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Plasma corticosterone of city and desert Curve-billed Thrashers, *Toxostoma curvirostre*, in response to stress-related peptide administration

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ABSTRACT

We compared the activity and responsiveness of the hypothalamo–pituitary–adrenal (HPA) axis of an urban (Phoenix, Arizona) and desert population of a male songbird species (Curve-billed Thrasher, *Toxostoma curvirostre*), by measuring plasma corticosterone in response to acute administration of corticotropin-releasing factor, arginine vasotocin, or adrenocorticotropin hormone. Urban adult male thrashers showed greater responsiveness than desert birds to an injection of arginine vasotocin or adrenocorticotropin hormone, suggesting a population difference in pituitary and adrenal gland sensitivity. Plasma corticosterone in response to corticotropin-releasing factor injection did, however, not differ between populations. The differential corticosterone response to arginine vasotocin and corticotropin-releasing factor may reflect effects of chronic stress or habituation, which are known to favor arginine vasotocin over corticotropin-releasing factor sensitivity. Efficacy of HPA negative feedback by glucocorticoids was determined by measuring plasma corticosterone in response to acute administration of the synthetic glucocorticoid dexamethasone. This administration decreased plasma corticosterone similarly in urban and desert thrashers, suggesting that the negative feedback of glucocorticoids on the HPA axis in the two populations was equally effective. The higher sensitivity of urban than desert thrashers to adrenocorticotropin hormone and arginine vasotocin may result from up-regulation of the HPA axis in urban birds. This up-regulation may in turn make it easier for city birds to cope with urban environment-associated stressors.

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1. Introduction

The hallmark of the vertebrate physiological response to stress is two-fold: activation of the sympathetic nervous system *via* catecholamines primarily released from the adrenal gland medulla and the release of glucocorticoids from the adrenal gland cortex. These responses enable an organism to mobilize energy stores and alter behaviors that maximize survival during a stressful event (Norris, 2006). Glucocorticoids are the end products of the hypothalamo–pituitary–adrenal (HPA) axis. At the onset of a perceived threat, parvocellular neurons of the avian hypothalamic paraventricular nucleus secrete corticotropin-releasing hormone (CRH) and arginine vasotocin (AVT), the avian homologue of mammalian vasopressin (AVP). In mammals, the actions of CRH during a stress response precede those of vasopressin, which has longer lasting effects (Herman et al., 1992; Ma and Aguilera, 1999). In mammals and birds, both neuropeptides stimulate the pituitary gland secretion of adrenocorticotropin hormone (ACTH; Zelena et al., 2004; Rich and Romero, 2005), which ultimately induces adrenal secretion of glucocorticoids, such as corticosterone (CORT) in birds.

Corticosterone regulates HPA activity through a classic negative feedback loop by acting at both the hypothalamus and pituitary gland (Young et al., 1995; Makino et al., 2002). This feedback may decrease CRH production and release (Aguilera et al., 2007) but research on rodents suggests that AVP is not directly affected by CORT (Dallman, 1993; Aguilera et al., 2007). A difference in feedback efficacy on CRH and AVT secretion may be important during “chronic” stress, here defined as persistently elevated plasma CORT combined with a reduced capacity to elevate CORT in response to acute stress. During chronic stress, the adrenal glands may continue to secrete CORT even after the stressor is no longer perceived. This can have deleterious impacts on energy balance, reproduction or immune function (Clinchy et al., 2004; Rich and Romero, 2005; Wingfield, 2005; Lightman, 2008). These processes have been extensively studied in mammals but are less studied in birds.

In nature, avian populations inhabiting different habitats often show varied seasonal responses to stress. For example, birds from climates where breeding opportunities are temporally limited (e.g., arctic, desert) can show lower CORT secretion during stress when breeding compared to other life-history stages (Astheimer et al., 1995; Wingfield et al., 1992; Fokidis et al., 2009). Limiting HPA activity during breeding may help avoid potentially deleterious consequences of elevated CORT levels, such as nest abandonment and suppression of

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reproductive physiology (Wingfield and Ramenofsky, 1997; Love et al., 2002), which could in turn decrease fitness.

Research investigating differences between populations have begun to focus on how anthropogenic environmental change can alter the HPA axis activity. Recent studies have identified differences in CORT secretion across urban–rural gradients (Partecke et al., 2006; Schoech et al., 2007; French et al., 2008; Fokidis et al., 2009), but the mechanisms involved are poorly understood. During the breeding season (March to July), urban Curve-billed Thrashers, *Toxostoma curvirostre,* increase plasma CORT in response to capture and handling stress more than conspecific birds living in desert areas (Fokidis et al., 2009). Desert thrashers may limit their acute stress response during the breeding season to avoid its interference with reproduction, since the reproductive window coincides with the food that becomes available shortly after the winter rains and before the very hot and dry summer (Wingfield et al., 1992; Fokidis et al., 2009). Outside the breeding season, initial plasma CORT (i.e., prior to application of handling stress or baseline) is higher in desert than urban birds, and during molt desert thrashers show stronger stress response than urban birds (Fokidis et al., 2009). Urban thrashers may be exposed to more frequent chronic (e.g., pollution, increased temperatures, and noise) and acute stressors (e.g., vehicles, humans, and feral predators). Exposure to such stressors, are far less common in desert-dwelling thrashers. Thus urban thrashers may require an active stress response during the breeding season, in contrast to desert birds that may need to modulate their acute stress response when breeding. An alternative situation can occur if consistent exposure to the above stressors results in habituation, here defined as attenuated stress responses as originally novel stressors over time are perceived as benign (Cyr and Romero, 2009).

