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EFFECTS OF MATERNAL STRESS ON PERFORMANCE BEHAVIOR OF LIZARD
OFFSPRING

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ABSTRACT

Optimal functioning of the hypothalamic-pituitary-adrenal (HPA) axis, and resulting production of glucocorticoids (GCs), can significantly impact how individuals cope with environmental challenges. Elevation in maternal GCs, including corticosterone (CORT), impact offspring phenotype, performance, and fitness. While many of these programmed developmental changes in offspring phenotype have been perceived as negative, it is hypothesized that these maternal GCs may be plastically enacting an adaptive response in offspring phenotype that can increase fitness. However, little is known of how this maternally-derived stress (MDS) adaptively effects offspring phenotype and prepares offspring to better survive in their post-natal environments. In order to investigate the adaptive potential of maternal stress, we first must quantify effects on fitness-relevant traits. I tested the hypothesis that maternal stress will alter fitness-relevant behavior of offspring expressed early in life. I manipulated CORT of gravid female Eastern Fence Lizards (*Sceloporus undulatus*) by dosing them daily with ecologically-relevant concentrations of CORT, to mimic those resulting from attack by fire ants (*Solenopsis invicta*). I measured righting ability and sprint speed of the resulting offspring soon after hatching and found no effect of maternal CORT on these performance behaviors. In contrast to previous results of elevated maternal CORT having outcomes on offspring, our results do not show an effect of maternal GCs on offspring phenotype. Future studies should examine the plastic potential of maternal CORT on other offspring phenotypes to discover the full effects of maternal stress on offspring fitness.

Key Words: maternal stress effects, maternally-derived stress, prenatal stress, phenotypic plasticity, developmental plasticity, glucocorticoids, corticosterone, stress hormones, offspring, eastern fence lizard, *Sceloporus undulatus*, performance behavior, fitness-relevant traits, locomotion, sprint speed, righting ability

TABLE OF CONTENTS

LIST OF FIGURES	iii
ACKNOWLEDGEMENTS	iv
Chapter 1 Introduction	1
Chapter 2 Methods	7
Chapter 3 Results	13
Chapter 4 Discussion	16
Chapter 5 Conclusion.....	19
BIBLIOGRAPHY.....	20

LIST OF FIGURES

- Figure 1. Effects of maternal CORT treatment were investigated on righting ability in eastern fence lizards at 7-10 days of age. Righting speed of offspring from CORT-treated mothers (red) did not differ from that of offspring from control mothers (blue). ANOVA: $F_{1,60}=0.012$, $P=0.914$. Bars represent means \pm 1 standard error. CORT: n=24 offspring from 13 mothers; Control: n=38 offspring from 19 mothers. 13
- Figure 2. Effects of maternal CORT treatment were investigated on sprint velocity in eastern fence lizards at 7-10 days of age. Maximum velocity of offspring from CORT-treated mothers (red) did not differ from that of offspring of control mothers (blue). ANOVA: $F_{1,17}=1.297$, $P=0.271$. Bars represent means \pm 1 standard error. CORT: n=10 offspring from 10 mothers; Control: n=10 offspring from 10 mothers. 14
- Figure 3. Effects of maternal CORT treatment were investigated on sprint acceleration in eastern fence lizards at 7-10 days of age. Maximum acceleration of offspring from CORT-treated mothers (red) did not differ from that of offspring of control mothers (blue). ANOVA: $F_{1,17}=0.015$, $P=0.904$. Bars represent means \pm 1 standard error. CORT: n=10 offspring from 10 mothers; Control: n=10 offspring from 10 mothers. 14
- Figure 4. Effects of maternal CORT treatment were investigated on sprint distance in eastern fence lizards at 7-10 days of age. Maximum distance of individual sprint bursts ran by offspring from CORT-treated mothers (red) did not differ from that of offspring of control mothers (blue). ANOVA: $F_{1,17}=1.206$, $P=0.287$. Bars represent means \pm 1 standard error. CORT: n=10 offspring from 10 mothers; Control: n=10 offspring from 10 mothers. 15

