



Effects of nutritional stress during different developmental periods on song and the hypothalamic–pituitary–adrenal axis in zebra finches



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ABSTRACT

In songbirds, developmental stress affects song learning and production. Altered hypothalamic–pituitary–adrenal (HPA) axis function resulting in elevated corticosterone (CORT) may contribute to this effect. We examined whether developmental conditions affected the association between adult song and HPA axis function, and whether nutritional stress before and after nutritional independence has distinct effects on song learning and/or vocal performance. Zebra finches (*Taeniopygia guttata*) were raised in consistently high (HH) or low (LL) food conditions until post-hatch day (PHD) 62, or were switched from high to low conditions (HL) or vice versa (LH) at PHD 34. Song was recorded in adulthood. We assessed the response of CORT to handling during development and to dexamethasone (DEX) and adrenocorticotrophic hormone (ACTH) challenges during adulthood. Song learning and vocal performance were not affected by nutritional stress at either developmental stage. Nutritional stress elevated baseline CORT during development. Nutritional stress also increased rate of CORT secretion in birds that experienced stress only in the juvenile phase (HL group). Birds in the LL group had lower CORT levels after injection of ACTH compared to the other groups, however there was no effect of nutritional stress on the response to DEX. Thus, our findings indicate that developmental stress can affect HPA function without concurrently affecting song.

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Introduction

Growth and developmental processes are sensitive to environmental factors, and early life adversity can have profound effects on behavior and physiology of animals (Barnes and Ozanne, 2011; Lindström, 1999). Birdsong is a trait that appears particularly sensitive to stressful developmental conditions (Spencer and MacDougall-Shackleton, 2011), which indicates that it may be a reliable indicator of developmental history and this may contribute to birdsong being a sexually selected trait (Nowicki et al., 1998, 2002). For songbirds such as the zebra finch (*Taeniopygia guttata*), development of a specific network of interconnected brain nuclei mediates song learning and production. Development of these brain regions and song learning behaviors begin soon after hatching and conclude at sexual maturity (Brainard and Doupe, 2002; Kirn, 2010). Because zebra finches do not modify their song elements in adulthood, any stress-induced deficits in song learning during early life may reliably indicate how well an individual was able to develop when confronted with stress. While there seems to be

some support for this hypothesis, the results are not uniform across studies (Table 1). These inconsistencies may partially be caused by the variation in types of stressors used and measures used to quantify song. To help resolve these inconsistencies, further studies are required that replicated previously used developmental stress protocols and include a comprehensive analysis of song parameters.

One way in which external environments can affect development is through glucocorticoids via activation of the hypothalamic–pituitary–adrenal (HPA) axis. Glucocorticoid receptors (GR) are present in the song control nuclei HVC and RA (robust nucleus of the arcopallium), implying that these areas are potential targets for glucocorticoids such as corticosterone (CORT; Shahbazi et al., 2011; Suzuki et al., 2011). Artificially increasing CORT can affect song-related behaviors and neural structures. For example, oral administration of CORT to hatchlings for approximately 30 and 50 days reduced song complexity of zebra finches and song sparrows (*Melospiza melodia*), respectively (Schmidt et al., 2013; Spencer et al., 2003), and HVC volume (proper name) of zebra finches (Buchanan et al., 2004). Administration of CORT via silastic implants for a longer duration (approximately 85 days) also reduced song learning accuracy of zebra finches (Shahbazi et al., 2011). Furthermore, song sparrows with larger song repertoires had larger HVC volumes and lower CORT concentrations in response to

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Table 1

Summary of studies of developmental stress on zebra finch song. Values for the duration of treatment represent days post-hatch, where 0 corresponds to the hatch date.

	Manipulation	Duration	Song complexity	Learning accuracy	Song rate
de Kogel and Prijs (1996)	Brood size reduction	0–50			↑
Tschirren et al. (2009)	Brood size enlargement	0–90			↑
Gil et al. (2006)	Brood size enlargement	0–90	=	=	
Holveck et al. (2008)	Brood size enlargement	0–30	=	↓	
Birkhead et al. (1999)	Protein reduction	0–30			=
Spencer et al. (2003)	Food accessibility	5–30	↓		=
Zann and Cash (2008)	Food accessibility	0–30	↓	=	
Brumm et al. (2009)	Food accessibility	5–30	=	↓	

stress (MacDougall-Shackleton et al., 2009; Pfaff et al., 2007; Schmidt et al., 2012). Collectively, these findings suggest that CORT may be a mechanism by which developmental stress affects song.

The timing of developmental stress may be particularly important because stressors will likely have stronger or weaker effects on traits depending on the timing of trait development relative to the timing of the stressor (Spencer and MacDougall-Shackleton, 2011). For instance, altering nutritional conditions during the age when cheek patches of male zebra finches are developing affected cheek patch expression, but altering nutritional conditions before that age did not (Honarmand et al., 2010; Naguib and Nemitz, 2007). Previous experimental studies on developmental stress and song using zebra finches have used either brood size or nutritional manipulations (see Table 1). Those that manipulate nutritional conditions directly usually terminate treatment once birds reach nutritional independence, around post-hatch day (PHD) 30 (e.g. Gil et al., 2006; Holveck et al., 2008; Spencer et al., 2003). However, zebra finch song-control regions HVC, RA and Area X develop and mature from approximately PHD 10–50 (Bottjer et al., 1985), coinciding with the behavioral development of song learning, which extends well past PHD 30. Thus, developmental stress after PHD 30 should likely affect zebra finch song development, but no studies to date have confirmed this.

