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Effects of developmental conditions on glucocorticoid concentrations in adulthood depend on sex and foraging conditions

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ABSTRACT

Developmental conditions in early life frequently have long-term consequences on the adult phenotype, but the adult environment can modulate such long-term effects. Glucocorticoid hormones may be instrumental in mediating developmental effects, but the permanency of such endocrine changes is still debated. Here, we manipulated environmental conditions during development (small vs. large brood size, and hence sibling competition) and in adulthood (easy vs. hard foraging conditions) in a full factorial design in zebra finches, and studied effects on baseline (Bas-CORT) and stress-induced (SI-CORT) corticosterone in adulthood. Treatments affected Bas-CORT in females, but not in males. Females reared in small broods had intermediate Bas-CORT levels as adults, regardless of foraging conditions in adulthood, while females reared in large broods showed higher Bas-CORT levels in hard foraging conditions and lower levels in easy foraging conditions. Female Bas-CORT was also more susceptible than male Bas-CORT to non-biological variables, such as ambient temperature. In line with these results, repeatability of Bas-CORT was higher in males (up to 51%) than in females (25%). SI-CORT was not responsive to the experimental manipulations in either sex and its repeatability was high in both sexes. We conclude that Bas-CORT responsiveness to intrinsic and extrinsic conditions is higher in females than in males, and that the expression of developmental conditions may depend on the adult environment. The latter finding illustrates the critical importance of studying of causes and consequences of long-term developmental effects in other environments in addition to standard laboratory conditions.

1. Introduction

Developmental conditions can have long-lasting effects on phenotypes and fitness prospects, and this has been extensively studied in recent years (Lindström, 1999; Metcalfe and Monaghan, 2001; Blount et al., 2003; Gil et al., 2004; Monaghan, 2008). However, such effects may be modulated by the environmental conditions experienced in adulthood (e.g. Reid et al., 2003; Taborsky, 2006; Costantini et al., 2014; Kriengwatana et al., 2014; Briga, 2016). Long-term effects of developmental conditions can be mediated by hormones, but interactions between endocrine signals and environmental conditions experienced during development and in adulthood are not well known.

Harsh conditions during early life stages are often referred to as 'developmental stress' (Spencer and MacDougall-Shackleton, 2011), and indeed the vertebrate stress axis, in particular glucocorticoid (GC) hormones can be potent mediators of phenotypic changes arising from early life challenges (Weaver et al., 2004). GCs are metabolic hormones involved in regulating a wide array of behavioral and physiological traits in both immature and adult vertebrates (Wingfield et al., 1998; Breuner and Hahn, 2003; Martins et al., 2007; Romero and Wingfield, 2015; Hau and Goymann, 2015; Hau et al., 2016). They mediate organismal adjustments to environmental conditions in two ways: first, at baseline concentrations, circulating GCs vary with predictable changes in metabolic demands resulting from daily and seasonal processes, like activity-rest cycles, work load and reproduction (Romero, 2004; Bonier et al., 2011; reviewed in Monaghan and Spencer, 2014). At these low levels, GCs regulate the availability of glucose to fuel daily processes, primarily via actions on the mineralocorticoid receptor (Romero, 2004; Romero and Wingfield, 2015; Hau et al., 2016). Second, whenever an individual is faced with unpredictable challenges such as the appearance of a predator, a rival or rapid environmental deterioration, GC concentrations increase rapidly (Sapolsky, 2000; Romero, 2004; Koolhaas et al., 2011; Hau et al., 2016). At such high stress-induced concentrations, GCs acutely redirect behaviors and physiology to emergency functions which include increased locomotor activity and rapid mobilization of energy stores, at the expense of

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processes like reproduction and immune function through actions on the glucocorticoid receptor (Romero, 2004; Romero and Wingfield, 2015; Hau et al., 2016).

In light of the importance of GCs for individual responses to environmental conditions, it is not surprising that GC functioning in adulthood is shaped by developmental experiences (Lendvai et al., 2009; Rensel et al., 2010; Banerjee et al., 2012). In bird species, this notion is supported by studies that have a) created challenging conditions to increase GC secretion during development by, e.g., increasing brood size, food deprivation, reduction of parental care (Honarmand et al., 2010; Rensel et al., 2010; Banerjee et al., 2012; Schmidt et al., 2012, 2014; Kriengwatana et al., 2014) or b) directly administrated exogenous GCs to the chicks (Spencer and Verhulst, 2007; Spencer et al., 2009; Schmidt et al., 2012, 2014; Crino et al., 2014). However, from the few studies that have examined phenotypic effects of early life conditions under varying adult environments, the role of GCs has remained unclear- either because the role of GCs has not been specifically tested (e.g. Costantini et al., 2014) or the effects of early life conditions on GCs concentrations have disappeared in adulthood (Kriengwatana et al., 2014).

In the current study, we therefore tested whether developmental conditions induced GC changes that lasted into adulthood in a long-term experiment on zebra finches (*Taenopygia guttata*). In a full factorial experimental design, we exposed birds to a combination of two treatments: a brood-size manipulation treatment that created benign vs. harsher conditions during development (small vs. large broods, creating differences in sibling competition and food provisioning), and a foraging treatment (easy vs. hard foraging conditions) that determined environmental conditions during adulthood. Both of our treatments were designed to be naturalistic: experimental brood sizes remained within the range observed in nature and the foraging treatment simulated natural variation in costs of obtaining food (Koetsier and Verhulst, 2011). Our long-term foraging manipulation is likely to induce effects that differ from those of short-term food restrictions often applied in studies testing for environmental effects on endocrine physiology (e.g. Lynn et al., 2010; Schmidt et al., 2014). All birds were maintained in outdoor aviaries during adulthood, which allowed for additional naturalistic effects of variation in climate. To standardize the breeding state of individuals and minimize reproductive activities, all birds were maintained in single-sex groups. Finally, we included equal numbers of males and females into the experiment to test for the existence of sex differences in responses to developmental and adult conditions. Indeed, there is some evidence for sex differences in the persistence of the effects of developmental conditions (Wilkin and Sheldon, 2009; reviewed in Jones et al., 2009) or in the nature of traits affected (Schmidt et al., 2012, 2015). However, whether sex-specific changes in GC concentrations are mediating such differences has yet not been investigated.