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Chapter 1

Introduction

In the face of environmental challenges, animals often increase glucocorticoids (GCs) resulting from activity of the hypothalamic-pituitary-adrenal (HPA) axis, which is fundamental in how animals cope with and respond to their environment (Wingfield et al., 1998; Boonstra, 2013). GCs play an important role in allowing individuals to cope with acute stressors such as predation, climate change, and limiting resources (Wingfield et al., 1998; Sapolski et al., 2000; Wingfield and Kitaysky, 2002; Romero, 2004). Maternal effects of increased GCs can have significant transgenerational impacts altering offspring phenotype, performance, and fitness (McCormick, 1998; Uller and Olsson, 2006; Meaney et al., 2007; Love et al., 2012). The characteristics of the maternal environment (e.g. food availability or predation risk) can affect offspring through effects of maternal hormones, specifically GCs during development (Seckl, 2004; Love et al., 2005; Love and Williams, 2008a). These GCs can provide offspring with information about post-natal environmental condition (Love et al., 2005). These hormonal maternal effects, termed maternally-derived stress (MDS) effects, have become a focus of research determining their role as an inducer of transgenerational phenotypic plasticity in offspring (Gluckman et al., 2005; Meaney et al., 2007; Love and Williams, 2008a,b; Love et al., 2012; Sheriff and Love, 2013).

Short-term negative effects of MDS include maladaptive changes to morphological, physiological, behavioral, and fitness-related phenotypes in offspring (Marshall and Uller, 2007; Sheriff and Love, 2013; Uller et al., 2013; Sheriff et al., 2017). For instance, effects from

gestational stress in rodent offspring include developmental disruption of the HPA axis, learning deficits, depression-like behavior, and suppression of genes in the hippocampal that lead to permanent changes in behavior (Lesage et al., 2001; Zagron and Weinstock, 2006; Abe et al., 2007; Bogoch et al., 2007; Meany et al., 2007). MDS exposure also leads to modified morphology of offspring resulting in reduced mass, body size, and body condition in species across many taxa (Lesage et al., 2001; Meylan and Colbert, 2004; Saino et al., 2005; Meany et al., 2007; Love and Williams, 2008b; Sheriff et al., 2009). These studies have all examined and supported the short term and once believed unavoidable negative outcomes of MDS in offspring (Love et al., 2012),

Increasingly, new found investigations of the alterations to offspring by MDS are being placed in an ecological framework by examining fitness consequences of these phenotypic effects (Marshall and Uller, 2007; Uller, 2008; Love et al., 2012; Sheriff and Love, 2013; Uller et al., 2013). The developmental programming of offspring phenotype are now thought to possibly be adaptive responses helping offspring cope when faced with ecological stressors (Meylan and Colbert, 2004; Love and Williams, 2008a; Sheriff et al., 2010). For example, elevated maternal GCs resulted in larger female offspring at hatching in side-blotched lizards (Sinervo and DeNardo, 1996); female three-spined sticklebacks who were exposed to a predatory stressor while pregnant produced larger eggs (Giesing et al., 2010), and exposure of free-ranging red squirrels to high density cues, resulting in elevated maternal GCs, gave birth to offspring with increased growth rates that are beneficially matched to the high density environmental conditions (Dantzer et al 2013). Various behavioral performance phenotypes may also be enhanced with MDS. In two species of lizards (*Lacerta vivipara* and *Sceloporus undulatus*), offspring exposed to maternal GCs exhibited increased anti-predator behavior: increased time to

emerge from shelter (Uller and Olsson, 2006) and increased time spent hiding and reduced response to tactile predator cues (Ensminger et al., unpubl data). Several studies found that after a single (intense or mild) prenatal stressful event, offspring had positive long-lasting enhancement in learning performance in adulthood (Cannizzaro et al., 2006; Fujioka et al., 2001). Locomotor activity may be one candidate behavior in which to examine the phenotypic plasticity caused by MDS that would enhance offspring fitness. For instance, pre-natal stress increased locomotor movement and activity in rats (Deminière et al., 1992), and juvenile flight performance and muscle development is positively affected by exposure to maternally derived GCs (Chin et al., 2009). A recent review indicates offspring who experienced elevated GCs and were in an environment that matched the maternal environment increased performance (Uller et al., 2013). Given the complexity of different environmental stressors and the contradictory results in offspring behavioral phenotypes, more studies investigating maternal GCs effects on locomotor performance phenotypes need to be conducted to better understand effects of maternal stress on offspring performance (Sheriff et al., 2017).

Challenging the traditional perspective of negative outcomes of MDS, the environmental matching hypothesis (Gluckman and Hanson, 2004; Love and Williams, 2008a; Monaghan, 2008; Sheriff and Love, 2013; Sheriff et al., 2017) proposes that MDS will have adaptive potential if the maternal environment matches that of the offspring's. Evidence is building that maternal stress may be adaptive in programming the offspring's phenotype to prepare them for future environments, by signaling the characteristics of the maternal environment that they will be born into (Love et al., 2005; Marshall and Uller, 2007; Love and Williams, 2008b; Uller, 2008; Sheriff and Love, 2013; Uller et al., 2013; Sheriff et al., 2017). Maternal GCs have been suggested as a mechanism for causing adaptive phenotypic responses in offspring depending on

the variation in environments (Meylan and Clobert, 2005; Love et al., 2009). For example, exposure to elevated MDS may potentially match embryonic performance traits to the expected quality of the newborns environment, for example, predation risk (Chin et al., 2009). Through trans-generational phenotypic plasticity, MDS may help individuals in adapting to changing environments (Meylan et al., 2012).