Stress during different periods of development may also have differential effects on song. In zebra finches, stress during the sensory phase can affect aspects of song learning, presumably by influencing neural representation of tutor songs (e.g. Holveck et al., 2008; Spencer et al., 2003; Zann and Cash, 2008). On the other hand, stress during the sensorimotor phase may have more potent effects on vocal performance because during this phase birds must learn to precisely coordinate motor movements to match neural representations of song (Podos et al., 2009; Sakata and Vehrencamp, 2012). Vocal performance includes aspects of song that are physically difficult to produce because it places great demands on birds' ability to perform rapid modulations of the syrinx, respiratory, and vocal tract motor systems (Podos et al., 2009). The ability to sing consistent or stereotyped renditions of a song could also be affected by developmental stress if it limits the amount of time young zebra finches are able to practice singing (see Pytte and Suthers, 2000). As described above, previous work shows that zebra finch song learning may be affected by developmental conditions, but whether vocal performance is also affected remains unresolved. So far, song rate has been the principle measure of the effects of developmental stress on vocal performance in zebra finches (Birkhead et al., 1999; Brumm et al., 2009; Gil et al., 2006; Spencer et al., 2003; Tschirren et al., 2009), but this measure may not be representative of true vocal performance capabilities (Podos et al., 2009).

Here, our aim was to determine the relationship between timing of developmental stress and adult song complexity and song performance in zebra finches, and to determine whether CORT mediates the effects of stress on song. More specifically, we addressed the following questions: (1) Does nutritional stress at different developmental periods have distinct effects on HPA axis? (2) Does nutritional stress during later juvenile development (PHD 30–60, when young are feeding independently) affect adult song learning and/or vocal performance and if so, can it be distinguished from the effects of early stress? We defined

nutritional stress as conditions that made finding and/or obtaining food more difficult without inducing a calorie deficit (Lemon, 1991), and followed a nutritional stress protocol previously used by Spencer et al. (2003), Zann and Cash (2008) and Brumm et al. (2009). An important advantage of our approach is that we can see how diverse aspects of song (including a relatively unexplored component, song stereotypy) are affected by nutritional stress during early periods, compared to later periods of development.

Materials and methods

Animals and manipulation

This study was conducted over two years (2011 and 2012). Growth and body mass of birds used in these experiments have been previously reported elsewhere (Kriengwatana et al. in review). Randomly paired adult male and female zebra finches from our breeding colony were each housed in a 36 × 43 × 42 cm cage with access to an external nest box (20 × 13.5 × 13.5 cm) and kept on a 14 h:10 h light:dark cycle at 22 °C. Pairs received grit, cuttlefish bone, seed (Living World premium finch seed; 11.0% protein, 5.9% lipid), and water ad libitum, and were supplemented with daily portions of hardboiled chicken eggs, cornmeal, and bread. All animal care and husbandry protocols were approved by the Animal Use Subcommittee at the University of Western Ontario (protocol #2007-089), and followed guidelines of the Canadian Council on Animal Care. Only broods with 4 or 5 nestlings at the start of treatment were included in our experiment. Nests were monitored daily for nesting activity and randomly assigned to treatment conditions after the first egg hatched.

Treatments began on PHD 5–6 and ended on PHD 61–62 (date of hatch is PHD 1). We manipulated food accessibility similar to Spencer et al. (2003), whereby birds in the high treatment (H) were given access to 65 g seed and 13.5 g egg-food daily, while birds in the low treatment (L) were given access to 50 g total of seed in a mixture containing a 1:3 ratio of seeds and woodchips (by volume), and 6.5 g egg-food daily. This manipulation forces zebra finches in the L treatment to search longer for seeds, but still allows them to obtain a similar amount of seeds per day as the H treatment (Lemon, 1991). This manipulation has been shown to negatively affect body mass, adult song control brain regions, and song characteristics of zebra finches (Buchanan et al., 2004; Lemon, 1993; Spencer et al., 2003; Zann and Cash, 2008).

Nutritional manipulation was separated into two phases: pre-nutritional independence (PHD 5 or 6–PHD 34 or 35) and post-nutritional independence (PHD 35 or 36–61 or 62). Birds experienced either the same conditions (H to H or L to L) for both phases, or different conditions during the pre- and post-nutritional independence phases (i.e. switched from H to L or L to H). This resulted in four treatment groups: HH, HL, LH, LL. After the treatment period, all birds were given ad libitum seed, and offspring were kept with their parents until PHD 90 to ensure that young males learned song from their fathers exclusively (Adret, 1993). After PHD 90, birds were kept in single sex groups of four to five individuals. Potential year effects were controlled statistically (see below). A total of 9 and 13 breeding pairs produced 33 and 58 experimental offspring in the first and second year of the study,

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