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Sex-dependent effects of maternal stress: Stressed moms invest less in sons than daughters

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Abstract

Multigenerational effects can have important and sex-dependent effects on offspring. Sex allocation theory predicts that females should differentially invest in sons and daughters depending on sex-specific fitness returns and costs of investment. Maternal stress-relevant (glucocorticoid) hormones may be one mechanism driving this effect. We investigated how maternal stress hormones differentially affected sons and daughters by manipulating levels of the glucocorticoid, corticosterone (CORT), in gravid female eastern fence lizards (*Sceloporus undulatus*) and quantifying reproductive investment and sex ratio of resulting clutches, and the mass, snout-vent length, and body condition of sons versus daughters at hatching. We found no effect of maternal CORT-treatment on the number or size of eggs laid or on the sex ratio of resulting offspring, but sons of CORT-treated mothers were shorter, lighter, and of poorer body condition at hatching than were sons of control mothers. We found no difference in size or condition of daughters with maternal treatment. Our results suggest that maternal stress, mediated by elevations in maternal CORT concentrations, can have sex-specific effects on offspring manifesting as lower investment in sons.

KEYWORDS

condition, multigenerational, offspring, sex allocation, sex-ratio, stress

1 | INTRODUCTION

Mothers can greatly influence the phenotype and future fitness of their offspring via maternal effects, such as altered oviposition site (Brown & Shine, 2004), nutrient allocation (Vaughan, Sferruzzi-Perri, & Fowden, 2012), and hormonal exposure (Schoech, Rensel, & Heiss, 2011). Effects can be sex-dependent; for example, maternal stress in rats impaired learning performance of sons but enhanced learning performance in daughters (Mueller & Bale, 2007). Given there are different optimal traits for sons versus daughters (e.g., sex differences in optimal offspring size; Langkilde & Shine, 2005), females can maximize the fitness of offspring by differentially investing in a particular sex. The sex that females should invest in may vary under different environmental conditions. For example, the Trivers-Willard hypothesis predicts that, under a restricted set of conditions, mothers in good condition should favor offspring of the sex with more variable reproductive value, and thus the evolutionarily less expensive sex (Trivers & Willard, 1973). Charnov (1982) more broadly predicts that any environment that has differential effects on fitness of males versus females should lead to sex-dependent allocations.

The mechanisms underlying sex-specific maternal investment are poorly understood (Veller, Haig, & Nowak, 2016); however, maternal

stress hormones (glucocorticoids; maternal CORT hereafter) may be one factor driving sex-dependent maternal effects (Sheriff et al., 2017). Maternal CORT is directly related to the environment experienced by the mother, such as predation risk, food availability, and competition, and has been shown to reduce maternal investment in offspring (Thierry, Massemin, Handrich, & Raclot, 2013) and mediate offspring phenotype (reviewed in Saino, Romano, Ferrari, Martinelli, & Møller, 2005; Sheriff & Love, 2013). For example, elevated CORT resulted in decreased size, body condition, and growth of Common lizard offspring (*Lacerta vivipara*; Meylan & Clobert, 2005). Similarly, maternal CORT treatments resulted in reduced offspring length, mass, and sprint performance in the viviparous lizard, *Pseudemoia entrecasteauxii* (Itonaga, Jones, & Wapstra, 2012; but see Cadby, Jones, & Wapstra, 2010 for an example of a lack of effect of maternal CORT on offspring). Maternal CORT may also alter maternal investment in offspring in a sex-dependent manner. In European starlings (*Sturnus vulgaris*), Love, Chin, Wynne-Edwards, and Williams (2005) found that experimentally elevated maternal CORT resulted in female-biased clutches, and lower mass and immune function in sons but not daughters. Similarly, elevated cortisol concentration in milk of rhesus monkey mothers correlated with an increased confident temperament factor in sons but not daughters (Sullivan, Hinde, Mendoza, & Capitanio, 2011).

Here, we tested the hypothesis that maternal CORT alters maternal investment in clutches (eggs per clutch, individual egg mass, and total clutch mass) and would result in a sex-dependent reduction in offspring investment using eastern fence lizards (*Sceloporus undulatus*). To test this hypothesis, we experimentally elevated maternal CORT to ecologically relevant levels and measured maternal investment in their clutches, and the sex ratio, size, and body condition of resulting offspring. Specifically, we predicted that CORT-treated females would have (i) fewer eggs per clutch (if they resorb or there is sex-specific mortality of embryos), but greater individual egg and overall clutch mass; (ii) sex-biased clutches; and (iii) sex-dependent effects on body size (body mass and length) and condition (mass by length comparison).

