Do Gravid Females Become Selfish? Female Allocation of Energy during Gestation

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ABSTRACT

Net energy availability depends on plasma corticosterone concentrations, food availability, and their interaction. Limited net energy availability requires energy trade-offs between self-maintenance and reproduction. This is important in matrotrophic viviparous animals because they provide large amounts of energy for embryos, as well as self-maintenance, for the extended period of time during gestation. In addition, gravid females may transmit environmental information to the embryos in order to adjust offspring phenotype. We investigated effects of variation in maternal plasma corticosterone concentration and maternal food availability (2 × 2 factorial design) during gestation on offspring phenotype in a matrotrophic viviparous lizard (*Pseudemoia entrecasteauxii*). Subsequently, we tested preadaptation of offspring phenotype to their postnatal environment by measuring risk-averse behavior and growth rate using reciprocal transplant experiments. We found that maternal net energy availability affected postpartum maternal body condition, offspring snout-vent length, offspring mass, offspring performance ability, and offspring fat reserves. Females treated with corticosterone allocated large amounts of energy to their own body condition, and their embryos allocated more energy to energy reserves than somatic growth. Further, offspring from females in high plasma corticosterone concentration showed compensatory growth. These findings suggest that while females may be selfish when gestation conditions are stressful, the embryos may adjust their phenotype to cope with the postnatal environment.

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Introduction

Animals must allocate energy to a number of key physiological processes, including self-maintenance (i.e., survival), reproduction, and growth. However, energy availability can be limited and varies according to temporal and spatial scales (e.g., Bronikowski and Arnold 1999; Mills et al. 2008). A large number of studies have investigated the energy trade-offs between survival and current reproduction: current reproduction may be costly to survival, especially when food levels are low (Shine and Schwarzkopf 1992; Schwarzkopf 1993, 1994; reviewed in Stearns 1976; Zera and Harshman 2001). Matrotrophic (i.e., mothers supply energy for the embryos during embryogenesis) viviparous animals, in particular, must simultaneously balance energy allocation to survival and to current reproduction during gestation in response to gestational conditions (e.g., energy availability) to avoid risk of maternal death (reviewed in Gaillard and Yoccoz 2003). The degree of maternal energy support for embryonic development during gestation may significantly affect offspring phenotype and, therefore, offspring fitness (Fowden et al. 2006; Micke et al. 2010; Cadby et al. 2011; Harris and Seckl 2011). Several studies have suggested that high maternal energy availability during gestation allows females to invest more energy in embryonic development. Such energy allocation is regarded as a selective advantage of matrotrophic reproduction (Trexler and DeAngelis 2003; Marsh-Matthews and Deaton 2006; Ostrovsky et al. 2009; Itonaga et al. 2012). If this is so, the relationship between food availability and the energetic costs of self-maintenance (i.e., net energy availability) during gestation may play a key role in the evolution of matrotrophic reproduction.

Energetic costs of self-maintenance may vary between individuals in response to ecological and physiological conditions, such as stress, body size, and immunity (French et al. 2007; Careau et al. 2008; Homyack et al. 2010). Most animals spend large amounts of energy on self-maintenance compared with reproduction and growth (Cruz-Net and Bozinovic 2004; Steyermark et al. 2005). For example, a viviparous reptile, *Sceloporus jarrovi*, allocates about 85% of its energy budget to self-maintenance (Congdon et al. 1982). Therefore, even small fluctuations in costs of self-maintenance during gestation may have significant impacts on energy allocation to current reproduction in matrotrophic viviparous animals.

Stressors increase secretion of the vertebrate glucocorticoids (e.g., corticosterone in reptiles or cortisol in mammals [Greenberg and Wingfield 1987; Guillette et al. 1995]). Corticosterone influences metabolic functions, such as regulating energy intake, storage, and mobilization (e.g., Astheimer et al. 1992; Wingfield et al. 1998; Sapolsky et al. 2000; Hayward and Wing-

field 2004). In general, short-term increases in plasma corticosterone concentration may improve the ability to cope with stressful conditions, such as predatory attacks and competition, by mobilization of stored energy resources to fuel increased locomotion activities, facilitating movement and foraging behavior (Astheimer et al. 1992; Belthoff and Dufty 1995; Miles et al. 2007). At the same time, however, corticosterone may downregulate processes such as reproduction and growth that are not required for immediate survival. Chronic elevation of plasma corticosterone concentration due to shortage of prey items, high predator density, high parasite load, or poor body condition can, for example, suppress reproduction (Tilbrook et al. 2000; Wingfield and Sapolsky 2003; Petes et al. 2007) because high plasma corticosterone concentration increases energy expenditure for self-maintenance (McEwen and Wingfield 2003; Cote et al. 2006; Lynn et al. 2010). Thus, elevated plasma corticosterone concentrations in reproducing females are typically viewed as having a negative impact on reproductive investment in terms of the energy budget.

