Variation in feather corticosterone levels in Alpine swift nestlings provides support for the hypo-responsive hypothesis

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ABSTRACT

In birds, feather corticosterone values (CORTf) are increasingly used as a retrospective and integrative proxy of an individual's physiological state during the period of feather growth. Relatively high CORTf values are usually interpreted as an indicator of exposure to energy-demanding or stressful conditions during feather growth. However, in nestlings this interpretation might not always hold true. The reasons are that, firstly nestlings (especially altricial ones) still develop their hypothalamo-pituitary-adrenal (HPA) reactivity during the growth of their feathers. Hence, at a young age, nestlings might be unable to mount a substantial adrenocortical stress response. Secondly, some species are able to down-regulate their metabolism during food scarcity and therewith probably also their CORT release. Consequently, CORTf values may not unambiguously reflect whether nestlings have suffered from energy-demanding or stress situations. Relatively high CORTf values might indicate either energy-demanding or stressful conditions ('stress responsive hypothesis'), or – conversely – favourable conditions during the period of feather growth ('hypo-responsive hypothesis'). In the altricial Alpine swift (*Tachymarptis melba*), we tested which factors help to distinguish between the two hypotheses by considering factors which affect CORT release (brood size, weather) and factors which are affected by high CORT levels (nestling size and condition). We measured CORTf in 205 nestlings over 7 years and collected data on brood size, body size, body condition and prevailing weather. Nestling CORTf values were positively correlated with body condition and negatively with adverse weather, supporting the hypo-responsive hypothesis. Results from the Alpine swift study, supplemented with a survey of the literature, show that relatively easily collected parameters on brood size, nestling size and condition, and environmental factors can help to distinguish between the two hypotheses. A meaningful interpretation of nestling CORTf should only be made in the context of species-specific traits.

1. Introduction

Corticosterone (CORT) is the main glucocorticoid in birds. It is secreted by the adrenal glands and its plasma levels increase to moderate levels to up-regulate the metabolism (e.g. as a response to cold ambient temperature; Jimeno et al., 2017), and to high levels in response to acute stressors (e.g. Müller et al., 2006) to induce a variety of physiological and behavioural changes for overcoming a threatening situation (Romero and Wingfield, 2016). Therefore, CORT is frequently used as an indicator to evaluate whether an individual was exposed to energy demanding or stressful situations.

Most of our knowledge about the release of CORT in response to stressors comes from research on plasma CORT which measures the momentary level of CORT circulating in the blood stream (Romero and

Reed, 2005). Because CORT is quickly released into the blood in response to stressors, plasma levels of CORT are suited to indicate exposure to immediate or ongoing stressors requiring a mobilisation of resources.

In birds, CORT is also deposited in feathers during their growth (CORTf) and thereby provides an integrative and historical record of an individual's CORT release during the period of feather growth (Bortolotti et al., 2009; Ganz et al., 2018; Jenni-Eiermann et al., 2015; Romero and Fairhurst, 2016). Hence, CORTf is increasingly used to indicate energetically demanding or stressful situations retrospectively and over a prolonged period of time (e.g. Fairhurst et al., 2012; Grava et al., 2013; López-Jiménez et al., 2016), although effects of relatively rare, short-lived stressors on CORTf are considered negligible (Romero and Fairhurst, 2016) and might be masked. Therefore, CORTf has been

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considered more useful for studying the cumulative effects of metabolic challenges and responses to environmental stressors that operate over longer time periods, or persistent individual differences in plasma CORT levels (Lind et al., 2020).

However, because of its integrative nature, CORTf values are challenging to interpret. Whether a given CORTf value reflects increased CORT release or baseline levels, needs to be evaluated indirectly by comparison with a control group (Lind et al., 2020) or by considering additional factors, which are known to be related with the adrenal activity (e.g. climatic factors and food availability; e.g. Bize et al., 2010; Jenni-Eiermann et al., 2008). In addition, young nestlings may exhibit a limited CORT response to stressors, although their hypothalamic–pituitary-adrenal (HPA) axis is fully developed (Romero and Wingfield, 2016). This might be due to a) ongoing maturation of the brain's ability to regulate the HPA axis (Sapolsky and Meany, 1986) and/or the sensory and brain functions, necessary to perceive a threatening stimulus as such (Sims and Holberton, 2000), or to b) a down-regulation of the metabolism to save energy during stressful periods (McKechnie and Lovegrove, 2002; Vuarin and Henry, 2014). As a result, CORTf of nestlings facing chronic stressors might be higher, similar, or lower compared with a control group not facing those challenges, as discussed below.

