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Initial reactivity and magnitude of the acute stress response associated with personality in wild great tits (*Parus major*)

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ABSTRACT

Phenotypic correlations, such as those between functionally distinct behavioral traits, can emerge through the action of selection on individual traits, on trait combinations, and through pleiotropic mechanisms. Steroid hormones are known to have pleiotropic effects on a suite of behavioral and physiological traits, including stable individual differences in coping with stress. Characterizing the stress axis in relation to personality, however, has typically focused on estimating baseline and peak levels of glucocorticoids, principally in captive animals. In contrast, the reactivity of the stress response—how quickly it turns on and persists—may better indicate the ability of an individual to cope with challenges, particularly in free-living animals. Using wild great tits (*Parus major*) we tested the hypothesis that cautious individuals respond to a standardized stressor with a more reactive stress response compared to bolder individuals. Wild birds were captured and tested for exploration behavior in a novel environment—an operational measure of personality in this species—and assessed separately for their glucocorticoid response to a standardized stressor. Slower explorers exhibited a greater elevation in glucocorticoid levels within the first three minutes after capture. Further, slower explorers reached a higher maximum CORT concentration and had higher total exposure to glucocorticoids during the stressor period. These data provide evidence that the temporal reactivity of the endocrine stress response, specifically its speed and magnitude, is associated with stable behavioral traits in free-living animals.

1. Introduction

Individual animals exhibit behavioral differences that are stable over time and across contexts (Gosling, 2001; Réale et al., 2007). Such behavioral differences are referred to as coping styles or personality, and have been shown to have a genetic (van Oers et al., 2005) and developmental basis (Stamps and Groothuis, 2010), and be under sexual (Schuett et al., 2010) and natural selection (Dingemanse et al., 2004; Quinn et al., 2009; Smith and Blumstein, 2008). The idea that hormones serve a key role in promoting such differences is a sustained hypothesis in animal behavior research (Williams, 2008). Stress hormones in particular are thought to be involved in one of the major axes of personality variation: the shy–bold continuum (Carere et al., 2010; Korte et al., 2005; Øverli et al., 2007).

The endocrine stress response is coordinated by the hypothalamic–pituitary–adrenal (HPA) axis. The HPA axis releases glucocorticoid hormones and one of the critical functions of this system is to cope with the demands of normal life, for example day–night rhythmicity, locomotor activity and metabolism (Landys et al., 2006). Moreover, the HPA axis is essential for coping with unpredictable, 'stressful' events, such as exposure to unfamiliar environments (Lendvai et al., 2011), inclement weather (Breuner and Hahn, 2003), or predators (Cockrem and Silverin, 2002; Eilam et al., 1999). The stress response consists of several components: First, the response is initiated within a few minutes after a stimulus (stressor, e.g., capture) is perceived, as glucocorticoids (and their upstream secretagogues) are secreted above baseline concentrations. Second, levels of glucocorticoids continue to increase in the blood until they reach a peak concentration, typically within 30–60 min. Third, a process of negative feedback reduces circulating glucocorticoid levels, allowing baseline levels to be re-achieved, thus enabling the animal to respond to future challenges. The main glucocorticoid in birds is corticosterone (CORT), and like many steroid hormones CORT can affect diverse regulatory and behavioral processes simultaneously. For example, elevated CORT

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stimulates locomotor activity and foraging when food reserves are low, but can also suppress non-essential and energetically demanding processes such as immune defense, reproductive physiology and behavior (Sapolsky et al., 2000).

Because a single hormone such as CORT can generate co-variation at multiple physiological levels (c.f., hormonal pleiotropy; (Ketterson and Nolan, 1999), and because the HPA axis can influence behavior directly, the pleiotropic effects of CORT might contribute to behavioral co-variation (Baugh et al., 2012; Korte et al., 2005; Øverli et al., 2005). In fact, several of the canonical behavioral traits that characterize personality (e.g., shyness in animals, neuroticism in humans; (Gosling, 2001) may relate to differences in how individuals respond hormonally to stressors (Koolhaas et al., 2007; Martins et al., 2007). Furthermore, there is often remarkable intra-population variation in concentrations of baseline and stress-induced CORT (Pottinger et al., 1992; Tort et al., 2001). Importantly, a portion of this variance has been shown to be repeatable among individual birds (Evans et al., 2006; Pottinger and Moran, 1994; Rensel and Schoech, 2011; Romero and Reed, 2008) and to have a heritable component (Brown and Nestor, 1973; Edens and Siegel, 1975; Evans et al., 2006; Satterlee and Johnson, 1988). On the basis of these established hormone–behavior relationships, glucocorticoid physiology has been hypothesized to underlie animal personality (Korte et al., 2005). Specifically, the HPA axis of shyer individuals is predicted to exhibit greater reactivity (Ellis et al., 2006). Operationally, 'reactivity' of the HPA axis has been used to refer to the magnitude of the stress response, including both the area under the curve (Juster et al., 2012) and the maximum concentration of stress hormones observed during a stress assessment (Wada et al., 2007)—definitions that deemphasize the temporal dimension. Nonetheless, studies probing the relationship between individual differences in behavior and stress physiology have yielded support for this first prediction (Baugh et al., 2012; Cockrem, 2007; Koolhaas et al., 1999; Lendvai et al., 2011; Mackenzie et al., 2009; Øverli et al., 2005). And while much can be gleaned from such studies, many have explored this question using captive or domesticated animals, which might differ in fundamental ways from wild organisms, particularly in their stress physiology (Calisi and Bentley, 2009; Dickens and Romero, 2009).