Despite the effects of maternal corticosterone on maternal energy budgets, exposure of embryos to corticosterone is essential for embryonic development because this hormone promotes normal maturation of the central nervous system, including the brain (reviewed in Harris and Seckl 2011). Furthermore, embryos are exposed to corticosterone of maternal origin during embryonic development, which can generate variation in offspring phenotype and life history in a variety of taxa (e.g., mammals: Kapoor and Matthews 2005; Harris and Seckl 2011; birds: Hayward and Wingfield 2004; Saino et al. 2005; reptiles: Meylan and Clobert 2005; Uller and Olsson 2006; Cadby et al. 2010; fish: Gagliano and McCormick 2009). This maternal corticosterone-induced phenotypic plasticity in offspring may be considered as a preadaptation to stressful environments (Dufty et al. 2002; Meylan and Clobert 2005; Love and Williams 2008; Gagliano and McCormick 2009). The embryos may receive environmental information (e.g., low food availability, which increases corticosterone secretion [see Kitaysky et al. 2001; Lynn et al. 2010]) through maternally transmitted corticosterone and adjust their phenotype during embryogenesis (reviewed in Groothuis et al. 2005; also see Cadby et al. 2010). For example, in common lizards, *Lacerta vivipara*, embryos exposed to a high concentration of corticosterone produced offspring with slow growth rates and high vigilance (Meylan and Clobert 2005; Uller and Olsson 2006). These offspring characteristics may enhance survival and reduce risk of predation, potentially in sex-specific ways (e.g., Sih 1997; Hayward and Wingfield 2004; Meylan and Clobert 2005), especially when predator density is high and/or when food availability is low, because risk of predation increases with foraging activity (Huey and Pianka 1981; Abrams 1991; Lima 1998). In addition, slow growth rate may be advantageous when food availability is low because of a reduction in energy requirements (Olsson and Shine 2002; Hayward and Wingfield 2004). Notably, if these preadaptations are to postnatal low net energy availability, maternal net energy availability during gestation may be the cue for the production of adaptive offspring risk-averse behavior (e.g., high vigilance and reduced risk of predation at foraging) and growth rate (Marshall and Uller 2007; Uller 2008).

In viviparous reptiles, links between the effects of maternally transmitted corticosterone (i.e., the maternal signal) during embryonic development and offspring preadaptation are currently neither well understood nor generalized compared with birds and mammals (see Cadby et al. 2010). Most of our knowledge in reptiles has come from studies that concentrated on using one species, *L. vivipara* (e.g., Meylan and Clobert 2004, 2005; Uller and Olsson 2006; Vercken et al. 2007). Maternal effects and their expression (in this case, maternal corticosterone) are context dependent and therefore vary between species and situations (e.g., Pen et al. 2010; Uller et al. 2011). Furthermore, transmission of maternal corticosterone to the embryos during gestation in viviparous reptiles has been demonstrated only in *Pseudemoia entrecasteauxii* (Itonaga et al. 2011*b*). Viviparity in reptiles has evolved on more than 100 independent occasions (Blackburn 1992), with considerable variation in physiological pathways, including placental structure (Blackburn 1992; Stewart and Thompson 2000; Blackburn and Vitt 2002). Variation in placental structure induces differences in placental functions among viviparous reptiles (Thompson et al. 2004, 2006). Therefore, the maternal signal (e.g., corticosterone concentration, which is related to energy availability and predation risk) may pass into the embryos differently between different species of viviparous reptiles. We currently lack empirical studies from different viviparous reptile species to understand how maternal signals may induce preadaptation of the offspring in viviparous reptiles.

In this study, we focused on how the interaction between maternal plasma corticosterone concentration and maternal food availability during gestation (using a 2 × 2 factorial design) affects both maternal and offspring phenotypic traits in a matrotrophic viviparous reptile. Risk-averse behavior and growth rate may be associated with fitness in reptiles (Sinervo and Adolph 1994; Cooper 1997; Warner and Andrews 2002; Martín et al. 2003). These characteristics in offspring may be determined by the maternal signal during embryonic development. Therefore, we also focused on whether risk-averse behavior (i.e., measuring time to re-emerge after simulated predatory attacks [see Uller and Olsson 2006]) and growth rates (using corticosterone-manipulated reciprocal transplant experiments [see Cadby et al. 2010]) are adaptive to postnatal conditions. To address these aims, we used a small viviparous lizard, *P. entrecasteauxii. Pseudemoia entrecasteauxii* are one of the few known viviparous lizards with significant matrotrophy (Itonaga et al. 2011*a*, 2011*b*; in this study). Their nutrient provisioning for embryonic development is roughly half from the yolk and half via the placenta (Stewart and Thompson 1993). In this species, therefore, variation in maternal plasma corticosterone concentration and maternal food availability (i.e., variation in maternal net energy gain) during gestation may significantly affect reproductive investment and, subsequently, offspring phenotype.

Table 1: Characteristics of maternal *Pseudemoia entrecasteauxii* and offspring from females that had combinations of the corticosterone (CORT) treatment and food supply throughout pregnancy

	High food supply		Low food supply	
	CORT treatment	Control	CORT treatment	Control
Total sample size	20	20	20	20
No. mothers giving birth	18	20	18	19
Gestation length (d)	49.3 ± 1.30	47.3 ± .70	49.6 ± 1.00	48.7 ± 1.00
Initial SVL (mm)	46.80 ± .89	45.97 ± .83	45.70 ± .57	47.20 ± .96
Postpartum SVL (mm)	47.5 ± .79	47.2 ± .77	46.6 ± .06	48.1 ± .88
Postpartum body condition[a]	.7 ± .23	.1 ± .21	−.1 ± .53	−.7 ± .22
Embryonic mortality (%)	10.0 ± 5.60	6.0 ± 3.20	12.0 ± 5.30	10.0 ± 4.40
Clutch size	3.21 ± .22	3.00 ± .22	3.11 ± .17	3.42 ± .19
Relative clutch mass	.3 ± .02	.3 ± .02	.3 ± .01	.3 ± .02
Offspring:				
SVL (mm)	20.6 ± .13 (18)	21.1 ± .19 (20)	20.4 ± .21 (18)	20.8 ± .18 (19)
Body mass (mg)	176.8 ± 3.2 (18)	192.3 ± 6.2 (20)	170.1 ± 5.1 (18)	184.0 ± 4.8 (19)
Sprint speed (m s^{-1})	.39 ± .02 (18)	.43 ± .01 (20)	.38 ± .02 (18)	.40 ± .02 (19)
Fat reserves relative to body mass[a]	.5 ± .23 (17)	−.5 ± .19 (19)	−.2 ± .23 (18)	.2 ± .25 (19)
Risk-averse behavior (s)	75.7 ± 20.6 (15)	84.8 ± 18.4 (17)	128.9 ± 37.4 (16)	83.4 ± 17.6 (14)