2 | MATERIALS AND METHODS

2.1 | Adult collection and husbandry

We captured 34 gravid female eastern fence lizards during April–May 2017 from two sites in the southeastern USA: Standing Stone State Park, Tennessee (SSSP: 36°28′25″N, 85°25′01″W) and Land-Between-the-Lakes National Recreation Area, Kentucky (LBL: 36°50′50″N, 88°05′02″W). These sites are ~25 km apart but similar in habitat and ecology of the resident lizards. Females were brought to the Pennsylvania State University and housed in plastic enclosures (56 × 40 × 30 cm, L × W × H) in same-treatment same-site pairs until laying; each female within a pair was at a different stage of gravidity to avoid them laying at the same time. Enclosures were furnished with a shelter that served as a refuge and basking perch, a water bowl, and moist sand for nesting. A 53-W halogen light bulb was setup at one end of the enclosure and provided heat for 8 hr each day (08:00 AM–04:00 PM), allowing the lizards to thermoregulate. Overhead lights were set to a 12:12 hr light:dark schedule (light: 07:00 AM–07:00 PM) and ambient room temperature was ~23.3°C. Adult lizards were fed crickets (*Acheta domestica*, dusted with calcium and vitamin supplements) three times per week, and water was available ad libitum.

2.2 | Maternal stress treatments

Females from each of the two sites were randomly assigned to one of two treatments: daily CORT elevation (SSSP: $n = 5$; LBL: $n = 9$) or control (SSSP: $n = 4$; LBL: $n = 16$). Maternal site of origin was included in initial statistical models and found to be nonsignificant, thus we removed this from further evaluation. To manipulate maternal CORT concentrations, we used a daily transdermal application of CORT solution (0.2 $\mu\text{L/g}$ of 4 mg CORT [$\geq 92\%$; Sigma C2505, Saint Louis, MO] dissolved in 1 ml of sesame oil vehicle [approximately 0.8 μg CORT/g lizard; range = 0.74–0.87 μg CORT/g]) or a vehicle only control. The volume (treatment or control) of solution applied to females' backs ranged from 1.6 to 4.3 μL . The relevant solution was applied to the middle of the lizards' backs using a pipette between 07:00 PM and 09:00 PM, after all lights had turned off and lizards had ceased activity for the evening. This minimized the invasiveness of these manipulations as the lizards did not need to be handled during dosing. The treatments were applied from capture until laying (9–75 days).

Due to the lipophilic nature of lizard skin, the oil and hormone were quickly absorbed into the blood stream (Belliure & Clobert, 2004). This application results in plasma CORT concentrations that are approximately twice those of baseline by 30 min after application, approximating increases resulting from nonlethal encounters with predatory fire ants (Graham et al., 2017), a chasing stressor (Trompeter & Langkilde, 2011), a heat stressor (Telemeo, Pers. Comm.), or a confinement stressor (Graham et al. 2012), and returning to baseline within 90 min after application.

2.3 | Clutch traits, sex ratio, and hatchling morphology

Enclosures were checked at least three times per day for eggs. When an egg clutch was discovered, we immediately collected the eggs and recorded the number of eggs (mean clutch size = 11 eggs, range: 7–16 eggs), and the mass of four randomly selected eggs and of the entire clutch (to the nearest 0.01 g). Since females were at different stages of gravidity, the mother could be easily identified visually and confirmed by palpating (female abdomens feel empty after laying). The clutches were transferred to a plastic container (5.5 × 7.5 cm, R × H), filled with moist vermiculite (~200 kPa), and sealed with plastic wrap and a rubber band (Langkilde & Freidenfelds, 2010; Warner, Radder, & Shine, 2009). Eggs were incubated at 31°C until hatching (mean \pm SD: 44 \pm 1.4 days later). The incubator was checked at least two times per day for hatchlings, and containers were rotated every other day to avoid any within-incubator effects of position.

Two control females died before laying. We were able to dissect out their eggs to obtain a count of their clutch size and resulting hatchlings. However, since these eggs may not have been fully developed, we did not measure their mass. We did, however, get viable hatchlings from one of these clutches.

Of the eggs that hatched (79 from 14 CORT-treated females and 159 from 20 control females), hatchling sex was determined via the presence (male) or absence (female) of enlarged post-anal scales (Haanel, Smith, & John-Alder, 2003), and mass (to the nearest 0.01 g) and snout-vent length (SVL, to the nearest 0.5 mm) were measured immediately. Body condition of each hatchling was calculated by dividing $\ln(\text{mass})$ by $\ln(\text{SVL})$. Since we could not determine the sex of unhatched eggs, we could not determine differential hatching success of sons versus daughters.

