events can modify the demand or even disrupt the normal cycle.

In many vertebrate species, including birds and rodents, corticosterone CORT is the principal glucocorticoid GC and is involved in the regulation of metabolism (Devenport et al. 1989) and immune responses (e.g. Bourgeon and Raclot 2006), as well as the responses to a wide range of stressors such as food shortage (e.g. Cockrem et al. 2006), contamination (Baos et al. 2006) and capture (e.g. Mueller et al. 2006). This wide range of functions would make CORT especially interesting as a potential mediator of trade-offs between investment in these different body functions. A better knowledge of natural levels of GC in wild species, including data on daily and seasonal variation, is thus desirable.

Most vertebrates have a diel rhythm in adrenocortical activity. The typical mammalian rhythm shows a peak in basal GC just before the active period, and GC levels decline afterwards but remain elevated during the most active period of their day–night cycle (e.g. Dallman et al. 1993). Some domestic birds (e.g. pigeons and chickens)

display CORT rhythms that match the typical mammalian rhythm (Joseph and Meier 1973; Lauber et al. 1987; Westerhof et al. 1994). Few studies on diel rhythms of wild birds have so far been published, but they show a “pre-active peak” in basal CORT at the end of the inactive period, followed by a rapid decrease in circulating CORT after the peak, while basal CORT during the most active period is generally low (captive Gambel’s white-crowned sparrows *Zonotrichia leucophrys gambelii*, Breuner et al. 1999; wild Nazca boobies *Sula granti*, Tarlow et al. 2003 and captive starlings *Sturnus vulgaris*, Romero and Remage-Healey 2000).

The thin-billed prion *Pachyptila belcheri*, like most Procellariiformes, is a highly pelagic seabird. Thin-billed prion parents feed their chicks infrequently, often with intervals of several days (Weimerskirch et al. 1995; Duriez et al. 2000; Quillfeldt et al. 2007a). For example, in the breeding season 2005 analysed in the present study, adults carried out foraging trips of 1–8 days (Quillfeldt et al. 2007b), resulting in intervals between feeds of 1 to 5 days. Such long feeding intervals allow thin-billed prions, like many of the smaller species of Procellariiformes, to avoid predation when they come to attend their chicks by nesting in burrows or crevices and only coming ashore at night (e.g. Brooke 2004). The chicks of these species thus experience a nocturnal feeding rhythm, but often, they go unfed for several nights.

In the present study, we measured basal levels of plasma CORT in chicks of the thin-billed prion during two events of predictable changes in demands, the daily activity pattern and the preparation for fledging. The aim of the present study of was

1. To determine how plasma CORT changes with the day–night cycle of chicks
2. To determine if the transition from the nest to the open sea (fledging) is accompanied by changes in plasma CORT, and
3. By comparing chicks fed more or less recently, to test how CORT secretion is modified according to increased allostatic load induced by nutritional stress.

## Materials and methods

### Study site and study species

The study was carried out at New Island Nature Reserve, Falkland Islands from January to March 2006. The thin-billed prion is a small and abundant subantarctic seabird, known to breed in two main areas: at Crozet and Kerguelen in the Southern Indian Ocean and at the Falkland Islands (and possibly on some islands off Tierra del Fuego; Cox

1980; Clark et al. 1984) in the Southern Atlantic Ocean, New Island holding the largest known breeding population.

The life cycle and basic biology of thin-billed prions have been described by Strange (1980). The author also provided the first growth curve for the body mass of chicks. At New Island, recent studies explored variability in provisioning and parent–chick interactions (Quillfeldt et al. 2003, 2006, 2007b). Thin-billed prions show the typical procellariiform pattern of a single-egg clutch and slow chick development, with an average fledging period of 50 days (Strange 1980). Thin-billed prions are burrow nesters, and we reached chicks in their nest chambers via short access tunnels in the roof of each burrow, capped with removable stone lids. This system facilitated rapid access to chicks, reducing overall disturbance. Marked nests were monitored for eggs and hatching chicks.

Adults arrived at the colony between 2140 and 0330 hours, although most feeding activity is registered just after dusk and finishes before midnight (unpublished data).

### Chick measurements and samples

When eggs were found, the hatching date was estimated from the egg density (see Quillfeldt et al. 2003), and the nest was not visited again until 3 days after the estimated hatching date.