Following the interpretations of plasma CORT, most studies measuring CORTf in nestlings assume that relatively high CORTf levels indicate energetically demanding or stressful conditions during feather growth, which stimulate the adrenal activity and lead to an increased CORT release (later on 'stress responsive hypothesis' e.g. Boves et al., 2016; Johns et al., 2018; Sapolsky et al., 2000; Sorensen et al., 2016). However, this assumption might not always be correct. For several bird species, especially altricial ones, it was shown that the HPA axis reactivity is lowest in the youngest nestlings (Bebus et al., 2020; Schwabl, 1999; Sims and Holberton, 2000; Walker et al., 2005) and reaches a stress reactivity similar to that of adults only shortly before fledging (e.g. Baos et al., 2006; Blas et al., 2006; Rensel et al., 2010; Wada et al., 2007). Since the HPA axis is necessary for hatching and therefore fully developed at this stage, a hypo-responsive period after hatch might be an adaption to prevent adding damage of high CORT levels on the developing neurons (for review see Romero and Wingfield, 2016). Such periods of hypo-responsiveness do not only occur dependent on the intrinsic developmental stage (reviewed in Wada, 2008). They were also observed under external stressful conditions in situations where altricial nestlings would not be able to increase parental feeding (Kitaysky et al., 2001b) thereby reducing maintenance energy costs and possibly growth (e.g. Müller et al., 2009). A reduced stress reactivity might also be expected in altricial nestlings which down-regulate their body temperature, metabolism and behavioural reactions during hunger stress and enter hypothermia (e.g. swifts, swallows; reviewed in McKechnie and Lovegrove, 2002; Vuarin and Henry, 2014). Since CORT is strongly positively associated with metabolic rate (Jimeno et al., 2017), one might expect that CORT release is dampened during hypothermia. Hence, at a young age and/or in stressful conditions low CORTf values might - in contrast to the stress responsive hypothesis - indicate stressful conditions. The scenario of a reduced stress reactivity (either intrinsically depending on developmental stage or through external stressful conditions) will be referred to as 'hypo-responsive hypothesis'. Therefore, for the interpretation of CORTf in nestlings, additional information is required to indicate whether nestlings up-regulate or down-regulate their metabolism as a response to energy-demanding or stressful conditions.

The objective of our study was to test, which of the two hypotheses – the stress- or the hypo-responsive hypothesis – best explains the variation in CORTf in nestling Alpine swifts (*Tachymarptis melba)*. This altricial bird species exclusively feeds on the wing and has the capability to enter hypothermia (Ruf and Geiser, 2015). In this study we considered factors that are relatively easily collected in field studies and are known to either affect CORT release (brood size, weather) or are affected

by CORT (nestling size and condition) (see below for the rationale and references). This allowed us to then carry out a survey of the literature on CORTf to discuss past results in the light of this new conceptual framework of variation in CORTf according to the two hypotheses (Table 1).

During adverse weather (low ambient temperature, rain, strong wind gusts) the availability of aerial insects is strongly reduced (Grüebler et al., 2008; Jenni-Eiermann et al., 2008) and Alpine swifts reduce or entirely stop feeding nestlings, which then experience hunger stress. Short periods of inclement weather and food restriction lead to Cort increase. However, during adverse weather Alpine swift nestlings may also down-regulate body temperature to a minimum of 18 °C (Bize et al., 2007) thereby reducing basal metabolic rate. Large broods increase sibling competition (e.g. for Alpine swifts Bize and Roulin, 2006) and begging behaviour, a behaviour facilitated by CORT (Kitaysky et al., 2001b). Therefore, CORT release in large broods may be increased (Saino et al., 2003; but see Bize et al., 2010; Crino et al., 2020; Gil et al., 2008). On contrary, a large brood may also hamper maturation and therewith HPA responsiveness.

Development and growth of nestlings are retarded in early life when CORT is repeatedly increased to stress levels (Almasi et al., 2012; Butler et al., 2010; Crino et al., 2014; Müller et al., 2009; Sapolsky et al., 2000) and feather growth and quality were impaired in experiments which applied exogenous CORT (e.g. Jenni-Eiermann et al., 2015; Romero et al., 2005). However, it was also shown that feather growth is maintained even during periods of reduced food intake or fasting (Jenni and Winkler, 2020) and hence no correlation between wing-length (which is dominated by feather-length) and CORTf might be found. Body condition is directly reduced by nutritional stress which has been shown to increase CORT secretion (e.g. Jenni-Eiermann et al., 2008; Kitaysky et al., 2001a; Pravosudov and Kitaysky, 2006).

Based on these findings, our predictions for the stress response hypothesis are a positive correlation between CORTf and adverse weather and brood size, and a negative correlation with body size measures and body condition, respectively (Table 1). In contrast, for the hyporesponsive hypothesis, we predict a negative correlation between CORTf and adverse weather and brood size, and a positive correlation with body size measures and body condition at a given age, respectively (Table 1).