2.4 | Statistical analyses

We analyzed the effect of maternal CORT-treatment on the suite of clutch and offspring traits (number of eggs per clutch, average egg mass, clutch mass, sex ratio, hatchling mass, hatchling SVL, and hatchling body condition) using separate analysis of variance (ANOVA) models. Our initial models of clutch traits (number of eggs per clutch, average egg mass, clutch mass, sex ratio) included an effect of maternal treatment (CORT-treated vs. control), with the additional predictor variables of maternal site of capture (site), number of times the mother was dosed (number of doses), and maternal post-laying mass. We removed non-significant ($P > 0.05$) predictor variables from our final models to preserve degrees of freedom, so our final models included

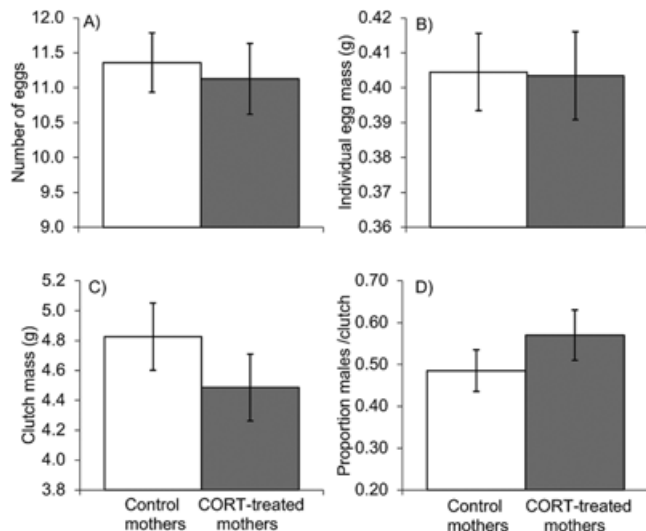


FIGURE 1 Traits of clutches laid by control females ($n = 20$) and those treated daily with exogenous corticosterone (CORT) while gravid ($n = 14$), showing the average (A) number of eggs in a clutch, (B) individual mass of eggs within the clutch, (C) mass of the entire clutch, and (D) sex ratio of offspring. Bars represent means ± 1 standard error

sex ratio model: treatment only; clutch size model: treatment and post-laying mass; egg mass model: treatment, number of doses, and post-laying mass; clutch mass model: treatment, site and post-laying mass. Our initial models of offspring morphology (mass, SVL, body condition) included maternal treatment, maternal site of capture, offspring sex, the interaction of these factors, and the number of doses. Maternal identity was included as a random effect (nested within treatment) to account for lack of independence among siblings. Only maternal site of capture did not significantly explain variation in offspring traits ($P > 0.05$) and was omitted from all final models. All analyses were conducted in JMP Pro 13 (SAS Institute Inc., Cary, NC, USA) with $\alpha = 0.05$.

3 | RESULTS

CORT-treated and control females produced a similar number of eggs (treatment: $F_{2,32} = 0.12$, $P = 0.73$; Figure 1A), and eggs and clutches of a similar mass (individual egg mass: $F_{3,28} < 0.01$, $P = 0.95$; clutch mass: $F_{3,28} = 1.31$, $P = 0.26$; Figure 1B,C).

Maternal CORT-treatment did not affect the sex ratio of resulting offspring ($F_{1,30} = 1.12$, $P = 0.29$; Figure 1D).

The effect of maternal CORT treatment on offspring mass, SVL, and body condition depended on the sex of the offspring (treatment \times sex: mass $F_{1,211} = 8.62$, $P < 0.01$; SVL $F_{1,213} = 4.11$, $P = 0.04$; condition $F_{1,211} = 8.55$, $P < 0.01$; Figure 2). Sons of CORT-treated females were 5% lighter, 3% shorter, and had 12% lower body condition than sons of control females, whereas control and CORT-treated females had daughters of similar mass, length, and body condition. Maternal CORT-treatment had an overall negative effect on offspring SVL (treatment: $F_{1,28} = 4.49$, $P = 0.04$) but not offspring mass or body condition (treatment: mass $F_{1,30} = 2.41$, $P = 0.13$; body condition $F_{1,29} = 3.96$, $P = 0.06$). Sons and daughters did not differ in these morphological traits overall