Note. Characteristics of maternal *P. entrecasteauxii* include gestation length, initial and postpartum snout-vent length (SVL), postpartum body condition, embryonic mortality, litter size, and relative clutch mass related to parturition from combinations of the corticosterone treatment (treatment and control) and food supply (high and low) throughout pregnancy, and characteristics of offspring include SVL, body mass, sprint speed, fat reserves relative to body mass, and risk-averse behavior at birth. Values are means ± SE (*n*).

[a]Student residual.

Material and Methods

Maternal Treatments during Gestation

We collected 80 female *Pseudemoia entrecasteauxii* in early pregnancy from the Peter Murrell Reserve in Kingston, southern Tasmania, Australia (41°50′S, 146°36′E; altitude 116 m) from October 15 to October 31, 2008, shortly after ovulation took place. The lizards were taken to the Herpetology Laboratory at the School of Zoology at the University of Tasmania, where they were measured for snout-vent length (SVL; ±0.01 mm) and weighed (±0.001 g). The presence of ovulated follicles was confirmed by palpation of the female's abdomen. We examined the effects of maternal plasma corticosterone concentration and maternal food availability during gestation on reproductive efforts using a 2 × 2 factorial design. Gravid *P. entrecasteauxii* were randomly assigned to one of four gestation conditions: (1) corticosterone treatment group with high food availability, (2) corticosterone treatment group with low food availability, (3) control group with high food availability, and (4) control group with low food availability.

The amount of food (high and low) per lizard during gestation was based on our standard husbandry conditions (i.e., six mealworms per lizard per week; e.g., Swain and Jones 2000) and average volume of food eaten during gestation in *P. entrecasteauxii* (Brown 1988). We fed nine mealworms per lizard per week for females in high food availability groups and four mealworms per lizard per week for females in low food availability groups. In addition, most mealworms that we supplied were eaten during the experiment. Maternal plasma corticosterone concentrations were artificially elevated using the noninvasive method of Knapp and Moore (1997), as previously used on Tasmanian skinks (*Niveoscincus ocellatus*) by our group (Cadby et al. 2010); dose and volume of treatment were adjusted for the mean body mass of *P. entrecasteauxii*. We made a corticosterone oil solution with 30 mg of authentic corticosterone (Sigma) in 10 mL of sesame oil. Females in the corticosterone treatment group (i.e., mimicked stressful condition; Meylan and Clobert 2005; Vercken et al. 2007; Cadby et al. 2010) were painted on their dorsal surface every 2 d with 4.0 μL of this corticosterone oil solution until parturition. Females in the control group were painted dorsally every 2 d with 4.0 μL of sesame oil (oil alone) until parturition (Cadby et al. 2010). To confirm a difference in mean plasma corticosterone concentrations between treatment groups, an additional 17 pregnant females were collected. Each of these females was allocated to either the corticosterone treatment or the control treatment for 1 wk. Three hours after their last treatment, blood was collected (nine samples from the corticosterone treatment group, eight samples from the control group) to determine plasma corticosterone concentrations using radioimmunoassay (see Jones and Bell 2004). There was a significant difference in plasma corticosterone concentration between treatment groups ($t = 2.200$, df = 11, $P < 0.0001$), with plasma corticosterone concentration being nearly three times higher in the corticosterone treatment group (133 ± 7.8 ng mL^{-1}) than the control group (45 ± 3.3 ng mL^{-1}).

Female *P. entrecasteauxii* were maintained in an air-conditioned room under bright fluorescent tube lighting (~20,000 lux) and ultraviolet lighting (14L : 10D). Each lizard was housed

Table 2: Summary of results of statistical analyses: effects of maternal corticosterone (CORT) treatment and maternal food availability (combinations of CORT treatment and control and high and low food supply) during gestation and their interaction on maternal and offspring characteristics in *Pseudemoia entrecasteauxii*

	CORT condition			Food supply			CORT condition × food		
Variable	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
Gestation length	2.21	1, 76	.14	.84	1, 76	.36	.30	1, 76	.58
Postpartum maternal SVL	1.02	1, 76	.32	.02	1, 76	.90	1.27	1, 76	.26
Postpartum maternal body condition	**6.99**	**1, 76**	**<.01**	**13.01**	**1, 76**	**<.01**	.01	1, 76	.94
Embryonic mortality	.78	1, 67	.38	.57	1, 67	.45	.01	1, 67	.92
Litter size	.07	1, 73	.80	.61	1, 73	.44	1.69	1, 73	.20
Relative clutch mass	1.90	1, 67	.17	.48	1, 67	.49	1.16	1, 67	.28
Offspring:									
SVL	**6.04**	**1, 71.5**	**.02**	1.70	1, 71.5	.19	.01	1, 71.5	.91
Body mass	**9.33**	**1, 67.9**	**<.01**	2.97	1, 67.9	.09	.04	1, 67.9	.84
Sprint speed	**4.04**	**1, 51.6**	**.04**	.52	1, 51.6	.47	1.39	1, 51.6	.24
Fat reserves relative to body mass	2.02	1, 69	.16	.01	1, 69	.92	**10.87**	**1, 69**	**<.01**
Risk-averse behavior	.21	1, 58	.65	.73	1, 58	.39	.13	1, 58	.72

