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Research paper

Evidence for condition mediated trade-offs between the HPA- and HPG-axes in the wild zebra finch

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ABSTRACT

Opportunistic breeding is a strategy used to maximize reproductive success in unpredictable environments. Birds that breed opportunistically are thought to maintain partial activation of the reproductive axis in order to rapidly initiate breeding when environmental conditions become suitable. The physiological mechanisms that modulate reproduction in seasonally breeding birds have been well explored. In contrast, the physiological mechanisms that allow opportunistic breeding birds to maintain a continued state of reproductive readiness has not been well established. Here, we tested the hypothesis that reproductive readiness is modulated through condition-mediated effects on the hypothalamic–pituitaryadrenal (HPA) axis and its downstream effects on corticosterone (CORT) secretion in wild zebra finches (*Taeniopygia guttata*). We examined the variation in body condition, HPA-axis activity (endogenous and adrenocorticotropic hormone (ACTH)-induced responses), and hypothalamic-pituitary-gonadal (HPG) axis activity activity (baseline and gonadotropin-releasing hormone (GnRH) induced testosterone and estradiol levels) in zebra finches across five sites in the Northern Territory in Australia. We found that birds at the sites in the lowest condition had the highest level of baseline and peak CORT. Additionally, males at the sites in the lowest condition had the highest fold increase in testosterone following a GnRH challenge. Across sites, birds with low body condition had high baseline, peak, and ACTH-induced levels of CORT. Our data suggest that reproductive readiness in opportunistically breeding birds is modulated by condition-mediated trade-offs between the HPA- and the HPG-axes. Further work is needed to understand the environmental conditions that influence reproductive activation in opportunistically breeding birds.

1. Introduction

Animals living in variable or unpredictable environments can maximize fitness by timing energetically expensive life history states (e.g. reproduction) to overlap with periods of high resource availability (Bronson, 1985; Wingfield and Kenagy, 1991). In unpredictable environments, resources can vary erratically within or between seasons driving high levels of variability in reproductive opportunities (Robin et al., 2009). Animals that breed in unpredictable environments (i.e. opportunistic breeders) are thought to continually maintain a state of reproductive readiness in order to rapidly exploit reproductive opportunities (Perfito et al., 2007). Consequently, unpredictable environments exert strong selective pressure for flexible physiological responses that enable animals to rapidly transition between life history stages to maximize fitness (Wingfield et al., 1992).

In birds, opportunistically breeding species are purported to lack periods of absolute reproductive refractoriness, but rather maintain some degree of a continuous state of reproductive readiness (reviewed in Cornelius et al., 2013; Hahn et al., 2008). In contrast to seasonally breeding birds that have dampened hypothalamic-pituitary-gonadal (HPG) axis activity and completely regressed gonads outside of the breeding season, some opportunistically breeding birds such as the Australian zebra finch (*Taeniopygia guttata*), maintain an active HPG axis and partially developed gonads even when not breeding (Perfito et al., 2007). Other species of opportunistically breeding birds such as Darwin's small ground finch (*Geospiza fuliginosa*), undergo complete collapse of gonads when not breeding (Hau et al., 2004), but potentially sustain a degree of reproductive readiness via maintenance of the central gonadotropic-releasing hormone (GnRH) system (Hahn et al., 2008). Maintaining a degree of tonic reproductive readiness allows

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birds to rapidly initiate reproduction behaviors when favourable conditions are encountered in unpredictable environments, such as the arid zone of Australia, where avian species have restricted and unpredictable breeding opportunities (Duursma et al., 2017).

While seasonally breeding birds are largely dependent on photoperiod to trigger changes in reproductive physiology (Dawson et al., 2001; Nicholls et al., 1988), opportunistic breeding birds initiate breeding in response to multiple environmental and social cues (Hahn, 1995; Hahn et al., 2005). One environmental cue that may be particularly informative to opportunistically breeding birds is food availability. In captive and free-living birds, food restriction has been associated with decreased testosterone and reproductive behaviors and increased levels of corticosterone (CORT; Fokidis et al., 2013; Lynn et al., 2003; Lynn et al., 2010). Elevated levels of CORT can inhibit reproduction via suppression of the HPG-axis (Wingfield and Sapolsky, 2003), disrupt parental and reproductive behaviors (Lynn et al., 2010; Silverin, 1986, 1990), and have been associated with reduced parental care and reproductive success in free-living birds (Criscuolo et al., 2005; Lendvai and Chastel, 2010; Miller et al., 2009). In birds, body condition has well-established links to both CORT response (e.g. Breuner and Hahn, 2003; Crino et al., 2017) and reproduction (e.g. Bety et al., 2003; Chastel et al., 1995). Reproductive readiness in opportunistic breeders may be modulated through changes in body condition and its downstream effects on the hypothalamic-pituitaryadrenal (HPA) and HPG-axes.