We have poor understanding of how MDS influences fitness (Groothuis et al., 2005; Love et al., 2005; Love and Williams, 2008a). This is because few studies have measured the effects of MDS in offspring from free-living females in an ecologically relevant framework during pre-natal development, the stage at which offspring are directly affected by MDS hormones (Sheriff and Love, 2013). Even fewer studies examine the long-term effects of MDS on offspring phenotype and fitness where effects in offspring phenotype may continue to be expressed (Seckl, 2004; Jarvis et al., 2006; Schoech et al., 2011). For example, a study examining the body size of house wrens after eggs were injected with GCs found that hatchlings were lighter in weight at hatching, but after compensatory growth, were heavier at fledging when compared with control offspring (Strange et al., 2016). Focusing studies on examining the effects MDS has on traits that directly influence fitness would increase our knowledge of the evolutionary and ecological significance of these maternally derived hormones (Chin et al., 2009). Only after we discover the alterations in phenotypes from MDS, specifically phenotypes relating to performance and fitness-relevant traits, can we begin to investigate the adaptive potential these changes have in offspring fitness.

In this study, I experimentally manipulated GCs in wild-caught adult female eastern fence lizards (*Sceloporus undulatus*) to examine how the maternal corticosterone (CORT), the key GC in reptiles (Romero, 2004), affects performance behaviors in their offspring. This is an

appropriate model species used to study maternal stress effects as it is simple to manipulate maternal CORT through transdermal application of the stress hormone, CORT, mimicking a natural CORT response in this lizard species to a non-lethal encounter with a predator (Trompeter and Langkilde, 2011; Graham et al., 2017) and the physiology of this organism has been well studied (Alder et al., 2009; Graham et al., 2016). Additionally, as there is no maternal care, alterations in offspring performance behaviors are not affected by maternal behavior (Klukowski and Nelson, 1998).

Here, I tested the effects of maternal CORT on the offspring performance behaviors of righting ability and sprint speed, which are ecologically important fitness traits known to affect prey capture, the ability to escape predation (Garland et al., 1990; Miles, 2004), and the ability to feed (Greenwald, 1974; Webb, 1986). Righting ability can assess an individual's performance capacity, where a physical inability to right itself may have consequences for its ability to escape predation (O'Donnell et al., 2007). Sprint speed is reliably measured with high repeatability (Bennett, 1980; Garland, 1985; Huey and Dunham, 1987). Maximal performance capacities for righting ability and sprint speed were analyzed to focus on the ability of an individual to perform maximally and be able to most accurately compare differences in performance behavior due to MDS (Garland and Losos, 1994; Losos et al., 2002).

I investigated the maternal stress effects on fitness-relevant performance parameters in offspring. With a growing body of studies examining the adaptive potential of MDS in preparing offspring to cope with high stressed environmental conditions (Gluckman et al., 2005; Meaney et al., 2007; Love and Williams, 2008a,b; Sheriff et al., 2010, Sheriff et al., 2011; Love et al., 2012; Sheriff and Love, 2013; Sheriff et al., 2017), I predicted that MDS would enhance offspring performance behaviors in faster righting speeds, faster sprint speeds, and longer sprint distances.

By investigating maternal effects on fitness-relevant traits I build on previous work to elucidate the transgenerational phenotypic effects MDS has on preparing offspring for future environmental conditions.

Chapter 2

Methods

Field Sites and Collection of Mothers

Gravid female eastern fence lizards were captured using a noose from two sites in the southeastern USA: Standing Stone State Park, Tennessee (36°28'25"N, 85°25'01"W) and Land-Between-the-Lakes National Recreation Area, Kentucky (36°50'50"N, 88° 5'2"W) (N=32). Females were toe clipped for individual identification and morphology measures were collected at capture including mass (g), snout-vent length (cm) (SVL), tail length (TL), right front limb (RFL), right hind limb (RHL) and sex. Gravidity of females was determined by abdominal palpation. Lizards were transported to Pennsylvania State University for further housing and experimental treatment.

