



## Sex-specific hypothalamic-pituitary-gonadal axis sensitivity in migrating songbirds



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### ABSTRACT

In seasonally migratory species, the overlap between the migratory and breeding life history stages is a balance between the physiological and behavioral requirements of each stage. Previous studies investigating the degree to which songbirds prepare for breeding during spring migration have focused on either circulating hormone levels or direct measures of gonadal recrudescence. In this study, we evaluated the phenology of breeding preparation in a long-distance migratory songbird, the Swainson's Thrush (*Catharus ustulatus*), by assessing hypothalamic-pituitary-gonadal (HPG) axis sensitivity with gonadotropin-releasing hormone (GnRH) bioassays throughout the migratory period. During spring migration both males and females had a significant response to GnRH injections as reflected in elevated testosterone levels. The magnitude of response to GnRH injections,  $R_{\text{potential}}$ , in females stayed consistent throughout spring migration; however,  $R_{\text{potential}}$  in males increased as the migratory season progressed. It is clear that at least some degree of endocrinological breeding development occurs either before or during spring migration in both sexes, however the phenology appears to be sex specific. In males this breeding development continues at a relatively steady pace throughout the migratory period while in females, relatively little endocrine breeding development occurs during migration. These sex-specific differences in the phenology of the endocrine breeding development warrant future investigations for both male and female songbirds. Moreover, research focused on how physiological breeding development is balanced with the expression of migratory traits in long-distance songbird migrants is needed.

### 1. Introduction

Testosterone (T) is a steroid hormone that mediates a wide-range of behavioral and physiological effects in songbirds and other vertebrates (Wingfield and Silverin, 2009; reviewed in Adkins-Regan, 2005). While T is linked to many actions throughout the annual cycle, it has been heavily studied in the context of the breeding season (e.g. Ramenofsky and Wingfield, 2006; but see DeVries et al., 2011; Ramenofsky et al., 1992, 1999; Schwabl et al., 1988; Soma, 2006). Many of the effects mediated by T, or its metabolites, are central to the expression of male breeding behaviors, including singing and aggressive territory defense (Adkins-Regan, 2005; Goymann and Wingfield, 2014; Wingfield et al., 2001). Testosterone, either as a prohormone for estradiol or in its own right, is also important for female reproduction and reproductive behaviors (Ketterson et al., 2005; Norris, 1997; Rosvall, 2013; Staub and De Beer, 1997). Typically peak levels of circulating T occur during the early breeding season in male songbirds, and several studies have

focused on circulating levels of T throughout the annual cycle to investigate breeding preparation and hypothalamic-pituitary-gonadal (HPG) axis activity (e.g. Jawor et al., 2006; Wingfield, 1984; see Ketterson et al., 2005). While only a few studies have investigated T variation in female songbirds, detectable levels are generally found at some point during the annual cycle and show within season variability in at least some species (e.g. Jawor et al., 2007; see Ketterson et al., 2005).

The coordination of physiological and behavioral traits associated with each stage of the annual cycle allows adequate time and energy for development and expression of those traits (Jacobs and Wingfield, 2000; Ramenofsky, 2011). In addition to the stages expressed by all birds (e.g., breeding, molt, non-breeding), migratory birds face the additional challenge of expressing spring and fall migration stages and, in some species, an additional molt. This increase in the number of stages in the annual cycle results in less flexibility in the timing of each stage and more overlap between successive stages (Ramenofsky, 2011).

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According to (Jacobs and Wingfield, 2000; Ramenofsky, 2011), each stage of the annual cycle can be represented by three distinct phases; development, mature expression, and termination. Due to energetic limitations, the mature expression of any two stages cannot overlap, although the development of one stage may overlap with the mature expression of or termination of preceding stages (Jacobs and Wingfield, 2000; Ramenofsky, 2011). In long-distance migrants, especially those breeding at northern latitudes, the opportunity to breed is limited to a relatively narrow time frame; thus proper timing of the mature expression of breeding upon arrival is crucial (Jacobs and Wingfield, 2000; Ramenofsky and Wingfield, 2006). Estimates suggest that physiological development of the breeding stage, including full activation of the HPG axis and complete gonadal recrudescence, takes approximately one month for songbirds before mature expression of breeding activity (e.g. Ramenofsky, 2011). Given the time constraints restricting long-distance migrants upon arrival on the breeding grounds, HPG-axis activity, leading to the production of gonadal steroids and gametes, should increase before or during spring migration. Males should be prepared to transition quickly to expression of breeding behavior once on the breeding grounds, including establishment of territory and mate attraction, if environmental conditions are conducive. Similarly, if environmental conditions are appropriate for breeding, females should arrive on the breeding grounds receptive to courting males since early initiation of breeding increases reproductive success (Smith and Moore, 2005; Wingfield and Ramenofsky, 2011). Thus, arriving individuals must have sufficiently developed HPG axis activity to promote the expression of these behaviors and to facilitate a quick transition to the breeding life-history stage. This development of the HPG axis and resulting gonadal steroid levels are an essential component of seasonal breeding preparation that may have other downstream effects on reproduction including recrudescence of gonads and expression of reproductive behaviors. While some male songbirds have detectable increases in T during their vernal migration towards the breeding grounds (Covino et al., 2015, 2016; Wingfield and Farner, 1978a, 1978b) this pattern is not universal (Bauchinger et al., 2007; Covino et al., 2015). Studies of breeding hormone fluctuations in migrating female songbirds are relatively rare but indicate that hormone levels, including T and estradiol, may not increase until after females reach the breeding grounds (Covino et al., 2015, 2016; Wingfield and Farner, 1978a, 1978b). Since circulating T levels do not reliably predict breeding readiness or timing in all species (Caro et al., 2006; Davies et al., 2015; Partecke et al., 2005; Schaper et al., 2012) studies incorporating more direct measures of HPG axis activity are necessary.

