



## Breaking down seasonality: Androgen modulation and stress response in a highly stable environment



Paulina L. González-Gómez<sup>a,b,\*</sup>, Loren Merrill<sup>c</sup>, Vincenzo A. Ellis<sup>d</sup>, Cristobal Venegas<sup>e</sup>, Javiera I. Pantoja<sup>e</sup>, Rodrigo A. Vasquez<sup>e</sup>, John C. Wingfield<sup>a</sup>

<sup>a</sup> Department of Neurobiology, Physiology, and Behavior, University of California Davis, 1 Shields Avenue, CA 95616, USA

<sup>b</sup> Instituto de Filosofía y Ciencias de la Complejidad (IFICC), Los Alerces 3024, Santiago, Chile

<sup>c</sup> Department of Zoology, LSW 420, Oklahoma State University, OK 74075, USA

<sup>d</sup> University of Missouri – St. Louis, MO, USA

<sup>e</sup> Instituto de Ecología y Biodiversidad (IEB), Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

### ARTICLE INFO

#### Article history:

Received 17 February 2013

Revised 2 May 2013

Accepted 3 May 2013

Available online 23 May 2013

#### Keywords:

Stable environments

Endocrine mechanisms

Corticosterone

Testosterone

Desert

*Zonotrichia*

### ABSTRACT

Previous studies show that most birds inhabiting temperate regions have well defined life history stages, and they modulate the production of testosterone (T) and corticosterone (CORT) in response to changes in seasonality. In this study we aimed to examine baseline and stress-induced levels of CORT and circulating T in relation with life history stages in the rufous-collared sparrow, *Zonotrichia capensis*. We carried out this study for a year in a population inhabiting riparian habitats in the Atacama Desert in Chile, one of the most climatically stable and driest places in the world. This environment shows minimal yearly change in average temperature and precipitation is virtually zero. We found individuals breeding, molting and overlapping breeding and molt year round, although most individuals were molting during March and in breeding condition during October. T levels were not related to individual breeding condition, and at population level they were not significantly different across sampling months. Baseline levels of CORT did not vary across the year. Stress-induced levels of CORT were suppressed during March when most of the birds were molting. This phenomenon was also observed in birds not molting during this period suggesting a mechanism other than molt in determining the stress-response suppression. Our results strongly suggest that in this study site, long-term extremely stable conditions could have relaxed the selective pressures over the timing of life history stages which was evidenced by the breeding and molt schedules, its overlap and endocrine profiles.

© 2013 Elsevier Inc. All rights reserved.

### 1. Introduction

Many vertebrate species experience a series of energetically costly events over the course of the annual cycle including reproduction, molt, and migration (Wingfield, 2005). These events require substantial investment of resources (Hoye and Buttemer, 2011), and are sufficiently costly that they cannot be undertaken simultaneously without fitness repercussions (Zera and Harshman, 2001). In non-migratory species breeding at mid- to high latitudes there is typically a pronounced temporal division of the most energetically demanding phases of breeding and molt, with minimal overlap between these activities at the individual level (Barta et al., 2006; Houston et al., 2005; Johnson et al., 2012). In fact, birds that overlap activities are observed to experience lower fitness than birds that, for example, finish breeding before initiating molt

(Nilsson and Svensson, 1996). Partitioning of molt from other life history stages is therefore assumed to be an adaptation that minimizes physiological demands (allostatic load, McEwen and Wingfield, 2003) while maximizing the allocation of productive energy to enhance lifetime fitness (Hahn et al., 2008; Mitchell et al., 2012). In migratory birds, the schedule of migration, molting and breeding are even more constrained mainly because individuals which delay molting or breeding migrate later (Stutchbury et al., 2011; Mitchell et al., 2012), and the optimal arrival time on the breeding grounds is crucial to obtain the best territories (Kokko et al., 2006). In addition, in seasonal environments reproductive success is strongly linked to the appropriate timing of breeding, when hatching matches peaks in food supply (e.g. Brinkhof et al., 1993; Lambrechts et al. 1996).