Maternal Housing

Adult females were housed in pairs of the same experimental treatments in plastic enclosures 46 x 40 x 30 cm (L x W x H). Enclosures were furnished with a plastic shelter that allows for elevated basking and refuge, a water bowl, and moist sand for females to lay eggs in. 53-W incandescent lamps were hung to one side of the tubs to allow a temperature gradient for thermoregulation and were lit for 8 hours a day from 8:00-16:00. Overhead room lights were set to a 12-hour light:dark cycle, with light from 07:00-19:00. Females were fed crickets (*Acheta domestica*) dusted with calcium and vitamin supplements three days a week to satiation and given water *ad libitum*.

Maternal CORT Treatment

At capture, females were randomly assigned one of two treatment groups, CORT treated (S=13) or control (C=19). CORT treated females received a topical application of 0.2 uL/g lizard of 4 mg CORT ($\geq 92\%$, Sigma C2505, Saint Louis, MO) in 1mL of sesame seed oil vehicle (0.8ug CORT/g lizard; Trompeter and Langkilde, 2011) while control mothers received the same volume of sesame seed oil vehicle. Both CORT and control solutions were applied to the lizards once per day between 19:00 and 21:00 after lights turned off to ensure lizard activity ceased and no disturbance was caused. Solutions were pipetted to the middle of the lizard's back. Treatments were applied from capture until laying (9-75 days). This ecologically relevant concentration of CORT mimics the stress hormone elevation caused by a variety of stressors, such as sublethal attacks by fire ants (Trompeter and Langkilde, 2011; Graham et al., 2017) heat stress (Telemeco et al., unpubl data), chasing stress (Trompeter and Langkilde, 2011) and restraint stress (Graham et al., 2012).

Egg Collection and Incubation

Adult female enclosures were checked for eggs three times a day: in the morning, mid-day, and evening during dosing. Immediately after eggs were located they were stored in plastic containers (11x7.5 cm D x H) filled with moist vermiculite (~ -200 kPa) and sealed with plastic wrap (Warner et al., 2009; Langkilde and Freidenfelds, 2010). Eggs were incubated at 31°C until hatching (mean \pm 1 SD: 44 ± 1.4 days later; Sinervo, 1990; Langkilde and Freidenfelds, 2011). The incubator was checked at least two times per day for hatchlings: first thing in the morning and afternoon. Eggs were rotated every other day among shelves and between shelves to prevent potential within incubator effects of position.

Hatchling Housing

Offspring were immediately measured and toe clipped for identification after hatching (n=24 offspring from 13 CORT-treated females; n=38 offspring from 19 control females).

Morphological measures taken include mass, SVL, TL, RFL, HFL, and sex. Two healthy hatchlings were randomly selected from the clutch to use in the behavior experiments.

Hatchlings were paired with another lizard from the same clutch in each plastic tub (27.5 x 15 x 20 cm L x W x H). Enclosures were furnished with a plastic basking site to allow thermoregulation, a water bowl, and paper towel substrate. 43-W incandescent lamps were hung to one side of the tubs to allow a temperature gradient for thermoregulation and kept lit for 8 hours a day from 8:00-16:00. Over head room lights were set to a 12-hour light:dark cycle from 7:00-19:00. Hatchlings were fed flightless fruit flies (*Drosophila melanogaster*) every day after four days of age and given water *ad libitum*.

Performance Behavior Experiments

Two performance behaviors, righting ability and sprint speed were conducted at 7-10 days after hatching. Two hatchlings from each clutch were used in the righting ability experiments (clutches S=13, C=19; individuals S=24, C= 38) and one hatchling from each clutch was used in the sprint speed experiments (clutches S=10, C=10; individuals S=10, C=10). All performance behaviors were tested on the same day for each lizard beginning with righting ability and ending with sprint speed. This order in behaviors allows for minimal impacts from the previous behavior test as righting ability is the less strenuous activity (Boronow and Langkilde, 2010). Trials were conducted during the lizard's active hours from 9:00-16:00. Lizards were acclimated to 33 ± 1 °C in an incubator for 30 minutes before testing righting ability and sprint

speed. This is the preferred body temperature which results in maximal locomotor performance in this species and was measured via cloaca (Huey and Dunham, 1987; Sinervo and Aldolph, 1989; Angilletta, 2001, Angilletta et al., 2002). Maximum performance capacities were analyzed to avoid inclusion of low or sub-maximal speeds and focus on the ability of an individual to perform maximally, excluding their unwillingness to perform (Garland and Losos, 1994). The variation in phenotypes should be reflected in the variation in maximal performance capacities (Losos et al., 2002). When all performance behaviors were complete, hatchlings were measured for mass, SVL, TL, RFL, and FHL.

