





Corticosterone profiles in northern cardinals (*Cardinalis cardinalis*): Do levels vary through life history stages?

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Highlights

- We assessed CORT in cardinals across sexes and multiple life history stages.

- Levels of CORT varied across the year with higher levels in non-breeding.
- Sexes differed in CORT levels in a complex fashion across life history stage.

Abstract

As animals move through life history stages, energy requirements for each stage will vary. Both daily and annual variation in the glucocorticoid hormones (specifically corticosterone, or CORT, in birds) helps provide the variable energy needed through life history stages. In many bird species, CORT is higher in the breeding season when energy demands can be quite high and is often lower in the non-breeding season. Additionally, CORT has a role to play in the response to stressful stimuli and the level to which CORT is elevated following stressful events can vary through the annual cycle as well. Here we report on baseline and stress-induced CORT levels in both sexes of northern cardinals, *Cardinalis cardinalis*, a non-migrating, year-round territorial species across life history stages. Corticosterone is overall higher in the non-breeding season than the breeding season in both sexes. Males tend to have higher levels of stress-induced CORT than females, although the observed patterns are complex. Our findings differ from one of the more common profile reported in songbirds where breeding season CORT tends to be higher than non-breeding levels. A strong influence may be the prolonged breeding season seen in cardinals; lower levels of CORT during breeding may guard against adverse

maternal effects, interruptions in breeding behaviors, or egg production. Additional investigation of species with similar ecologies to northern cardinals, and more populations of cardinals, may show that annual glucocorticoid profiles are more labile than previously appreciated.

Introduction

Non-captive animals annually experience a wide variety of environmental conditions, changes in food availability, and variation in predator activity that all factor into the development of distinct life history stages (LHS) with a regular annual profile of activities that impact energetic demands and that can vary in the number of stages expressed in a species-specific pattern (Wingfield, 2008). Individuals move through breeding and non-breeding stages which can incur very different energetic demands, and, costs during breeding can vary with the sex of the individual. In birds, a significant number of species undergo energetically expensive migrations after and prior to breeding. All bird species experience, at the very least, an annual molt of body feathers. Ultimately, all of these activities impact the physiology and energetic demands of individuals. Hormones are an influential mechanism for the movement of individuals through LHSs and the glucocorticoids (specifically corticosterone, or CORT, in birds) also assist in providing the variable energy needed as individuals move through their annual cycle (Romero and Wingfield, 2016).

Changes in GC levels can lead to changes in blood glucose, body temperature, foraging and feeding activities, and alter how the body stores fat (Angelier et al., 2008, Astheimer et al., 1992, Dawson et al., 1972, Gray et al., 1990, Harvey et al., 1986, Landys et al., 2006, Lõhmus et al., 2006, Palokangas and Hissa, 1971, Rogers et al., 1993, Saldanha et al., 2000, Siegel, 1980, Wingfield et al., 1998); all of which can be important as individuals move through LHSs. In birds, studies of CORT levels through LHSs often have mixed results across species which can be a testament to the underlying physiological complexities associated with energetic demands and evolutionary histories. For example, in some species colder winter temperatures may force an increase in energy expenditure to compensate for body heat lost to the external environment leading to generally higher CORT in the winter followed by lower levels of CORT during breeding, potentially to avoid the deleterious effects elevated CORT may have on breeding behaviors (Angelier and Chastel, 2009, Hayward and Wingfield, 2003). Conversely, in some species, higher CORT during breeding might facilitate foraging behavior for finding offspring food and facilitate higher levels of glucose in circulation during a time period of high physical activity, lower levels of CORT may then be seen outside of breeding (Romero, 2002). What sort of profile is observed may vary strongly with the ecology of the organism under assessment. Considering both ecology and general GC profiles is needed to better understand flexibility in this hormone type and how it functions in physiology and behavior (Romero and Wingfield, 2016, Sapolsky et al., 2000).

A complicating factor for the GCs is that they also have a role to play in stress responses where they will elevate sharply following a stressful event. Defining stress, stress responses, and what stress encompasses has been a topic of much debate (Korte et al., 2005, McEwen and Wingfield, 2003, Romero and Wingfield, 2016, Romero et al., 2009, Sapolsky et al., 2000). This is largely due to individual, population, and species variation in what is seen as a stressor and in how robust individual stress responses are.

Following a simplistic definition stressors are situations that either disrupt, or even just threaten to disrupt, homeostasis (Chrousos and Gold, 1992) with stressors described as being either predictable or unpredictable. Predictable stressors (e.g. annual changes in food availability, daily temperature changes) are transient and can be anticipated; i.e., as the seasons move from summer to fall to winter, cooler temperatures are going to occur and food availability will change. Predictable stressors generally take the form of daily physical, energetic, and social demands associated with LHSs (Landys et al., 2006). Unpredictable stressors also force an organism to make changes in order to survive.