Although several studies have noted links between endocrine breeding development (e.g. increasing T levels) and expression of migratory characteristics (Owen et al., 2014; Ramenofsky and Németh, 2014; Tonra et al., 2011), some of the behavioral and physiological effects linked to high T levels may be antagonistic to the expression of the migratory syndrome (Ketterson et al., 2015) and a successful migratory journey. For example, T-mediated territoriality while *en route* may be costly when a migrant is time constrained, which is especially likely during spring passage. High concentrations of T may negatively impact lipogenesis and fuel deposition rates potentially interrupting migratory behavior (Deviche, 1995; Ketterson et al., 1991). In contrast, several studies have indicated that the expression of various migratory traits is linked to increasing T levels (Deviche, 1995; Rowan, 1925, 1929; Weise, 1967). For example, the expression of migratory characteristics including fattening, mass gains, and migratory restlessness, may be dampened or delayed when T is absent (King and Farner, 1962; Lofts and Marshall, 1961; Morton and Mewaldt, 1962; Schwabl et al., 1988; Schwabl and Farner, 1989; Stetson and Erickson, 1972). Further, the administration of exogenous T induces the expression of migratory behaviors in captive birds (Owen et al., 2014; Tonra et al., 2011, 2013).

Increases in HPG-axis sensitivity that outpace increases in circulating T levels may reflect an overlap between migration and breeding life history stages that avoids the antagonistic effects of prolonged T

elevation during migration (see Covino et al., 2016). While levels of circulating T or other breeding hormones (luteinizing hormone, estradiol, dihydrotestosterone) may reflect reproductive condition, individuals may express short-term fluctuations in hormone levels for many reasons (Deviche et al., 2006; Wingfield et al., 1990). These short-term fluctuations may mask seasonal changes, especially in studies of free-living birds where confounding variables may be difficult to control. Gonadotropin-releasing hormone (GnRH) bioassays in which exogenous GnRH is administered, sometimes called GnRH challenges, test the sensitivity of the HPG axis vis-à-vis determining the physiological capacity of an individual to elevate T (Jawor et al., 2006; Schoech et al., 1996; Wingfield et al., 1979, 1991). Through the administration of a large dose of GnRH, researchers, in essence, flood the GnRH receptors of the anterior pituitary (Bentley et al., 2006; Goymann and Wingfield, 2004; Wingfield et al., 1991). This effectively tests the sensitivity of the anterior pituitary to GnRH and, subsequently, that of the gonads to LH. The resulting elevation in T, termed the  $R_{\text{potential}}$  of an individual (Goymann et al., 2007), reveals the overall sensitivity of the HPG axis and, since this approach requires only a single capture, it is easy to use with free-living individuals (e.g. Covino et al., 2016; DeVries et al., 2011, 2012). Variation in  $R_{\text{potential}}$  may be due to changing sensitivity to GnRH, LH, or a combination of the two. That said, this technique provides reasonable quantification of endocrinological breeding development and previous studies have found  $R_{\text{potential}}$  to relate to ornament size (McGlothlin et al., 2008), breeding success (Cain and Pryke, 2017; McGlothlin et al., 2010), and body condition (Davies et al., 2015).

In this study we sought to investigate one component of endocrinological breeding development represented by HPG axis sensitivity, in male and female birds during their spring migration. To do so we determined the  $R_{\text{potential}}$  in Swainson's Thrushes (*Catharus ustulatus*) at different points along their migratory route as they traveled towards their breeding grounds. Although an earlier study did not find changes in the seasonal levels of baseline T (non-GnRH stimulated T) in this species during migration (Covino et al., 2015), we predicted that their HPG axis sensitivity (tested via GnRH challenge;  $R_{\text{potential}}$ ) would increase during migration (Goymann et al., 2007). Specifically, we expected that  $R_{\text{potential}}$  would increase as birds migrate towards their breeding destination, where higher levels of T are required for the expression of breeding traits. Given that both sexes must be prepared for breeding activities and behaviors upon arrival on the breeding grounds, we also predicted that both males and females would have a higher  $R_{\text{potential}}$  when sampled closer to their breeding grounds.

## 2. Materials and methods

### 2.1. Study species and study sites

Our focal species was the Swainson's Thrush (hereafter thrush), a long-distance Nearctic-Neotropical migrant that breeds in the Rocky Mountains, throughout North American boreal forests, and along the Pacific coast and winters in southern Central America and eastern South America (Fig. 1). As in Covino et al. (2015), we captured migrating thrushes throughout vernal migration at one southern site (from 6 April through 12 May) and one northern site (from 10 May through 2 June) during 2012–2014. Our study encompassed the entirety of thrush migration at both study locations. Our southern site is relatively far from the Swainson's Thrush breeding grounds (at least 1400 km to closest edge of the breeding range) and is located along the northern coast of the Gulf of Mexico in Cameron Parish, Louisiana (29° 45' N 93° 30' W). Our northern site is relatively close to the breeding grounds for this species (< 200 km to closest edge of the breeding range) and is located on an island off the New England coast in York County, Maine (42°58' N, 70°36' W; Fig. 1). We also captured birds at a site along the Gulf of Mexico coast in Mobile County, Alabama (30° 15' N 88° 05' W), during fall migration from 20 September through 8 October 2014, to enable

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