Righting Ability

Once the 30-minute acclimation period was complete, hatchlings were removed from incubators and cloacal temperature was immediately measured using a thermocouple probe. If cloacal temperature was not $33 \pm 1^\circ\text{C}$, hatchlings were returned to the incubator until necessary cloacal temperatures were reached. Once that temperature was reached, hatchlings were tested for righting ability. Righting ability was measured in a plastic container (27.5 x 15 x 20 cm L x W x H) with a paper towel substrate, and a hanging lamp to increase visibility and to assist hatchlings in maintaining appropriate cloacal temperatures.

Righting ability was tested by placing hatchlings on their backs and allowing them to flip themselves over until all four appendages made contact with the ground. Four complete righting ability flips were conducted with a 10 second recovery period between each flip (Losos et al., 2002). If a hatchling did not immediately flip, their chests were gently tapped with the bristle end of a paint brush until a flip occurred. If a hatchling took over 30 seconds to flip or the flip was influenced by the researcher's fingers, the flip was considered sub-maximal and excluded from

analysis (following Losos et al., 2002). Righting ability experiments were recorded in slow motion (240 fps) with the camera view focused downward. Videos were analysed in Tracker version 4.9.8 and examined frame-by-frame. The beginning of each flip was characterized by the first frame a lizard began to lift its shoulder off the ground. The end of each flip was the frame where the hatchling's four limbs made complete contact with the ground. From this, righting ability was measured as the total number of frames it took for a hatchling to right itself. The fastest righting speed from the four flips was used in analysis. Once four successful flips were achieved, the hatchling was removed and allowed a one-hour recovery period before beginning sprint experiments. During the first half hour, the hatchling recovered in room temperature ($\sim 24^{\circ}\text{C}$) and then moved for the second half hour to the incubator to acclimate to $33 \pm 1^{\circ}\text{C}$.

Sprint Speed

After the acclimation period was complete, hatchlings were removed from the incubator and cloacal temperature immediately measured. If cloacal temperature reached $33 \pm 1^{\circ}\text{C}$, sprint speed experiments would begin. Sprint speed was tested by allowing a hatchling to run down a 1-meter long race track (122 x 8 x 9 cm L x W x H) chased by the bristle end of a paint brush. The bottom of the racetrack was marked with scratches to create traction and a cloth bag was attached to the end of the track to provide shelter. Five lamps hung above the track to increase visibility and provide heat to the hatchlings during sprint speed trials.

If hatchlings paused during a run, they were encouraged to commence running by touching their tail with the bristle end of a paint brush. If a hatchling turned around, did not move, or the track was not completed, the sprint was defined as submaximal and discarded from analysis (following Losos et al., 2002). Four complete sprints were conducted with a one-hour

recovery period between sprints (Losos et al., 2002). The first half of the recovery period occurred at room temperature (~ 24 °C) while for the second half, the hatchlings were moved to the incubator to acclimate to 33 ± 1 °C. Sprint experiments were recorded in slow motion (240 fps) and analysed frame-by-frame in Tracker version 4.9.8. Since hatchlings do not sprint long distances in the laboratory, I discovered that bursts of 5 cm or greater were an accurate determination of maximum sprints. Therefore, all bursts of 5 cm or greater were analysed frame-by-frame and measures of maximum velocity, maximum acceleration, and distance of burst were extracted. The maximum values among all four sprint experiments including maximum velocity, maximum acceleration, and maximum distance were used in analysis.

Statistical Analysis

All analyses were conducted using JMP Pro (v12, SAS Institute Inc., Cary, NC, USA). I used an analysis of variance (ANOVA) to compare the effect of maternal CORT treatment on hatchling maximum righting speed, maximum sprint velocity, maximum sprint acceleration, and maximum sprint distance. Hatchling sex, mass, site, SVL, TL, RFL, and RHL did not significantly explain variation in our dependent variables in any of our models ($p > 0.300$); thus, were removed from the final model to preserve degrees of freedom. Maternal ID was included as a random effect with offspring as repeated measures to control for non-independence of these offspring in righting ability analysis. Maternal ID was not included as a random effect in sprint speed analysis as only one offspring was used in experiments per mother. Significance was determined to be a p-value < 0.05 and results were presented as ± 1 standard error (SE).

Chapter 3

Results

Maternal treatment had no effect on any measured hatchling behavior. Maternal CORT had no significant effect on hatchling maximum righting speed (ANOVA: $F_{1,60}=0.01$, $P=0.914$, Figure 1), maximum sprint velocity (ANOVA: $F_{1,17}=1.297$, $P=0.271$, Figure 2), maximum sprint acceleration (ANOVA: $F_{1,17}=0.015$, $P=0.904$, Figure 3), or maximum sprint distance within a single burst (ANOVA: $F_{1,17}=1.206$, $P=0.287$, Figure 4).

