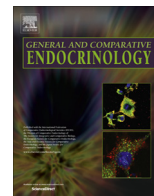




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The number of life-history stages does not influence the androgen responsiveness to male–male interactions: Sedentary and migratory black redstarts (*Phoenicurus ochruros*) do not elevate testosterone in response to simulated territorial intrusions

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ABSTRACT

High plasma levels of testosterone at the beginning of the breeding season adjust male physiology for mating and promote territorial behavior in birds. Conversely intra-sexual competition may elicit a temporary increase in circulating testosterone. Male black redstarts (*Phoenicurus ochruros*) from migratory populations show the expected increase in baseline testosterone during early breeding, but circulating testosterone levels do not change in response to male–male interactions. Because sedentary populations express fewer life-history stages they may be more flexible in timing of life-history stages and more responsive to environmental modulation of hormone concentrations. Therefore, we tested whether the androgen responsiveness to male–male interactions differs between migratory (6 life-history stages) and sedentary black redstarts (3 life-history stages) during early breeding, predicting that in contrast to migratory birds, sedentary birds would modulate testosterone in response to simulated territorial intrusions (STI). In contrast to our prediction, sedentary males did not modulate post-capture testosterone levels in response to simulated territorial intrusions. Males of both populations increased testosterone after an injection of gonadotropin releasing hormone (GnRH), demonstrating that they were capable of increasing testosterone. Interestingly, in sedentary males the GnRH injection elicited a higher testosterone response in STI males than in control males. The two populations did not differ in their behavioral response to the STIs, except that sedentary males spent less time close to the decoy. In combination with previous data from black redstarts and other socially monogamous and biparental birds our current study adds to the growing evidence that current theory regarding hormone-behavior relationship needs to be refined.

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1. Introduction

Most organisms live in seasonal environments and time successive life-history stages according to predictable changes in environmental cues (Jacobs and Wingfield, 2000; Wingfield, 2008). The finite-state-machine model (Jacobs and Wingfield, 2000; Wingfield, 2008) suggests that animals living in environments with large seasonal changes express more life-history stages than animals living in environments with a low degree of seasonal change. Because hormones are involved in the regulation of

development, onset and termination of life-history stages, the numbers of stages and the degree of overlap may influence the neuroendocrine mechanisms and their control by environmental cues (Wingfield, 2008). In particular, the finite-state-machine theory predicts that species or populations expressing more life-history stages (e.g. migratory, compared to sedentary populations) should be less flexible in timing and thus, the succession of life-history stages may be under tighter hormonal control. Furthermore, if life-history stages are tightly controlled they may be less susceptible to environmental modulation (Goymann, 2009; Wingfield, 2008, 2005). In addition, it has been proposed that birds breeding at higher latitudes have higher peaks of plasma testosterone than lower latitude birds (reviewed in Garamszegi et al., 2008). However, these differences may be driven by differences in life history rather than latitude per se (Goymann and Landys, 2011;

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Goymann et al., 2004). Accordingly, specific life-history traits, such as short and synchronous breeding seasons may be more important determinants of hormone profiles than latitude.

Sex steroids are important regulators of the breeding life-history stage. Testosterone, for example, is involved in spermatogenesis, the development of secondary sexual characters (reviewed by Adkins-Regan, 2005), sexual (Ball and Balthazart, 2004; Beach and Inman, 1965), and territorial behavior within a reproductive context (e.g. Canoine and Gwinner, 2002; Wingfield et al., 1990, 2001; Wingfield, 1984). At the same time social interactions such as competition for territories or mates may feed-back on hormone secretion, potentially leading to an increase in testosterone during male–male conflicts (Harding, 1981). The challenge hypothesis predicts a short-term rise in circulating testosterone in response to male–male interactions, especially in socially monogamous species (Wingfield et al., 1990; termed $R_{\text{male–male}}$ by Goymann et al., 2007a). Indeed, male–male interactions produce a rapid increase in plasma testosterone levels in males of socially monogamous species of a variety of vertebrate taxa (reviewed by Hirschenhauser and Oliveira, 2006). However, in the majority of birds that have been experimentally tested so far, males fail to elevate testosterone during male–male challenges (Addis et al., 2010; Apfelbeck and Goymann, 2011; Deviche et al., 2012; DeVries et al., 2012; Landys et al., 2010; Scriba and Goymann, 2010; Villavicencio et al., 2013; and older studies reviewed by Goymann et al., 2007a; Goymann, 2009). The finite-state-machine theory offers one possible explanation for the lack of $R_{\text{male–male}}$ in some birds. If the tightness of hormonal control mechanisms increases with the number of life-history stages, then those avian species (or populations) expressing more life-history stages may also be less responsive to social modulation of hormones (i.e. to avoid interference with the control mechanism; Goymann, 2009). Here, we test this idea by comparing testosterone dynamics in males from two populations of one bird species that differ in the number of life-history stages.

