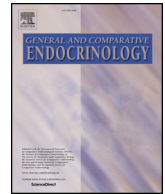




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## Survival and reproductive costs of repeated acute glucocorticoid elevations in a captive, wild animal

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## ABSTRACT

Organisms are continuously encountering both predictable and unpredictable ecological stressors within their environment. The activation of the hypothalamic-pituitary-adrenal (stress) axis is a fundamental process allowing animals to cope with and respond to such encounters. A main consequence of HPA axis activation is the release of glucocorticoid hormones. Although short-term glucocorticoid elevations lead to changes in physiological and behavioral processes that are often adaptive, our understanding of fitness consequences of repeated acute elevations in glucocorticoid hormones over a longer time period is largely lacking. This is of particular current importance as animals are facing a significant increase in exposure to stressors including those associated with human-induced rapid environmental change. Here, we test fitness-relevant consequences of repeated exposure to glucocorticoids in the absence of natural challenges, by treating wild-caught gravid female eastern fence lizards (*Sceloporus undulatus*) with a daily transdermal dose of a glucocorticoid hormone until laying. This treatment causes an increase in plasma glucocorticoids that mimics the natural response lizards have when they encounter a stressor in the wild, without confounding effects associated with the encounter itself. This treatment reduced females' reproductive success (hatching success) and survival. Further, glucocorticoid-induced reductions in reproductive success were greater when females had experienced higher temperatures the previous winter. This demonstrates the potential significant consequences of repeated exposure to acute elevations in glucocorticoid hormones. Additionally, the costs of repeated glucocorticoid elevation may be further exaggerated by an individual's previous experience, such as the potential compounding effects of winter warming increasing animals' vulnerability to increased glucocorticoid levels during spring breeding.

### 1. Introduction

Understanding how organisms respond to stressors in their environment is of increasing importance in a rapidly-changing world (Bijlsma and Loeschcke, 2005; Sih et al., 2011). An organism's response to environmental perturbations or challenges is mediated by the physiological "stress" response, a suite of neuroendocrine processes characterized by activation of the hypothalamic-pituitary-adrenal axis (HPA) and subsequent release of glucocorticoid hormones (Sapolsky, 2002). Glucocorticoid hormones function to simultaneously maintain physiological homeostasis and facilitate appropriate reactions to and recovery from environmental stressors (Wingfield et al., 1998; Sapolsky 2002; McEwen and Wingfield, 2003).

Although some definitions of stress and stressors necessitate a

reduction in performance or fitness (Schulte, 2014), the physiological response to an ecological stressor – including glucocorticoid elevation – has generally been assumed to be an adaptive mechanism by which immediate survival is prioritized (Boonstra, 2013; Breuner et al., 2008; Sapolsky et al., 2000; Wingfield et al., 1998). Though some studies have reported negative fitness outcomes of chronic stressor exposure (Boonstra et al., 1998; Boonstra and Singleton, 1993; Bradley et al., 1980; Cyr and Michael Romero, 2007), there is limited evidence for fitness effects of repeated short-term elevations in glucocorticoids (Breuner et al., 2008, but see Cote et al., 2006), or direct relationships between ecologically meaningful concentrations of glucocorticoids and variation in fitness more generally (Bonier et al., 2017; Crespi et al., 2013; Hau et al., 2016).

Short-term elevations of glucocorticoid hormones have the potential

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to have lasting impacts on individuals. Frequent short-term increases in glucocorticoid hormones are likely to be energetically expensive, particularly given these hormones are directly associated with energy balance (Haase et al., 2016; Sapolsky et al., 2000). Glucocorticoids at high levels have been linked with reduced body weight and condition (De Vos et al., 1995; Klein, 2015); changes in food intake (Cote et al., 2006; Osborne, 2015); elevated rates of metabolism (DuRant et al., 2008; Haase et al., 2016); and suppressed immune function (McCormick et al., 2014). Further, studies have correlatively linked baseline glucocorticoid levels (Romero and Wikelski, 2010; Cabezas et al., 2007) and glucocorticoid reactivity (Blas et al., 2007) to variation in survival, while others have linked stressor-induced (predation risk) changes in glucocorticoids to changes in survival and reproduction (MacLeod et al., 2018; Zanette et al., 2011). Studies that have investigated direct links between glucocorticoids and fitness (in terms of survival and reproductive success) have largely used implants, which constantly release hormones and may not appropriately mimic the natural, short-term responses to ecological stressors (Hau et al., 2016; Crossin et al., 2016). However, a study in the common lizard *Lacerta vivipara* showed that daily elevations of corticosterone, a primary glucocorticoid in vertebrates, significantly influenced food consumption and activity levels, and enhanced male survival (Cote et al., 2006). In the same species, daily maternal glucocorticoid elevations resulted in male offspring with higher survival (Meylan and Clobert, 2005). Together, these results indicate a likely mediating effect of short-term elevations of glucocorticoids on fitness that should be further explored.

Here, we test the hypothesis that ecologically relevant changes in glucocorticoid levels directly affect fitness. Specifically, we examined the effects of frequent (daily), short-term increases (to ecologically relevant levels) in glucocorticoids in gravid, eastern fence lizards, *Sceloporus undulatus*. These lizards are subject to a variety of stressors in their environment, the physiological effects of which have been well-studied, allowing us to mimic natural glucocorticoid responses to stressors under controlled laboratory conditions (e.g., Trompeter and Langkilde, 2011; McCormick et al., 2017). Previous work has linked glucocorticoids to increased survival in males (Cote et al., 2006); however, given the increased energetic demands imposed by reproduction (Crespi et al., 2013), and negative effects of environmental stressors on reproductive female survival in other species (MacLeod et al., 2018), we predicted that elevated glucocorticoids during gestation should result in decreased adult female survival and reduced reproductive output in terms of offspring hatching success.