In a first step we verify whether the factors supposedly affecting CORT (weather and brood size) are indeed correlated with the parameters supposedly affected by CORT (body size and body condition). In a second step we evaluate how both, the factors affecting CORT and those being affected by CORT, can be used to distinguish between the two hypotheses according to the predictions given in Table 1. Thirdly, the results, complemented with a survey of the literature, were used to evaluate parameters which help to distinguish between the two

Table 1

Expected correlations of nestling CORTf with factors known to either affect CORT release (adverse weather, brood size) or to be affected by CORT (nestling size, body condition) in nestlings based on two different hypotheses. The stress responsive hypothesis predicts an increase in CORT release under stressful conditions. The hypo-responsive hypothesis predicts an increase of CORT release with nestling development or because of a down-regulation of CORT release under (transient) adverse conditions. The arrows indicate an expected positive or negative correlation, a dash no correlation. The significant correlations found in this study for Alpine swift nestlings are indicated in bold.

	Correlation of CORTf under the	
	stress responsive hypothesis	hypo-responsive hypothesis
Adverse weather	↗	↘
Brood size	↗	↘
Nestling size	↘[1] —[2]	↗[1] —[2]
Body condition	↘	↗

[1] for body size measurements.
[2] for wing-length.

hypotheses.

2. Methods

2.1. Study species

Alpine swifts are colonial and can live up to 26 years in the wild. They breed for the first time at the age of 2 or 3 years and produce one clutch of 1 – 4 eggs/year until death (Tettamanti et al., 2012). Alpine swifts are socially monogamous with males and females sharing parental duties equally from incubation to fledging, which takes place 50 to 70 days after hatching (Bize et al., 2004). Nestlings hatch naked and grow their body feathers simultaneously between 10 and 50 days of age (Arn-Willi, 1960).

2.2. Study site and general field procedures

Data come from an Alpine swift colony of ca. 50 breeding pairs located in Solothurn, Switzerland, where there is an individual based monitoring of all the nestlings and adults since 1999. For the present study, feathers were collected during the years 2008 to 2014. Each year, nests were visited regularly to determine clutch size and hatching date of the first egg (denoted day 0), brood size at hatching and brood size at fledging (later on brood size). At day 50 (mean $\pm$ SE: 50.4 $\pm$ 0.11; range 47–64) after hatching, body mass of each nestling was measured to the nearest 0.1 g, sternum-length to the nearest 0.1 mm and wing-length to the nearest mm. Between 4 and 10 feathers were plucked from the white patch of the breast. Nestlings were individually recognized by ringing them with a numbered ring 10 days after hatching. Weather data were received from the Swiss meteorological station Bern-Zollikofen, located at about 40 km from Solothurn. Note that none of the seven study years was an extremely poor year in terms of environmental conditions.

For this study, we randomly selected one nestling per brood for keeping costs within limits, which resulted in feather samples and biometric measurements at day 50 collected from 205 nestlings between 2008 and 2014 (see Table 2 for a description of the sample sizes per year).

Bird capture, ringing and measurements were performed under the legal authorisation of the Federal Office for the Environment, Forests and Landscapes. The ringing licence number of PB is 2235.

2.3. Analysis of CORTf

CORTf was measured in two body feathers per nestling. The length of these two feathers was measured to the nearest mm and they were weighed to the nearest µg before being minced together with scissors in small pieces (<5mm) into a soda glass centrifuge tube. Feather mass was kept within narrow limits (mean $\pm$ SE: 4.57 $\pm$ 0.038 mg). 6 ml methanol (analytical or HPLC grade) were added, and the samples were placed in a sonicating water bath for 30 min at room temperature, followed by incubation at 50 °C in a water bath for 10 h (overnight). Methanol was separated from the feather material by filtration through a Whatman filter paper no. 4 into a new centrifuge tube. The feather remnants and original sample tube were washed with 2 ml methanol and filtered into the tube with the previous filtrate. Methanol extracts were then placed in a SBHCONC/1 Sample Concentrator and evaporated under a constant stream of nitrogen gas at 50 °C. Dried extracts were stored in the freezer and re-suspended in 250 µl assay buffer for CORT measurement.

CORTf was measured in duplicate in a total of six plates with a commercial enzyme immunoassay (EIA, Enzo Life Sciences, Inc.) and calculated via a standard curve run in duplicate on each plate. Cross-reactivites with related steroids are: Corticosterone (100%), Deoxycorticosterone (21.3%), Desoxycorticosterone (21.0%), Progesterone (0.46%), Testosterone (0.31%), Tetrahydrocorticosterone (0.28%), Aldosterone (0.18%), Cortisol (0.046%), and < 0.03% for Pregnenolone, Estradiol, Cortisone, 11-dehydrocorticosterone acetate. Plates were read with a Bio-Rad Benchmark spectrophotometer at 405 nm. A chicken plasma sample (mean $\pm$ SE: 46.86 $\pm$ 1.65 ng/ml) was measured in duplicate as internal control on each plate to calculate intra- (7.99%) and inter-assay (8.98%) variation. Dilution curves of a pool sample of Alpine swift feathers extracted as described were parallel to the standard curve. To test extraction efficiency, 21 Alpine swift feather samples of known CORT concentration were spiked. The mean recovery was 93.37% $\pm$ 2.33 (mean $\pm$ SE, range 74.06–111.88).