Note. Significant results are in bold. SVL, snout-vent length.

individually in a plastic terrarium (300 mm × 200 mm × 100 mm) that contained paper pellets as a substrate, one terra-cotta saucer and one wooden block as a basking site, and one plastic plate as a shelter; water, supplemented with multivitamins, was available ad lib. Basking heat was supplied by a 25-W spotlight positioned ~80 mm above a basking surface. The basking lights were turned on 12 h d^{-1}, which reflected the natural basking opportunities during gestation in Tasmania (Wapstra et al. 2009, 2010; While and Wapstra 2009). The thermal gradient in each plastic terrarium was 12°–40°C. These conditions allowed free thermoregulation when the basking lights were on. All lizards were maintained in these conditions until parturition. Each plastic terrarium was positioned randomly within the experimental group and was repositioned weekly to minimize position effects.

Maternal and Offspring Characteristics

For each female, the following data were recorded: gestation length, postpartum SVL (±0.01 mm), postpartum mass (±0.001 g), litter size, and relative clutch mass. Gestation length was estimated by assuming that all females ovulated more or less synchronously, using a start date of November 1 (for a similar justification, see Swain and Jones 2000; Wapstra et al. 2009; Uller et al. 2011). Relative clutch mass was calculated as total offspring mass/postpartum female body mass immediately after parturition (Vitt and Congdon 1978; Shine 1980). Postpartum body condition was subsequently calculated as the residual of the regression of log-transformed postpartum mass and postpartum SVL (because of the allometry of body size; e.g., Cadby et al. 2010). For all offspring, we recorded whether they were born alive or dead, their SVL (±0.01 mm), and body mass (±0.1 mg) at birth. Sprint speed (m s^{-1}), as a measure of whole-body performance (Wapstra 2000), was measured on the day of birth. Before the sprint trials, each lizard was held in a petri dish in a water bath (28° ± 1°C) for 30 min to reach the optimal temperature for sprinting for this species (Melville 1998). Sprint time along the track (120 cm long × 8 cm wide), which was lined with fine sandpaper for traction, was recorded by five equally spaced (20 cm) infrared light beams. The fastest sprint speed over a 20-cm distance was taken as the maximum sprint speed (e.g., Melville and Swain 2003). Lizards were encouraged to run by occasional gentle taps on the tail using a soft paint brush.

One offspring from each litter was used to measure risk-averse behavior on the day of birth following the methodology of Uller and Olsson (2006). Each offspring was transferred individually from its home cage to a large test area (500 mm × 400 mm × 350 mm) with sand substrates containing several wooden blocks and plastic plates for shelter at one end and basking heat supplied by a 25-W spotlight positioned ~80 mm above one terra-cotta saucer at the other end. When released into the large test area, offspring soon moved to a basking spot, and they usually stayed (some of them moved around the test area, but they soon returned to a basking spot) until we started tests. A predator attack was mimicked by startling and chasing the lizard with a paintbrush, at which time it disappeared under the shelters. The time from the simulated attack until the lizard reappeared and resumed basking was used as a measure of risk-averse behavior. The trial was discontinued if the lizard did not reappear after 10 min (see Uller and Olsson 2006).

In litters of two or more offspring, one offspring was selected haphazardly and killed on the day of birth to determine dry fat reserves. Each offspring was killed by decapitation after injection of phenolbarbitone (500 μL kg^{-1}) diluted to 1 : 100. *Pseudemoia entrecasteauxii* store fat as both abdominal fat bodies and in caudal fat stores. The abdominal fat bodies were dissected out, transferred to a preweighed (±0.1 mg) Eppendorf tube, and dried in a 60°C oven for at least 2 d; the tube was reweighed

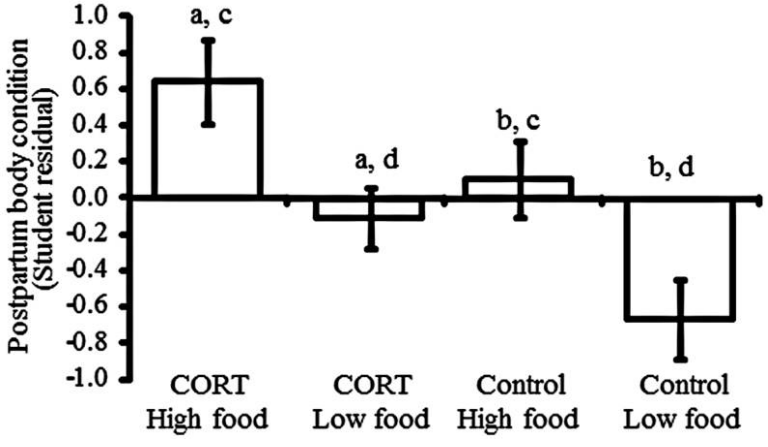

Figure 1. Postpartum maternal body condition in *Pseudemoia entrecasteauxii*. Terms indicate the maternal gestation condition: CORT, females that had the corticosterone treatment; control, females that had the control treatment (i.e., oil alone); high food, high food supply; low food, low food supply. Values are means ± SE. Letters indicate significance.