Previous results from this long-term experiment have documented that fitness consequences of developmental conditions depend on the adult environment: birds reared in large broods had a decreased survival rate compared to conspecifics raised in small broods, but only when experiencing the hard foraging environment (Briga et al., 2017). Furthermore, differences between treatments have been found in blood glucose levels (Montoya et al., in review), metabolic rate (Koetsier and Verhulst, 2011; Briga, 2016) and social behaviour (our unpublished observations) of adult birds. Our experiment therefore also addresses whether GCs may be involved in mediating these broad phenotypic effects.

We quantified two GC traits, baseline and stress-induced corticosterone (the main GC in birds) in adult birds to test whether (1) the consequences of developmental experiences depend on the quality of the adult environment; (2) natural climatic variations induce differential responses among treatment groups; (3) sex differences exist in responses to treatments and climate; (4) the effects of treatments, climate or sex differ for baseline and stress-induced corticosterone. For brevity, from here on we refer to baseline- and stress-induced corticosterone as Bas-CORT and SI-CORT respectively.

2. Materials and methods

2.1. Animals and treatments

Housing and rearing conditions of the birds are described in Briga et al. (2017). In brief, birds were randomly mated and pairs were housed in cages (80 × 40 × 40 cm) with nesting material and drinking water, sepia and a commercial seed mixture. When the oldest chick was maximally 5 days old, chicks were weighed and randomly cross-fostered to create small (2, sometimes 3 chicks) and large (6, sometimes 5 chicks) broods. These brood sizes are within the range observed in the wild (Zann, 1996). From 35 until approximately 100 days old, young birds were housed in indoor aviaries (153 × 76 × 110 cm) with up to 40 other young of the same sex and two male and female adults (tutors) to foment sexual imprinting. After reaching 100 days of age, individuals were assigned randomly to one of eight outdoor aviaries (310 × 210 × 150 cm), evenly distributed between easy and hard foraging environments. Each aviary contained individuals of one sex, and an approximately equal number of birds reared in small and large broods. The manipulation is described in detail in Koetsier and Verhulst (2011). Briefly, in each aviary a food container (120 × 10 × 60 cm) with 5 holes on each side was suspended from the ceiling. In the easy foraging environment food-boxes had perches just below the holes, allowing birds to perch while eating (low foraging costs). In the hard foraging environment the perches were absent, forcing birds to stay on the wing when obtaining food (high foraging costs). The experiment was started in December 2007, and young birds were periodically added to the aviaries to maintain a density of approximately 20 birds per aviary (see Briga et al., 2017 for details). Thus each aviary contained birds of different ages, ranging from 0.88 to 8.81 years in the data presented in this paper.

Ambient temperature was recorded each hour in the aviaries, and in our analyses we used the temperature in the hour before baseline blood samples were taken. Structural size was measured when the birds were fully grown (age > 100 days) and was taken to be the average tarsus and head + bill length after transformation to a standard normal distribution. Body mass was measured monthly, and was highly repeatable (Briga, 2016). To minimize disturbance we did not measure body mass during blood sampling but instead used the mass measurement closest in time to the blood sampling date. Residual body mass was calculated as the residuals of the linear regression of body mass on structural size, to obtain a mass component independent of size.

2.2. Blood sampling protocol

Blood was collected in May 2014 and May 2015. We sampled only one bird per aviary on each day, to avoid disturbance effects on CORT levels of conspecifics. Each sampling day, four aviaries were sampled between 10:00–12:00 h, and another four between 14:00–16:00 h. The entire sampling period lasted one month each year. Sexes, ages and treatments were balanced for each sampling date and time, and the sequence of aviaries sampled each day was randomized. The identity of the bird to be sampled was pre-determined and target birds were marked with color-rings to facilitate their individual identification when catching. In total, we obtained blood samples for Bas-CORT and SI-CORT from 91 birds in 2014 (Table 1;

Table 1
Sample sizes by sex, treatments (small vs. large brood size, easy vs. hard foraging environment) and year. Some individuals were sampled in both years, and the total number of individuals sampled is therefore shown in brackets.

	Small broods				Large broods			
	Easy		Hard		Easy		Hard	
	2014	2015	2014	2015	2014	2015	2014	2015
Males	12	16	13	17	9	14	11	15
Females	12	18	13	13	12	13	9	14
Total	58 (42)		56 (44)		48 (36)		49 (40)	

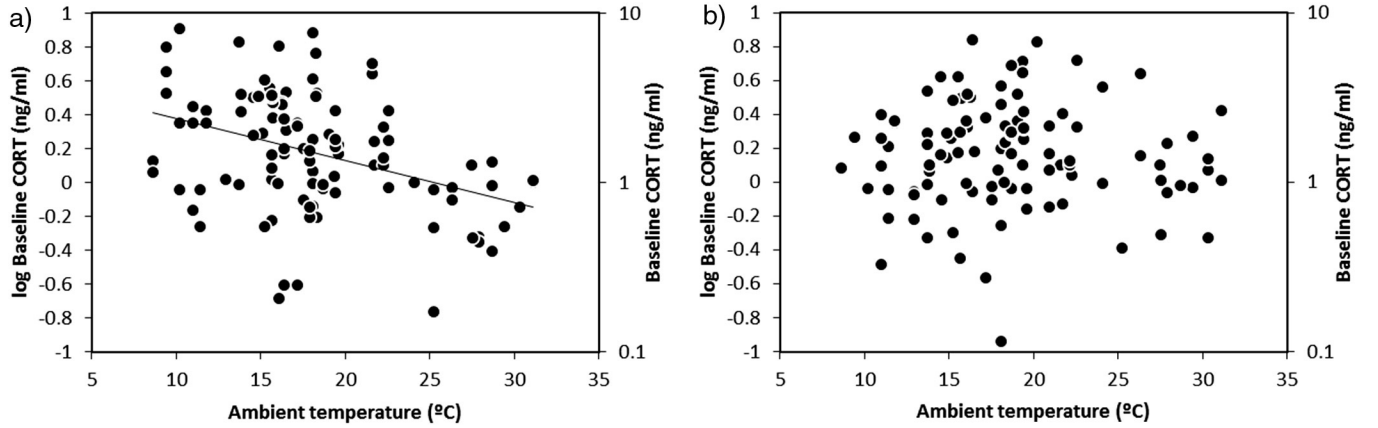

Fig. 1. Baseline CORT concentrations in relation to ambient temperature in (a) females and (b) males.

ages: 0.88–8.29 years, mean = 3.82) and 120 birds in 2015 (Table 1; ages: 0.93–8.81 years, mean = 3.33). 49 of these birds were sampled in both years, the second sample being taken on the date as close as possible to that of the previous year.