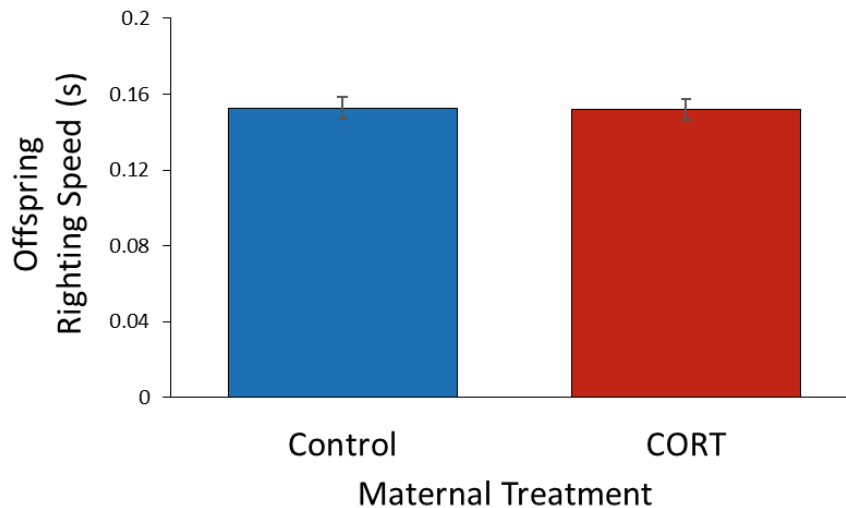


Figure 1. Effects of maternal CORT treatment were investigated on righting ability in eastern fence lizards at 7-10 days of age. Righting speed of offspring from CORT-treated mothers (red) did not differ from that of offspring from control mothers (blue). ANOVA: $F_{1,60}=0.012$, $P=0.914$. Bars represent means \pm 1 standard error. CORT: $n=24$ offspring from 13 mothers; Control: $n=38$ offspring from 19 mothers.

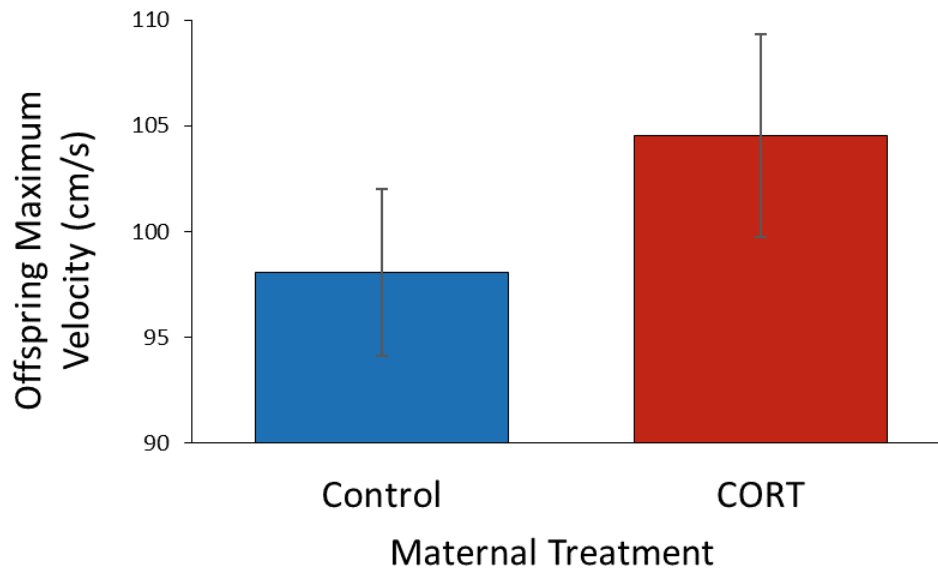


Figure 2. Effects of maternal CORT treatment were investigated on sprint velocity in eastern fence lizards at 7-10 days of age. Maximum velocity of offspring from CORT-treated mothers (red) did not differ from that of offspring of control mothers (blue). ANOVA: $F_{1,17}=1.297$, $P=0.271$. Bars represent means \pm 1 standard error. CORT: $n=10$ offspring from 10 mothers; Control: $n=10$ offspring from 10 mothers.