(±0.1 mg) to determine the dry mass of the abdominal fat bodies. To estimate the mass of caudal fat storage for each sample, we used the method of Chapple and Swain (2002), modifying the volume of diethyl ether for the small size of the offspring. The tail was removed at the highest fracture plane, cut into small pieces, and transferred to a preweighed (±0.1 mg) Eppendorf tube. The tail was then dried in a 60°C oven for at least 2 d, and the tube was reweighed (±0.1 mg). The dried tail mass was calculated as (dried tail + tube mass) − tube mass. The dried tail was then immersed in diethyl ether (1 mL) for at least 2 d to dissolve the lipid stores and then transferred to fresh preweighed (±0.1 mg) Eppendorf tubes and placed in a fume cabinet overnight to allow the diethyl ether to evaporate completely. The tube was then reweighed (±0.1 mg) to determine the mass of tail minus fat, and the mass of fat was calculated accordingly.

Offspring Growth Rate

One offspring per litter was selected haphazardly. We measured offspring growth rate in response to postnatal corticosterone treatment using reciprocal transplant experiments. Offspring were allocated into one of two treatments (either postnatal corticosterone treatment or postnatal control group). This means that the postnatal corticosterone treatments for half of the offspring were identical to those their mothers had experienced during gestation, while the other half of the offspring received a postnatal treatment different from that experienced by their mothers. Every 2 d, we painted either 0.5 μL of corticosterone oil solution (i.e., the same corticosterone concentration as for mothers) or 0.5 μL of sesame oil (oil alone) onto the dorsal surface of offspring. Offspring were otherwise held as described for females. Offspring were fed human baby food (Heinz pear flavor) and supplemented with multivitamins, calcium powder, and protein powder three times per week. We measured offspring SVL weekly for 5 wk (e.g., Wapstra 2000; Cadby et al. 2010). Growth rate was calculated using the slope of the least squares regression line of offspring SVL against time.

All research was carried out with the approval of the Animal Ethics Committee (A0010213) of the University of Tasmania and a permit from the Department of Primary Industries, Water, and Environment (FA08176).

Statistical Analyses

All statistical analyses were performed with SAS 9.1 for Windows.

Maternal Characteristics. Differences in initial maternal SVL between maternal treatments were examined using one-way ANOVA. Influence of maternal gestation conditions (i.e., corticosterone treatment and food availability) on maternal characteristics—including gestation length, postpartum SVL, postpartum body condition, litter size, and relative clutch mass—were examined using full-model two-way ANOVA. Maternal corticosterone treatment (corticosterone treatment, control) and food availability (high, low) were considered as fixed factors. We have also examined embryonic mortality among treatments. It was evaluated with generalized liner mixed models using the GLIMMIX procedure in SAS. Embryonic mortality was as proportion of stillborn offspring plus undeveloped eggs in a litter. Maternal corticosterone treatment (corticosterone treatment, control) and food availability (high, low) were considered as fixed factors, and the analysis considered the full model including interactions. Assumptions of normality were checked by examining plots of standardized residuals against estimated values and the normal probability curve of the residuals.

Offspring Characteristics. The influence of maternal gestation conditions (i.e., corticosterone treatment and food availability) and their interaction on offspring phenotype—including SVL,

