



Effects of early-developmental stress on growth rates, body composition and developmental plasticity of the HPG-axis



Tara M. Farrell^{a,c,*}, Amanda Morgan^{b,c}, Yanina Sarquis-Adamson^{b,c}, Scott A. MacDougall-Shackleton^{a,b,c}

^a Department of Psychology, University of Western Ontario, Canada

^b Department of Biology, University of Western Ontario, Canada

^c Advanced Facility for Avian Research, University of Western Ontario, Canada

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ABSTRACT

In altricial songbirds, food restriction in early development has adverse effects on various physiological systems. When conditions improve birds can accelerate growth, but this compensatory strategy is associated with long-term adverse consequences. One system affected by altered growth rates is the hypothalamic–pituitary–gonadal (HPG) axis. Here, we subjected European starlings, *Sturnus vulgaris*, to an unpredictable food manipulation from 35 to 115 days of age. We assessed the effects of the treatment by measuring overall body mass and body composition during and following the treatment period (i.e., accelerated growth). In adulthood, we measured the long-term effects of the treatment on overall body mass, testis volume, and HPG axis function in both sexes by quantifying androgen levels before and after a gonadotropin-releasing hormone (GnRH) challenge. During the treatment period, treatment birds had less body fat than controls. Following the treatment period, treatment birds weighed more than controls, but these gains were attributed to changes in lean mass. In adulthood, treatment males had lower baseline androgen levels, but there was no difference in peak androgen levels compared to controls. Treatment females did not differ from controls on any of the androgen measures. However, females that accelerated growth faster following the termination of the treatment had lower integrated androgen levels. When faced with limited developmental resources, birds may alter the developmental trajectory of physiological systems as a compensatory strategy. Such a strategy may have long-term consequences on endocrine regulation that could affect courtship and reproductive behaviors.

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1. Introduction

Quality of the early-life environment is instrumental in shaping the developing phenotype, particularly for altricial songbirds that are born in an immature state. When environmental conditions are poor, physiological development may deviate from the normal trajectory, a process which is typically known as developmental plasticity (Debat and David, 2001; McMillen and Robinson, 2005). An evolved strategy to mitigate poor rearing conditions is to compensate once conditions improve by extending the developmental period through adjusting growth rates and resource allocation (Schew and Ricklefs, 1998). For example, nestlings reared in food-restricted environments exhibit marked developmental plasticity in body mass growth. Growth is slow while the restriction is

enforced, accelerated once it is removed (i.e., compensatory, catch-up, or accelerated growth), but ultimately these birds achieve adult weight comparable to nestlings reared under control conditions (Brumm et al., 2009; Killpack et al., 2014; Nowicki et al., 2002; Schmidt et al., 2012; Zann and Cash, 2008; but see Pravosudov et al., 2005). Accelerating growth can be beneficial in the short-term, but there are costs associated with this strategy. For instance, in zebra finches (*Taeniopygia guttata*) accelerated growth has been linked in adulthood to reduced cognitive ability and altered exploration of new environments (Fisher et al., 2006; Krause and Naguib, 2011), increased resting metabolic rates (Crisuolo et al., 2008), and reduced resistance to oxidative damage (Alonso-Alvarez et al., 2007).

In the later juvenile period, physiological development continues after birds have achieved asymptotic body size. Solely quantifying changes in overall body mass may fail to capture differential growth of body components (i.e., fat and lean mass) in the juvenile period. Through changes in feeding behavior, diet quality and energy requirements, birds can undergo rapid physiological

* Corresponding author at: Department of Psychology (Social Sciences Building, Room 7400), University of Western Ontario, 1151 Richmond Street, London, Ontario N6A 5B8, Canada.

E-mail address: tfarrel2@uwo.ca (T.M. Farrell).

changes which may not be detected through total body mass (Dykstra and Karasov, 1992; Lindström et al., 2000; Pierce and McWilliams, 2004; Piersma and Lindström, 1997; Piersma et al., 1999). Increases in lean mass results from growth of muscles, organs, feathers, and skeletal tissue (O'Connor, 1977), while increases in fat mass suggest that surplus resources are being stored for later use (Ashton and Armstrong, 2002; Reid et al., 2000). Recently, developmental studies have quantified changes in body composition to assess how birds allocate resources when food is restricted. These studies use destructive techniques (i.e., the bird is killed to complete the analysis) to illustrate which systems birds prioritize when faced with limited resources and/or are energetically more costly to develop (Killpack and Karasov, 2012; Killpack et al., 2014). One limitation of destructive techniques is birds cannot be assessed repeatedly throughout development or into adulthood. Quantitative magnetic resonance (QMR) allows the accurate, rapid, and repeatable assessment of an animal's body composition via nondestructive means (Guglielmo et al., 2011; McWilliams and Whitman, 2013). QMR is able to quantify changes in wet lean mass (not structural tissues feather and bone) and fat mass (Guglielmo et al., 2011). A recent study using QMR in zebra finches found that the largest determinant of body fat in adulthood was nutritional conditions experienced during the juvenile period, more so than nutritional conditions of the nestling period (Kriengwatana et al., 2013). QMR is an excellent tool to quantify long-term differences in growth patterns when birds develop in challenging environmental conditions.