Bas-CORT samples were taken within 2 min after opening the door of the aviary. Blood samples were taken from the brachial vein and collected in heparinized microcapillary tubes stored on ice until centrifugation. Immediately after collecting the first sample (Bas-CORT) the birds were placed into an opaque cotton bag (restraint stressor), and a second blood sample (SI-CORT) was taken after 20 min. In total, no more than 150 μl of blood were taken per individual (this includes 2 further samples taken later on the same day as part of a complementary study). After blood sampling, each bird was put into a separate cage with food and a heat lamp to recover before being released back into the aviary (usually within 20 min). Plasma was separated from all samples and stored at −20 °C until analyzed.

2.3. Hormone analysis

We determined plasma CORT concentrations using an enzyme immunoassay kit (Cat. No. ADI-900-097, ENZO Life Sciences, Lausen, Switzerland), following previously established protocols (Ouyang et al., 2015). Samples taken from one individual in each year were placed in neighboring wells, but in other respects samples were randomly distributed. Briefly, aliquots of either 10 μl (for Bas-CORT) or 7 μl plasma (SI-Cort) along with a buffer blank and two positive controls (at 20 ng/ml) were extracted with diethylether. After evaporation, samples were redissolved in 280 μl assay buffer. On the next day, two 100 μl duplicates of each sample were added to an assay plate and taken through the assay. Buffer blanks were at or below the assay's lower detection limit (27 pg/ml). In 2014, intra-plate coefficient of variation (CV; mean ± SE) was 9.63 ± 5.1% and inter-plate CV was 15.23 ± 3.2% (n = 10 plates). In 2015, the intra-plate CV was 11.43 ± 7.05% and inter-plate CV was 9.99 ± 2.67% (n = 16 plates). Samples with CV's > 20% were re-assayed when there was sufficient plasma. Final CORT concentrations were corrected for average loss of sample during extraction, which is 15% in our laboratory (Baugh et al., 2014).

2.4. Statistics

To test our hypotheses we constructed a general linear mixed model, sequentially including the following sets of variables: 1) non-biological variables: ambient temperature, date (as a continuous variable in which 1 = first sampling day, 27th of April), sampling round (morning/afternoon), and sampling sequence (1–4, as four birds were sampled per round and date); 2) individual traits not affected by experimental treatments: sex and age. These steps served to develop a background model for step 3), which incorporated experimental treatments: brood size and foraging. In a final step, 4) we tested for effects of structural size and residual body mass (see below), as body mass is affected by our foraging treatment (Briga, 2016). In all models the following random effects were retained regardless of their contribution to the model fit: individual identity, year and assay plate. Aviary number was not

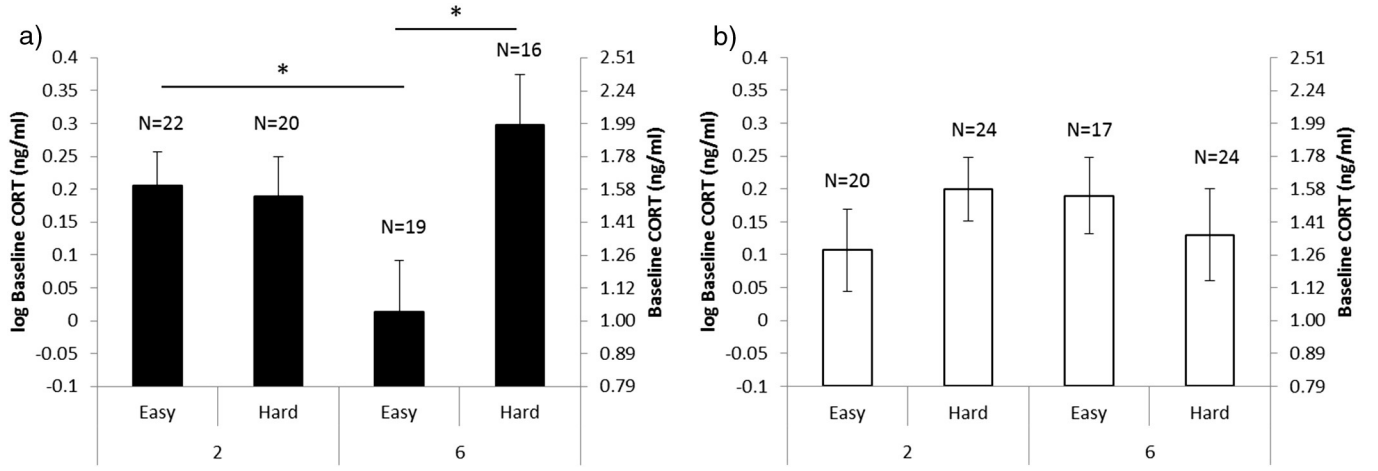

Fig. 2. Baseline CORT concentrations (± s.e.) in relation to manipulated brood size (2 vs. 6 chicks) and foraging environment (easy vs. hard) in (a) females and (b) males. Note that sample sizes refer to number of individuals whereas number of samples per sex and treatment is higher, due to the 49 individuals sampled in both study years. Baseline CORT was independent of either manipulation in males (Table 2b), while in females there was a significant interaction between the two manipulations (Table 2a).

included because it explained a negligible part of the variance in all models.

While building the four models described above, we used backward elimination of least significant terms, except for the main effects of age, brood size and foraging treatment which were kept in the following step regardless of significance. We did this because age effects may diverge between treatments and because treatment groups may differ in structural size and residual body mass, respectively (Briga, 2016). After model selection, the Akaike Information Criterion (Akaike, 1973) was also considered to confirm that the final models had the lowest AIC values. We tested all two- and three-way interactions that included at least two of the following factors: sex, brood size treatment, foraging treatment.