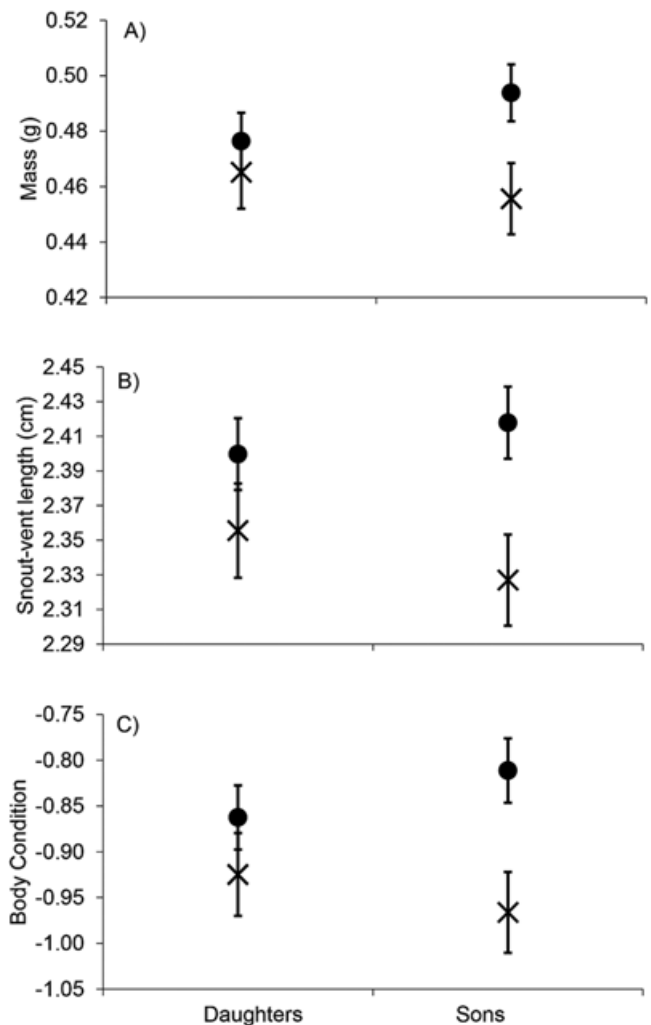


FIGURE 2 Morphology of offspring from control females (circles; $n = 159$) and those treated daily with exogenous corticosterone (CORT) while gravid (crosses; $n = 79$), showing the average (A) mass, (B) snout-vent length, and (C) body condition at hatching. Points represent means ± 1 standard error

(sex: mass $F_{1,212} = 0.73$, $P = 0.39$; SVL $F_{1,214} = 0.20$, $P = 0.65$; body condition $F_{1,211} = 0.10$, $P = 0.76$). Maternal identity explained a significant amount of the variation in all models of offspring traits ($P < 0.01$).

4 | DISCUSSION

We tested the hypothesis that maternal CORT would reduce maternal investment into clutches (eggs per clutch, individual egg mass, and clutch mass), and reduce investment into sons (female biased clutches and smaller sons) using eastern fence lizards. We found no difference in clutch investment; control and CORT-treated females had similar number of eggs laid, individual egg, and total clutch mass. Maternal CORT treatment did not affect offspring sex-ratio; however, compared to control females, CORT-treated females had sons with lower body mass, shorter SVL, and reduced body condition. There was no difference in daughters between treatments. Our results thus

suggest that maternal CORT alters offspring phenotype in a sex-dependent manner.

Exposure of females to CORT typically decreases investment into reproduction (Meylan & Clobert, 2005; but see Love & Williams, 2008). We did not, however, detect a reduction in reproductive investment by CORT-treated females in terms of the number of eggs or the mass of individual eggs or the entire clutch. This could be due in part to the captive environment. Reproductive investment can be limited by energy availability (Olsson & Shine, 1997), and CORT can redistribute energy away from reproduction (Greenberg & Wingfield, 1987). Our females were not food limited (fed frequently and there was no difference in post-laying condition), which may have masked any effects of CORT on clutch investment (see French, McLemore, Vernon, Johnston, & Moore, 2007). It is also possible that CORT did not affect females' allocation of energy to reproduction.