The hormonal changes associated with the timing and duration of different life history stages are complex, but metabolic demands are considered linked to plasma levels of corticosterone (CORT) while testosterone (T) levels are associated with territory establishment and onset of breeding, at least in males. During regular

\* Corresponding author. Address: Department of Neurobiology, Physiology, and Behavior, University of California Davis, 1 Shields Avenue, Davis, CA 95616, USA.

E-mail address: [plgonzalezgomez@ucdavis.edu](mailto:plgonzalezgomez@ucdavis.edu) (P.L. González-Gómez).

life history stages, CORT regulates metabolic functions such as energy intake, storage, and mobilization (Sapolsky et al., 2000; Landys et al., 2006). In contrast, stress-induced elevation of CORT involves a variety of physiological and behavioral changes that allocate resources toward immediate survival (Wingfield et al., 1998; Landys et al., 2006). In this context, changes in plasma CORT levels can affect timing of breeding and molting directly as well as indirectly by promoting activities incompatible with molt and breeding (Murphy, 1996; Breuner et al., 1998). CORT may also indirectly increase energy expenditure with the potential to limit resources devoted to reproduction and feather growth (Romero et al., 2005). Consequently, despite high levels of variability in CORT plasma levels (Romero, 2002; Wingfield, 2005), a widespread pattern is the suppression of both baseline and stress induced CORT levels during the parental phase of breeding and the post-breeding (prebasic) molt relative to breeding (Cornelius et al., 2011).

On a predictable, seasonal basis, environmental signals such as the annual changes in photoperiod, precipitation, and food abundance regulate the progression of life history stages through, for example, stimulation of the hypothalamic–pituitary–gonad (HPG) axis that in turn regulates T increases in males and acquisition of a territory and onset of breeding (Wingfield, 2008; Perfíto et al., 2007). However, prolonged high levels of T can have detrimental effects such as decreases in body mass and fat stores, depressed immune activity and ultimately decreased survival (e.g., Dufty, 1989; Ketterson and Nolan, 1992; Hillgarth and Wingfield, 1997; Wingfield and Soma, 2002). In addition, high T levels can interfere with molt (Runfeldt and Wingfield, 1985; Schleussner et al., 1985). Nolan et al. (1992) showed that birds maintained at artificially elevated levels of T beyond the end of the breeding season, postponed or suppressed molt. Consequently, many avian species exhibit a marked breeding season where T increases and remains elevated for most of the breeding period (Farner and Wingfield, 1980; Wingfield, 1984). In environments where seasonality is less clearly delineated and typically reduced to two general seasons (i.e., wet and dry seasons), such as the tropics, year-round territorial species display continuously low levels of T, or T remains undetectable year round compared with species in seasonal environments (Levin and Wingfield, 1992; Goymann et al., 2004; Moore et al., 2004a). Despite studies in tropical environments, the hormonal regulation of life history stages in highly stable environments is poorly understood. In this context our goal was to assess life history stages and circulating levels of T and CORT in rufous-collared sparrow (*Zonotrichia capensis peruviansis*) in the Atacama Desert, the driest and oldest extant desert on Earth (Hartley et al., 2005; Supplemental materials Fig. 1). In this extremely stable climate the environmental cues to molt or breed are minimal. Despite variations in photoperiod are roughly 2 h, which eventually could be considered as a proximate cue since birds in the tropics can respond to differences <1 h (Hau et al., 2008), variations in temperature and precipitations are low. The annual average temperature is  $18.75 \pm 0.04$  with minimal temperatures of  $13.5 \pm 0.18$  and maximal of  $24.0 \pm 0.08$  °C (Dirección Meteorológica de Chile, 2011). In terms of water and food availability, even though precipitation is extremely infrequent in the coastal desert region (i.e., roughly 0.5 mm per year), several streams flow from Los Andes and provide water and conditions for abundant riparian vegetation in the valleys. In our study site the valleys present similar climatic characteristics however San Jose River (Azapa Valley) can be classified as an endorheic basin where water is pumped to the surface to sustain agricultural activities, presenting a flow of 0.58 l/s. This flow can increase in 0.7 times between January and March every 4 or 5 years mainly associated with heavy rain in the Andes region during “El Niño” events. In contrast, the Lluta basin is exorheic and water naturally flows year round with a flow of roughly 600 l/s (Cade-Idepe Consultores,