We investigated the source of variation along the HPA axis that may account for these differences in CORT secretion between breeding urban and desert thrashers. Specifically, we compared (1) differences in sensitivity of the pituitary gland to CRH and AVT; (2) differences in the responsiveness of the adrenal glands to ACTH injection; and (3) differences in negative feedback induced by administration of the synthetic glucocorticoid dexamethasone (DEX). This information can be used to assess whether urban birds show symptoms of chronic stress, habituation, or differences in the regulation of their HPA axis activity compared to desert birds. If urban thrashers are chronically stressed, we predict they would produce greater amounts of CORT due to increased adrenal sensitivity to ACTH compared to desert birds. This increased CORT production would decrease CRH secretion, via a negative feedback loop. In contrast, AVT release which is thought to be impervious to the negative feedback action of CORT may increase which would translate to increased pituitary sensitivity to AVT in urban compared to desert birds. If urban birds down-regulate their HPA activity as a result of habituation, we predict *decreased* secretion of the entire HPA axis, which would ultimately decrease sensitivity to ACTH, AVT, and CRH injections, and DEX would have an increased ability to decreased CORT secretion in urban compared to desert birds. If urban thrashers up-regulate their HPA activity, we predict *increased* sensitivity in all aspects of the HPA axis so that ACTH, AVT, and CRH injections have a greater ability to increase CORT levels in urban birds compared to desert birds. In addition, we predict that DEX would also have a greater capacity to limit CORT secretion, in urban as compared to desert birds. This is the first study to investigate intraspecific differences at multiple levels of the HPA axis between rural and urban animal populations.

2. Methods

2.1. Model species and study populations

Curve-billed Thrashers are common Sonoran Desert songbirds in Phoenix, Arizona, although they are found at lower population densities than in the surrounding desert (Green and Baker, 2003). This species is non-migratory and defends a permanent territory year-round against conspecific intrusion (Tweit, 1996). Thus physiological differences among populations likely result from local environmental factors and not from those associated with distant wintering grounds.

The study was conducted in a Sonoran desert site and in urban areas of the cities of Phoenix and Scottsdale. The desert site was the McDowell Mountain Sonoran Preserve and the adjoining Regional Park (940 acres and 21,099 acres, respectively), which is located at the northern periphery of Phoenix and 4 km from the fringe suburban developments of Troon and Fountain Hills. Urban sites included high- and low-income residential housing tracts, commercial areas, business districts, and manicured city parks of various sizes, and their sampling was governed primarily by authorized access. Previous research documented consistent differences in acute stress responses over several years between thrashers inhabiting various areas of Phoenix and those from several Sonoran Desert localities to the north, west, and south of the city, and there is little evidence for differences in stress physiology within urban localities (Fokidis, *unpublished data*). The current study is confined to two populations but the results likely apply to urban–desert comparisons across a number of localities.

2.2. Field capture and initial blood collection

The study was conducted between February and April 2008, which coincides with the early (incubation) to middle (early nestling) stages of the breeding season in this species (Tweit, 1996). Adult male thrashers (presumably defending active territories) were lured and captured in mist nets using conspecific playback recordings and all bird captures took place between 0500 and 1100 h.

Within 3 min of capture, approximately 300 μL of blood was collected from the right jugular vein into a heparinized 0.3 mL syringe with a 29.5 gauge needle. These samples were used to determine pre-injection (*hereafter* initial) plasma CORT. Birds (mean body mass ~80 g) then received either an intrajugular control injection of 0.9% NaCl solution (*hereafter* “Saline”), or one of the following treatments (see below). The order of these treatments was originally randomized, but once this order was established, treatments were given systematically and independently between the populations. There were no apparent differences in the breeding phenology between urban and desert bird populations.

Some birds (6 urban and 6 desert) were bled using the standard 30 min capture and handling protocol outlined by Fokidis et al. (2008, 2009), but received no injection. Results from these birds (*hereafter* “Bleed”), were compared to those from saline-injected birds to determine whether the act of injection alters the stress response. All blood samples were kept on ice until plasma was separated by centrifugation and then stored at −80 °C until assayed for CORT.

Sex of the birds was confirmed as male by the presence of a developed cloacal protuberance, and body mass (±0.1 g) and wing chord (±1 mm) was also measured for each bird. All birds received a uniquely numbered aluminum United States Geological Survey leg band and were released at the site of capture. All procedures followed the guidelines established by the Arizona State University Institutional Animal Care and Use Committee (protocol # 06-850R) and site access was authorized by the Arizona Game and Fish Department, the United States Fish and Wildlife Service, Cities of Phoenix and Scottsdale Parks and Recreation Departments, and various private landowners.

2.3. Pituitary sensitivity to CRH and AVT

To test the pituitary sensitivity to CRH and AVT, birds were injected *via* the jugular vein with either ovine CRH (*Sigma-Aldrich Co. Cat* # C3167) or AVT (*Sigma-Aldrich Co. Cat* # V0130). These injections

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