General and Comparative Endocrinology 235 (2016) 78–88

Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

Research paper

The seasonal glucocorticoid response of male Rufous-winged Sparrows to acute stress correlates with changes in plasma uric acid, but neither glucose nor testosterone

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A R T I C L E I N F O

Article history:
Received 24 July 2015
Revised 9 May 2016
Accepted 8 June 2016
Available online 9 June 2016

Keywords:
Annual cycle
Antioxidant
Glycemia
Passerine
Seasonality
Sparrow

A B S T R A C T

We sought to clarify functional relationships between baseline and acute stress-induced changes in plasma levels of the stress hormone corticosterone (CORT) and the reproductive hormone testosterone (T), and those of two main metabolites, uric acid (UA) and glucose (GLU). Acute stress in vertebrates generally stimulates the secretion of glucocorticoids, which in birds is primarily CORT. This stimulation is thought to promote behavioral and metabolic changes, including increased glycemia. However, limited information in free-ranging birds supports the view that acutely elevated plasma CORT stimulates glycemia. Acute stress also often decreases the secretion of reproductive hormones (e.g., T in males), but the role of CORT in this decrease and the contribution of T to the regulation of plasma GLU remain poorly understood. We measured initial (pre-stress) and acute stress-induced plasma CORT and T as well as GLU in adult male Rufous-winged Sparrows, *Peucaea carpalis*, sampled during the pre-breeding, breeding, post-breeding molt, and non-breeding stages. Stress increased plasma CORT and the magnitude of this increase did not differ across life history stages. The stress-induced elevation of plasma CORT was consistently associated with decreased plasma UA, suggesting a role for CORT in the regulation of plasma UA during stress. During stress plasma GLU either increased (pre-breeding), did not change (breeding), or decreased (molt and non-breeding), and plasma T either decreased (pre-breeding and breeding) or did not change (molt and non-breeding). These data provide only partial support to the hypothesis that CORT secretion during acute stress exerts a hyperglycemic action or is responsible for the observed decrease in plasma T taking place at certain life history stages. They also do not support the hypothesis that rapid changes in plasma T influence glycemia.

1. Introduction

Animals are regularly exposed to events (e.g., predation and inclement weather) that incite a stress response. Hormonal and physiological changes that occur during this response include the release of catecholamines and the activation of the hypothalamic-pituitary-adrenal (HPA) axis, which controls the production and secretion of glucocorticoids. A component of the stress response consists of a rapid (within minutes) increase in plasma glucocorticoids above resting (initial) levels (Mora et al., 2012). As understood from mammalian studies, glucocorticoids act synergistically with catecholamines and glucagon to stimulate glycogenolysis and gluconeogenesis, ultimately increasing plasma glucose (GLU) and its availability to the brain, muscles, and other tissues (Eigler et al., 1979; Mcmahon et al., 1988; Sapolsky et al., 2000). This, in turn, is thought to improve the chances of survival in a threatening situation (Astheimer et al., 1992; Sandi et al., 1996; Sapolsky et al., 2000; Miles et al., 2007).

The hyperglycemic effect of glucocorticoids is observed in domestic poultry (Kobayashi et al., 1989; Yuan et al., 2008). However, the few studies investigating effects of acute stress on glycemia in wild birds have yielded variable results. For example,

Abbreviations: ANOVA, analysis of variance; CORT, corticosterone; CP, cloacal protuberance; GLU, glucose; HPA, hypothalamic-pituitary-adrenal axis; IQ, interquartile interval; KW test, Kruskal-Wallis test; MST, mountain standard time; MW test, Mann-Whitney *U*-test; P, probability; rmANOVA, repeated measure analysis of variance; SNK test, Student-Newman-Keuls test; T, testosterone; UA, uric acid.

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http://dx.doi.org/10.1016/j.ygcen.2016.06.011
0016-6480/

acute stress increased plasma GLU in free-ranging Abert's Towhees, *Melozone aberti* (Davies et al., 2013) and captive European Starlings, *Sturnus vulgaris*, but in the latter case only at certain times during the daily and annual cycle (Remage-Healey and Romero, 2001, 2002). By contrast, acute stress did not influence glycemia in captive Curved-billed Thrashers, *Toxostoma curvirostre* (Fokidis et al., 2011) and decreased it in free-ranging Rufous-winged Sparrows *Peucaea carpalis* (RWSP; Deviche et al., 2014). In all these species, acute stress increased plasma glucocorticoids (primarily corticosterone (CORT) in birds), indicating that this increase was not necessarily accompanied with elevated glycemia.

Birds differ from other vertebrates in that they normally maintain high glycemia and yet are resistant to the effects of oxidative stress that are generally associated with elevated plasma GLU (Braun and Sweazea, 2008). Surprisingly, the regulation of GLU metabolism has received little investigation in wild birds, with studies primarily focusing on migrating birds (Jenni and Jenni-Eiermann, 1998; Maillet and Weber, 2006; reviewed in Scanes and Braun, 2013). Migration includes extended periods of physical exertion and is characterized by numerous metabolic and endocrine adjustments that are specific to this life history stage (Speakman and Selman, 2003; Landys et al., 2004). Whether information on the control of glycemia in migratory birds applies to sedentary species is, therefore, uncertain.