If chicks were present on our first visit, we determined the hatching dates of chicks (to the nearest day) by calibrating wing length against wing growth in chicks of known age. Chicks were weighed twice daily at 0730 and 1930 hours to the nearest 1 g using a digital balance. Meal sizes and feeding frequencies were estimated from the evening and morning weights, by correcting the mass differences for metabolic mass loss using the equations given in Quillfeldt et al. (2003).

An index of chick body condition at 1930 hours was calculated as described by Quillfeldt et al. (2006), as present mass relative to the mean mass for study chicks of each age ( $m_{\text{mean}}$ ), using the following formula:  $BC = m \times 100 / m_{\text{mean}}$ . BC of prefledglings at the time of last sampling ranged between 84 and 124 and was independent from the age at sampling ( $R=0.015$ ,  $df$  15,  $P=0.956$ ) and the Julian date ( $R=-0.045$ ,  $df$  15,  $P=0.868$ ). Blood samples (0.2–0.4 ml) were collected after capture by hand by puncture from the brachial vein in heparinised capillaries within 2 min from burrow opening to the end of blood sampling. Blood samples were immediately transferred to 0.5-ml tubes and kept on ice until centrifugation. Plasma was stored frozen at  $-20^{\circ}\text{C}$ .

Blood samples for the analysis of the diurnal rhythm were taken in two 24-h rounds from a group of four different chicks each 3 h starting at 0600 hours on 1

February (32 chicks in total), and again from 10 February. Chicks (age range 24–46 days for analysis of diurnal rhythm) were either sampled only once, or in the case of double sampling, sampling points were in contrasting time periods of the day–night cycle, such that we avoided pseudo-replication within time periods. Chicks sampled during the night (0000 or 0300 hours) were weighed to ascertain whether they had been fed. If they had effectively been fed until the time of sampling, we grouped them in the “fed” group.

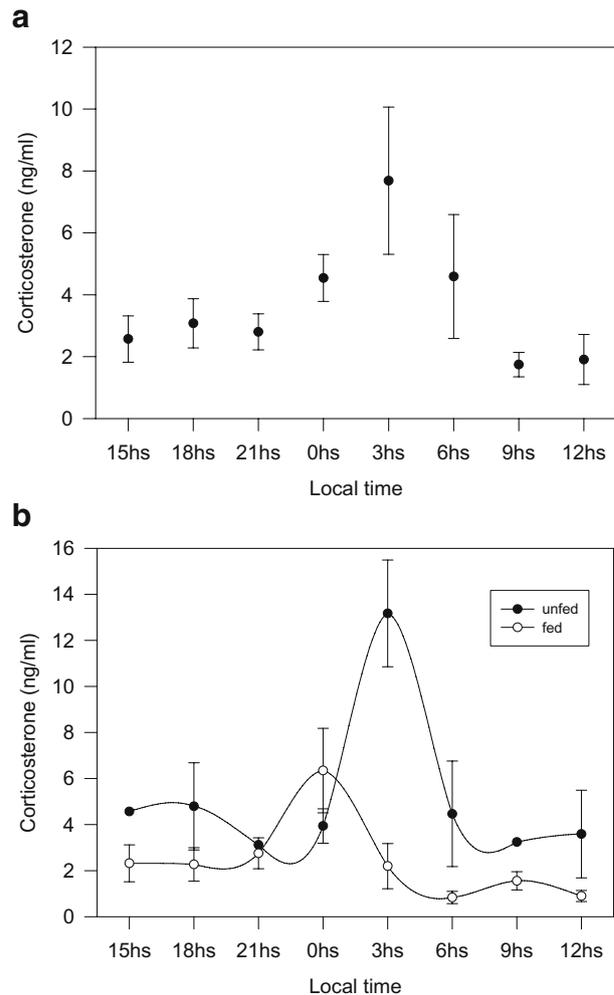
For the analysis of pre-fledging patterns, we took all blood samples during the day (0900 to 1800 hours). Chicks were sampled every 2–4 days during the pre-fledging period, and only the last sample before fledging of each chick was included. We obtained pre-fledging samples from 16 chicks (8 from chicks in the morning before fledging, 7 chicks 1 day earlier and 1 chick 2 days earlier). Of these chicks, nine were recently fed (in the night before sampling), while seven were unfed, and the two groups are compared. The eight birds sampled the morning before fledging contained four fed and four unfed chicks, and moreover, we controlled for age in the analysis; thus, we can exclude an influence of sampling bias.

