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Territorial aggression in urban and rural Song Sparrows is correlated with corticosterone, but not testosterone

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ABSTRACT

Urban songbirds of several species more vigorously defend their territories in response to conspecific song playback than do their rural counterparts, but the hormonal basis of this behavioral difference is unclear. It is well established in vertebrates that both testosterone and corticosterone affect the intensity of territoriality. Previous studies have found no evidence that initial (i.e., immediately following territorial challenge, but prior to restraint) plasma testosterone accounts for the elevated territorial aggression of urban birds. Determining if testosterone still contributes to urban-rural differences in territoriality requires also assessing males' abilities to transiently increase plasma testosterone (in response to an injection of gonadotropin-releasing hormone). We tested whether these hormones are correlated with the territorial response to conspecific song playback in urban and rural male Song Sparrows (*Melospiza melodia*) in Montgomery County, Virginia. We found that the elevated territorial aggression of urban sparrows was not related to variation in either initial plasma testosterone or the ability to transiently increase testosterone. In contrast, despite no overall habitat difference in initial corticosterone, levels of this hormone were positively correlated with territoriality in urban and rural sparrows. Furthermore, for a given level of corticosterone, urban sparrows were more territorially aggressive. Our findings suggest that initial corticosterone may either play a role in the regulation of persistent differences in territorial behavior between free-ranging urban and rural male Song Sparrows or be affected by the intensity of behavioral response to territorial challenge.

1. Introduction

Territorial aggressive behavior between conspecifics is found throughout the animal kingdom and is used to defend finite resources, such as mates, territories, and food (Brown, 1964; Grant, 1993; Stamps, 1994). The intensity of resource defense is predicted to be related to the defendability of the resource, with increasing intensity as resources become more limited or spatially aggregated (Brown, 1964; Grant, 1993; Stamps, 1994). Rapid environmental change, such as urbanization, can modify many of the factors that determine resource defendability and, in turn, potentially affect the intensity of territorial behavior. Indeed, songbirds living in urbanized areas frequently express more intense territoriality in response to simulated territorial intrusions than do their conspecifics living in nearby rural areas (Abolins-Abols et al., 2016; Davies and Sewall, 2016; Evans et al., 2010; Fokidis et al., 2011; Foltz et al., 2015; Scales et al., 2011; but see Atwell et al., 2014 for an exception to this pattern). However, the hormonal mechanisms that mediate this urbanization-related disparity remain unclear (Davies and Sewall, 2016; Fokidis et al., 2011), and multiple hormones, in particular testosterone and corticosterone, potentially play a role (Haller, 2014; Partecke et al., 2005, 2006; Wingfield et al., 2006). Elucidating the hormonal basis of phenotypic adjustments to urbanization has the potential to simultaneously shed light on how animals respond to environmental change and provide insight into the function and evolution of hormonally-mediated traits.

The frequency and intensity of conspecific aggression in territorial vertebrates has traditionally been linked to circulating levels of androgens (testosterone in most vertebrate classes; Wingfield et al., 2006, 2001). Indeed, experimentally increasing circulating testosterone using implants can elevate the intensity of territoriality, and decreasing testosterone by removing the testes or pharmacologically blocking testosterone's actions can reduce territoriality (Canoine and Gwinner, 2002; Hau et al., 2000; Schwabl and Kriner, 1991; Soma et al., 1999; Wingfield and Hahn, 1994). However, there is inconsistency in the relationship between testosterone and territorial aggression (Apfelbeck et al., 2013; Goymann, 2009; Goymann et al., 2007, 2015; Wingfield et al., 2006, 1987). In birds, elevated testosterone levels correlate with territorial aggression in some (e.g., Hau et al., 2000; McGlothlin et al.,

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Table 1
The location and land use for each study site sampled. We used the semi-automated method described by Seress et al. (2014) to estimate land use (see methods for more details).