2.4. Statistical analysis

CORTf values were expressed per mm feather-length (pg/mm) (following Bortolotti et al., 2009; Jenni-Eiermann et al., 2015) and ln-transformed before analysis in all models to ensure normality of the residuals. For each individual separately, the mean of daily ambient temperature (°C), daily sum of rain (mm) and daily maximum wind gusts (m/s) (later called ambient temperature, rain, wind) were calculated for day 10 to 50 of each nestling (the period of nestling feather development; for sternum-length, which reaches its final length at about 30 days of age, the first 30 days were taken). Body condition was expressed as the residuals of a linear regression of body mass (g) against wing-length (mm). Annual variation in weather condition, reproductive traits and nestling phenotypic traits are presented in Table 2.

To test the effect of environmental, individual and nest conditions on body size and body condition, we fitted a General Linear Model with temperature, rain, wind, age of nestling (days), season (hatching day; 1

Table 2

Annual means (±SD) of CORTf, weather parameters recorded during nestling feather development (day 10 to 50 for each nestling), reproductive success, and nestling biometric traits at day 50 after hatching. Feathers were collected at 50 days of age from one randomly chosen nestling per brood per year (number of nestlings). F and P values are results from one-way ANOVAs testing for annual variation in traits. For each trait, years not connected by the same letter are significantly different using post-hoc Student *t*-test comparisons.

	2008	2009	2010	2011	2012	2013	2014	$F_{6,198}$	P
Number of nestlings	30	29	32	36	23	27	28		
Feather CORT at day 50 (pg/mm)	1.32[A] ± 0.40	2.13[A,B] ± 1.89	4.48[C] ± 2.60	4.43[C] ± 1.64	2.36[B] ± 1.54	5.40[D] ± 2.16	1.34[A] ± 0.34	27.60	<0.001
Weather condition during nestling feather development (10–50 days)									
Mean ambient temperature (°C)	18.83[A] ± 0.10	17.98[B] ± 0.26	19.48[C] ± 0.41	17.35[D] ± 0.10	18.38[E] ± 0.14	19.86[F] ± 0.50	17.39[D] ± 0.29	341.1	<0.001
Sum of rain (mm)	2.98[A,B] ± 0.06	4.65[D] ± 0.29	2.67[C] ± 0.79	4.05[E] ± 0.20	2.76[B,C] ± 0.16	3.05 [A] ± 0.17	6.73[F] ± 0.58	360.7	<0.001
Maximum wind gust (m/s)	6.06[A] ± 0.04	6.30[C] ± 0.20	5.82[B] ± 0.29	5.74[B] ± 0.14	6.20[A,C] ± 0.05	6.21[C] ± 0.18	6.27[C] ± 0.57	22.10	<0.001
Reproductive success									
Brood size at fledging	2.63[A] ± 0.62	2.63[A] ± 0.49	2.13[B] ± 0.61	2.22[B] ± 0.76	2.35[A,B] ± 0.65	2.11[B] ± 0.75	2.36[A,B] ± 0.83	2.95	0.009
Nestling phenotype at day 50									
Body mass (g)	95.17[A] ± 8.16	98.19[A,B] ± 6.27	98.02[A,B] ± 9.66	100.14[B] ± 8.25	96.62[A,B] ± 9.97	97.43[A,B] ± 7.92	94.77[A] ± 9.43	1.49	0.183
Wing-length (mm)	215.9[A,B] ± 7.41	215.8[A,B] ± 9.76	216.6[A,B] ± 7.64	216.1[A,B] ± 6.81	210.2[C] ± 9.04	218.4[A] ± 8.15	213.9[B,C] ± 9.66	2.42	0.028
Sternum-length (mm)	40.19[A] ± 1.48	39.81[A,B] ± 1.36	39.33[B,C] ± 1.16	39.71[A,B] ± 1.31	38.71[C] ± 1.30	39.22[B,C] ± 1.80	39.63[A,B] ± 1.30	3.09	0.006

May = 1), and brood size as explanatory covariates, year (7 levels: 2008–2014) as explanatory factors, and wing-length, sternum-length and body condition, respectively, as dependent variables.

To examine intrinsic and environmental effects on CORTf, a Linear Mixed Model was fitted with lnCORTf as dependent variable and mean ambient temperature, rain, wind, brood size at fledging, wing-length, body condition as fixed explanatory covariates and year as fixed explanatory factors. Plate number was included as random factor (6 levels: plates 1–6) to account for inter-plate variation. Sternum-length was included in the initial model, but then removed as sternum-length was highly correlated with wing-length and inclusion of sternum-length did not show any additional effect on CORTf.

All the statistical models were run in SPSS 12.0 for Windows.

3. Results

The seven study years differed markedly in CORTf, weather conditions, reproductive success and nestling phenotype. Significant differences between years were found for CORTf, ambient temperature, rain, wind gusts, brood size, wing- and sternum-length, but not for body mass (Table 2).