### Hormone analysis

Baseline plasma corticosterone levels were assessed by radioimmunoassay at the Centre d’Etudes Biologiques de Chizé (CEBC) as detailed in Lormée et al. 2003. All samples were run in one assay. As blood samples were collected within 2 min of capture, they were considered to reflect baseline levels of corticosterone (Romero and Reed 2005). Detection limit was 100 pg/ml, and the lowest measurement was 0.3 ng/ml. Intra-assay coefficient of variation was 12% ( $n=6$  duplicates).

### Statistical analysis and data presentation

Statistical tests were performed in SPSS 11.0. For general linear models (GLM), we included partial eta-squared values ( $\eta^2$ ) as a measure of effect sizes (i.e. the proportion of the effect + error variance that is attributable to the effect). The sums of the partial eta-squared values are not additive (e.g. [http://web.uccs.edu/lbecker/SPSS/glm\\_effectsize.htm](http://web.uccs.edu/lbecker/SPSS/glm_effectsize.htm)). Means are given with standard errors. In Fig. 1b, smoothed lines were fitted using Sigma plot 8.0 to indicate temporal patterns and to make the instant visual distinction of the two groups easier. Regression lines were fitted in Fig. 3 where only the last data point was included for each of 16 chicks followed to fledging, to show the difference in the two groups that was statistically treated by GLM.



**Fig. 1** Diurnal cycle of corticosterone in thin-billed prion chicks **a** all chicks, **b** fed and unfed chicks separate. Means are derived from eight chicks for each sampling point and given with standard errors

## Results

### Diel rhythm

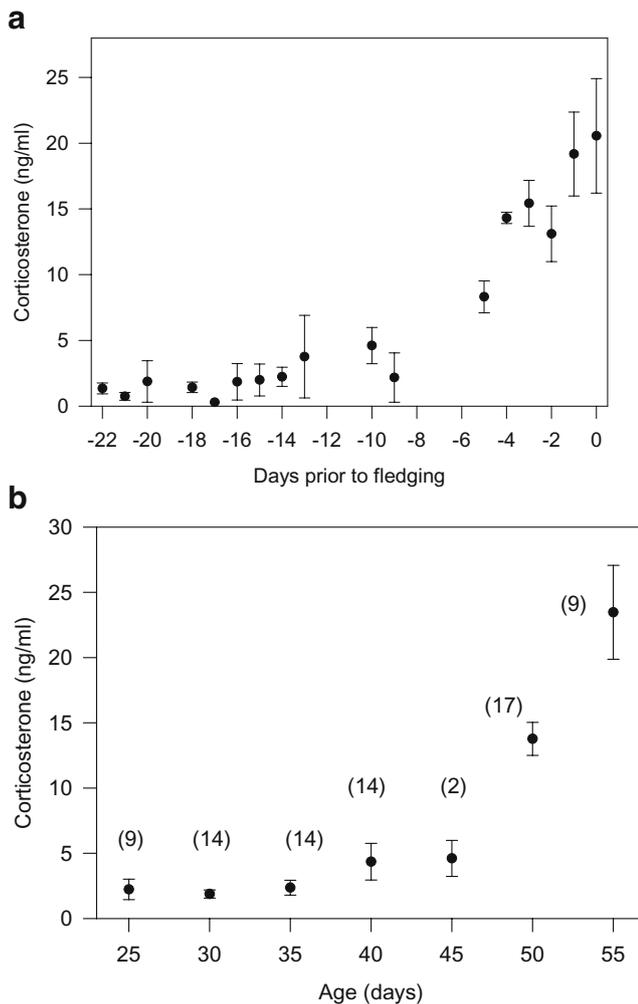
Chicks had a clear daily pattern of CORT secretion (Fig. 1a), and increased values corresponded with the active phase, i.e. the night. Chicks fed during the observed night had low CORT compared to unfed chicks, except at midnight (Fig. 1b). Their CORT peak was earlier and lower than that of unfed chicks (Fig. 1b). Chick that did not receive a meal had a strong increase of CORT in the middle of the night (0300 hours) when the main feeding time had passed. Unfed chicks also secreted more CORT throughout the whole following day (Fig. 1b, mean 0900 to 2100 hours for fed chicks,  $2.0 \pm 0.3$  ng/ml; unfed chicks,  $4.0 \pm 0.8$  ng/ml;  $t$  test,  $t=2.9$ ,  $df 40$ ,  $p=0.006$ ). The two groups did not differ in CORT at midnight ( $p=0.187$ ), but unfed chicks had significantly higher levels at 0300 hours (Fig. 1b; fed

chicks,  $2.2 \pm 1.0$  ng/ml; unfed chicks,  $13.2 \pm 2.3$  ng/ml; *t* test,  $t=4.4$ , *df* 6,  $p=0.005$ ).