In this study we extended this line of investigation to test the idea that variation in stress reactivity—including both its onset and magnitude—is associated with behavioral differences in wild birds. Specifically, variation in the initiation phase of the glucocorticoid response might play a role in acute coping behavior, while its magnitude might have longer term consequences, including how effectively an individual can endure a subsequent stressor and which individuals survive stressful natural events (Romero and Wikelski, 2010).

We used wild great tits (*Parus major*), tested in a standardized way for both exploration behavior and stress responses. Great tits have become a model vertebrate for the study of animal personality, in part because this species has been studied from an ecologically informed perspective. Previous research in this species has shown that exploration behavior in a novel environment (open field test; Verbeek et al., 1996) is a repeatable behavioral trait over long periods of time (Dingemanse et al., 2002), is correlated with mate choice (van Oers et al., 2008), aggression (van Oers et al., 2004; Verbeek et al., 1996), territorial behavior (Amy et al., 2010), learning (Titulaer et al., 2012), reproductive success (Both et al., 2005; Quinn et al., 2009), and survival (Dingemanse et al., 2004). We thus used exploration behavior as an operational measure of great tit personality. Further, heritability studies of wild (Dingemanse et al., 2002; Quinn et al., 2009) and captive great tits (Drent et al., 2003; van Oers et al., 2004) have demonstrated a high degree of heritability in exploration behavior, and a genetic correlation between exploration behavior and stress physiology (Baugh et al., 2012; Carere et al., 2003). In the present study we tested the hypothesis that slower explorers exhibit a more reactive (earlier elevation and greater magnitude) endocrine stress response.

2. Materials and methods

2.1. Study system

The Westerheide study area near Arnhem, The Netherlands (52° 0′ 38″ N, 5° 50′ 30″ E) is a forest of approximately 100 ha and hosts a large long-term study population of color-ringed personality-typed wild great tits. Since personality has been shown to be a trait that is consistent over time, we did not retest individuals of known personality, but conducted new tests upon first capture of unringed individuals. We carried out behavioral testing and hormone sampling on separate dates to avoid the potential confounding effects that the bleeding experience might have on performance in the behavior assay, and vice versa. Because we could not target the collection of specific individuals, we instead sampled birds opportunistically for hormones and behavior, resulting in a median interval between behavioral testing and hormone sampling of 28 days (mean ± SD: 145 ± 300 d). Our exploration assay has been shown to estimate persistent characteristics of an individual (Carere et al., 2005; Dingemanse et al., 2002), indicating that the scores have a high explanatory power across prolonged periods of time.

2.2. Behavioral testing

Birds were caught with mist nets near feeding stations in Westerheide and transported for approximately 0.5 h in transport boxes to a custom designed housing and behavioural testing facility (Heteren, The Netherlands) where they were kept overnight in individual cages (0.9 × 0.5 × 0.4 m) in a room that shares a common wall with the test chamber. Exploration behavior was measured separately for each individual following a standardized protocol using a test chamber (2.0 × 4.0 m, 2.5 m high) with five artificial 'trees' as a novel environment (for details see Dingemanse et al., 2002). On the morning following capture (0800–1200) each bird was released individually from its cage directly into the test chamber without handling, by opening a sliding door on the chamber side of the common wall. After entry into the chamber, we monitored behavior for 2 min and recorded the number of tree visits and hops and flights between and within perches (e.g., branches of the artificial trees, sliding doors, floor). We calculated the exploration scores by summing all hops and flights per individual. Exploration scores are known to vary seasonally (increasing as the breeding season approaches) but remain repeatable at the individual level (Dingemanse et al., 2002). We therefore corrected for 'July date', which is the number of days from 1 July onward (exploration scores from the sample ($n = 86$): mean = 23.09, SD = 9.46, range = 5.7–49.9). All individuals in this study were tested for the first time during their lives, thus precluding any effects of habituation to the testing conditions (Dingemanse et al., 2002). Behavioral testing was conducted blindly and independently of hormone sampling and measurement. Birds were released at their site of capture within a few hours following behavioral testing.

2.3. Hormone sampling

In the autumn of 2010 we captured birds for the measurement of plasma CORT using a standardized handling-restraint protocol to examine initial and stress-induced concentrations (Romero et al., 1997). By sampling plasma CORT during the non-breeding season, when hormone levels fluctuate less (Romero and Wingfield, 1998), and by sampling during a restricted time of day