In mammals, and to a lesser extent birds, environmental stressors exert organizational effects on the hypothalamic–pituitary–adrenal (HPA) axis and glucocorticoid production (Lupien et al., 2009; McMillen and Robinson, 2005; Schoech et al., 2011). Glucocorticoid regulation is intimately linked with the regulation of another important endocrine system: the hypothalamic–pituitary–gonadal (HPG) axis (Rivier and Rivest, 1991; Viau, 2002). In mammals, stressors can alter HPG axis function, resulting in reduced gonadal steroids and, thereby, altered reproductive function (Hardy et al., 2005; Kyrou and Tsigos, 2008; Nepomnaschy et al., 2004; Tsigos et al., 1999). The avian HPG axis largely develops in the embryo and the first few weeks of life, but exhibits plasticity several months after hatch and across reproductive years (Ottinger and Bakst, 1995; Sockman et al., 2004). Androgens, such as testosterone (T) and dihydrotestosterone (DHT), are gonadal steroid hormones that modulate physiological and behavioral traits necessary for reproduction (Balthazart, 1983; Wingfield et al., 1990). For example, increased T levels are associated with better song quality and enhanced immune function in male European starlings (*Sturnus vulgaris*; Duffy and Ball, 2002; Ball and Balthazart, 2010) and an increased likelihood of acquiring and maintaining a breeding site in female spotless starlings (*Spongipellis unicolor*; Veiga and Polo, 2008). However, elevated T levels are also associated with reduced parental care (Eens et al., 2007). In birds, only one study in song sparrows (*Melospiza melodia*) has examined how early developmental experiences may program HPG axis function into adulthood: males treated with glucocorticoids early in life had higher baseline T levels, while females treated with glucocorticoids, or subjected to food-restriction, had lower estradiol levels than control females (Schmidt et al., 2014). Thus, a stressful rearing environment may alter a bird's allocation of resources, such that reproductive function is altered through changes to HPG axis function.

In the current study, we reared juvenile starlings on an unpredictable food supply treatment that is known to have detrimental effects on several physiological, neural and behavioral measures in starlings (Buchanan et al., 2003; Farrell et al., 2011) and song sparrows (Schmidt et al., 2014; Schmidt et al., 2012, 2013a,b). We monitored the effects of the treatment on body mass and body

condition during, and following, the treatment period to determine if unpredictable food access altered growth of fat and lean tissue. In adulthood, we assessed the long-term effects on body mass and quantified the size of testes in adult males while they were in breeding condition. For both sexes, HPG axis function was measured by assessing androgen levels using a gonadotropin-releasing hormone (GnRH) challenge. A GnRH challenge allows for the assessment of reproductive condition of the animal (Wingfield et al., 1979), as well as inference of the hormonal response an individual would issue in a socially challenging situation (Jawor et al., 2007). We predicted birds raised in our treatment group would grow more slowly during the treatment, faster once the treatment ceased (i.e., exhibit accelerated growth), but there would be no long-term effect on adult body mass. We also predicted that birds from the treatment group would have less fat and lean mass during treatment, but would compensate after the restriction by gaining more fat and lean mass. We predicted that male and female birds from the treatment group would have reduced androgen production compared to controls. Furthermore, as accelerated growth is known to be associated with costs later in life (Metcalfe and Monaghan, 2001), we predicted that individuals with more accelerated growth would have reduced androgen production in adulthood.

2. Methods

2.1. Subjects and treatment

We collected starlings as nestlings around London, Ontario (42° 98'N, 81°25'W) during May and June 2012. These are the same birds that were used in a previous study examining the effects of early-life stress on female song preferences (Farrell et al., 2015a). We brought nestlings into captivity when they were approximately 13.0 ± 3.9 (SD) days of age. Shortly after capture, we took a small blood sample (<50 μ L) by piercing the brachial vein with a 26-gauge needle, extracted the DNA from whole blood, and used polymerase chain reaction (PCR) to genetically sex all birds (Griffiths et al., 1998). We housed all nestlings by nest in small bowls lined with tissue paper placed inside a cage ($76 \times 46 \times 45$ cm). We fed nestlings our hand-rearing diet, a mixture of commercial chick starter, wheat germ, carrots, hardboiled egg, grit, and vitamins (Prime avian vitamin supplement, Rolf C. Hagen Inc., Montreal, QC, Canada), *ad libitum* until the birds were feeding independently. We then transitioned birds to chick starter feed and separated birds into individual cages (same size as above) at 33.2 ± 1.7 (SD) days of age. At this time, within each nest, we randomly assigned birds to control or unpredictable conditions (i.e., the treatment group) counterbalancing across sex (see Table 1).

Table 1

Samples size by treatment condition and sex across the different phases of the experiment.

Treatment group	Sex	Treatment period	Post-treatment period	GnRH challenge + testis volume (males only)
Control	Male	17	9	9
	Female	9	9	8
Treatment	Male	17	9	8
	Female	12	12	12
Total		55	39	37 (17)

Eight males from both control and treatment groups were sacrificed on the final measurement day of the treatment period for a separate study. One control female and one treatment male died before the GnRH challenge and testis volume measurements could be taken.

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