However, it is important to note that unpredictable stressors often do not present the individual with immediate life-threatening demands like some predictable stressors can. Instead, they present conditions that are deteriorating, and this directly forces an organism to make adjustments to better its chances of survival; e.g., stay and brood eggs with an ensuing storm or abandon your brood and prioritize your own survival. One major similarity between both types of stressors is that once a disturbance passes, a recovery phase is entered and the individual can potentially

return to its appropriate LHS (Wingfield et al., 1998). In some cases, with prolonged, unpredictable stressors, the organism isn't given a chance to enter into the recovery phase, and this is where a line can be drawn between acute and chronic stress, with all the damages that can accrue over time as a result of chronic stress pathology (Wingfield et al., 1994) including muscle mass loss (De La Cruz et al., 1981, Tomas et al., 1979), suppression of the immune system (Sapolsky et al., 2000), and increased susceptibility to disease (Hanssen et al., 2004), potentially resulting in the death of an organism (see Romero and Wingfield, 2016 for additional description). As with baseline levels of CORT, stress induced levels have been shown to vary seasonally (Romero, 2002). Variation in how GCs change at both baseline and stress-induced levels through LHSs needs assessment in the face of a species ecology to better understand how this hormone class functions.

This work examines the annual CORT profile (baseline and stress-induced levels) in both sexes of a population of northern cardinals (*Cardinalis cardinalis*) in the southeastern United States across multiple LHSs, non-breeding, pre-breeding, and breeding. Cardinals are a resident species with a relatively long breeding season (6+ months, Halkin and Linville, 1999). Socially monogamous pairs (often paired for life) remain on their territories year-round and display territorial behavior year-round (Gentry, 2015). Individuals are known to temporarily join feeding flocks in the winter (Halkin and Linville, 1999) but return to their territories regularly (Gentry, 2015). Pairs are biparental with respects to offspring feeding (Halkin and Linville, 1999, Jawor and

Breitwisch, 2004, Jawor et al., 2004, Linville et al., 1998). However, during incubation, females alone incubate, and they alone brood offspring early in nestling life, while males provide brooding females with food (Halkin and Linville, 1999; Jawor and Breitwisch 2006). Cardinals lay 1–5 eggs (typically 2–3 in this study population) per clutch and typically produce 3–5 clutches in a season, but pairs have been documented having up to 10 clutches during a single breeding season (Jawor, 2002). Due to their preference for edge habitat, these open-cup nesters often suffer high nest depredation rates with up to 75% of nests depredated within a single breeding season and re-nest quickly (M.S. DeVries, unpubl. data). Previous work investigating baseline and stress-induced CORT in cardinals has focused on males and has shown that male stress responses can vary throughout the year, are influenced by exogenous application of adrenocorticotrophic hormone (ACTH), and can be altered by levels of urbanization, food availability, and social interactions (Barron et al., 2012, Fokidis, 2016, Wright and Fokidis, 2016). Here we assess whether males and females show variation in baseline levels of CORT and CORT elevation following handling stress across three general time periods.

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Section snippets

Field methods and blood collection

Cardinals were captured using mist nets for collection of baseline (blood collected <3 min upon capture to more accurately reflect unstressed condition, Romero and Reed, 2005) and stress-induced CORT levels (after 30 min of restraint) from August 2012-July 2013 (total $n = 127$; males $n = 69$; females $n = 58$) at the Lake Thoreau Environmental Research and Education Center (Hattiesburg, Mississippi, United States, 31.34° , -89.42°). Upon capture birds were removed from mist nets and a blood sample...

Life history stage variation in baseline and Stress-Induced Corticosterone in males and females

In males, baseline CORT varied across LHSs ($F_{2,41} = 8.46$, $P = 0.0008$; Fig. 1). Post hoc comparisons using the Tukey HSD test indicated that baseline CORT for males in the non-breeding season ($21.12 \text{ ng/ml} \pm 12.6$) was significantly higher than that of baseline CORT in the pre-breeding ($10.42 \text{ ng/ml} \pm 7.2$) season. Stress-induced CORT also varied across LHSs ($F_{2,41} = 4.83$, $P = 0.0131$). Post hoc comparisons using the Tukey HSD test indicated that stress-induced CORT in the non-breeding...

Discussion

Here we show in this population of northern cardinals that both sexes display variation in baseline and stress-induced CORT levels across LHSs. Cardinals displayed an increase in CORT with restraint, regardless of stage, as has been shown in males in other populations of this species (Barron et al., 2012, Fokidis, 2016). We observed the highest levels of baseline and stress-induced CORT in both sexes during the non-breeding season, similar to what Fokidis (2016) found for just male cardinals in ...

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Research data for this article

 *Data not available / Data will be made available on request*

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