When analyzing SI-CORT as the dependent variable, we included Bas-CORT as a covariate in the models. We did this to separate the effects of stress-induced from those of Bas-CORT, as the two traits can be correlated ($r = 0.3$ in our population, unpublished data). However, we also ran all models on SI-CORT without including Bas-CORT as covariate and obtained qualitatively similar results.

All statistical analyses were performed using R version 3.2.1 (R Core Team, 2015) with the function "lmer" of the R package lme4 (Bates et al., 2014). In the main models, R^2 was obtained with the function "r.squaredGLMM" of the R package MuMIn (Bartoń, 2013). Logarithmic transformations were performed to normalize Bas-CORT and SI-CORT. After model selection all residuals showed a normal distribution.

3. Results

When pooling all data, there was no difference between the sexes in either average Bas-CORT ($F_{141.76} = 0.25$, $p = 0.617$) or in average SI-CORT ($F_{148.67} = 0.03$, $p = 0.869$) concentrations. However, preliminary analysis of Bas-CORT revealed multiple three-way interactions including sex, and we therefore analyzed data for the sexes separately to facilitate the interpretation of the statistical models. We subsequently checked whether the findings differed significantly between the sexes in an analysis of the pooled data.

3.1. Baseline CORT

- *Non-biological variables*: Female Bas-CORT decreased with increasing ambient temperature (Table s1a, Fig. 1a), whereas male Bas-CORT was independent of temperature (Table s1b, Fig. 1b). This sex difference was significant (pooled data: Temperature × Sex: $F_{157.5} = 9.35$, $p = 0.0026$). In females, the association between Bas-CORT levels and temperature differed between foraging treatments, independently of developmental conditions (Table s3a, Fig. s1): the relationship between Bas-CORT and temperature was significantly steeper in the hard (-0.10 ± 0.016) compared to the easy foraging treatment (-0.039 ± 0.017), and both differed significantly from 0 (hard: $t_{47} = -4.29$, $p < 0.0001$; easy: $t_{53} = -2.20$, $p = 0.032$). Date, time of the day and processing sequence were not correlated with Bas-CORT in either sex (Table s1). Thus, of all non-biological variables tested, Bas-CORT associated negatively only with temperature in females, and this association was more pronounced in hard environmental conditions.
- *Age*: Introduction of age into the model, either as a linear or quadratic term, did not explain a significant amount of variation in Bas-CORT in either sex (Table s2). Thus, we found no evidence for age-associated changes in Bas-CORT.
- *Treatments*: Bas-CORT concentrations of males were not affected by either treatment or their interaction (Table s3b, Fig. 2b). In contrast, Bas-CORT concentrations of females were affected by both experimental treatments, as indicated by a significant interaction between foraging and brood size treatments (Table s3a, Fig. 2a). Post-hoc analyses showed that for females from small broods, adult foraging conditions had little effect on Bas-CORT ($F_{38.9} = 0.24$, $p = 0.63$, Fig. 2a). In contrast, for females from large broods Bas-CORT levels varied with foraging conditions, with Bas-CORT levels being higher in the hard compared to the easy foraging treatment ($F_{25.3} = 6.67$, $p = 0.016$, Fig. 2a). Interestingly, the Bas-CORT levels of females from small broods were intermediate between those of females from large broods kept under easy ($F_{37.6} = 4.55$, $p = 0.038$, Fig. 2a) and hard foraging conditions, albeit not significantly for the latter comparison ($F_{22.3} = 2.03$, $p = 0.16$, Fig. 2a). The differences between the sexes were significant (Foraging Treatment × Brood Treatment × Sex: $F_{137} = 5.41$, $p = 0.022$; Brood Treatment × Sex: $F_{137} = 5.28$, $p = 0.023$; Foraging Treatment × Sex: $F_{134.8} = 2.27$, $p = 0.13$). Thus, Bas-CORT levels in females but not in males were susceptible to environmental quality during development and in adulthood (Fig. 4).

Table 2
Baseline CORT concentrations (log transformed) in relation to non-biological variables, age, experimental treatments, size and mass in (a) Females (main model, $R^2 = 0.77$), and (b) Males (main model, $R^2 = 0.61$). Temp = Ambient temperature; BroodTreat(6) = Brood treatment (large); ForTreat(H) = Foraging treatment(hard). Note that these final models are also the best fitting ones according to Akaike Information Criterion (Akaike, 1973) and may not include terms with significant *p*-values.

a	Estimate	s.e.	d.f.	F	p
Intercept	1.426	0.351			
Temperature	−0.037	0.014	83.05	24.961	<0.0001
ForTreat(H)	0.546	0.401	60.86	5.690	0.021
BroodTreat(6)	−0.521	0.175	54.68	1.214	0.276
Size	−0.139	0.093	56.75	0.054	0.817
Mass	−0.294	0.074	88.62	15.697	0.0002
Temp × ForTreat(H)	−0.052	0.021	49.21	6.123	0.017
ForTreat(H) × BroodTreat(6)	0.767	0.247	50.65	9.615	0.003
ForTreat(H) × Size	0.320	0.178	65.65	3.211	0.078
Rejected terms					
ForTreat(H) × Mass	−0.042	0.254	87.69	1.969	0.164
BroodTreat(6) × Mass	−0.280	0.169	78.45	0.002	0.967
BroodTreat(6) × Size	−0.169	0.201	65.58	0.007	0.934
ForTreat(H) × BroodTreat(6) × Mass	0.547	0.340	87.61	2.588	0.111
ForTreat(H) × BroodTreat(6) × Size	0.310	0.361	59.27	0.734	0.395

