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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)	