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# 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.

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#### 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

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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 nonaggressive) and if individuals engaged in aggressive behavior were physiologically capable of elevating T above circulating levels following an STI.

#### Materials and methods

#### 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 aggressive encounters within the peak of inter-male competition, all birds in this study (n = 55) were captured within the month of March during the years assessed. To determine if circulating T is elevated during aggressive interactions, male cardinals were subjected to one of two treatments: passive capture (n = 26) or capture during an aggressive encounter (n = 29). All birds were captured and processed between 0600 and 1200 h and individuals were not repeatedly sampled across treatments or years. Upon capture, time of extraction was noted and birds were processed following procedures described for cardinals by DeVries et al. (2011). Processing included blood collection for hormone analyses, administration of GnRH injections (see below), banding, and recording morphometric measures as part of ongoing research. At the conclusion of processing, all birds were released from the point of capture. All procedures performed in this study were in accordance with the Animal Behaviour Society's 'Guidelines of the treatment of animals in behavioral research and teaching' and the EU Directive 2010/63/EU for animal experimentation. Further, this work was conducted under USFWS Banding Permit #23479, MS Department of Wildlife, Fisheries, and Parks Scientific Collecting Permit #0201101 and approved by USM IACUC protocol #08081401. Salvage of adult cardinals for taxidermic decoy preparation under USFWS Special Purposes Permit #MB135338-0.

#### Passive sampling

Twenty-six (26) individuals (2009, n = 16; 2010, n = 6; 2011, n=4) were captured passively while foraging at baited (e.g. sunflower seed, cracked corn) mist nets and Potter traps. Considering that cardinals are difficult to capture passively during this period of peak territoriality (i.e. March), simultaneous use of numerous nets/traps (8+ each) was required. Nets/traps were assessed every 20 min by multiple field assistants and captures were immediately transported to a central location for processing (mean handling time: 11 min, range: 1-26 min). In a prior study, handling time (defined as time of bird extraction until first blood collection) and levels of corticosterone (CORT) did not negatively impact T levels in cardinals (DeVries et al., 2011) and we report similar findings here (see Results). After blood sampling to assess circulating levels of T, twenty-four birds (24) were then administered GnRH injections (see below) to quantify the gonad's ability to elevate T levels (2009, n = 16; 2010, n = 6; 2011, n=2; 2 additional birds were subjected only to initial blood sampling due to impending inclement weather).

#### Simulated territorial intrusions

Simulated territorial intrusions (STIs) were used to capture twenty-nine (29) individuals (2009, n=2; 2010, n=7; 2011, n = 20) engaged in aggressive encounters. Each STI consisted of placing a male cardinal taxidermy mount (taxidermy model produced in a stereotypical aggressive posture assumed by cardinals) and a batterypowered speaker (Altec Lansing iM207 Orbit) between two parallel mist nets in the center of a focal male's territory. At the onset of each trial, camouflaged observers retreated 10-15 m away from the nets and began a randomly selected recording of male cardinal song/vocalizations from a non-population source (Cornell Lab of Ornithology, Macaulay Sound Laboratory) with a MP3 player (SanDisk Sansa Clip). Trial length was 30 min or until capture of the focal male. If territory owners did not respond to the STI within 30 min of the onset of the vocalization broadcast, the trial was aborted. Latency to respond (LTR) was recorded (within 300 s: n = 14, within 301-599 s: n = 5, post 600 s: n = 10; mean: 417 s; range: 19–1560 s) and defined as the first appearance of the focal male at the site of the 'intrusion'. Capturing male cardinals during STIs proved challenging, resulting in a relatively low capture percentage for the capture effort (30 captures/80 attempts = 37.5% capture success). Considering that some studies suggest an increase in T levels during STIs requires at least 10 min of stimulation by an 'intruder' (Wingfield and Wada, 1989), our pilot work attempted to initially attract individuals to the decoy with subsequent capture 10 min after the initial exposure. Yet, we had little success consecutively attracting male cardinals to the 'intrusion', especially if the individual attacked the decoy on the initial approach. STI techniques were therefore modified and all individuals in this study were captured on their initial approach to the 'intruder'. Interestingly, levels of T did not demonstrate a significant relationship with STI duration or LTR (see Results below).

Upon capture, STI duration was noted (within 300 s: n = 14, within 301–599 s: n = 5, post 600 s: n = 10; mean: 540 s; range: 30–3180 s) and birds were extracted and bled within 3 min to assess circulating T levels. In 2011, a subset of males captured during STIs (n = 18) was also administered GnRH injections (see below) within 5 min of net extraction to quantify if the gonad could further increase T production after the aggressive encounter.

#### **GnRH** injections

GnRH injections were administered to all individuals (passive and STI captures) following procedures described for cardinals by DeVries et al. (2011). After capture, a blood sample was collected ( $\sim$ 75  $\mu$ l plasma) from venipuncture of the alar wing vein to quantify initial

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