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Does sex matter? Differential responses to corticosterone administration in the zebra finch

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ABSTRACT

Because of potentially deleterious effects of chronic stress, physiological measurements of stress hormones (in birds, corticosterone (CORT)) are often used to determine the consequences of natural or human-induced change. Often, it is assumed that CORT levels will be similar between the sexes and the results are pooled. However, recent studies have reported sex differences in CORT concentrations in avian species. As zebra finches (*Taeniopygia guttata*) are one of the most widely used bird species in laboratory studies worldwide, potential sex-specific differences in hormone metabolism, as well as the clearance rate of oral doses of exogenous CORT, are highly relevant. The results of this study show that female zebra finches have a significantly higher baseline CORT than males, which could partially be a product of differential responses to semi-isolation. In addition, a single dose of exogenous CORT resulted in different blood profiles between the sexes over time, though exogenous CORT was cleared from blood within 90 min following treatment in both sexes. Interestingly, exposure to multiple doses of exogenous CORT resulted in elevated CORT levels 24 h after treatment in both sexes. These results highlight the need for further investigations into potential sex differences in hormone metabolism, as well as possible cumulative effects of repeated stress.

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1. Introduction

All living organisms need to maintain a dynamic equilibrium with their environment in order to survive. In vertebrates, the activation of the hypothalamic–pituitary–adrenocortical (HPA) feedback system by stressors facilitates immediate escape from life-threatening situations, such as predation attempts (Wingfield et al., 1998; Saino et al., 2005; Denver, 2009). Acute stressors redirect energy from non-essential body processes and activities towards short-term survival, thus negatively affecting growth, reproduction, digestion, and inflammatory responses (Pravosudov et al., 2001; Wingfield and Kitaysky, 2002). These effects are short-term, as the HPA feedback mechanism operates efficiently and the system rapidly returns to baseline (Wingfield et al., 1998). However, if animals are unable to escape the source of stress, feedback signals are weakened, and the HPA system remains activated (Pravosudov et al., 2001). Under chronic stress, the short-term physiological or behavioural changes that ameliorate stress and promote survival can become deleterious and affect long-term fitness by suppressing digestion, growth, reproduction, and immune function (Wingfield et al., 1998; Sims and Holberton, 2000; Pravosudov et al., 2001; Wingfield and Kitaysky, 2002; Rich and Romero, 2005).

The recent surge of interest in the effects of stress has identified sex-specific differences in stress responses in a number of avian species. Although circulating corticosterone (CORT) levels are comparable between sexes in several species, possibly because they experience similar external environmental pressures (e.g., black-legged kittiwakes (*Rissa tridactyl*) (Kitaysky et al., 1999); Western screech owl (*Otus kennicottii*) (Dufty and Belthoff, 1997) and common diving petrel (*Pelecanoides urinatrix*) (Smith et al., 1994)), other studies have reported sex differences in CORT concentrations in a range of species (e.g., Northern spotted owls (*Strix occidentalis caurina*) (Wasser et al., 1997); Adelie penguins (*Pygoscelis adeliae*) (Ninnes et al., 2010); and Gambel's white-crowned sparrow (*Zonotrichia leucophrys gambelii*) (Astheimer et al., 1994)). Still more studies have identified seasonal sex differences in circulating CORT, as well as sex-specific changes according to life history stage. For example, the red-footed booby (*Sula sula*) displays significant decreases in baseline CORT in females during chick-rearing, while baseline CORT remained elevated in males (Lormee et al., 2003). The species-specific results of these studies highlight the need for further investigations regarding potential sex differences in stress hormone metabolism in a wider range of species.

We examined the change in circulating CORT of male and female zebra finches (*Taeniopygia guttata*) in response to a single oral

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dose of CORT and if a physiological re-setting of baseline CORT is initiated with repeated CORT treatments (to simulate the downstream effects of repeated stress events). Given that the number of studies utilising oral CORT treatments has increased over the past couple of years, it is important to know the effect on circulating CORT profiles, if there are sex-specific effects, and determine how quickly the exogenous CORT is cleared from the system. Animals generally experience natural peaks and troughs in circulating CORT in response to their environment (Breuner et al., 1998; Lynn et al., 2010), and repeated CORT treatments may provide useful information regarding the effect of recurring stress on an animal living in an unstable, unpredictable environment. The benefit of using exogenous CORT is that there is no evolutionary response to this, thus endogenous levels remain constant (Breuner et al., 2012), allowing us to look at downstream effects and determine the clearance rate of the hormone.

