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Baseline corticosterone and stress response in the Thorn-tailed Rayadito (*Aphrastura spinicauda*) along a latitudinal gradient

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ABSTRACT

Glucocorticoids are essential for life and their secretion is regulated by the hypothalamic–pituitary–adrenal axis (HPA). The HPA axis is often divided into two components: baseline glucocorticoids levels and stress response glucocorticoids levels, which are affected by changes in ambient temperature and productivity among others factors. An approximation to evaluate how a species copes with these changes is to evaluate differences of this hormone amongst populations of the same species that inhabit places ideally presenting all the possible combinations of temperature and productivity. We aimed to evaluate whether environmental temperature or productivity, represent challenges in terms of stress in the Thorn-tailed Rayadito (*Aphrastura spinicauda*). We examined circulating baseline levels of CORT and stress responses from three populations, covering the whole geographic distribution of the species across large gradients in weather conditions. If low temperature influences baseline CORT levels, we expect higher levels of this hormone in the southernmost population (higher latitude). However, if productivity is the factor that influences baseline CORT levels, we expect the contrary pattern, that is, lower values of this hormone in the southernmost population (more productive environment). We observed that baseline CORT levels presented lower values in the southernmost population, supporting the environmental productivity hypothesis. Secondly, we tested the hypothesis that individuals breeding at higher latitudes should have a lower stress response than individuals breeding at lower latitudes. Contrary to our expectations, we found that stress response did not vary among populations in any of the three years. We concluded that low environmental temperatures did not represent a stress situation for the Thorn-tailed Rayadito if food abundance was sufficient to support energetic demands.

1. Introduction

Responses to biotic and abiotic cues typically involve the hypothalamic–pituitary–adrenal cortex (HPA) axis, culminating in the release of glucocorticoids (e.g., Sapolsky et al., 2000; Wingfield, 2003; Romero et al., 2009). Glucocorticoids are essential for life as they regulate or support a variety of important cardiovascular, metabolic, immunologic, and maintain daily homeostatic energetic balance (Harvey et al., 1984; Dallman et al., 1993). The HPA axis is often divided into two components: baseline glucocorticoids levels and stress response glucocorticoids levels (Romero, 2004). The first is an approximation of the seasonal baseline level that the animal should maintain to be able to cope with the predictable demands of the current life-history stage (Landys et al., 2006; Bókony et al., 2009), so it reflects long-term adaptation. The former, (stress response: the increase in baseline glucocorticoids levels to the level reached in 30 min) best reflect short-term plastic responses to environmental perturbations (Romero, 2002; Wingfield, 2013).

In birds, unexpected periods of inclement weather, such as storms, or low environmental temperatures can increase baseline corticosterone (CORT) (e.g., Passeriformes: Wingfield et al. 1983; Wingfield, 1985; Rogers et al., 1993; Breuner and Hahn, 2003; Ouyang et al., 2012; Apodiformes: Bize et al., 2010; Pelicaniformes: Smith et al., 1994; and Charadriiformes: Satterthwaite et al., 2012), the primary glucocorticoid in birds (Wingfield, 1994; Sapolsky et al., 2000; Romero, 2004). In addition, de Bruijn and Romero (2011) observed that small drops in ambient temperature (e.g., 3 °C) mimicking a natural storm, was sufficient to increase baseline CORT levels, in the European Starlings (*Sturnus vulgaris*), presumably due to the higher energetic cost demanded by low temperatures.

Not only low ambient temperatures, but also low habitat quality (i.e., low food availability or low productivity) can raise baseline CORT levels. Increased levels of this hormone, as a result of low habitat quality, has been registered in Black-legged Kittiwakes

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(*Rissa tridactyla* – Kitaysky et al., 1999; Lanctot et al., 2003; Buck et al., 2007), Common Murres (*Uria aalge* – Kitaysky et al., 2007), American Redstarts (*Setophaga ruticilla* – Marra and Holberton, 1998) and Barn Swallows (*Hirundo rustica* – Jenni-Eiermann et al., 2008). However difficulties arise when these two factors (temperature and productivity) co-vary and thus emerging patterns are equally consistent with alternative scenarios. For example, Ouyang et al. (2012) observed higher levels of baseline CORT levels in Great Tits, *Parus major*, in a year of low ambient temperatures that coincided with lower food availability. Separating the roles played by each of these factors is challenging, particularly in the field, because of the impossibility to manipulate ambient temperature and productivity. Although supplementary experiments can be performed, they present some disadvantages (see Desy and Batzli, 1989). So, an approximation to evaluate how a species copes with changes in temperature and productivity is to evaluate differences of this hormone amongst populations of the same species that inhabit places ideally presenting all the possible different combinations of temperature and productivity.

Here we studied three populations of a passerine bird, the Thorn-tailed Rayadito (*Aphrastura spinicauda*) in Chile. This species is ideal to evaluate whether temperature or productivity represents challenges in terms of stress, because the distribution range of this species encompasses regions with strong differences in weather condition and productivity. Compared with the central and northernmost populations, the southernmost population (lower latitude) presents lower annual temperatures, higher annual precipitations and higher productivity (Table 1). Although the northernmost and the central population are similar in the aforementioned variables, they differed in the magnitude of annual variance, as is reflected in the coefficient of variations: the central population presents more seasonality in temperatures and precipitations (Table 1). In addition Thorn-tailed Rayadito presents larger clutch sizes (a life-history trait that can influence baseline CORT levels Criscuolo et al., 2006), and higher body weights towards the south. So, if low temperature influences baseline CORT levels, now called “low temperature hypothesis”, we expected higher levels of this hormone in the southernmost population in relation to the central and northernmost populations. However if productivity is the main factor influencing baseline CORT levels, we propose: “productivity environmental hypothesis”, we expected lower values of this hormone in the southernmost population because this population represents the most productive environment.