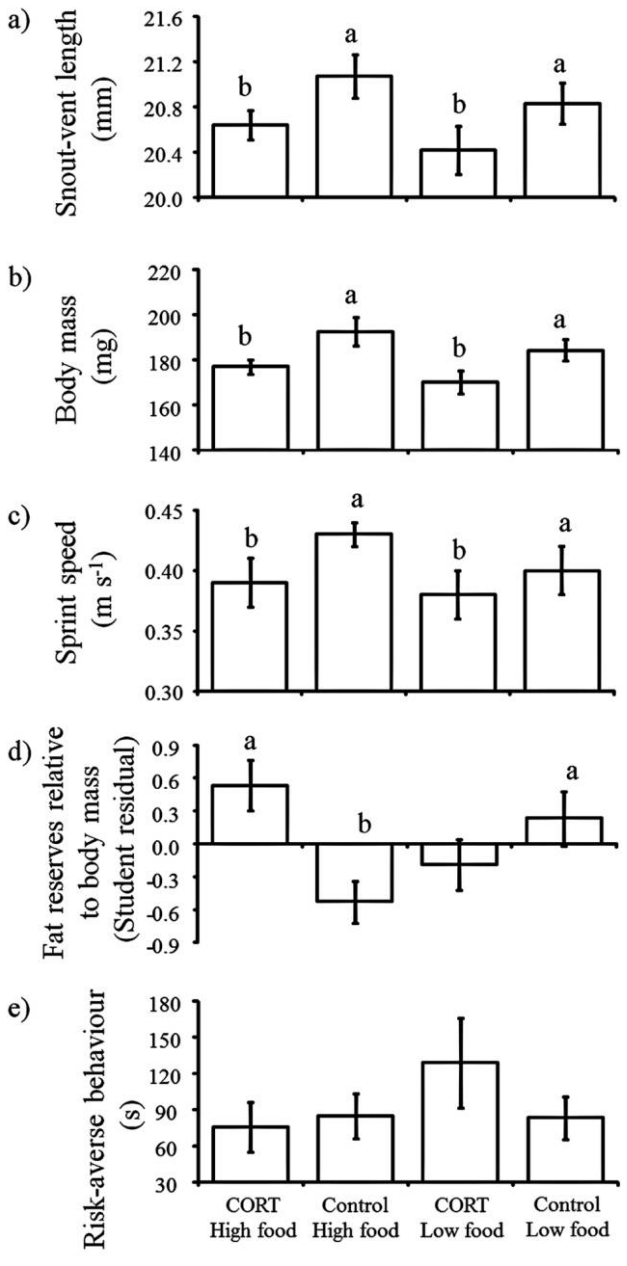

Figure 2. Characteristics of offspring *Pseudemoia entrecasteauxii*, including snout-vent length (*a*), body mass (*b*), sprint speed (*c*), fat reserves relative to body mass (*d*), and risk-averse behavior (*e*) at birth from females that had combinations of the corticosterone (CORT) treatment and food supply throughout pregnancy. Terms indicate the maternal gestation condition: CORT, females that had the corticosterone treatment; control, females that had the control treatment (i.e., oil alone); high food, high food supply; low food, low food supply. Values are means ± SE. Letters indicate significance.

body mass, and sprint speed—were examined using full mixed-model ANOVA. In the mixed-model ANOVA, maternal identity was treated as a random factor to account for litter effects. Fat reserves and risk-averse behavior were examined using full-model two-way ANOVA. In general, body mass and fat reserves are positively correlated (Sinervo et al. 1991). In this study, this assumption was supported overall ($r^2 = 0.4502$, $P < 0.0001$) and also within each maternal treatment. To examine differences in offspring fat reserves, we therefore used residuals (i.e., fat reserves relative to body mass), which were generated from a regression analysis of all values for offspring fat reserves (abdominal fat bodies plus caudal fat storage) against offspring body mass. Maternal corticosterone treatment and maternal food availability during gestation were considered as fixed factors. Data for offspring body mass were square root transformed, and data for offspring sprint speed and risk-averse behavior (time to re-emerge) were log transformed to meet the assumptions of ANOVA.

Offspring Growth Rate. We used a full-model three-way ANOVA to analyze the effect of maternal corticosterone treatment and maternal food availability during gestation, offspring postnatal corticosterone treatment, and their interactions on offspring growth rate. Maternal corticosterone treatment, maternal food availability, and offspring postnatal corticosterone treatment were considered as fixed factors. Data for growth rate were square root transformed to meet the assumptions of ANOVA.

Results

Maternal characteristics and offspring characteristics at birth (for all live-born offspring) from each maternal treatment are summarized in table 1, and the statistical results are summarized in table 2. There was no difference in initial maternal SVL among treatments ($r^2 = 0.03$, $F_{3,77} = 0.77$, $P = 0.52$). There were no differences in maternal characteristics—including gestation length, postpartum maternal SVL, litter size, and relative clutch mass—among treatments (tables 1, 2). Postpartum maternal body condition was influenced by both maternal corticosterone treatment during gestation and maternal food availability during gestation, but not by their interaction (table 2). Both females treated with corticosterone during gestation and females with abundant food during gestation had high postpartum maternal body condition (fig. 1). There was no difference in embryonic mortality between maternal treatments (tables 1, 2).

Maternal corticosterone treatment during gestation influenced offspring SVL and offspring body mass and had marginally significant effects on offspring sprint speed, although there was no effect of maternal food availability during gestation and no interaction effect of maternal corticosterone and maternal food availability during gestation on these offspring phenotypic traits (table 2). Corticosterone-treated females produced smaller and lighter offspring with slower sprint speed than the control females (SVL: Cohen's $d = 0.53$, effect-size $r = 0.27$; body mass: Cohen's $d = 0.65$, effect-size $r = 0.31$; sprint speed: Cohen's $d = 0.35$, effect-size $r = 0.17$; fig. 2*a*–2*c*).

All females (control or corticosterone treated) with low food availability during gestation tended to produce small offspring,

Table 3: Summary of results of statistical analyses: effects of maternal corticosterone (CORT) treatment and maternal food availability (combinations of CORT treatment and control and high and low food supply) during gestation, postnatal offspring CORT treatment (postnatal CORT treatment and postnatal control), and their interactions on offspring growth rates in *Pseudemoia entrecasteauxii*

Source	*F*	df	*P*
Maternal plasma CORT	1.01	1, 49	.30
Maternal food	1.18	1, 49	.28
Offspring plasma CORT	**5.18**	**1, 49**	**.02**
Maternal plasma CORT × maternal food	.24	1, 49	.63
Maternal plasma CORT × offspring plasma CORT	**5.28**	**1, 49**	**.02**
Maternal food × offspring plasma CORT	.64	1, 49	.43
Maternal plasma CORT × maternal food × offspring plasma CORT	1.91	1, 49	.17

Note. Significant results are in bold.

although the results were not significant (table 2; fig. 2*a*, 2*b*). The interaction between maternal corticosterone treatment and maternal food availability during gestation affected offspring dry fat reserves relative to body mass (table 2). Post hoc tests (Ryan-Einot-Gabriel-Welsch multiple range tests) revealed that corticosterone-treated females with high food availability and control females with low food availability during gestation produced offspring with larger fat reserves relative to body mass than the control females with high food availability (fig. 2*d*). Differences in absolute fat reserves among treatments were very similar to fat reserves relative to body mass (interaction between maternal corticosterone treatment and maternal food availability during gestation: $F_{1,69} = 4.98$, $P = 0.0289$; full-model two-way ANOVA). Maternal gestation conditions (i.e., corticosterone treatment and food availability) and their interaction did not affect offspring risk-averse behavior (fig. 2*e*). Overall, there were strong effects of corticosterone treatment on most offspring traits as well as effects of the interaction between corticosterone and food treatments on only offspring fat reserves relative to body mass.