Random factors

	Variance
Bird ID	0.131
Year	0.080
Assay plate	0.092
Residual	0.174

b	Estimate	s.e.	d.f.	F	p
Intercept	0.384	0.077	38.27		
Rejected terms					
ForTreat(H)	0.208	0.248	61.81	2.194	0.143
BroodTreat(6)	0.251	0.244	61.56	2.956	0.090
Size	0.136	0.179	71.04	2.712	0.104
Mass	0.126	0.127	90.11	3.388	0.069
ForTreat(H) × BroodTreat(6)	0.107	0.353	63.21	0.092	0.762
BroodTreat(6) × Mass	0.272	0.181	91.14	4.592	0.035
ForTreat(H) × Size	−0.148	0.291	69.04	2.771	0.100
ForTreat(H) × Mass	−0.313	0.231	79.51	0.027	0.869
BroodTreat(6) × Size	−0.275	0.265	65.82	1.151	0.287
ForTreat(H) × BroodTreat(6) × Mass	0.693	0.406	81.03	2.918	0.091
ForTreat(H) × BroodTreat(6) × Size	1.005	0.426	71.04	5.573	0.021

Random factors

	Variance
Bird ID	0.255
Year	0.000
Assay plate	0.007
Residual	0.218

- *Size and mass:* In females, higher residual body mass was associated with lower Bas-CORT concentrations (Table 2a, Fig. 3a). In contrast, in males there was no association between residual body mass and Bas-CORT (Table 2b, Fig. 3b). The difference between the sexes was highly significant (Pooled data: Body Mass × Sex: $F_{190.6} = 15.97$, $p < 0.0001$). A trend for larger individuals in hard foraging conditions having higher Bas-CORT concentrations was found in both males and females (Table 2), possibly reflecting higher energy needs of large individuals in particular when foraging is costly.

3.2. Stress-induced CORT

- *Non-biological variables*: Female SI-CORT concentrations were affected by date (with SI-CORT concentrations being lower later in the season, Fig. s2) and time of day, being lower in the afternoons (Table s4a). None of these variables affected SI-CORT levels in males (Table s4b). With pooled data, the sex difference regarding the time of day was confirmed (Time of day × Sex: $F_{134.5} = 4.36$, $p = 0.038$), whereas there was no effect of sampling date (Date × Sex: $F_{134.5} = 0.75$, $p = 0.39$). Thus, SI-CORT was affected by different non-biological variables than Bas-CORT, but again only in females.
- *Age, Treatments, Size and Mass*: Age (Table s5a–b), treatments (Table s6a–b, Fig.5a–b) or size and mass (Table 3a–b) did not affect SI-CORT and this was consistent for both sexes. Hence, in contrast to Bas-CORT, SI-CORT levels were little affected by environmental variables.

3.3. Repeatability

Repeatability was calculated for the 49 individuals (22 males, 27 females) that were sampled in both years. The repeatability of Bas-CORT in males was high (51%, Table 4) and twice that of females (23–26%, Table 4). In contrast, the repeatability SI-CORT was equally high for both sexes (approx. 50%, Table 4, Fig. 6). Whether these estimates were extracted from the null models or from the final models (i.e. with covariates or additional random effects, Table 4) made little difference. Thus, the repeatabilities of CORT traits were overall high (~50%), but halved for Bas-CORT levels in females, which were the most affected by environmental conditions.

4. Discussion

Our study confirmed that the long-term effects of early developmental challenges can depend on environmental conditions during adulthood, because females reared in large broods modulated Bas-CORT concentrations with respect to the quality of their adult environment, while this phenomenon was not observed in females reared in small broods or in males. Specifically, females that experienced harsh developmental conditions had low Bas-CORT concentrations in the easy foraging treatment, but increased Bas-CORT in the hard foraging environment. Thus, our results show that being reared with many siblings leads to long-term changes in the hormonal organization of individuals, thereby determining the way in which individuals cope with environmental conditions during adulthood.

Our finding that females from large broods had particularly low Bas-CORT concentrations in the easy foraging environment was unexpected, because previous studies have associated developmental challenges with increased, not decreased, CORT levels in later stages of life (e.g. Spencer et al., 2009; Kriengwatana et al., 2014; Schmidt et al., 2014). Growing up with a large number of siblings increases competition within the nest, but also reduces per capita food provisioning by the parents (Briga, 2016). Both food restriction and increased begging have been related to higher Bas-CORT levels in nestlings in previous studies (Kitaysky et al., 2001a, 2001b; Honarmand et al., 2010). It is therefore possible that in our study birds coming from large broods had higher Bas-CORT as nestlings, even though in adulthood we found no differences in Bas-CORT concentrations between individuals from different developmental treatments. This suggests either that early life effects on Bas-CORT were present, but manifested themselves only during development, or that they persisted into adulthood but were then modified by the adult environment. Further experiments, which include the collection of blood samples from developing birds would be required to solve this question. Conversely, the pattern found in females from large broods living in the hard foraging environment is as expected, as increased work load is known to increase Bas-CORT concentrations (e.g. Bonier et al., 2011; Landys et al., 2006). To our surprise, Bas-CORT of females reared in small broods did not respond to the foraging treatment. We know that individuals from our study population that grow up in small broods can cope better with their environment because their lifespan is not affected by the foraging treatment, in contrast to that of birds reared in large broods (Briga et al., 2017). The fact that these individuals do not increase Bas-CORT concentrations in a hard adult environment suggests that they can compensate somehow for the increased workload. Hence, together with the survival data our findings suggest that individuals raised in small broods are less sensitive (or, more resilient) to the effects of challenging conditions during adulthood.

We found a striking difference between the sexes in the responsiveness of CORT to developmental and adult environmental conditions, with females showing stronger Bas-CORT responses than males (Fig. 4). Even SI-CORT, which generally showed little environmental responsiveness in our experiment, was related to sampling