Wing- and sternum-length of the Alpine swift nestlings were not related to the three weather variables or brood size, while there was a significant year effect (Table 3). In contrast, body condition was negatively related with brood size, i.e., nestlings of large broods had a lower body condition, while there was no year effect.

CORTf showed a significant negative relationship with wind, a positive relationship with body condition and differences between years, while temperature, rain, body size and brood size were not significantly related with CORTf (Table 4, Fig. 1).

4. Discussion

Among the factors that could affect CORT, which in turn might influence traits of Alpine swift nestlings, we identified that brood size had an impact on body condition, while weather had no significant effect on size measures or body condition. For CORTf we found a positive correlation with body condition and a negative with strong wind (Fig. 1). Hence, CORTf was high during favourable environmental conditions and in nestlings in good condition. These results clearly support the hypo-responsive hypothesis (Table 1).

Alpine swift nestlings had a lower body condition at day 50 when raised in a large brood, while body size was not affected by environmental, nest- or individual factors. The measures of body size used here (wing- and sternum-length), both reflecting the flight machinery, seem to have a high priority; hence (moderately) adverse conditions - none of the seven study years was an extremely bad year - affected body condition, rather than the size of the flight apparatus, when nestlings are close to fledging. Remarkably, in nestling Alpine swifts, body condition was found to be favoured at the expense of wing and sternum growth earlier in the development (Bize et al., 2006). This change in allocation of resources to different tissues likely mirrors a shift in priorities, with body reserves being essential to ensure survival during the early growth

phase and the flight apparatus being essential to ensure fledging and survival in this extreme aerial bird (Liechti et al., 2013).

We found that CORTf was related to body condition and wind, but not significantly to other weather factors, body size or brood size, although the direction of the slopes tended in the same direction, i.e., better conditions were generally related to higher CORTf (Fig. 1). Moreover, CORTf differed significantly between the study years. Most nestlings of a year grow concurrently and hence experience similar weather conditions (averaged over the 50 days of growth) with little variation within a year. Therefore, we included year as a factor to control for these annual variations.

In the following we discuss the various parameters which may be used to facilitate the interpretation of CORTf in nestlings and to distinguish between the stress responsive and the hypo-responsive hypotheses, in the light of other studies.

Adverse weather conditions reduce the availability of insects in the air (Grüebler et al., 2008) which in Alpine swifts leads to reduced or no feeding by the parents and, depending on the duration of adverse weather, to hunger in the nestlings, and eventually to starvation (Glutz von Blotzheim and Bauer, 1980). Short bouts of adverse weather increase circulating CORT in Alpine swift nestlings transiently (Bize et al., 2010), but apparently do not translate into a long-lasting effect resulting in elevated CORTf (in accordance with the conclusion by Romero and Fairhurst, 2016). It remains to be shown whether plasma CORT in starving Alpine swift nestlings that entered a hypothermic state (Bize et al., 2007; Ruf and Geiser, 2015) is indeed decreased because of a down-regulated metabolism or because of a retarded development.

