



Testosterone elevation and response to gonadotropin-releasing hormone challenge by male Northern Cardinals (*Cardinalis cardinalis*) following aggressive behavior

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Abstract

There is much discrepancy about the relationship between testosterone (T) and male aggressive behavior. For example, in birds, males of many species significantly elevate T levels during inter-male conflict. However, this is not universal, and in species where males typically do not elevate T during aggressive interactions, concentrations of the hormone are often assumed to be circulating at maximum levels. We examined if male northern cardinals (*Cardinalis cardinalis*) significantly elevated T during simulated territorial intrusions (STIs). We also examined if individuals had the capacity to further elevate T levels in response to gonadotropin-releasing hormone (GnRH) injections immediately after an aggressive encounter. Our results indicate that male cardinals do not significantly elevate T levels in response to STIs, but have the physiological capacity to significantly elevate T in response to GnRH injections following aggressive interactions. This implies that T levels of individuals captured during STIs were not at maximum concentrations. However, additional findings in this study also suggest the possibility that prolonged social instability could elicit significant elevations in T in males of this species, warranting further investigation.

Highlights

- ▶ We examined if male cardinals significantly elevate testosterone levels in aggressive contexts.
- ▶ Males were injected with gonadotropin-releasing hormone (GnRH) following aggressive behavior.
- ▶ Testosterone levels of birds subject to STIs were not significantly higher than passive captures.
- ▶ Males captured in

aggressive contexts could elevate testosterone in response to GnRH injection.

Introduction

Testosterone's (T) influence on aggressive behavior in male vertebrates has been researched extensively (reviewed in Goymann et al., 2007). However, definitive relationships between T and male aggression are not fully established due to variation in T's impact on aggressive behavior among vertebrate species (Wingfield et al., 2006). For example, in birds, a correlation between elevated levels of T and male aggression exists for some species (e.g., Wingfield, 1984, Beletsky et al., 1990, Hau et al., 2000, McGlothlin et al., 2007), but not others (e.g., Hunt et al., 1999, Moore et al., 2004, Lynn and Wingfield, 2008, Apfelbeck and Goymann, 2011). Such discrepancy of T's impact on male aggression among avian species warrants further investigation of this hormone–behavior relationship (Lynn, 2008).

Many studies examining the relationship between T and territorial behavior provide support for the 'challenge hypothesis' (Wingfield et al., 1990), which suggests that inter-male competition is enhanced by transient elevations in T above levels required for breeding physiology. In the field, such investigations are frequently accomplished through the use of simulated territorial intrusions (STIs) that stage a relatively short-term aggressive interaction between a male territory owner and a simulated 'intruder' (i.e. a decoy or captive live individual) placed within the focal bird's

territory. Males of numerous avian species have demonstrated higher levels of T than their respective breeding concentrations following an STI, therefore supporting the challenge hypothesis (reviewed in Goymann et al., 2007). Conversely, many studies do not provide support for the challenge hypothesis as male birds of many species do not elevate T above seasonally average levels in response to STIs (reviewed in Goymann et al., 2007). In these latter species, male T concentration is sometimes presumed to be circulating at maximum levels, thus inhibiting transient elevations of the hormone. Quantifying if males are physiologically capable of elevating T above circulating levels observed in response to an STI has received little attention (but see Apfelbeck and Goymann, 2011). Therefore, it remains unclear whether males who do not elevate T above normal circulating levels when presented with a simulated intruder are incapable of producing higher androgen concentrations, or if they are physiologically capable of elevating T, but do not during aggressive contexts.

Northern Cardinals (*Cardinalis cardinalis*, hereafter: cardinals) are year-round temperate zone residents ranging from Central America to southern Canada (Halkin and Linville, 1999). Breeding pairs are socially monogamous and display longer periods of reproduction (6+ months, Halkin and Linville, 1999) and territoriality (almost year-round, little territorial behavior observed in Oct. and Nov.) than most temperate zone species (Jawor, 2007). Territories are often occupied by the same pair for consecutive breeding seasons (Halkin and Linville, 1999) and paternal care of offspring may be essential (Linville et al., 1998).

Prior work suggests that male cardinals captured in passive contexts (e.g. foraging) have low, but detectable, levels of T year-round with little fluctuation between breeding and non-breeding seasons (Jawor, 2007). However, it was unknown if infrequently observed elevated T (see Jawor, 2007) supported aggressive interactions among male cardinals and if T concentrations observed within this behavioral context were at maximum.