2004). Flows are more regularly registered in Lluta, causing until 6-fold increase in discharge between January and March every year. In addition, Lluta presents higher levels of salinity than the San Jose River. These differences in salinity probably explain the higher levels of agricultural activities in Azapa valley where over the past few years the cultivable surface has increased 5-fold (Torres and Acevedo 2008). As a result of the increments of agricultural activity, semirural areas rich in vegetables, arthropods and seeds are common, creating habitats for some passerine birds, as rufous-collared sparrow (see Estades and Temple, 1999).

Our study model was the rufous-collared sparrow, a species distributed from southeastern Mexico to the Southernmost tip of South America, Cape Horn in Chile. Along this range, populations experience diverse habitats including urban areas, coastal and xeric environments, grasslands, chaparral and edges of tropical and temperate forests and alpine meadows (Estades and Temple, 1999; Class et al., 2011; Maldonado et al. 2012). Populations of rufous-collared sparrows through Central and South America exhibit different patterns of timing and duration of their life-history stages (Kalma, 1970; King, 1973; Moore et al., 2005; Class et al., 2011; Busch et al., 2010; Addis et al., 2010, 2011). Breeding and molting have been described to be unimodal seasonal and mostly mutually exclusive in most of *Zonotrichia*'s distribution range in Latin America (Wolf, 1969; Kalma, 1970; Miller, 1959; Moore et al., 2005; Davis, 1971; King, 1973) with the exception of high-altitude populations in Colombia where birds were observed to breed and molt twice a year (i.e., bimodal schedule) but without overlapping between both stages (Miller, 1962; Miller and Miller, 1968). In all of these environments individuals experience some degree of seasonality or environmental cues that modulate timing of life history stages. Very few studies have examined life history stages in an organism that lives in an area with minimal environmental change. In this study, we explored the link between life history stages, T and CORT in a stable environment to better understand the trade-offs involved between molt and reproduction, and the relation between endocrine mechanisms and environmental cues that shape most of the life schedules in vertebrate species.

## 2. Material and methods

### 2.1. Species, study site and morphological measures

In our focal species, *Z. capensis*, males are territorial and socially monogamous, and both males and females exhibit parental care (Chapman, 1940; Miller and Miller, 1968). They are described as mainly granivorous, however they have been observed to consume insects and fruits depending on the environment that they inhabit and time of year (Novoa et al., 1996). To assess life history stages and endocrine profiles, and to determine the relationship between circulating hormone levels and breeding and molt conditions in this species, we carried out a field study in the Atacama Desert in Northern Chile. The extremely dry conditions in this place are maintained by several factors: (i) the Pacific Anticyclone along the coast generates a thermal inversion layer; (ii) the Andes Mountains act as a barrier blocking the humid influence of the Amazonian region, and (iii) the cold Humboldt marine current originating in Antarctica limits seawater evaporation (Cereceda et al., 2002). These conditions result in an extremely stable environment characterized by daily coastal morning fog and year round constant temperature (see Supplemental materials, Fig. 2). For example, in the year of this study, the maximum and minimal temperatures averaged  $23.29 \pm 2.63$  °C and  $18.79 \pm 1.84$  °C respectively. These temperatures are similar to those recorded in the last 50 years (Torres and Acevedo, 2008). We collected blood samples and phenology data for a week at

Download English Version:

<https://daneshyari.com/en/article/5901214>

Download Persian Version:

<https://daneshyari.com/article/5901214>

[Daneshyari.com](https://daneshyari.com)