The zebra finch, an Estrildid finch native to Australia, is an avian model system that is characterized by its propensity to breed opportunistically (Serventy, 1971; Zann, 1996). The zebra finch is distributed over 75% of continental Australia in habitats ranging in seasonal climatic variation from temperate, arid, to semi-tropical environments (Zann, 1996). In unpredictable habitats, zebra finches are thought to maintain an activated reproductive system in order to rapidly initiate breeding in response to sporadic and unpredictable precipitation (Perfito et al., 2007). Early reports suggested that zebra finches initiate reproduction within hours of rainfall following a drought (Immelmann, 1963). However, evidence from a seven year study in the grassland biome at Alice Springs suggests a longer lag time between precipitation and reproduction in wild zebra finches with reproduction being highest around four months after a significant rainfall event (Zann et al., 1995). Likely, wild zebra finches integrate a broad suite of environmental cues to determine when best to time breeding events (Hahn et al., 2008).

Although the natural history of wild zebra finches has been well established (Zann, 1996), few studies have examined the physiological mechanisms that modulate reproductive readiness in wild zebra finches. A notable exception is research by Perfito et al. (2007) who examined differences in the reproductive readiness of zebra finches at two sites which varied in the predictability of rainfall. Perfito et al. (2007) found that male zebra finches at the unpredictable site maintained a greater degree of gonad development and higher levels of luteinizing hormone when not breeding, compared to birds from the predictable site. Birds from the unpredictable site were in lower condition compared to birds from the predictable site, but birds had no difference in baseline or stressed-induced CORT levels between the sites, suggesting that CORT does not modulate reproductive readiness in zebra finches (Perfito et al., 2007).

Here, we expand upon the work by (Perfito et al., 2007) by looking at population level differences in HPA- and HPG-axis activity, body condition, and breeding activity of zebra finches at five variable sites across a broad geographic area in the arid interior of Australia which varies in rainfall predictability. We examined these physiological trade-offs in zebra finches at five sites that were likely to reflect the quite variable environmental conditions that typically prevail in the heterogenous landscape of arid Australia (Morton et al., 2011). We evaluated differences in HPA- and HPG-axes activity, body size, and condition between sites and examined the relationship between body condition and endocrine responses. We examined site differences in breeding activity, and recent precipitation events and examined associations between local precipitation and endocrine responses. We predicted that zebra finches would differ between sites in body condition due to spatial and temporal variation in resource availability that typifies the Australian interior. Furthermore, we predicted that zebra finches in poorer condition would have elevated HPA-axis activity, dampened HPG-axis activity, and would be less likely to have bred recently.

2. Methods

2.1. Field sites, trapping, and blood collection methods

We trapped wild zebra finches to measure morphometric variation from 9-September – 15th-October 2014 (early summer) at five field sites located in the Northern Territory, Australia (Fig. 1). The field sites were located on private land and were chosen opportunistically based on the presence of zebra finches and the cooperation of the landowners. The sites were located between 106.4 and 594.1 km apart. We sampled birds a second time at the same sites from 10th – 28th of November 2014 (mid-summer) to evaluate HPA- and HPG-axis activity and measure morphometrics. We trapped wild zebra finches between 6:30am and 12:00 pm using mist nets, positioned at artificial water holes, used for watering stock.

We obtained an initial blood sample to measure baseline levels of hormones within three minutes of the birds being captured in the net for CORT and within five minutes for T. For CORT, samples collected within three minutes are considered to reflect baseline levels (Romero and Reed, 2005). For T we found no association between hormone levels and the amount of time it took to collect an initial blood sample after a bird made contact with the net ($T = 0.38$, $P = .70$), a result that is consistent with other published data (Prior et al., 2017). To collect blood, we punctured the alar vein with a 27-gauge needle and collected 25–50 μl of blood with heparinized microcapillary tubes. We stored the blood on ice (<7.5 h) until it could be centrifuged to separate plasma from red blood cells (7000 rpm for ten minutes). After separation, the plasma was isolated and stored at -20 °C until the samples were transported to Deakin University on dry ice and stored at −80 °C until assayed. After the initial blood sample was obtained, birds were exposed to one of the three endocrine treatments (stress response, ACTH challenge, or GnRH challenge) described below. Males and females were targeted equally and all birds included in these treatments were adults.

We utilized data collected from the Australian Government Bureau of Meteorology (BOM) to help infer differences in precipita-

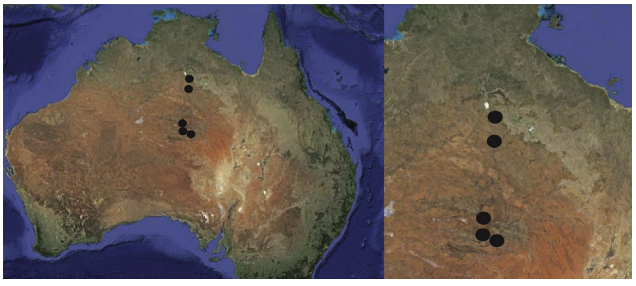

Fig. 1. A map of the five field sites used in this study (sites number 1–5 south to north). Images from Google Earth.

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