A GLM with CORT as dependent variable, age of the chick as covariate, and hour of the day and feeding status (fed/unfed) as factors detected an overall effect of hour ( $F=3.6$ ,  $p=0.003$ ,  $\eta^2=0.341$ ) and feeding status ( $F=7.7$ ,  $p=0.008$ ,  $\eta^2=0.136$ ), with a significant interaction between the two factors ( $F=4.1$ ,  $p=0.001$ ,  $\eta^2=0.371$ ). Age did not influence CORT in this sample ( $F=2.1$ ,  $p=0.151$ ,  $\eta^2=0.042$ ).

### Fledging

Chicks had highly elevated CORT in the last days before fledging (Fig. 2) after progressive increase during the last week before fledging (Fig. 2a), corresponding to chick ages 50 days and older (Fig. 2b). We compared the last sample (2–0 days before fledging) of chicks that had been fed during the previous night and chicks that had not been fed.



**Fig. 2** Pre-fledging pattern of corticosterone secretion in thin-billed prion chicks **a** relative to the observed time of fledging, **b** relative to chick age. Data are pooled by age pentads, with the starting age of each pentad marked at the axis. Sample sizes are indicated

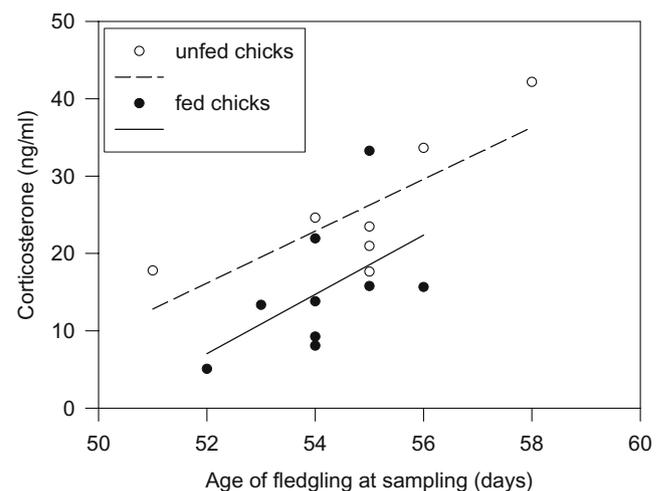
When controlling for age among the pre-fledging samples, unfed chicks had higher CORT ratios than fed chicks, although age was the overall more important parameter (Fig. 3, GLM with CORT as dependent, age as covariate and “fed/unfed” as factor; influence of age,  $F=10.1$ ,  $p=0.007$ ,  $\eta^2=0.436$ ; influence of feeding,  $F=5.2$ ,  $p=0.040$ ,  $\eta^2=0.286$ ). Regression lines in Fig. 3 illustrate the relations found in the GLM, i.e. increase with age and difference between the fed and unfed group. In contrast, pre-fledging CORT was independent of chick body condition (GLM with CORT as dependent and age and body condition as covariates; influence of age,  $F=10.7$ ,  $p=0.006$ ,  $\eta^2=0.451$ ; influence of body condition,  $F=0.3$ ,  $p=0.582$ ,  $\eta^2=0.024$ ).

### Discussion

In the present study, we present the first complete diel CORT rhythm in (nocturnally active) chicks of Procellariiformes showing a nocturnal peak. We present the first data on the hormonal changes close to fledging in Procellariiformes, and moreover, we show that CORT secretion during both processes is influenced both by external and internal factors.

#### Day–night rhythm

We reported previously (data of 2003 in Quillfeldt et al. 2006) that CORT in the plasma of chicks of thin-billed prions was higher at midnight than in the daytime. We have here added data of the complete 24-h cycle and observed a similar pattern.