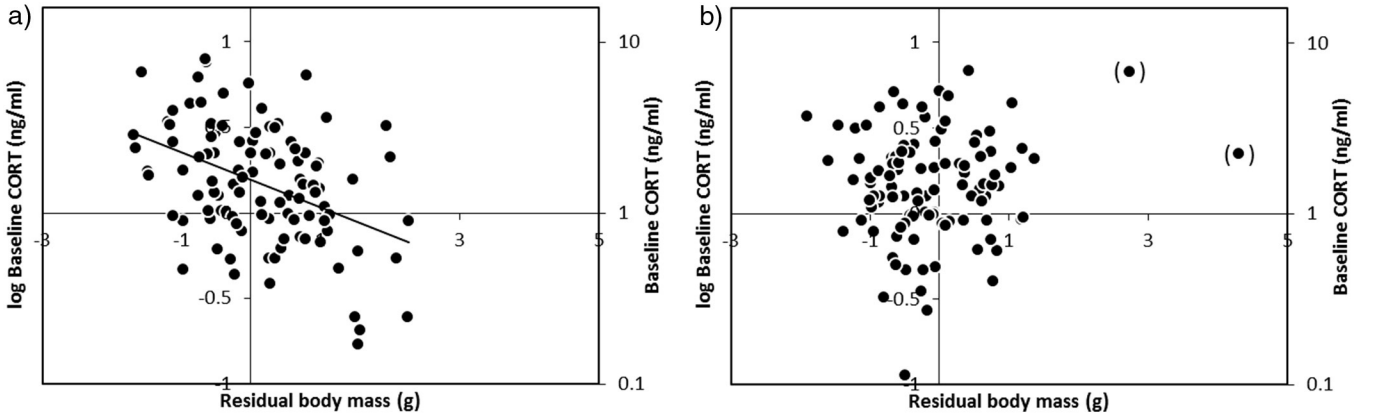

Fig. 3. Baseline CORT concentrations in relation to residual body mass in (a) females and (b) males. In the graph for males, two outliers that were excluded from the analyses are presented between brackets.

Table 3
Stress-induced CORT concentrations (log transformed) in relation to non-biological variables, age, experimental treatments, size and mass in (a) Females (main model, $R^2 = 0.64$) and (b) Males (main model, $R^2 = 0.55$). Temp = Ambient temperature; Time(aft.) = Time of day(afternoon); BroodTreat(6) = Brood treatment (large); ForTreat(H) = Foraging treatment(hard). Note that these final models are also the best fitting ones according to Akaike Information Criterion (Akaike, 1973) and may not include all the terms with significant *p*-values.

a	Estimate	s.e.	d.f.	F	p
Intercept	2.786	0.153	91.97		
BasCORT	0.098	0.035	97.39	7.794	0.006
Date	−0.019	0.006	61.07	11.978	0.001
Time (aft.)	−0.344	0.110	96.72	9.783	0.002
Rejected terms					
ForTreat(H)	0.100	0.192	67.32	1.573	0.214
BroodTreat(6)	−0.208	0.195	69.62	0.920	0.341
Mass	0.088	0.110	75.61	0.087	0.769
Size	0.014	0.135	64.68	1.415	0.239
ForTreat(H) × Size	−0.212	0.233	69.59	2.745	0.102
ForTreat(H) × Mass	−0.371	0.230	85.83	0.905	0.344
BroodTreat(6) × Size	0.052	0.188	68.96	0.013	0.911
BroodTreat(6) × Mass	0.013	0.157	80.94	2.493	0.118
ForTreat(H) × BroodTreat(6)	0.148	0.280	66.71	0.279	0.599
ForTreat(H) × BroodTreat(6) × Mass	0.453	0.309	86.14	2.144	0.147
ForTreat(H) × BroodTreat(6) × Size	−0.142	0.336	62.95	0.178	0.675

Random factors

	Variance
Bird ID	0.153
Year	0.000
Assay plate	0.000
Residual	0.154

b	Estimate	s.e.	d.f.	F	p
Intercept	2.284	0.122	76.89		
BasCORT	0.160	0.044	97.57	13.283	0.0004
Rejected terms					
ForTreat(H)	−0.174	0.201	67.56	0.076	0.783
BroodTreat (6)	−0.258	0.201	66.07	0.077	0.782
Mass	−0.073	0.105	82.47	1.705	0.195
Size	−0.283	0.147	74.57	0.124	0.726
ForTreat(H): Mass	0.231	0.190	77.89	2.975	0.089
ForTreat(H): Size	0.281	0.239	73.71	1.604	0.209
BroodTreat(6): Mass	0.093	0.195	86.84	0.679	0.412
BroodTreat(6) × Size	0.401	0.219	71.94	4.008	0.049
ForTreat(H) × BroodTreat(6)	0.432	0.294	68.64	2.152	0.147
ForTreat(H) × BroodTreat(6) × Size	−0.105	0.362	77.78	0.085	0.772
ForTreat(H) × BroodTreat(6) × Mass	0.119	0.341	78.33	0.120	0.730

Random factors

	Variance
Bird ID	0.148
Year	0.000
Assay plate	0.014
Residual	0.161

date and time of day in females, but not in males. The sex difference in environmental responsiveness was confirmed by the sex difference in Bas-CORT repeatability, which was lower in females (repeatability = 23%) compared to males (repeatability = 51%). Thus the sex-difference in environmental responsiveness was not due to unidentified or stochastic environmental effects on Bas-CORT in males, but can instead be attributed to an intrinsic difference between the sexes.

Some of the observed environmental effects on CORT in females were expected, because they affect energy expenditure. For example, female Bas-CORT decreased with increasing ambient temperature and residual body mass. Periods with warmer weather, which likely induced a slower metabolic rate, were shown previously to be related to lower Bas-CORT levels (Jenni-Eiermann et al., 2008; Lendvai et al., 2009; de Bruijn and Romero, 2011). The negative correlation found in females between Bas-CORT and residual body mass is also in agreement with previous studies (Kitaysky et al., 1999; Jenni-Eiermann et al., 2008; Jaatinen et al., 2013; Hau et al., 2016), and may reflect heavier individuals having a lower mass-specific metabolic rate. The apparent environmental insensitivity in male CORT traits is therefore surprising, because findings in our study population indicate male and female metabolism to be equally sensitive to ambient temperature, residual body mass and environmental quality (Briga, 2016). Likewise, the experimental effects on lifespan and survival trajectories were indistinguishable between the sexes (Briga et al., 2017). Further experiments are needed to test whether the association between metabolic rate and Bas-CORT is sex-dependent, and whether this explains the sex difference in environmental responsiveness of Bas-CORT. One way in which such a difference could arise is when individual variation in level of the Bas-CORT/metabolic rate association is larger in males, leading to a weaker association on the between-individual level, which would be consistent with the higher repeatability found for male Bas-CORT.