Exogenous administration of gonadotropin-releasing hormone (GnRH) can assess if an individual's circulating T levels are at maximum (e.g. Jawor et al., 2006, DeVries et al., 2011). Injections of GnRH stimulate the anterior pituitary to release luteinizing hormone (LH), which promotes T production by the testes. Pre-injection and post-injection levels of T are compared to assess if an individual has the physiological capacity to elevate T. GnRH injections have been used to assess reproductive axis activity in males of several songbird species (e.g. Moore et al., 2002, Jawor et al., 2006, Spinney et al., 2006, Busch et al., 2008, Apfelbeck and Goymann, 2011, DeVries et al., 2011). However, to our knowledge, only Apfelbeck and Goymann (2011) administered GnRH injections to males following an aggressive encounter (i.e. an STI). Findings from Apfelbeck and Goymann (2011) suggest that male black redstarts (*Phoenicurus ochururos*), a migratory, territorial European songbird, do not elevate T levels above average breeding concentrations in response to STIs, but have the physiological capacity to do so (Apfelbeck and Goymann, 2011). We performed a similar investigation with cardinals, a species in which males exhibit comparable behavior to male black redstarts (e.g. highly

territorial, social monogamy, etc.). The objectives of this study were to determine if circulating T levels of male cardinals varied with behavioral context (aggressive vs non-aggressive) and if individuals engaged in aggressive behavior were physiologically capable of elevating T above circulating levels following an STI.

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Field methods

This study was conducted during the month of March in 2009, 2010, and 2011 in Hattiesburg, Mississippi, USA at the Eubanks/Lake Thoreau (ELT-USM) property owned by the University of Southern Mississippi (USM). Male territorial aggression (e.g. song, conspecific conflict, etc.) in this population of cardinals can be observed as early as December with a subsequent peak in March prior to the onset of breeding in April. Therefore, to quantify if elevated T levels accompanied male responses to...

Initial testosterone levels

Results indicate that initial levels of T of male cardinals captured passively or during aggressive contexts did not significantly differ (Table 1, Fig. 1). CORT levels of passively captured individuals were significantly higher than individuals captured during STIs (independent samples *t*-test: $t_{47}=10.48$, $P=0.0001$), but there was no significant relationship between initial levels of CORT, handling time, or mass on initial T levels of both treatments (Table 1). However, there was a significant...

Discussion

Similar to recent studies reporting a lack of a relationship between elevated T and territorial aggression in males of some tropical avian species (reviewed in Goymann et al., 2007), our data show that levels of T were not significantly elevated in male cardinals responding aggressively to STIs. Our results also demonstrate that male cardinals were physiologically capable of elevating gonadal T in response to GnRH injections delivered immediately after an STI, suggesting that circulating T...

Conclusions

Our findings suggest that male cardinals do not significantly elevate T levels in response to STIs, but have the physiological capacity to do so. Thus far, males of at least two songbird species (i.e. black redstarts, northern cardinals) have demonstrated that a lack of significant T elevation during aggressive interactions was not due to the bird's inability to produce greater amounts of the

hormone. Considering that both species share several behavioral characteristics (e.g. social monogamy,...

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Citation Excerpt :

...Levels of T in circulation are typically elevated at the beginning of the breeding season, when competition for mating opportunities is high, and then T levels decline as behavioral efforts shift to parental care (Wingfield et al., 1990). This cross-stage shift in T production has been well demonstrated in males (Hirschenhauser and Oliveira, 2006), and is potentially more dramatic in females (DeVries et al., 2012; George and Rosvall, 2018; Jawor et al., 2007). Cross-stage shifts may also alter correlations between T and sexually selected traits, such that these traits are strongly integrated with T during competition for mates, but more independent from T during periods of parental care (Ketterson et al., 2009; Lipshutz et al., 2019a)....

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...Experimental stimulation of the HPG axis with exogenous GnRH injections has mitigated these concerns by flooding the HPG axis with GnRH and quantifying an individual's maximal T output after a standardized waiting period. Results are nonetheless mixed: T levels produced in response to GnRH injections are correlated with suites of T-mediated traits, including territorial aggression, parental care, and ornamentation in dark-eyed juncos (McGlothlin et al., 2008), but they are not correlated with parenting or aggression in Northern cardinals (*Cardinalis cardinalis*) (DeVries et al., 2012). T responses to GnRH challenge also track morph-related differences in T-mediated traits in male white-throated sparrows (*Zonotrichia albicollis*) (Spinney et al., 2006) and side-blotched lizards (*Uta stansburiana*) (Mills et al., 2008), but average T responses to GnRH do not differ among morphs in male red-backed fairy-wrens (*Malarus melanocephalus*) (Barron et al., 2015) or Gouldian finches (*Erythrura gouldiae*) (Cain and Pryke, 2017)....

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...Our results highlight the importance of using saline controls to determine whether animals can elevate T in response to exogenous GnRH. Many studies do not use saline controls in conjunction with GnRH injections (e.g., Husak et al., 2009; Jawor et al., 2007; Rosvall et al., 2014- but see Covino et al., 2017; Covino et al., 2018; DeVries et al., 2012; Spinney et al., 2006). In some cases, saline injections may be less relevant or necessary, for example, when GnRH challenges are administered to all

individuals as an assay of an endocrine phenotype, which is then related to some other individual trait (e.g., Cain and Pryke, 2016; Mcglothlin et al., 2008)....

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