	Site name	Latitude (N)	Longitude (W)	Meters above sea level	Cells with high building density	Cells with high vegetation density	Cells with paved surfaces	Mean vegetation density	Mean building density	Urbanization index	Number of behavioral trials
Urban	Virginia Tech campus (North)	37°13′49″	80°25′24″	632	19	35	94	1.28	1.03	3.56	13
	Radford College campus	37°08′14″	80°33′04″	561	15	29	92	1.29	1.01	3.35	8
	Virginia Tech campus (South)	37°13′21″	80°25′11″	642	14	50	87	1.50	1.03	2.53	16
Rural	Heritage Park	37°14′21″	80°27′44″	602	0	100	25	2.00	0.18	−1.73	11
	Virginia Tech Kentland Farm	37°11′46″	80°34′57″	534	0	97	3	1.95	0.03	−2.03	1
	Stroubles Creek restoration area	37°12′19″	80°26′49″	608	0	100	2	2.00	0.00	−2.20	18

2007; Ros et al., 2002; Smith et al., 2005; Wingfield, 1984), but not all species (e.g., Apfelbeck and Goymann, 2011; Deviche et al., 2012; Hunt et al., 1997; Moore et al., 2004; Silverin et al., 2004). Three studies have examined whether initial (i.e., prior to handling and restraint) plasma testosterone accounts for the elevated territorial aggression of urban birds. Plasma testosterone did not account for the more intense territoriality of urban male Curve-billed Thrashers (*Toxostoma curvirostre*), and Abert's Towhees (*Melozone aberti*), in Phoenix, Arizona (Fokidis et al., 2011), while testosterone was actually lower in urban Dark-eyed Juncos (*Junco hyemalis*), in San Diego, California, which are *less* aggressive than their montane counterparts (Atwell et al., 2014). We have also found that initial levels of this hormone do not account for elevated aggression in urban male Song Sparrows (*Melospiza melodia*), in Blacksburg and Radford, Virginia (Davies and Sewall, 2016). The available evidence, therefore, suggests that initial plasma testosterone is not related to the elevated territorial aggression of urban birds.

On top of seasonal changes in initial testosterone, levels of this hormone can also transiently increase during agonistic interactions in some species. These transient testosterone increases are thought to enhance inter-male aggression (i.e., the challenge hypothesis; Goymann, 2009; Goymann et al., 2007; Wingfield et al., 1990). One approach to study the ability to transiently increase testosterone is to use a gonadotropin-releasing hormone (GnRH) challenge, which consists of quantifying testosterone release in response to a standardized injection of GnRH (Cain and Pryke, 2017; Davies et al., 2016, 2015; DeVries et al., 2012; Goymann et al., 2015; Jawor et al., 2006; Wingfield et al., 1979). Just one study, to our knowledge, has investigated whether variation in conspecific territoriality between urban and rural birds is related to the ability to transiently increase testosterone. GnRH-induced testosterone was positively related to aggression in Dark-eyed Juncos, but there was no difference between urban San Diego and montane (rural) juncos (Atwell et al., 2014). It is worth noting that the San Diego junco system contradicts most other studies of urban territorial aggression in that the urban birds are less aggressive than their rural counterparts. Thus, in cases where urban birds are more territorial than their rural counterparts, it is unknown whether the ability to rapidly increase testosterone secretion accounts for this behavioral disparity. The first aim of our study, therefore, was to test whether the ability to produce testosterone in response to GnRH injection is related to variation in conspecific territorial aggression between urban and rural male Song Sparrows. We predicted that the intensity of territorial aggression will be positively related to the ability to transiently increase testosterone and, therefore, that urban males would have higher GnRH-induced testosterone.

In addition to testosterone, it is well established in a range of vertebrates that aggressive conflicts are associated with plasma glucocorticoids (for reviews see Haller, 2014; Summers et al., 2005). Glucocorticoids modulate aggressiveness by altering the activity of brain regions that control aggression (Hayden-Hixson and Ferris, 1991a, 1991b). Indeed, acutely increasing glucocorticoid levels elevates aggressiveness, while acutely inhibiting glucocorticoid synthesis or receptor binding suppresses aggressiveness in vertebrates (Chang et al., 2012; Hayden-Hixson and Ferris, 1991b; Kruk et al., 2004; Mikics et al., 2004; Munro and Pitcher, 1985; Schjolden et al., 2009). Just one study in an urbanization context has investigated whether initial corticosterone (the primary glucocorticoid in birds) is related to the intensity with which territorial individuals respond to conspecific song playback. Fokidis et al. (2011) found no relationship between corticosterone and territorial response in male Curve-billed Thrashers or Abert's Towhees. In their study of urban and rural male Dark-eyed Juncos in Los Angeles, California, Abolins-Abols et al. (2016) found that initial corticosterone was not related to territorial aggression a day after the stress of capture. However, the study was not designed to determine whether territorial aggression prior to acute stress was related to initial corticosterone. Because of the role of glucocorticoids in mediating territorial aggression, the second aim of our study was to test whether variation in