CORT-treated females did not produce female-biased clutches as expected. Several mechanisms have been proposed that could have resulted in CORT-treated females having altered sex ratios, including incubation temperature (Janzen, 1994; Robert & Thompson, 2001; Robert, Thompson, & Seebacher, 2003), maternal body condition (Cameron & Linklater, 2007), quality of diet (Warner, Lovern, & Shine, 2007), and hormone concentrations (Bonier, Martin, & Wingfield, 2007; Love et al., 2005; Pryke, Rollins, Buttemer, & Griffith, 2011; Warner et al., 2009). In species where sex is genetically determined, these typically need to occur before or around the time of fertilization (Cameron & Linklater, 2007; Komdeur, Magrath, & Krackow, 2002; Sheldon & West, 2004; Sheldon, Andersson, Griffith, Örnberg, & Sendecka, 1999). In our study, females were captured post-fertilization and so these are unlikely candidates. Post-fertilization, sex ratios could also be altered by females resorbing embryos of a particular sex (Gosling, 1986; Krackow, 1992), or to male specific mortality (Burger & Zappalorti, 1988; Love et al., 2005; Warner et al., 2009). We found no evidence of this.

Despite no difference in the number or size of eggs, or sex ratio of hatchlings, CORT treatment did affect offspring traits. The effects of maternal CORT on offspring have been shown to vary between species (e.g., Cadby et al., 2010; Warner et al., 2009; Itonaga, Jones, & Wapstra, 2012) and can have a sex-dependent effect (e.g., Love et al., 2005; Sullivan et al., 2011). In this study, CORT-treated females appeared to invest less into their sons; sons hatched lighter and smaller but daughters were unaffected by maternal CORT treatment. We were unable to determine the sex of individual eggs (all eggs from a clutch were incubated together), but it is possible that females differently provisioned male versus female eggs. There was substantial variation in egg size within a clutch (up to 25%; this study), so females may have invested less into eggs that would produce sons. Females may also have differentially invested protein and lipids into the eggs of sons versus daughters. Eggs of CORT-treated mothers contain less protein and more lipid than eggs of control mothers (Ensminger et al., unpubl. data). Yolk proteins are implicated in embryonic and hatchling development, and eggs with lower protein levels produced smaller hatchlings (Roulston & Cane, 2002; Shepherd, Crowther, Desai, Hales, & Ozanne, 1997). Since CORT-treated mothers had smaller sons, it is possible that these females allocated less protein

to eggs of male offspring, but not female offspring. Quantifying the amount and composition of nutrients allocated to male versus female eggs would be informative in this regard. An alternative mechanism for the smaller size of sons of CORT-treated females could be differential sensitivity of male versus female embryos to CORT (Love et al., 2005), since CORT applied to females at these doses more than doubles the concentrations of CORT in the yolk of eggs immediately after laying (Ensminger et al., unpubl. data). There could also be effects of CORT on maternal behavior (e.g., thermoregulation; Preest & Cree, 2008), which could have had sex-specific effects on offspring.

Our results, thus, show that CORT-treated females are investing more in daughters (i.e., they are investing as much as control females), seemingly at the cost of their sons. CORT-implanted female side-blotched lizards (*Uta stansburiana*) were found to also invest more in daughters than sons (Sinervo & Denardo, 1996). This pattern is predicted if preferentially investing in daughters provides an evolutionary advantage in poor environments (Love et al., 2005). Overall, larger eastern fence lizard hatchlings have been shown to have increased survival (Parker & Andrews, 2007), possibly explained by larger hatchlings having greater competitive advantage and growth rate throughout their development and usually becoming bigger adults (Sorci, Clobert, & Belichon, 1996). Larger female hatchlings, specifically, may also have greater reproductive output as adults (Reynolds & Gross, 1992; Tinkle & Ballinger, 1972). Within this species, males are not limiting and females are able to reproduce as long as they are of reproductive size. Possibly, in poor environments CORT-treated females are providing their daughters with an advantage from hatching, allowing them to reach a larger size at maturation, which is correlated with fecundity (Tinkle & Ballinger, 1972). Further, only 42% of males reproduce even in good environments (Haelen et al., 2003), and investing in sons when conditions are poor may not guarantee success. Thus, in poor environments mothers may be maximizing their evolutionary fitness by preferentially investing in the evolutionarily safer sex; their daughters.

Our results support the hypothesis that CORT may be a mechanism driving sex-specific reproductive investment. In our study, this effect was expressed as a decrease in the size and condition of sons of CORT-treated versus control mothers rather than an increase in investment in daughters, likely because lower-quality females, that maintained individual egg and clutch size, were not capable of directly investing more resources in one sex (i.e., daughters). Investing in daughters when environmental conditions are poor may reflect a strategy to maximize lifetime fitness by investing in the safer sex. This study adds to growing evidence that maternal CORT may provide a mechanistic link between maternal quality and sex-biased investment in offspring. There is further need for future studies examining the fitness consequences of CORT-induced reductions in reproductive investment to continue to assess any sex-specific effects, and importantly to examine the potential adaptive significance of these effects.

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