We found in the present study of thin-billed prions that fed chicks as well as unfed chicks exhibited a CORT peak during the night, but elevated CORT levels were not sustained throughout the night. The CORT peak of fed chicks was earlier and lower than that of unfed chicks (Fig. 1b). The pattern of CORT changes described in this paper for prion chicks is also similar to that found in several mammals, including humans: Baseline CORT increases slightly right before feeding (suggesting a shift in food anticipatory activity; Woodley et al. 2003), and food intake is associated with a decrease in baseline CORT (Mistlberger 1994; Hau and Gwinner 1996).

The basal CORT rhythm is thought to regulate energy intake, mobilisation, and deposition (Dallman et al. 1993). The pre-active peak in CORT observed in so many vertebrates may be in anticipation for the physiological changes associated with the transition from the inactive to the active period. However, chicks of thin-billed prions are not fed every night, they only received meals every 1.8 days on average during February (e.g. Quillfeldt et al. 2007b). Thus, it would not seem adaptive to become active and prepare for food intake at the beginning of every night if chicks cannot be sure to be fed. In fact, we have observed on video in a related species (Wilson's storm-petrel *Oceanites oceanicus*) that arriving adults had to wake up their sleeping chicks before being able to feed (Quillfeldt, unpublished data).

The early peak at midnight in chicks that had received meals until this time may thus reflect the stimulation of chicks by arrival of the parent and feeding and their increased activity during vigorous begging. Chick feeding and begging sessions can be as short as 10 min, or extend over a longer period, up to 90 min (Quillfeldt et al. 2006, 2007b). Most adults will leave soon after feeding their chick, and thus, this short burst of activity may explain the narrow peak of elevated CORT at midnight in fed chicks and rapid decline afterwards. This pattern is also consistent with the observation that induced activity can result in elevated CORT levels. For example, Jessop et al. (2002) demonstrated increased CORT values in green turtles *Chelonia mydas* after experimentally induced nocturnal activity, compared to turtles that were asleep.

Unfed chicks, in contrast, increased CORT highly towards the end of the night. This is a time when arrival of an adult is already very unlikely, and chicks may need to mobilise energy from their internal stores to produce heat and survive the coldest part of the night. CORT may then be increased to promote availability of lipid energy from adipose tissue stores (e.g. Dallman et al. 1993). The peak in CORT of unfed chicks may also be explained by frustration, as has been shown for rats (Romero et al. 1995). After training rats to drink at the same time of day for 30 min for 2–3 weeks, the frustration of presenting empty water bottles

resulted in increased corticosterone concentrations, similar to the pattern observed in the present study.

The only other investigation of a nocturnal bird, to our knowledge, is of young captive Western screech-owls *Otus kennikottii*. Dufty and Belthoff (1997) found the highest CORT levels during the inactive period; however, the difference to the active period was not great. It is possible that they missed the peak CORT values because they sampled only two time points, as they took night time samples 1 hour after dark at 2230–2300 hours and daytime samples at 1300–1500 hours. In addition, the owl chicks were disturbed each day during cleaning and handling for other studies, and feeding apparently took place during the day, too. These methodological problems may explain the differences in the results between Dufty and Belthoff (1997) and the present study.

In the present study, we sampled nest-bound chicks, and we do not have data on diel rhythm in adult thin-billed prions because they only attend the colony at night (except during the incubation and guard stage). Many adult procellariiform seabirds also feed extensively at night when they exploit zooplankton rising to the surface in their vertical diel migration. However, in contrast to the nest-bound chicks, adults also feed and travel during the day. Thus, adults would not seem to have a phase of sleep during their normal daily rhythm and are an exception to the general pattern observed in most animals, which are active only during one part of the day–night cycle (e.g. Aschoff 1981).

### Fledging

Fledging in many bird species involves complex parent–chick interactions (Davies 1976). In contrast, fledging in young petrels occurs in the absence of contemporaneous parental influences (e.g. Brooke 2004). Although thin-billed prions are normally not deserted by the parents before fledging, prion fledglings emerge from their burrows and leave for the sea on their own (personal observations). Thus, fledging has to be triggered internally.