Prior work on the black redstart (*Phoenicurus ochruros*), a small, insectivorous, and territorial songbird indicates that testosterone shows a strong seasonal pattern with high levels in spring, when territories are established, intermediate levels during the rest of the breeding season, and low levels in autumn (Apfelbeck et al., 2013). Males respond aggressively, but do not elevate plasma testosterone when challenged by a real or a simulated territorial intrusion, by a multiple simulated territorial intrusion, or when removing a territory neighbor. Black redstarts thus, do not support the predictions of the challenge hypothesis for socially monogamous birds with biparental care (Apfelbeck and Goymann, 2011; Apfelbeck et al., 2011; Villavicencio et al., 2013). Previous work on this species has focused on migratory populations expressing six life-history stages: spring migration, breeding, molt, autumn territoriality, autumn migration and wintering. In southern Europe, sedentary populations of black redstarts exist (Bueno, 1992) and they express only three life-history stages: breeding, molt and non-breeding. If social modulation of testosterone is more likely to occur in birds displaying fewer life-history stages, then we hypothesized that sedentary redstarts should modulate testosterone in response to male–male interactions. To test this hypothesis we compared territorial behavior, post-capture and GnRH-induced testosterone concentrations in males from one sedentary and two migratory black redstart populations. The sedentary population in Spain had already started to breed, allowing us to establish comparisons with either (i) a migratory population sampled at the same time of the year, during active northward migration across the Mediterranean sea (i.e. same dates, but different life-history stages) or (ii) a migratory population in Germany sampled later in the year, during early breeding (i.e. different dates, but the same life-history stage as the sedentary population). We assessed both

post-capture and GnRH-induced testosterone levels to exclude the possibility that birds were not capable of elevating testosterone during male–male interactions ($R_{\text{male–male}}$), because they may have been producing the hormone at their maximal rate even before the social challenge (Goymann, 2009). Further, the GnRH-treatment allowed us to test whether the populations differed in their maximum physiological capacity to produce testosterone (termed $R_{\text{potential}}$ by Goymann et al., 2007a; see also e.g. Moore et al., 2002).

2. Material and methods

We conducted this study on one sedentary and two migratory populations of black redstarts. The resident, non-migrant population was located in southern Spain, in the natural reserve Torcal de Antequera (Malaga, Andalusia; 36°N, 4°W, 1100–1200 m above sea level). Males were sampled during early breeding (between March 17th and April 1st in 2012) when they courted females and females started nesting (i.e. the mating stage). One migratory population was sampled during migration on Ponza, a small island in the Tyrrhenian Sea of Italy (40°55' N, 12°58' E, 0–100 m above sea level) that is frequently used by migrants as a stop-over site (samples were collected during active northward migration, between March 14th and March 27th in 2011). The second migratory population was sampled in Upper Bavaria, Germany in villages in the vicinity of the Max-Planck-Institut für Ornithologie (47°N, 11°E, 500–600 m above sea level). Males of this population arrive on the breeding grounds between mid-March and beginning of April. Once territories are established and weather conditions permit they start to breed at the end of April. We sampled males when they were actively defending territories and mating with females, which started to nest (i.e. the mating stage between April 20th and May 13th in 2010 and April 11th and May 6th in 2011).

Black redstarts show delayed plumage maturation with second-year males (i.e. males in their first breeding season) resembling females and attaining their black coloration with white wing patches only after their first postnuptial molt (Landmann, 1996). Because this phenotypic difference between second-year and older males could relate to differences in behavior or testosterone concentrations (Schwarzova et al., 2010) we considered age differences throughout the manuscript.

2.1. Experimental procedure

On the breeding grounds males were caught with two different protocols: (i) STI males were caught with mealworm-baited ground traps following a simulated territorial intrusion, during which we placed a stuffed decoy onto a male's territory and played-back black redstart songs for 20 min. (ii) Control males were caught with mealworm-baited traps either passively while searching for food, or within 10 min of the onset of playing back black redstart song (assuming that testosterone concentrations do not change within 10 min of playback presentation; Wingfield and Wada, 1989). To avoid pseudo-replication we used four different stuffed males in full adult plumage as decoys and songs from 20 different adult males. For the STI group territorial behavior was assessed during 20 min after placing the dummy and starting playbacks. We recorded the following behaviors: latency to first approach within 5 m of the decoy (response latency), total time spent within 5 m of the decoy, frequency of head nodding, number of songs and attacks. All behaviors were scored by the same observer (CPV), and the frequency was defined as total number of events per 20 min. After 20 min of STI, traps were activated to catch the territorial male. All males were caught with ground traps and tree traps baited with mealworms. We caught 13 control males with short playback (latency to be caught: 4.5 ± 1.7 min (mean \pm 95%

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