In addition, zebra finches are the most widely studied passerine species worldwide (Griffith and Buchanan, 2010), and are important model species in laboratory studies, hence potential sex-specific differences in hormone metabolism are highly relevant. Most studies of stress responses in zebra finches have examined breeding/pair-bonded birds (e.g., Remage-Healey et al., 2003) or juveniles (e.g., Spencer and Verhulst, 2007), but sex differences in CORT levels, particularly the clearance rates of exogenous CORT administration, in non-breeding birds have either attracted less attention, or not been reported. We hypothesise that non-breeding zebra finches of both sexes will display similar baseline CORT levels, as seen in several previous studies on zebra finch (Remage-Healey et al., 2003; Perfito et al., 2007; Wada et al., 2008), but may demonstrate sex differences in CORT clearance rates, as reported in studies on other avian species. These studies suggest that male birds are more sensitive to stressors than females, as they displayed greater plasma CORT concentrations than females did in response to peptide injections (Schmeling and Nockels, 1978; Madison et al., 2008) and exposure to acute stress (Schoech et al., 1999; Marin et al., 2002).

2. Methods

2.1. Study species and housing

Zebra finches were captured from the La Trobe University colony (3rd and 4th generation offspring from wild-caught parents), and housed in individual cages divided in two for the duration of experimentation. The total size of each cage was 104 cm (W) × 43 cm (D) × 48 cm (H). Birds were housed in semi-isolation, where their cages allowed for visual and acoustic interaction between conspecifics. Prior to capture and individual housing, the birds were kept in same-sex groups in large flight aviaries. The birds were placed in individual housing for a minimum of eight days prior to commencing experimentation to familiarise them with the experimental set-up. All birds had free access to a seed mix (consisting of equal parts red panicum, yellow panicum and Japanese millet), as well as water, cuttlefish bone and shell grit. Fresh endive lettuce was provided three times per week.

2.2. CORT dosage

CORT was orally administered by micropipette, and each dose consisted of 0.01 mg CORT (C2505-500MG; Sigma–Aldrich, St. Louis, MO, USA) in 20 μl of peanut oil, resulting in an average CORT dose of 1 μg/g body weight. Control birds received 20 μl of peanut oil alone. Peanut oil was utilised as it is innocuous and does not have phytoestrogenic properties (Thompson et al., 2006; Gam et al., 2011).

We chose to use exogenous CORT, rather than presenting the birds with a perceived stressor or threat, to minimise differences in threat perception between individuals. Previous studies have utilised CORT injections, but the injection itself appears to induce elevated CORT responses (Remage-Healey and Romero, 2001; Loiseau et al., 2008; Spencer and Verhulst, 2008). In comparison, oral CORT treatments have been shown to elicit a short-term increase in circulating CORT similar to that which occurs in response to an environmental stressor (Spencer and Verhulst, 2007, 2008; Monaghan et al., 2012).

2.3. Blood sampling

Blood samples were collected in 75 μl heparinised capillary tubes after puncture of the brachial vein with a 26 gauge needle. Blood samples for each bird took approximately 30 s to collect after puncture, and within 3 min of initial disturbance to prevent any handling-induced stress impacting the sample (Romero and Romero, 2002). The samples were centrifuged at 4500 rpm for 15 min, and the plasma stored at −80 °C for later analysis.

All sampling was carried out at approximately the same time of day (1400–1600 h EST) to control for circadian fluctuations in circulating hormone levels, as the intensity of the CORT response to stressors may show natural fluctuations throughout the day (Carere et al., 2003; Pike and Petrie, 2005). Each bird was bled four times in total, with no more than two blood samples per week. The interval between successive bleeds was 24 h or greater to ensure birds had sufficiently replenished blood volumes between bleeds, and the HPA axis was not elevated due to previous sampling.

2.4. Enzyme immunoassay

Total CORT levels in plasma were measured using CORT EIA kits (#500655; Cayman Chemical Co., Ann Arbor, MI, USA) according to the manufacturer's recommendations. All samples were diluted 1:10 in buffer (Banerjee and Adkins-Regan, 2011; Banerjee et al., 2011) and ran in duplicate with the average of both readings used for the analysis. Six 96-well plates were used in total and a separate standard curve was run on each plate. The detection limit was 0.3 ng/ml, and the average intra-assay coefficient of variation was 8.57% (range: 6.4–10%). The inter-assay coefficient of variation calculated on a pooled blood sample across all plates was 5.3%. The cross-reactivity is 100% for CORT, 11% for 11-dehydrocorticosterone and 7% for 11-deoxycorticosterone.

2.5. Experiment 1: CORT response to a single CORT treatment

Previous studies have identified that circulating CORT returns to baseline by 2 h after CORT administration in zebra finch nestlings (Spencer and Verhulst, 2007, 2008). In these studies, blood samples were taken at 10, 30 and 120 min after treatment. This experiment aimed to refine the clearance rate in non-reproductive adults, by taking blood samples at 10, 20, 30, 60 and 90 min after treatment.

Baseline blood samples were taken in all birds 2 days before CORT treatment ($n = 77$; 41 males and 36 females). To minimise the number of blood samples drawn from each bird, they were divided into 5 groups where blood samples were taken at the following time intervals after CORT dosage: group 1 – 10 min, group 2 – 20 min, group 3 – 30 min, group 4 – 60 min and group 5 – 90 min as outlined in Fig. 1.

2.6. Experiment 2: CORT response to multiple CORT treatments

Baseline blood samples were taken in all birds ($n = 62$; 33 males and 29 females) the day before treatment. These birds had

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