We have here shown that CORT increases dramatically during the days pre-fledging, making it highly likely that CORT may be involved in the physiological and behavioural adjustments necessary for successful fledging and post-fledging survival. As mentioned above in the context of the diel CORT rhythm of unfed chicks, GCs promote the availability of lipid energy from adipose tissue stores (Dallman et al. 1993). In fact, experimental GC increase can influence free fatty acids in a dose-dependent manner (in rats, Mukherjee and Mukherjee 1973), such that GCs affect lipid mobilisation more strongly at higher concentrations. Thus, the high CORT levels observed around fledging may support lipid mobilisation needed to fuel first

flight and help the fledgling to survive until it encounters the first prey.

In line with the present results, CORT has been found to increase during the fledging and dispersal of juveniles of other cavity-nesting birds (American kestrels *Falco sparverius*, Heath 1997; screech owls *Otus asio* and *O. kennicottii*, Belthoff and Dufty 1998; pied flycatchers *Ficedula hypoleuca*, Kern et al. 2001), although the absence of a CORT increase before nest departure in snowy owls *Nyctea scandiaca* suggests that this mechanism is not universal in birds (Romero et al. 2006).

In burrowing petrels, as in many other cavity-nesting birds, the fledging process is particularly marked and dramatic. From the confinement of the burrow, the young petrel leaves to the open sea, where it has to fly, feed and navigate independently. Moreover, fledging in petrels is at the same time the point of independence and dispersal. Birds with a less marked fledging process may not need a strong fledging signal as observed here (Heath 1997). For example, young greylag geese do not show a CORT increase when approaching fledging (Frigerio et al. 2001).

Analyses of fledging age have repeatedly suggested that reaching a critical wing length may determine fledging age (tree swallows *Tachycineta bicolor*, Michaud and Leonard 2000; pied flycatchers *Ficedula hypoleuca*, Kern et al. 2001; rhinoceros auklets *Cerorhinca monocerata*, Deguchi et al. 2004; Leach's storm-petrels *Oceanodroma leucorhoa*, Mauck and Ricklefs 2005). Because wing length is one parameter determining wing loadings, a large enough wing length must be paramount for successful first flight. However, it is difficult to imagine how chicks may judge and respond to their wing length per se, and thus, a physiological internal mechanism is needed to either translate wing length or be correlated with some measure of cumulative growth rate.

CORT has been found to inhibit feather growth (Romero et al. 2005); once fledging has started, high CORT levels might effectively slow down or inhibit further feather growth, and this should be noticeable in the patterns of wing and tail growth. Mauck and Ricklefs (2005) noted that pre-fledging mass loss in Leach's storm-petrels coincided with the time when structural growth was finished.

#### Influence of body condition and energy stores

With the present data, we examined two predictable changes in demands, the daily activity pattern and the preparation for fledging. Superimposed on these cycles, prion chicks also have to deal with fluctuations in environmental conditions and thus feeding rate (e.g. Quillfeldt et al. 2007a). Times of nutritional stress may lead to increased baseline CORT levels in seabirds (e.g. black-legged kittiwakes *Rissa tridactyla*, Buck et al. 2007;

Adelie penguins *Pygoscelis adeliae*, Cockrem et al. 2006). By comparing chicks fed more or less recently, we tested how CORT secretion in thin-billed prion chicks is modified according to their feeding history and thus nutritional stress.

In the present study, the basal levels of CORT in unfed chicks during the day were twofold elevated compared with fed chicks, but the difference during the night peak was much greater (sixfold). This suggests that the non-attendance of chicks induced a greater allostatic load than the diel cycle itself. This is in line with previous results that indicate that diel and seasonal elevations in GCs fall well below stress-related concentrations (e.g. Breuner et al. 1999; Gwinner et al. 1992; Schwabl et al. 1991).

In contrast, in the case of fledging, age (or the time remaining to fledging) was the most important parameter determining CORT levels, and the increase was as dramatic as usually reported for stress-related concentrations. However, stress levels in response to handling in thin-billed prions remain to be investigated.

In summary, we have found that during two predictable changes in demands with a difference in magnitude and timing, both the internal and external component influence GC state, but the external (environmental) component is more important in diel rhythm and the internal (life-history) component in fledging.