Cory's Shearwater nestlings provided with less food by the parents than controls showed lower CORTf levels (Fairhurst et al., 2012) which was interpreted by the authors as an adaptive response to minimize the extent of physiological damage caused by chronically elevated CORT. Procellaride nestlings are able to reduce their body temperature by at least 10 °C in response to food scarcity (Boersma, 1986; Ricklefs et al., 1980) further supporting the hypo-responsive hypothesis. In contrast, black kite nestlings showed elevated plasma CORT during low ambient temperature (López-Jiménez et al., 2016) which supports the stress responsive hypothesis. Black kite nestlings develop in an open nest and
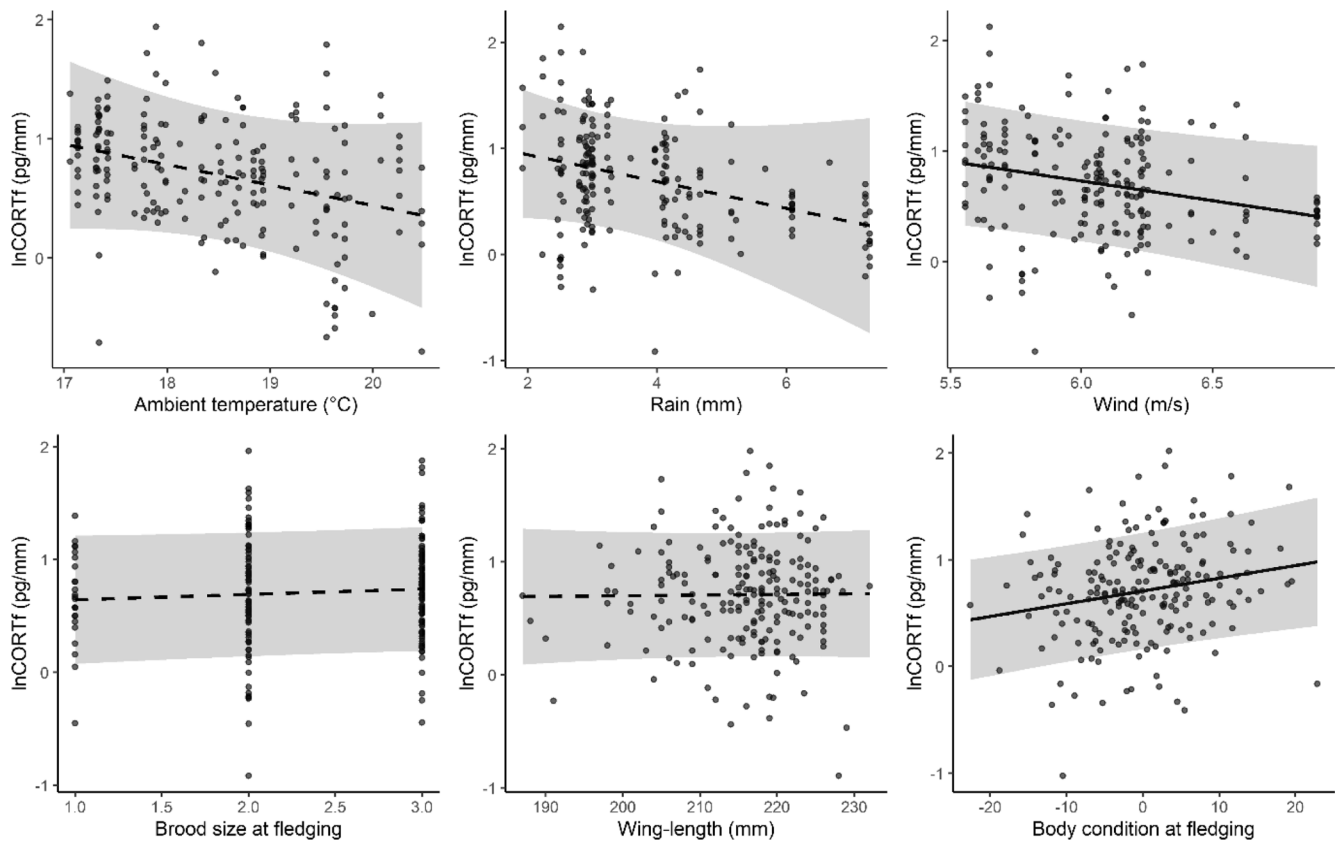
Table 4

Linear Mixed Model with lnCortf (pg/mm) as response variable, plate number as random factor, and mean daily ambient temperature (°C), rain (mm) and wind (m/s) during days 10–50 of each nestling, brood size at fledging, wing-length (mm) and body condition at ca. 50 days of age, respectively, as fixed explanatory variables and year (7 levels: 2008–2014) as fixed factor. Estimates ± SE, F-value and P-values are indicated (bold if significant at the P < 0.05 level).

	Estimate ± SE	F-value	P
Temperature	−0.171 ± 0.15	1.337	0.249
Rain	−0.127 ± 0.11	1.350	0.247
Wind	**−0.355 ± 0.18**	4.054	**0.046**
Brood size	−0.048 ± 0.05	0.779	0.379
Wing-length	0.001 ± 0.00	0.016	0.900
Body condition	**0.012 ± 0.01**	6.811	**0.010**
Year		2.723	**0.044**

Table 3

General Linear Models with wing-length (mm), sternum-length (mm) and body condition at ca. 50 days of age as response variable and mean ambient temperature (°C), rain (mm) and wind (m/s), respectively, during days 10–50 of each nestling (days 10 – 30 for sternum-length), brood size at fledging, hatching day (1 = 1 May), exact age (days) as fixed explanatory variables and year (7 levels: 2008–2014) as fixed factor. Estimates ± SE (P-value) are reported for the explanatory variables only. Differences between years are presented in Table 2. Significant effects were indicated in bold.

	Temperature	Rain	Wind	Brood size	Hatching day	Age	year
Wing (mm)	−2.571 ± 2.43 (0.292)	0.099 ± 1.80 (0.957)	−0.397 ± 2.96 (0.894)	−0.964 ± 0.87 (0.267)	−0.052 ± 0.12 (0.663)	0.292 ± 0.41 (0.475)	**(0.010)**
Sternum (mm)	0.176 ± 0.42 (0.679)	0.303 ± 0.31 (0.337)	0.191 ± 0. 52 (0.713)	−0.007 ± 0.15 (0.961)	−0.031 ± 0.02 (0.140)	−0.092 ± 0.07 (0.198)	**(0.005)**
Body condition	3.496 ± 2.34 (0.137)	−2.558 ± 1.73 (0.142)	0.035 ± 2.85 (0.990)	**−2.00 ± 0.83 (0.017)**	−0.026 ± 0.12 (0.820)	−0.263 ± 0.39 (0.504)	(0.114)

Fig. 1. Relationships of lnCORTf (pg/mm) with mean daily ambient temperature (°C), rain (mm), wind (m/s) during days 10 – 50 of each nestling, respectively, brood size at fledging, and wing-length (mm) and body condition at day 50, respectively. Plots show regression lines from the Linear Mixed Model in Table 4 (solid: significant, dashed: non-significant) with 95% confidence intervals. Dots are partial residuals of the model given in Table 4.

are not known to down-regulate their body temperature. It therefore seems plausible that they need to increase their metabolic rate for thermoregulation.