Resistance to the effects of oxidative stress that are associated with high glycemia in avian species is thought to involve circulating antioxidants such as uric acid (UA), a product of amino acid catabolism (Cohen et al., 2007; Braun and Sweazea, 2008). In many avian species, plasma UA decreases during an acute stress response, but this effect is not universal (Cohen et al., 2007; Davies et al., 2013, 2014). The decrease may result from UA being used in antioxidant actions associated with the metabolic effects of elevated CORT. However, the relationship between UA and both CORT and GLU remains unclear.

The CORT stress response of temperate region birds often changes seasonally and concurrently with transitions between life history stages (e.g., reproduction, molt, and in some species migration (Remage-Healey and Romero, 2000; Romero, 2002; Cyr et al., 2008). If a primary role of CORT is to regulate GLU metabolism, then it would be expected that seasonal and stress-induced changes in plasma CORT would be consistently associated with corresponding changes in plasma GLU. Naturally occurring seasonal changes in the CORT stress response can, therefore, be used to mechanistically investigate the relationship between this hormone and plasma GLU and UA.

In addition to its above roles, the CORT stress response is believed to limit the amount of energy that is directed to non-essential functions such as digestion, immune defense, and reproduction (Angelier et al., 2007), and to redirect energy to activities and metabolic processes that are critical for survival (Wingfield and Sapolsky, 2003). In some circumstances, acute stress decreases the activity of the hypothalamic-pituitary-gonadal (HPG) axis and the secretion of reproductive hormones, including testosterone (T) in male birds (Cyr and Romero, 2007; Schoech et al., 2009; Goutte et al., 2010; Deviche et al., 2012, 2014). As the acute stress response is associated with increased plasma CORT (Lynn et al., 2010; Deviche et al., 2012, 2014), these observations are often taken to suggest a causal relationship between an increase in plasma CORT and a concurrent decrease in plasma T. However, recent evidence, including from the species investigated here (Deviche et al., 2012), indicates that changes in plasma CORT such as during stress or social interactions, are not necessarily associated with changes in the opposite direction in plasma T (Goutte et al., 2010). These observations suggest a lack of or more complex proximate relationships between these hormones.

In many free-ranging male birds, plasma T varies seasonally, decreasing from high levels during breeding to low levels during molt and outside the breeding period (Dawson, 1983; Wingfield, 1984; Goymann et al., 2007). A primary function of T is to promote reproductive behaviors, but mammalian studies demonstrate a regulatory role of T also in carbohydrate, fat, and protein metabolism (reviewed in Kelly and Jones, 2013). These studies overwhelmingly point to an anabolic function of T, acting to increase glycogen synthesis and decrease plasma GLU (Leonard, 1952; Bergamini et al., 1968; Marin et al., 1992; Haffner et al., 1994; Ramamani et al., 1999; Kelly and Jones, 2013). The relationship between T and GLU in birds remains, however, poorly defined: few studies on this subject have been performed in free-ranging subjects and in chickens, research involving experimental manipulation of plasma T has yielded inconsistent results (Lepkovsky et al., 1967; Chen et al., 2005).

Due to the sparse number of studies investigating changes in metabolites during acute stress in free-living birds, the primary objective of the present study was to use such birds to clarify the relationships between CORT, T, GLU, and UA. To this aim, we measured pre-stress (initial) and acute stress-related plasma CORT and T across seasons in relation to plasma GLU and UA in free-living male RWSPs. This Sonoran Desert passerine breeds in association with the summer monsoon, and adults are sedentary and maintain the same territory year-round (Lowther et al., 1999). Thus, results are not influenced by the potentially confounding effects of factors related to seasonal migration or dispersion.

In a previous but independent study on adult male RWSP, we sampled birds shortly before (June) and during (July and August) the breeding season, as well as during post-breeding molt (September; Deviche et al., 2014). In response to stress, plasma CORT and T of these birds consistently increased and decreased, respectively, with the CORT response to stress showing attenuation during molt. Plasma metabolites (UA and GLU) were measured only in samples collected from breeding and molting sparrows, so that no data on this subject are available for birds sampled at other life history stages. In order to expand our understanding of how acute stress influences plasma CORT, T, UA, and GLU, to better understand relationships between these hormones and metabolites, and to test the robustness of these relationships, we measured all four plasma chemicals in RWSP sampled not only before and during breeding as well as molt, but also during winter, when birds are not molting and their reproductive system is quiescent.

Given the demonstrated role of CORT in regulating GLU metabolism in mammals, we hypothesized that CORT exhibits a similar function in wild birds. Based on previous work showing a decrease in plasma GLU and UA during acute stress (Deviche et al., 2014), we predicted a negative correlation during stress between changes in plasma CORT and those in both plasma GLU and UA. We then utilized the seasonally variable CORT stress response to investigate the relationship between plasma CORT and T during the stress response. If the hypothesis that acute stress-associated elevated plasma CORT is responsible for the concurrent decrease in plasma T is supported, we predicted a consistent inverse relationship between these hormones across life history stages. We also investigated the potential of T to influence plasma GLU and, for this, utilized stress-induced and seasonal changes in plasma T and GLU. We predicted that if T modulates plasma GLU, changes in plasma T, be they related to the life history stage or resulting from stress, would be consistently associated with changes in plasma GLU.

In a recent study on Blue Tits, *Cyanistes caeruleus*, changes in plasma GLU during stress were associated with changes in ambient temperature: the higher the minimum ambient temperature the night preceding capture, the more plasma GLU increased during stress (Kaliński et al., 2014). To our knowledge this type of relationship has not been researched in other free-ranging