## 2. Materials and methods

### 2.1. Study species, capture, and housing

The eastern fence lizard is a small, diurnal lizard found across the south-eastern portion of the United States (Powell et al., 2016). The glucocorticoid response of this species to a number of environmental stressors has been well-studied, including social stressors (Klukowski and Nelson, 1998; Smith and John-Alder, 1999), and to encounters with a key predator, the invasive red imported fire ant (*Solenopsis invicta*), with which the eastern fence lizard coincides across the southern part of their range (Graham et al., 2012; Langkilde, 2009a). Other physiological responses to ecological stressors have also been shown in this species (Angilletta et al., 2013; Levy et al., 2015). We captured female *S. undulatus* from three populations in southern Alabama (Geneva State Forest, Blakeley State Park, and Conecuh National Forest) in April and May of 2015 and 2016. Upon capture, we measured mass (to nearest 0.01 g) and snout-vent length (SVL, mm), and blood samples were collected from the postorbital sinus. Mean interaction time (from first seeing the lizard to completing blood sampling) was  $241.5 \pm 141.5$  s (mean  $\pm$  1 s.e.; approximately 4 min). Gravidity was determined by abdominal palpation upon capture (Graham et al., 2012) and non-gravid females were released.

Gravid females were housed in opposite-treatment pairs (CORT and vehicle-control) in plastic tubs ( $46 \times 40 \times 30$  cm L  $\times$  W  $\times$  H) in a temperature-controlled room ( $21 \pm 1$  °C) from capture until laying (a mean duration of  $35.5 \pm 16.7$  days). Tubs contained plastic perches and shelters, water bowls, and moist sand in which females could lay eggs. Heat was provided by a 60-W incandescent light bulb suspended over one end of each tub for 8 h a day to maintain a daytime temperature of approximately 32 °C, with the cooler end of the tub maintaining a temperature of approximately 21 °C, allowing lizards to behaviourally thermoregulate. Overhead lights were maintained on a 12:12 light:dark schedule (0700–1900 h). Food (live crickets, *Acheta domestica*, dusted twice weekly with calcium, vitamins, and minerals) was provided every other day, and water was available *ad libitum*.

### 2.2. Experimental glucocorticoid treatment

Gravid females were randomly assigned to either the control or experimental treatment group. Groups were made identifiable by placing a small dot of color-coded nail polish (free of formaldehyde, toluene and dibutyl phthalate; Pure Ice, New York, NY) on the lizards' backs. From capture until laying, females in the experimental group received a daily transdermal application of a corticosterone solution (hereafter CORT, the primary glucocorticoid in reptiles; Meylan and Clobert, 2005), corrected for their body weight ( $0.2 \mu\text{L/g}$  lizard of 4 mg CORT [ $\geq 92\%$ , Sigma C2505, Saint Louis, MO] in 1 mL of sesame seed oil vehicle, resulting in doses of  $0.8 \mu\text{g}$  CORT/g body mass). Females in the control group received a dose of the sesame seed oil vehicle only. CORT or control solutions were applied with a pipette to the middle of their back between 1930 and 2030 h. This timeframe was chosen as this was during the lizards' resting period, minimizing disturbance by researchers. There is no evidence of strong diel patterns in CORT secretion in this species (Trompeter and Langkilde, 2011). Handling the lizards was not required for this treatment. A time-series experiment showed that this dosage results in a short-term increase in CORT, doubling baseline levels by 30 min post-dosing (mean baseline CORT  $9.97 \text{ ng/ml} \pm 1.81$ , mean 30 min post-dosing CORT  $21.77 \text{ ng/ml} \pm 4.37$ ), with CORT returning to baseline levels by 90 min post-dosing (mean 90 min post-dosing CORT  $11.80 \text{ ng/ml} \pm 1.29$ ; see Appendix S1). Note that there is likely to be variation between individuals in the time and level of the CORT peak post-dosing.

This procedure and dosage has been shown in prior experiments to successfully mimic the increase in plasma CORT after non-lethal exposure to fire ants (McCormick et al., 2017; Owen et al., 2018), as well as periods of heat stress (R. Telemeco, pers. comm.). Similar levels of CORT are also achieved by employing a chasing (Trompeter and Langkilde, 2011) and restraint stressor (Graham et al., 2012), suggesting that this level of CORT-increase approximates the glucocorticoid response to short term, ecologically-relevant stressors in this species rather than reflecting pharmacological levels. Thus, as well as being relatively non-invasive (allowing us to avoid any potential confounds with handling stress, stress of dosing by injection, etc.) this treatment allows us to mimic the short-term increase in CORT experienced by free-living lizards who encounter natural stressors daily, rather than the sustained release of hormone implants (e.g. Breuner et al., 2008; Crossin et al., 2016) or pharmacologically high levels (Boonstra, 2013).

Tubs were checked multiple times daily for signs of egg-laying (freshly dug sand, the presence of nesting holes, mass loss/shape change in females). Upon laying, eggs were immediately transferred to plastic containers filled with moist vermiculite ( $-200$  kpa) and sealed with plastic wrap. Containers were kept in temperature-controlled incubators ( $30 \pm 1$  °C), and rotated regularly to avoid position effects, until hatching (after approximately 45 days). This protocol has been successfully employed as part of a number of studies (e.g. Langkilde and Freidenfelds, 2010; Swierk and Langkilde, 2013; Trompeter and Langkilde, 2011), with hatching success (proportion clutch hatched)

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