In summary, adverse weather conditions reduce food intake and/or increase maintenance energy requirements (thermoregulation) in nestlings. Depending on whether nestlings increase metabolism (increased begging, thermoregulation) or not, weather as an auxiliary parameter can help distinguishing between the stress responsive and the hyporesponsive hypotheses.

Another factor related to nestling CORT concentration is brood size. Experimentally enlarged broods lead to increased sibling competition (Bize and Roulin, 2006; Saino et al., 2003) and a reduced parental provisioning rate per individual. However, whether or not plasma CORT is increased in nestlings of large broods is inconsistent. Begging behavior is facilitated by CORT (Kitaysky et al., 2001b), and an increase of plasma CORT in experimentally enlarged broods was found in barn swallows *Hirundo rustica* (Saino et al., 2003) but not in other species (Alpine swift, zebra finch *Taeniopygia guttata,* spotless starling *Sturnus unicolor,* blue tit *Cyanistes caeruleus,* pied flycatcher *Ficedula hypoleuca)* (Bize et al., 2010; Crino et al., 2020; Gil et al., 2008; Lobato et al., 2008).

In our study, brood size significantly affected body condition. Alpine swift nestlings of large broods had a reduced body condition probably indicating a hampered development as also reported for wild nestling zebra finches (Crino et al., 2020), but brood size did not affect CORTf of the Alpine swift nestlings. In house sparrow nestlings of broods which suffered nestling mortality, relatively high CORTf levels were found, suggesting sibling competition for food (Salleh Hudin et al., 2017); based on the stress responsive hypothesis, the authors argued that CORTf was accumulated at the beginning of the nestling phase when the broods were large and sibling competition high. According to our predictions these results would also support the hypo-responsive

hypothesis, especially because they found a positive correlation between CORTf and body condition. López-Jiménez et al. (2016) measured CORTf in black kite nestlings and predicted, in line with the developmental based hypo-responsive hypothesis, higher CORTf in broods with a single nestling. However, they found low CORTf levels in singletons and in the first nestling of multi-nestling broods, while subordinate nestlings had higher levels. They concluded an effect of the social environment on CORTf levels, likely reflecting an increased allostatic load imposed by the oldest, dominant nestling on its younger siblings, which is in line with the stress responsive hypothesis. In great tits *Parus major*, brood size enlargement in the less favorable coniferous habitat resulted in increased CORTf, while brood size reduction in lower CORTf than in controls, and there was no effect of brood size manipulation on CORTf in the favorable deciduous habitat (Lodjak et al., 2015). This supports the stress responsive hypothesis and indicates an increased sibling competition with increasing brood size in the suboptimal habitat.

In summary, the effect of brood size on CORTf apparently depends on whether there is pronounced sibling hierarchy and competition which may lead either to allostatic load in subordinates (supporting the stress responsive hypothesis) or to a delayed development (supporting the hypo-responsive hypothesis). Obviously, a mixture of both, or no effect of brood size, may also occur.

It was repeatedly shown that an experimentally prolonged increase of plasma CORT depresses growth of bone structures (e.g. tarsus, bill), feathers, and mass gain in nestlings (e.g. Almasi et al., 2012; DesRochers et al., 2009; Müller et al., 2009; Spencer and Verhulst, 2007; Strochlic and Romero, 2008). However, whether the effect of transiently high plasma CORT levels on biometrics can be detected via CORTf is controversial. In common buzzard *Buteo buteo* nestlings which developed under natural conditions an inverse relationship of CORTf with body mass was reported (Martínez-Padilla et al., 2013). Other studies

showed no relationship between CORTf and feather growth rate, mass or length (Beaugeard et al., 2019; Harms et al., 2010; Will et al., 2014) or a positive relationship with feather growth rate and/or feather mass in nestlings fed *ad libitum* (Patterson et al., 2015; Salleh Hudin et al., 2017).

The use of size measures may pose two difficulties. First, compensatory accelerated growth may countervail a transient reduction of growth. Hence, despite stressful conditions during a certain period of growth (which may or may not lead to increased CORTf), final size may be similar to unstressed conspecifics (Bize et al., 2003). Second, structures that are particularly important for post-fledging survival may maintain growth under stressful conditions, or may be more prone to compensatory growth, than other structures (Müller et al., 2009). For example, some species will not reduce their feather growth rate when stressed (Grace et al., 2017). Our findings for the Alpine swift nestlings also suggest no effect of adverse weather on the size of the flight apparatus (at least with the weather experienced during the study years which excluded very bad periods) which is of prime importance after fledging, and hence no correlation of size with CORTf. As in our study, no correlation between CORTf and size was reported for wild juvenile house sparrows, although urban birds had higher CORTf than rural ones (Beaugeard et al., 2019) and the authors hypothesized that a potential negative relationship between CORTf and body size during early development might have been blurred by compensatory growth later on.