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#### References

- Aschoff J (1981) Handbook of behavioral neurobiology. Plenum, New York
- Baos R, Blas J, Bortolotti GR, Marchant TA, Hiraldo F (2006) Adrenocortical response to stress and thyroid hormone status in free-living nestling white storks (*Ciconia ciconia*) exposed to heavy metal and arsenic contamination. *Environ Health Perspect* 114:1497–1501
- Belthoff JR, Dufty AM Jr (1998) Corticosterone, body condition and locomotor activity: A model for dispersal in screech-owls. *Anim Behav* 55:405–415
- Bourgeon S, Raclot T (2006) Corticosterone selectively decreases humoral immunity in female eiders during incubation. *J Exp Biol* 209:4957–4965
- Breuner CW, Wingfield JC, Romero LM (1999) Diel rhythms of basal and stress-induced corticosterone in a wild, seasonal vertebrate, Gambel's white-crowned sparrow. *J Exp Zool* 284:334–342
- Brooke M (2004) Albatrosses and petrels across the world. Oxford University Press, Oxford

- Buck CL, O'Reilly KM, Kildaw SD (2007) Interannual variability of Black-legged Kittiwake productivity is reflected in baseline plasma corticosterone. *Gen Comp Endocrinol* 150:430–436
- Clark GS, Goodwin AJ, von Meyer AP (1984) Extension of the known range of some seabirds on the coast of southern Chile. *Notornis* 31:321–324
- Cockrem JF, Potter MA, Candy EJ (2006) Corticosterone in relation to body mass in Adelie penguins (*Pygoscelis adeliae*) affected by unusual sea ice conditions at Ross Island, Antarctica. *Gen Comp Endocrinol* 149:244–252
- Cox JB (1980) Some remarks on the breeding distribution and taxonomy of the prions (Procellariidae: *Pachyptila*). *J S Austral Mus* 18:91–121
- Dallman MF, Strack AM, Akana SF, Bradbury MJ, Hanson ES, Scribner KA, Smith M (1993) Feast and famine: critical role of glucocorticoids with insulin in daily energy flow. *Front Neuroendocrinol* 14:303–347
- Davies NB (1976) Parental care and the transition to independent feeding in the young Spotted flycatcher (*Muscicapa striata*). *Behaviour* 59:280–295
- Deguchi T, Takahashi A, Watanuki Y (2004) Proximate factors determining age and mass at fledging in rhinoceros auklets (*Cerorhinca monocerata*): intra- and interyear variations. *Auk* 121:452–462
- Devenport L, Knehans A, Sundstrom A, Thomas T (1989) Corticosterone's dual metabolic actions. *Life Sci* 45:1389–1396
- 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
- Duriez O, Weimerskirch H, Fritz H (2000) Regulation of chick provisioning in the thin-billed prion: an interannual comparison and manipulation of parents. *Can J Zool* 78:1275–1283
- Frigerio D, Möstl E, Kotrschal K (2001) Excreted metabolites of gonadal steroid hormones and corticosterone in greylag geese (*Anser anser*) from hatching to fledging. *Gen Comp Endocrinol* 124:246–255
- Gwinner E, Zeman M, Schwabl-Benzinger I, Jenni-Eiermann S, Jenni L, Schwabl H (1992) Corticosterone levels of passerine birds during migratory flight. *Naturwissenschaften* 79:276–278
- Hau M, Gwinner E (1996) Food as a circadian Zeitgeber for house sparrows: the effect of different food access durations. *J Biol Rhythms* 11:196–207
- Heath J (1997) Corticosterone levels during nest departure of juvenile American kestrels. *Condor* 99:806–811
- Jessop TS, Limpus CJ, Whittier JM (2002) Nocturnal activity in the green sea turtle alters daily profiles of melatonin and corticosterone. *Horm Behav* 41:357–365
- Joseph MM, Meier AH (1973) Daily rhythms of plasma corticosterone in the common pigeon, *Columba livia*. *Gen Comp Endocrinol* 20:326–330
- Kern MD, Bacon W, Long D, Cowie RJ (2001) Possible roles for corticosterone and critical size in the fledging of nestling pied flycatchers. *Physiol Biochem Zool* 74:651–659
- Lauber JK, Vriend J, Oishi T (1987) Plasma corticosterone in chicks reared under several lighting schedules. *Comp Biochem Physiol* 86A:73–78