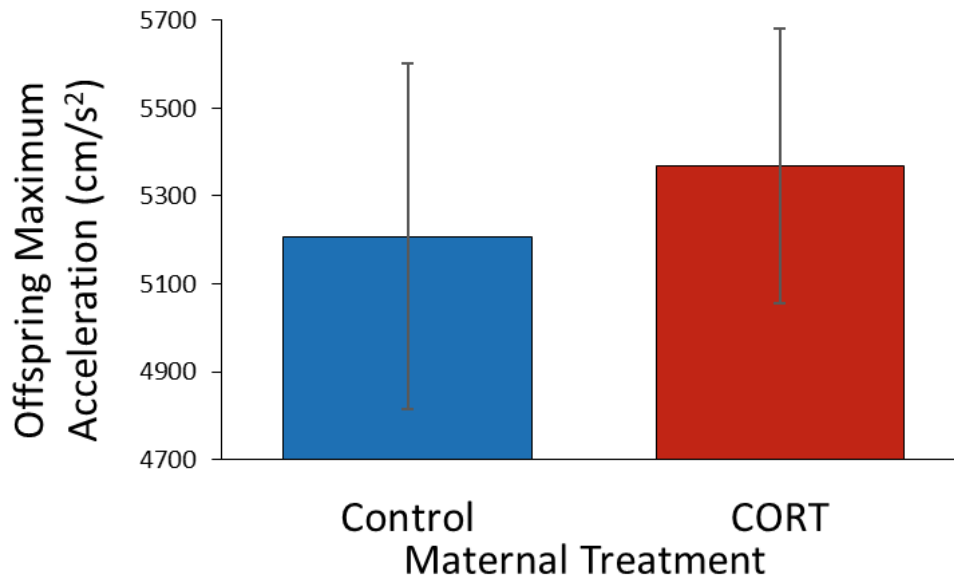


Figure 3. Effects of maternal CORT treatment were investigated on sprint acceleration in eastern fence lizards at 7-10 days of age. Maximum acceleration of offspring from CORT-treated mothers (red) did not differ from that of offspring of control mothers (blue). ANOVA: $F_{1,17}=0.015$, $P=0.904$. Bars represent means \pm 1 standard error. CORT: $n=10$ offspring from 10 mothers; Control: $n=10$ offspring from 10 mothers.

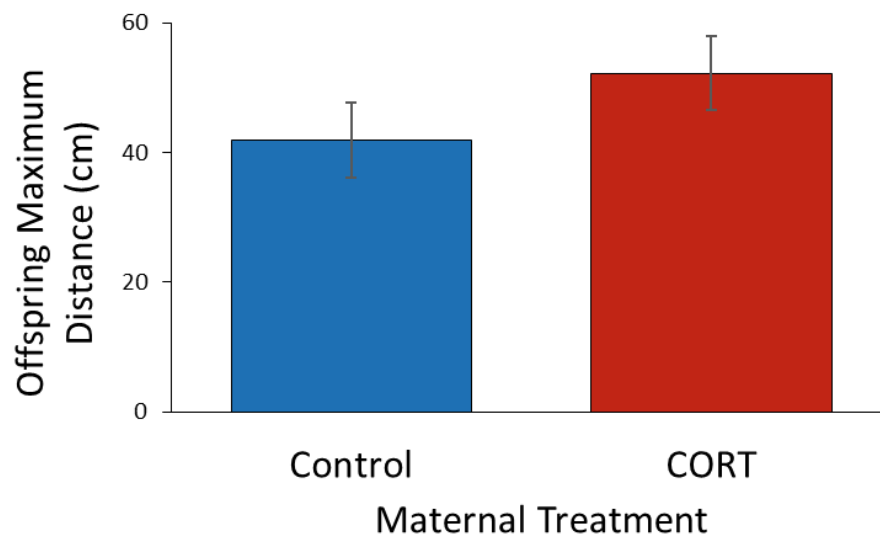


Figure 4. Effects of maternal CORT treatment were investigated on sprint distance in eastern fence lizards at 7-10 days of age. Maximum distance of individual sprint bursts ran by offspring from CORT-treated mothers (red) did not differ from that of offspring of control mothers (blue). ANOVA: $F_{1,17}=1.206$, $P=0.287$. Bars represent means \pm 1 standard error. CORT: n=10 offspring from 10 mothers; Control: n=10 offspring from 10 mothers.

Chapter 4

Discussion

Here, I investigated the transgenerational effects of maternal CORT on performance behaviors in lizard offspring. Specifically, I predicted that the maternal stress effects would prepare offspring for a high stress environment by increasing their performance (Love et al., 2012), this should result in faster righting speeds, sprint velocities, sprint accelerations, and longer sprint distances by offspring from CORT-treated mothers. However, I found no effect of maternal stress on the fitness-relevant performance of any of the tested behaviors in eastern fence lizards. To our knowledge, this is one of the first experiments examining consequences of elevated maternal GC effects on offspring locomotor performance which will help build the limited knowledge of maternal CORT effects on offspring phenotype.