Although baseline CORT levels serve to maintain energy balance, high levels of this hormone results in the interruption of the normal life-history stage (such as reproduction, migration, etc.) and triggers an emergency life-history stage that allows the individual to temporarily move away from the source of perturbation or endure it, while adopting many energy saving behaviors that allow it to cope (Wingfield, 2003). In birds, elevated levels of this hormone during breeding decreases reproductive behavior promoting nest abandonment (e.g., Astheimer et al., 1992; Love et al., 2004; Moore and Zoeller, 1985; Ouyang et al., 2012; Sapolsky, 1985; Silverin, 1986; Wingfield and Silverin, 1986; Silverin et al., 1989). These observations led to the formulation of the capricious conditions hypothesis (CCH) that predicts in species breeding in extreme and unpredictable environments and with restricted breeding periods (e.g., high latitude locations), that the stress response in general should be suppressed (Cornelius et al., 2012). And that this suppression would be observed especially during the parental phase of the reproductive cycle: the breeding environmental hypothesis (Wingfield, 1994; Wingfield et al., 1995a). Although some studies have supported the CCH hypothesis, with suppression of stress response in populations at higher latitudes (e.g., Cornelius et al., 2012; Silverin et al., 1997), others have detected invariant induced CORT during parental phases (e.g., Angelier et al., 2009; Breuner et al., 2003; Chastel et al., 2005), or even increased hormonal stress responsiveness in populations at higher latitudes (e.g., Wingfield et al., 1995b). Additionally, it has been proposed that the stress response is expected to depend upon parental care strategy, and individuals of the sex expressing more parental care should have a lower stress response than individuals of the sex expressing less, or no, parental care (Wingfield et al., 1995a). So, we tested the CCH hypothesis and the parental care hypothesis in Thorn-tailed Rayadito. If the stress response is down-regulated in the higher latitude population, presumably because of more severe environment due to unpredictable snowstorms and low environmental temperature, we should observe suppression of the stress response in southernmost populations. Because the Thorn-tailed Rayadito present a socially monogamous mating system where both members of the pair contribute to nest-building, incubation, and feeding of nestlings and fledglings (Moreno et al., 2007), the parental care hypothesis predicts absence of differences in stress responses between sexes.

Investigations of northern hemisphere populations reveals modulations of the adrenocortical responses to acute stress may have ecological bases related to gender, season, social status, climatic events and presence of predators. Such bases are also important in the southern hemisphere although few studies to date have tried to determine whether southern populations modulate the

Table 1

Geographical origin, climatic data, values of reproductive function (e.g., clutch size) and biometry (mass at fledgling, mass of adults) for three populations of rayaditos during two years in Chile[a]. DMi = Martonne aridity index, Clutch size = number of eggs, Nestling mass (g) = weight of nestlings at 13 days old, Adult mass (g) = weight of adults when nestling were 13 days old.

Population	Year	Precipitations (SD)	Coefficient of variation	Temperature (SD)	Coefficient of variation	DMi (SD)	Coefficient of variation	Clutch size	Nestling mass	Adult mass
Northern	2010	134.70 (1.93)	1.43	10.80 (1.88)	17.41	0.56 (0.67)	119.64	2.71 (0.68)	12.74 (1.43)	11.82 (0.92)
	2011	186.90 (2.12)	1.13	11.18 (1.90)	16.99	0.79 (1.79)	226.58	2.59 (0.74)	12.73 (1.73)	11.89 (0.85)
Central	2008	160.23 (5.69)	3.55	15.04 (5.01)	33.32	0.73 (1.59)	217.81	3.13 (0.72)	14.34 (1.19)	11.62 (0.91)
	2010	193.10 (4.59)	2.38	14.31 (5.04)	35.22	0.97 (1.37)	141.24	3.27 (1.00)	14.05 (1.81)	11.15 (1.00)
	2011	144.40 (3.69)	2.56	14.44 (4.94)	34.21	0.66 (1.12)	169.69	3.42 (0.90)	13.57 (1.89)	11.07 (0.96)
Southern	2008	325.38 (2.50)	0.77	4.58 (4.09)	89.30	2.05 (1.15)	11.00	5.00 (0.55)	14.37 (1.49)	11.90 (0.79)
	2010	412.80 (2.69)	0.65	6.49 (2.82)	43.45	2.10 (1.13)	22.22	4.68 (1.04)	14.75 (1.25)	12.58 (1.53)
	2011	340.90 (2.25)	0.66	5.92 (3.64)	61.49	2.16 (1.08)	50	4.85 (0.93)	14.87 (1.1)	12.3 (0.77)

The de Martonne (DMi) aridity index was calculated following di Castri and Hajek (1976), based on the average of monthly temperatures and precipitation. The index is low in hot, dry deserts (low productivity) and high in cool, wet areas (high productivity). The mean annual temperature (calculated as the average of the monthly temperatures) and total annual precipitation are reported. The variances of precipitation (σ^2 P) temperature (σ^2 T) and de Martonne index (σ^2 DMi) were estimated from the mean of monthly values.

[a] Climatic data was collected from <http://www.ceazamet.cl, http://www.meteochile.gob.cl/>.