Since the developmental manipulation affected CORT traits in females but not in males, it is possible that the observed sex differences in CORT in adulthood arose from males and females responding differently to the number of siblings they were reared with. This pattern is consistent with other studies on our study species showing interactions between sex and endocrine traits during early development (Griffith and Buchanan, 2010) and that females were more susceptible to early-life stressors than males (De Kogel, 1997; Verhulst et al., 2006; Schmidt et al., 2012). Sex differences in resource allocation to different physiological systems may lie at the base of sex-specific effects of developmental conditions (Wilkin and Sheldon, 2009; Schmidt et al., 2015). Mechanistically, such sex differences could result from the interactions between the HPA axis and the reproductive (hypothalamus-pituitary-gonadal, HPG) axis that secretes sex steroids (Schmidt et al., 2014; reviewed in Hau et al., 2016). Previous work in mammals and humans found that the actions of sex steroids on the HPA axis indeed differ between the sexes (Toufexis et al., 2014; Deak et al., 2015; reviewed in Handa and Weiser, 2014 and Panagiotakopoulos and Neigh, 2014). Further research is needed to determine whether in avian species these interactions underlie the divergent responses to developmental conditions in males and females.

Several studies have reported variable repeatability values for Bas-CORT and SI-CORT, and overall find repeatabilities for SI-CORT to be higher compared to Bas-CORT (Grace and Anderson, 2014; Romero and Reed, 2008; Wada et al., 2008; Ouyang et al., 2011; Small and Schoech, 2015; Vitousek et al., 2014). Repeatability estimates reflect a combination of the repeatability of properties of individual animals, including their behaviour at the time of sampling, and the repeatability of the environment in which they are sampled (which also affects their behaviour at the time of sampling). That the repeatability of SI-CORT is generally higher than the repeatability of Bas-CORT is not surprising therefore, because the setting in which an animal finds itself during the measurements (standardized restraint protocol), including its behaviour, is likely to be more repeatable for SI-CORT than for Bas-CORT. The context dependence of the repeatability estimates makes it difficult to evaluate more generally to what extent baseline or SI-CORT are repeatable traits. In the present study, the moderate-high repeatabilities found for CORT traits suggest that individuals from our population, especially males, can be characterized by their baseline and SI-CORT levels. This will in part reflect that the conditions in which they were measured were well controlled, and repeatabilities, in particular of Bas-CORT are likely to be consistently lower in more natural conditions, because these will be more variable.

We found Bas-CORT and SI-CORT to be affected by entirely different factors. In females, Bas-CORT varied with ambient temperature, developmental and adult treatments and residual body mass.

Table 4
Repeatabilities and variance components of random effects in both sexes for (a) baseline CORT and (b) stress induced CORT concentrations (both log transformed). Shown are variances and individual repeatabilities as extracted from the null model, containing two random factors only (Bird Identity and Plate), and variances and individual repeatabilities as extracted from the final models as presented in Tables 2 and 3.

a

Bas-CORT	Null model 98 samples of 49 individuals				Main model 98 samples of 49 individuals			
	Females ($N = 27$)		Males ($N = 22$)		Females ($N = 27$)		Males ($N = 22$)	
	Variance	Repeat.	Variance	Repeat.	Variance	Repeat.	Variance	Repeat.
Bird ID	0.13	**23.21%**	0.20	**51.03%**	0.12	**25.70%**	0.20	**51.03%**
Plate	0.17	–	0.00	–	0.12	–	0.00	–
Year	–	–	–	–	0.11	–	0.00	–
Residual	0.26	–	0.19	–	0.11	–	0.19	–

b

SI-CORT	Null model 98 samples of 49 individuals				Main model 98 samples of 49 individuals			
	Females ($N = 27$)		Males ($N = 22$)		Females ($N = 27$)		Males ($N = 22$)	
	Variance	Repeat.	Variance	Repeat.	Variance	Repeat.	Variance	Repeat.
Bird ID	0.18	**44.86%**	0.17	**50.59%**	0.16	**50.75%**	0.18	**50.30%**
Plate	0.05	–	0.00	–	0.00	–	0.00	–
Year	–	–	–	–	0.00	–	0.01	–
Residual	0.17	–	0.17	–	0.16	–	0.17	–

In contrast, none of these variables were related to SI-CORT concentrations. Instead, date and sampling time of day affected SI-CORT, and again only in females. Since SI-CORT concentrations shift an individual into an emergency life-history state, such responses are perhaps less dependent on direct effects on metabolic rate and more by other individual characteristics not addressed in this study, such as the genetic makeup. Indeed, SI-CORT has been shown to be more heritable compared to Bas-CORT (Jenkins et al., 2014). A strong genetic basis can be expected for individual traits with direct effects on fitness, and hence SI-CORT may potentially be more susceptible to evolutionary change in response to selection compared with Bas-CORT.

In the context of conservation physiology, the possibility has been considered that Bas-CORT of a population inhabiting a particular site or habitat may be indicative of the quality of that site or habitat as experienced by that population (reviewed in Dantzer et al., 2014,