Offspring Growth Rate

An interaction between maternal corticosterone treatment and offspring postnatal corticosterone treatment significantly influenced offspring growth rates (table 3). Post hoc tests showed that among offspring that had the postnatal control treatment, offspring from corticosterone-treated females showed faster growth rates (0.012 ± 0.001 mm d^{-1}, birth at small SVL) than offspring from control females (0.009 ± 0.001 mm d^{-1}, birth at large SVL; fig. 3). In addition, this faster offspring growth rate offset the differences between maternal treatments in SVL at birth by week 5 postbirth ($F_{1,29} = 0.52$, $P = 0.4756$; one-way ANOVA).

Discussion

We expected to find strong effects of maternal net energy availability during gestation on offspring characteristics because both maternal plasma corticosterone concentration and maternal food availability during gestation affect maternal net energy gain (Preest and Cree 2008; Tsai et al. 2009) and, therefore, the degree of reproductive investment. While it is possible that low food levels may have had a direct effect on maternal plasma corticosterone (Kitaysky et al. 1999; Lynn et al. 2010), given that the two treatments did not interact strongly, we are confident that our treatments altered female energy pathways in two independent ways as we intended. We demonstrated that in *Pseudemoia entrecasteauxii*, maternal net energy availability during gestation affected postpartum maternal body condition (effects of both maternal corticosterone treatment and maternal food availability), offspring SVL, offspring body mass, offspring performance ability (effects of maternal corticosterone treatment), and offspring fat reserves (effects of an interaction between maternal corticosterone treatment and maternal food availability). In addition, the strong effects of corticosterone on both maternal and offspring phenotypic traits imply that some of these phenotypic traits may be determined by direct maternal corticosterone effects rather than maternal net energy effects because maternal corticosterone can alter the energy allocation between physiological processes (e.g., Frigerio et al. 2001). Further, it is well established that corticosterone has powerful direct effects on embryonic development and consequently affects phenotypic traits (e.g., Fowden and Forhead 2004; Fowden et al. 2006).

Female *P. entrecasteauxii* treated with corticosterone during gestation exhibited higher postpartum body condition than control-treated females (fig. 1) at a cost to their offspring (i.e., females with high body condition produced small offspring). This finding suggests that gravid *P. entrecasteauxii*, if stressed, may spend more energy on self-maintenance (i.e., enhance maternal survival) than on current reproduction and, as described by Marshall and Uller (2007), is regarded as a selfish maternal effect, where mothers reduce current reproductive investment and gain long-term fitness benefits. Priority of energy allocation may depend on other life-history traits, including longevity and survival risk (Schwarzkopf 1994). *Pseudemoia entrecasteauxii* are annual breeders (Murphy et al. 2006), and if adult *P. entrecasteauxii* show high survival rates, allocation of more energy

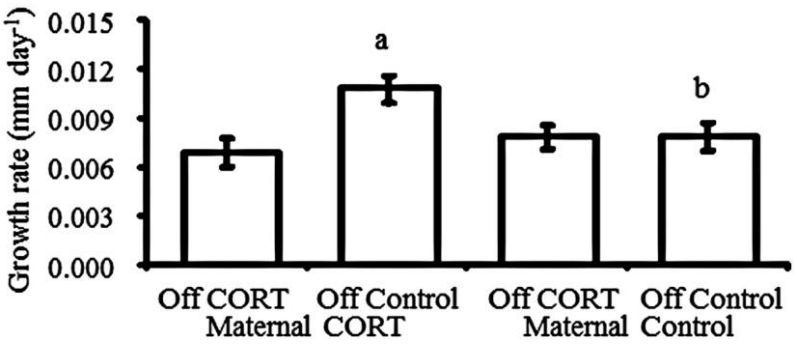

Figure 3. Results of the interaction between maternal corticosterone (CORT) treatment during pregnancy and postnatal offspring CORT treatment on offspring growth rates over 5 wk in *Pseudemoia entrecasteauxii*. Terms indicate the experimental condition: maternal CORT, females that had the corticosterone treatment; maternal control, females that had the control treatment (i.e., oil alone); off CORT, offspring that had the corticosterone treatment; off control, offspring that had the control treatment (i.e., oil alone). Values are means ± SE. Letters indicate significance.

into survival rather than current reproduction may be selected when gestation conditions are stressful. In reptiles, low postpartum maternal body condition may induce low survival rates in the following year (Avery 1970; Bonnet et al. 1999), but high body condition can enhance reproductive output in the following season (Doughty and Shine 1998). In contrast, *Niveoscincus ocellatus*, another matrotrophic lizard with annual reproduction, did not demonstrate a selfish strategy in response to elevated maternal stress levels (Cadby et al. 2010). This suggests that there are species-specific strategies regarding energy allocation (Bonier et al. 2009). Presumably, such differences may reflect differences between species in life-history traits, such as adult mortality.