There are several potential explanations for this result: 1) the stress of handling individuals and placing them into captivity may have stressed females enough that control mothers baseline GCs were similar to those of CORT-treated mothers. However, captivity does not increase baseline GC levels in this species above levels of free-living animals in the wild (Langkilde, unpublished).

2) The CORT dosage concentration that was applied may not have elevated CORT-treated mother's plasma CORT levels. As this dose consisted of lipophilic molecules, it was quickly absorbed by the high lipid concentrated lizard skin (Belluore and Clobert, 2004), and

transdermal application of this CORT dose significantly elevated plasma CORT levels in CORT-treated mothers (Trompeter and Langkilde, 2011).

3) Maternal CORT may not have entered the egg to affect offspring. However, the maternal CORT treatment used in this study resulted in an increase in the yolk CORT levels of eggs (Ensminger et al., unpublished). Additionally, stress-related hormones are passed through eggs and result in increased CORT levels in eggs in both avian (Saino et al., 2005) and aquatic species (Sopinka et al., 2016). It is thus likely that offspring eggs were exposed to increases in CORT associated with maternal CORT elevations.

4) Maternal CORT may not have affected offspring phenotypes. However, there is evidence of altered phenotypes in offspring due to MDS in morphology, anti-predator performance, learning performance, and locomotor activity in a variety of taxa, including in the species used in this study (Deminière et al., 1992; Fujioka et al., 2001; Uller and Olsson, 2006; Cannizzaro et al., 2006; Giesing et al., 2010; Uller et al., 2013; Ensminger et al, unpubl data). Additionally, positive effects of MDS have been observed in other survival-relevant traits such as increased flight performance and enhanced flight muscles in juvenile European starlings (Chin et al., 2009). It is interesting that I found no effect, either positive or negative, of maternal CORT treatment in offspring performance behavior phenotypes despite showing effects in other offspring phenotypes of various species. These results suggest that the increased elevation of maternal GCs do not developmentally program offspring performance phenotype. More studies across species investigating maternally derived stress effects on muscle physiology needs to be explored to understand the mechanisms in which maternally derived stress may affect various performance behaviors.

Future directions of this research would be to examine MDS effects in other behaviors of this and other species to investigate MDS interactions on phenotypic plasticity. Elevated CORT during development has been found to not only effect offspring at hatching but additionally, later in life (reviewed in Seckle, 2004) (e.g. increased responsiveness of HPA axis in adulthood in Japanese quail (Hayward et al., 2006) and impairment of GC response in adults of wistar rats (Barbazanges et al., 1996)). Examining these effects later in the life of offspring would give a larger picture on the long-term effects of MDS on performance behavior phenotypes where few studies have examined these effects into adulthood (Schoech et al., 2011). Similarly, research on the effects of individual personality and how these may interact with effects of maternal CORT on performance behaviors will be important since variation in individual personality, specifically bold and shy personalities, can cause differing reactivity in stress responsiveness (Carere and Oers, 2004; Schjolden et al., 2005; Koolhaas et al., 2007; Clary et al., 2014). Further research focused on the phenotypic plasticity of MDS in manipulating phenotypes that are advantageous to offspring in various environments, including the maternal environment, would be key to determining the adaptive potential of MDS in helping offspring cope with future environmental conditions (Sheirff et al., 2017).

Chapter 5

Conclusion

The study of maternal stress effects on phenotypic traits has intensified and become an influential field of study (Sheriff et al., 2017). Scientists are increasingly questioning the ability of maternal stress to be effective in altering phenotypes and investigating the plastic potential of phenotypes to MDS (Marshall and Uller, 2007; Love and Williams, 2008a,b). While there exist opposing results of adaptive and maladaptive consequences of maternal stress, this study's goal was to investigate the effects of maternal CORT on fitness relevant performance behaviors that can influence survival in a species. Our results do not support the hypothesis that maternal CORT can alter offspring behaviors of righting ability and sprint speed. Interestingly, due to these results, they suggest that maternal CORT does not affect these performance behaviors in eastern fence lizard offspring. Further research examining fitness-relevant consequences of effects of maternal CORT on offspring performance and muscle physiology will be critical to determine if MDS has an effect on other performance behaviors in this lizard species and if so, what those effects may be. Only after we discover the possible plastic potential MDS has on offspring performance phenotypes, can we begin to investigate the role of MDS in adaptively altering phenotypes to benefit offspring fitness.

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