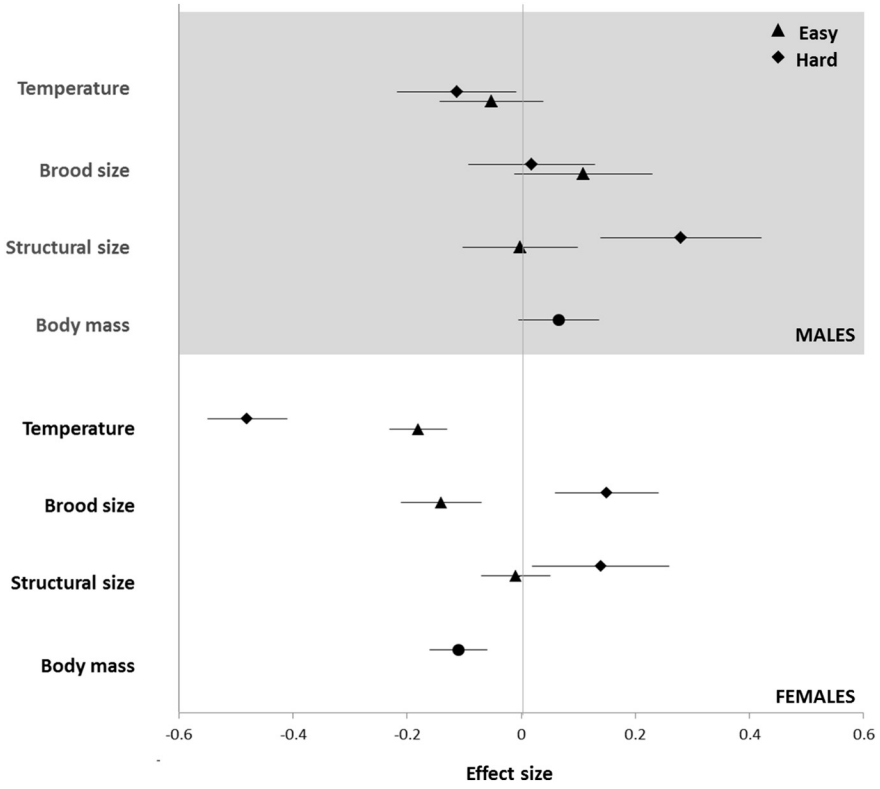

Fig. 4. Effect sizes (calculated as Cohen's D, Cohen, 1988) of the main variables affecting baseline CORT concentrations. To make effect size comparable across traits and sexes, all the independent variables were transformed to standard normal distributions and all effect sizes are based on the same model for the two sexes separately (main model for females, Table 2a). Data are split by foraging treatment for a better interpretation of the significant interactions. As data are split by sex and treatments error bars of effect sizes cannot be used to infer significance as derived from the models of the pooled data.

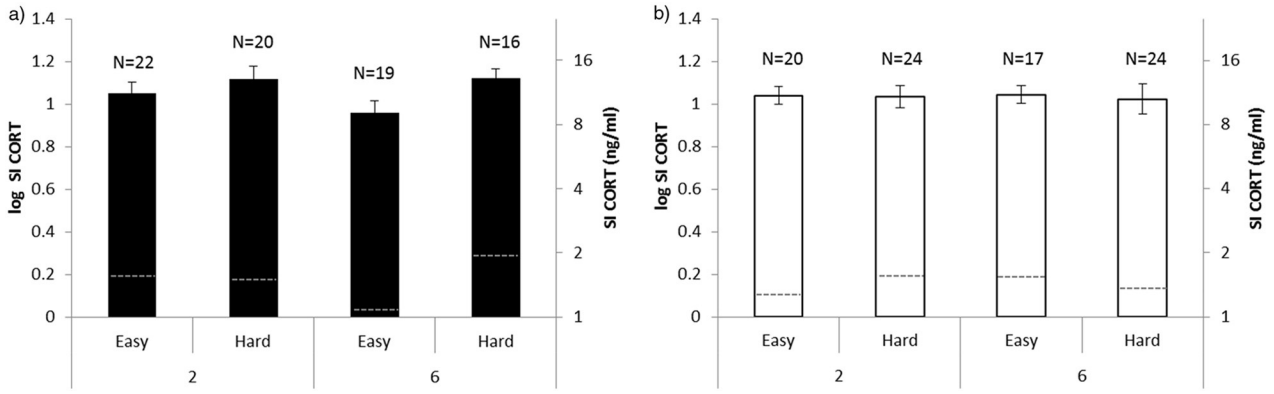

Fig. 5. Stress-induced CORT concentrations (±s.e.) in relation to manipulated brood size (2 vs. 6 chicks) and foraging environment (easy vs. hard) in (a) females and (b) males. Sample sizes refer to number of individuals whereas number of samples per sex and treatment is higher, due to the 49 individuals sampled in both years. Grey dashed lines in the bars indicate category specific average baseline CORT levels.

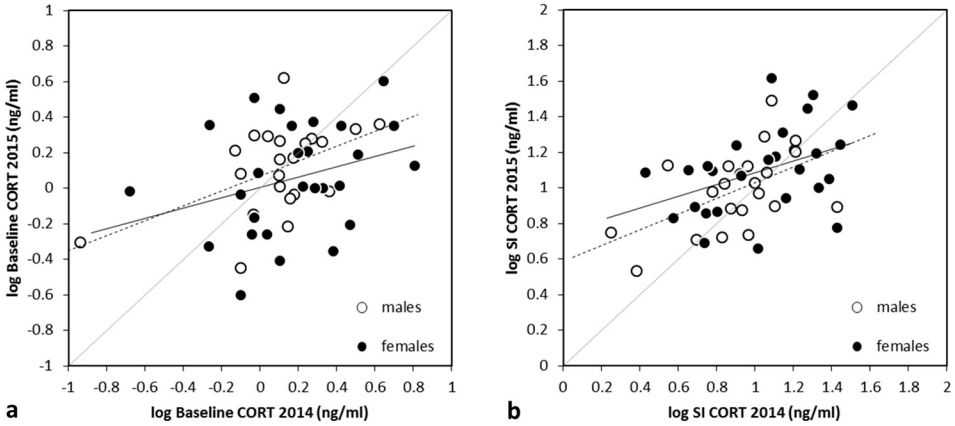

Fig. 6. Repeatabilities for (a) baseline CORT and (b) stress-induced CORT concentrations. Filled circles (and continuous line) represent females ($N = 27$). Open circles (and dotted line) represent males ($N = 22$). Grey lines represent y = x.

Madliger and Love, 2015). Testing for such a relationship conclusively in a natural setting is difficult, if only because individuals are not randomly distributed over low and higher quality habitats (e.g. Van De Pol et al., 2006). Our manipulation of a key aspect of habitat quality, namely the net intake rate of food, is therefore also of interest from the perspective of conservation physiology. In our study, foraging environment did not affect Bas-CORT in males, or in females when pooled across birds reared in small and large broods. This implies that large differences in habitat quality can exist that superficially do not affect Bas-CORT - unless phenotypic quality can be assessed independently, which will usually be difficult.

5. Conclusions

Males and females differed in their responsiveness to environmental variation regarding CORT traits. Females were more responsive than males, and their Bas-CORT was far more affected by environmental variation, while there was no sex-difference in average CORT concentrations. It would be of interest to unravel the extent to which this can be attributed to a difference in Bas-CORT function between males and females. Our results also illustrate that adult environments of different quality are needed to comprehensively investigate the long-term effects of developmental conditions.

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