Production of small offspring by female *P. entrecasteauxii* treated with corticosterone during gestation (fig. 2) may be interpreted as a negative (to offspring) transmissive effect (sensu Marshall and Uller 2007) rather than as an adaptive response (e.g., Marshall and Uller 2007). However, when we take the offspring fat reserves into account (i.e., effects of an interaction between maternal corticosterone treatment and maternal food availability), the observed offspring phenotype may be a preadaptation to stressful environments. We found that small offspring had larger fat reserves relative to body mass than large offspring (fig. 2), suggesting that when stressed, embryo *P. entrecasteauxii* may allocate more energy to fat reserves rather than to somatic growth, which may enhance offspring survival in a stressful postnatal environment (Kitaysky et al. 1999; Hayward and Wingfield 2004; Lynn et al. 2010). However, when gestation conditions are too adverse (e.g., in this case, the elevated corticosterone treatments with low food availability), maternal nutrient support to embryos may be very limited, resulting in small offspring with potentially poor fat reserves (see also Cote et al. 2010). However, small offspring size in not necessarily maladaptive. Advantages of small offspring size have been shown in the viviparous *Lacerta vivipara* (e.g., Meylan and Clobert 2005; Vercken et al. 2007). Small body size may reduce predation risk when predator density is high (Hayward and Wingfield 2004), and when food is limited, small offspring may show high survival rates because they require little energy for self-maintenance compared with larger offspring (Olsson and Shine 2002; Oksanen et al. 2003). Thus, we suggest that in *P. entrecasteauxii*, small size and large fat reserves relative to body mass may have advantages in stressful postnatal environments, but this may not be possible in all situations when maternal net energy availability is compromised even further.

The small offspring produced by the corticosterone-treated females grew rapidly if allocated to the postnatal control group compared with other offspring (fig. 3). We suggest that rapid growth rate in nonstressful environments may be advantageous because in *P. entrecasteauxii*, large adult body size in both sexes is an important component of reproductive success (i.e., courtship and fecundity; Stapley 2006, 2008; Stapley and Keogh 2006; our unpublished data: maternal initial SVL and litter size showed a strong positive relationship). Therefore, rapid growth in offspring *P. entrecasteauxii* may be important to offset negative impacts of maternal corticosterone during embryonic development on offspring size when conditions allow. Indeed, we found that among postnatal control-treated offspring, the significant differences in offspring SVL that resulted from maternal corticosterone treatment had disappeared by 5 wk postbirth. Some studies have suggested that compensatory growth may be associated with significant costs, such as high mortality, especially when energy availability is limited (Olsson and Shine 2002; Dmitriew and Row 2007; Donelson et al. 2009). We do not know the impacts of these fitness trade-offs related to energy allocation under natural conditions for our study species. It is possible that the costs of compensatory growth in *P. entrecasteauxii* may be low because we found that compensatory growth occurred only when the postnatal net energy availability was high.

In this study, offspring with fast growth rates in response to postnatal corticosterone treatments may result from maternal corticosterone-induced offspring programming. In *P. entrecas-*

teauxii, circulating maternal plasma corticosterone is directly transferred into the embryos (Itonaga et al. 2011*b*) and consequently may affect offspring metabolic programming (e.g., modification of the development of the control center for hormonal systems [i.e., hypothalamo-pituitary-adrenal axis]). It is well documented in the mammalian literature that maternal glucocorticoid exposure during embryogenesis induces metabolic programming in offspring to cope with the stressful postnatal environment (reviewed in Fowden et al. 2005; also see Love and Williams 2008). Similarly, in mammals, development of a thrifty phenotype (i.e., metabolic adaptation, which results in a reduced requirement of energy for growth) during embryogenesis as a result of malnutrition can lead to increased growth and fat deposition if postnatal nutrient availability is higher than predicted in utero (Hales and Barker 2001; Ozanne and Hales 2002; Symonds et al. 2003). Development of a thrifty phenotype may also occur in *P. entrecasteauxii* during embryogenesis because *P. entrecasteauxii* demonstrates high levels of matrotrophic reproduction, which has a great scope for energetic programming. In *P. entrecasteauxii*, therefore, the embryo may be able to adjust their own phenotypic traits—including body size, fat reserves, and metabolic rate—in response to the maternal signal during gestation to enhance their own fitness.

In contrast to previous studies (e.g., Meylan and Clobert 2005; Cadby et al. 2010), we observed differences in offspring growth rates in response to postnatal treatments (corticosterone versus controls). In addition, we found no maternal effects on offspring risk-averse behavior. This finding is also inconsistent with a previous study (Uller and Olsson 2006) that found that in *L. vivipara*, maternal corticosterone treatment during gestation affected risk-averse behavior of the offspring. However, maternal effects do not necessarily translate to effects on all offspring phenotypic traits, and effects vary within and between species and situations (Janczak et al. 2007; Warner et al. 2009; Cadby et al. 2010; Mainwaring et al. 2010; Pen et al. 2010; Uller et al. 2011). *Pseudemoia entrecasteauxii* are a wary and secretive species (Hutchinson et al. 2001). Therefore, stressors such as predation may not link to preprogramming of offspring risk-averse behavior in this species.

In conclusion, our findings suggest that, when exposed to adverse conditions, gravid *P. entrecasteauxii* preferentially allocate energy to their own body condition rather than to current reproduction. At the same time, their offspring display phenotypic plasticity in response to factors such as maternally transmitted corticosterone and/or restricted energy supply. As a result, females may store energy for survival and future reproduction and adapt offspring phenotype to postnatal environments. In this study, we found novel effects of elevated maternal corticosterone during gestation on phenotypic traits, including postpartum maternal body condition and offspring growth rate. However, we do not know whether such findings are a species-specific response to stressors. Further investigations using a variety of viviparous reptiles will be required if these questions are to be answered. Such studies will also contribute to our understanding of the evolutionary significance of matrotrophic viviparity in reptiles.

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