- Lormée H, Jouventin P, Trouve C, Chastel O (2003) Sex-specific patterns in baseline corticosterone and body condition changes in breeding red-footed Boobies *Sula sula*. *Ibis* 145:212–219
- Mauck RA, Ricklefs RE (2005) Control of fledging age in Leach's storm-petrel, *Oceanodroma leucorhoa*: chick development and pre-fledging mass loss. *Funct Ecol* 19:73–80
- Michaud T, Leonard ML (2000) The role of development, parental behavior, and nestmate competition in fledging of nestling tree swallows. *Auk* 117:996–1002
- Mistlberger RE (1994) Circadian food anticipatory activity: formal models and physiological mechanisms. *Neurosci Biobehav Rev* 18:171–195
- Mueller C, Jenni-Eiermann S, Blondel J, Perret P, Caro SP, Lambrechts M, Jenni L (2006) Effect of human presence and handling on circulating corticosterone levels in breeding blue tits (*Parus caeruleus*). *Gen Comp Endocrinol* 148:163–171
- Mukherjee SP, Mukherjee C (1973) Control of rat adipose tissue metabolism by cortisone in relation to epinephrine. *Am J Physiol* 224:898–903
- Quillfeldt P, Masello JF, Strange IJ (2003) Breeding biology of the thin-billed prion *Pachyptila belcheri* at New Island, Falkland Islands, in the poor season 2002/2003: egg desertion, breeding success and chick provisioning. *Polar Biol* 26:746–752
- Quillfeldt P, Masello JF, Strange IJ, Buchanan KL (2006) Begging and provisioning of thin-billed prions *Pachyptila belcheri* is related to testosterone and corticosterone. *Anim Behav* 71:1359–1369
- Quillfeldt P, Strange IJ, Masello JF (2007a) Sea surface temperatures and behavioral buffering capacity in Thin-billed prions: breeding success, provisioning and chick begging. *J Avian Biol* 38:298–308
- Quillfeldt P, Strange IJ, Segelbacher G, Masello JF (2007b) Male and female contributions to provisioning rates of thin-billed prions *Pachyptila belcheri* in the South Atlantic. *J Ornithol* (in press)
- Romero LM, Reed JM (2005) Collecting baseline corticosterone samples in the field: is under 3 min good enough? *Comp Biochem Physiol A* 140:73–79
- Romero LM, Remage-Healey R (2000) Daily and seasonal variation in response to stress in captive starlings (*Sturnus vulgaris*): corticosterone. *Gen Comp Endocrinol* 119:52–59
- Romero LM, Levine S, Sapolsky RM (1995) Adrenocorticotropin secretagog release - Stimulation by frustration and paradoxically by reward presentation. *Brain Res* 676:151–156
- Romero LM, Strohlic D, Wingfield JC (2005) Corticosterone inhibits feather growth: Potential mechanism explaining seasonal down regulation of corticosterone during molt. *Comp Biochem Physiol A* 142:65–73
- Romero LM, Holt DW, Maples M, Wingfield JC (2006) Corticosterone is not correlated with nest departure in snowy owl chicks (*Nyctea scandiaca*). *Gen Comp Endocrinol* 149:119–123
- Schwabl H, Bairlein F, Gwinner E (1991) Basal and stress induced corticosterone levels of garden warblers, *Sylvia borin*, during migration. *J Comp Physiol B* 161:576–580
- Strange IJ (1980) The thin-billed prion, *Pachyptila belcheri*, at New Island, Falkland Islands. *Gerfaut* 70:411–445
- Tarlow EM, Hau M, Anderson DJ, Wikelski M (2003) Diel changes in plasma melatonin and corticosterone concentrations in tropical Nazca boobies (*Sula granti*) in relation to moon phase and age. *Gen Comp Endocrinol* 133:297–304
- Weimerskirch H, Chastel O, Ackermann L (1995) Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the thin-billed prion *Pachyptila belcheri*. *Behav Ecol Sociobiol* 36:11–16
- Westerhof I, Mol JA, Van den Brom WE, Lumeij JT, Rijnberk A (1994) Diurnal rhythms of plasma corticosterone concentrations in racing pigeons (*Columbia livia domestica*) exposed to different light regimens, and the influence of frequent blood sampling. *Avian Dis* 38:428–434
- Woodley SK, Painter DL, Moore MC, Wikelski M, Romero LM (2003) Effect of tidal cycle and food intake on the baseline plasma corticosterone rhythm in intertidally foraging marine iguanas. *Gen Comp Endocrinol* 132:216–222