Hence, even if structural development was hampered for a certain period, it might not be discernible when measuring biometrics of birds shortly before or after fledging. Our observation that body size was not affected by weather or brood size indicates that body size does not seem a decisive parameter for distinguishing between the two hypotheses in our study. A way to retrospectively identify a transient stressful phase and to achieve an improved temporal resolution, is the analysis of feather growth bars and CORTf of feather segments (Ganz et al., 2018; Jenni-Eiermann et al., 2015). However, this needs larger feathers than the small body feathers used in our study for measuring CORTf with conventional EIA.

For body condition, similar difficulties concerning its relationship with CORTf might show up as with body size. Body condition is dependent on food intake which in turn depends on weather conditions, environmental and social factors. Therefore, as for structural growth, a transient low body condition may be compensated during later favourable times (Müller et al., 2009). Furthermore, some species have a natural recession of body mass towards the end of the nestling phase of nestlings in good condition, while those in worse condition do not show such an excess of body mass. Hence, the relationship between CORTf and body condition may depend on the time of measurement (i.e., during a transient low or a transient peak in condition).

We found a significant positive correlation between body condition close to fledging and CORTf in the Alpine swift nestlings, which supports the hypo-responsive hypothesis. Similarly, a study in house sparrow nestlings showed that individuals of parents with access to supplementary food and which were in good body condition, had significantly elevated CORTf levels (Salleh Hudin et al., 2017); however the authors based their interpretation on the stress responsive hypothesis and assumed a time effect with stressful events during early breeding and compensatory growth and mass gain later on. In other studies negative relationships between CORTf and body condition of nestlings were found which were interpreted as the consequence of increased allostatic load due to a bad nutritional status (Harms et al., 2010; Lamb et al., 2016; López-Jiménez et al., 2016) or due to experimentally increased plasma CORT (Fairhurst et al., 2013).

5. Conclusions

The main aim of this study and brief review of the literature is to highlight that the interpretation of CORTf in nestlings is not straightforward, as it might be when investigating plasma CORT levels. Contrasting interpretations of high and low CORTf values can coexist. Here,

we presented two alternative hypotheses associated with different underlying mechanisms. Additional information is required to distinguish not only between the stress responsive and hypo-responsive hypotheses, but also to differentiate whether a hypo-responsive reaction to stress is due to an intrinsic, developmental process or due to metabolic down-regulation triggered by external stressors. Only then CORTf can be interpreted correctly. To further our understanding of CORTf in nestlings, more information is needed in at least three fields.

First, the two proposed hypotheses need more scrupulous testing. For example, it remains untested how long a period of suboptimal feeding may last until it translates in elevated CORTf under the stress hypothesis; how the development of the adrenocortical capacity to respond to a stressor is related to CORTf and depends on the developmental mode (altricial or precocial); whether nestlings in hypothermia have low levels of plasma CORT and whether or not this modifies CORTf; which species may suppress CORT release under stressful conditions (as shown in Cory's shearwaters; Fairhurst et al., 2012).

Second, as shown in the present study and literature review, many of the easily obtainable parameters that may distinguish between the two hypotheses also need verification. For example, weather factors and brood size are good indicators to better define the ambient conditions during nestling development and to distinguish between the two hypotheses. However, as discussed above, they might still leave room for contrasting interpretations if standing alone. Additional factors, such as size measures and body condition, might help, but are also not clear-cut. Therefore, if possible, more information needs to be gathered. Of major importance is knowledge about the amount of food available to the nestling because of the direct effect of hunger stress on CORT release, and information about how the species in question reacts to hunger (e.g., increased begging or hypothermia). Also, information about sibling competition would be helpful to assess the possible level of stress the nestlings might be exposed to. In any case, findings have to be interpreted in the context of species-specific traits (e.g., altricial / precocial) and ambient conditions (e.g., weather). In brief, a thorough knowledge of the biology of the species is needed.

Third, the way of CORT deposition into the feather must be considered. CORTf is incorporated in a time-dependent manner and therefore dependent on feather growth rate. The slower feathers grow, i.e., the longer a feather segment is exposed to the circulation in the feather pulp, the higher is its CORTf concentration (Bortolotti et al., 2008; Jenni-Eiermann et al., 2015). Hence, if feather growth rate varies between groups or with factors of interest, CORTf may reflect feather growth rate rather than an integrated measure of exposure to plasmatic CORT. Therefore, feather growth rate, although not considered in this study, is potentially an important measure that can be determined retrospectively by measuring growth bars if repeated measurements of growing feathers are not feasible.

6. Authors' contribution

PB and SJE designed the study. PB did the entire field work. SJE and JOM performed the lab assays and analysed the data. SJE led the writing of the manuscript. All authors contributed substantially to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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