

Effects of pregnancy on body temperature and locomotor performance of velvet geckos

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ABSTRACT

Pregnancy is a challenging period for egg laying squamates. Carrying eggs can encumber females and decrease their locomotor performance, potentially increasing their risk of predation. Pregnant females can potentially reduce this handicap by selecting higher temperatures to increase their sprint speed and ability to escape from predators, or to speed up embryonic development and reduce the period during which they are burdened with eggs ('selfish mother' hypothesis). Alternatively, females might select more stable body temperatures during pregnancy to enhance offspring fitness ('maternal manipulation hypothesis'), even if the maintenance of such temperatures compromises a female's locomotor performance. We investigated whether pregnancy affects the preferred body temperatures and locomotor performance of female velvet geckos *Amalosia lesueurii*. We measured running speed of females during late pregnancy, and one week after they laid eggs at four temperatures (20°, 25°, 30° and 35 °C). Preferred body temperatures of females were measured in a cost-free thermal gradient during late pregnancy and one week after egg-laying. Females selected higher and more stable set-point temperatures when they were pregnant (mean = 29.0 °C, T_{set} = 27.8–30.5 °C) than when they were non-pregnant (mean = 26.2 °C, T_{set} = 23.7–28.7 °C). Pregnancy was also associated with impaired performance; females sprinted more slowly at all four test temperatures when burdened with eggs. Although females selected higher body temperatures during late pregnancy, this increase in temperature did not compensate for their impaired running performance. Hence, our results suggest that females select higher temperatures during pregnancy to speed up embryogenesis and reduce the period during which they have reduced performance. This strategy may decrease a female's probability of encountering predatory snakes that use the same microhabitats for thermoregulation. Selection of stable temperatures by pregnant females may also benefit embryos, but manipulative experiments are necessary to test this hypothesis.

1. Introduction

Pregnancy is a challenging period for squamate reptiles because of the energetic and physiological costs imposed by developing eggs and embryos. During late gestation, females encumbered with eggs or developing embryos may suffer a substantial reduction in locomotor performance (Bauwens and Thoen, 1981; Seigel et al., 1987; Shine, 1980; Van Damme et al., 1989; Webb, 2004; but see Zamora-Camacho et al. (2014)). Pregnant females may also bask overtly or spend more time basking (Schwarzkopf and Shine, 1991), which in concert with their handicapped running speeds, could potentially increase a female's risk of predation (Shine, 1980). In addition, females may also modify

their thermoregulatory regimes or strategies during pregnancy, and pregnant females may maintain higher, lower or more thermally stable temperatures than males or non-reproductive females (Charland, 1995; Chiaraviglio, 2006; Lourdais et al., 2008; Peterson et al., 1993; Webb et al., 2006; but see Zamora-Camacho et al. (2016)).

Two hypotheses have been proposed to explain the observed shifts in female body temperatures during pregnancy. The 'maternal manipulation hypothesis' posits that because embryos are sensitive to temperature fluctuations during development, selection should promote female traits that enable embryos to develop under more favourable or stable conditions than would otherwise be available (Shine, 1995, 2012). Maternal traits that could enhance offspring

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viability include precise thermoregulation during pregnancy (Webb et al., 2006), careful selection of nest sites (Shine and Harlow, 1996) and shivering thermogenesis (Shine et al., 1997). Because up to one third of embryonic development occurs in utero in egg laying species, these adaptive traits should be present in both oviparous and viviparous taxa (Andrews and Mathies, 2000). An alternative hypothesis for maternal thermoregulatory changes during pregnancy suggests that females adopt behaviour that maximise their lifetime reproductive success, irrespective of whether such changes entail costs to developing embryos (Schwarzopf and Andrews, 2012a). Thus, females might select higher temperatures during pregnancy to increase their sprint speeds and ability to escape from predators (Schwarzopf and Andrews, 2012a). Maintenance of higher temperatures could also accelerate embryogenesis (Angilletta et al., 2000), allowing females to reduce the period during which they are encumbered with eggs or embryos, thereby increasing their chances of survival and reproduction in the future (Schwarzopf and Andrews, 2012a).

Here, we investigate whether female velvet geckos, *Amalosia lesueurii* (formerly *Oedura lesueurii*, Oliver et al. (2012)) modify their thermoregulatory regimes during pregnancy. Velvet geckos are small, long-lived lizards that occupy rock outcrops which also are inhabited by predatory snakes that feed on geckos (Webb and Shine, 1998a). To thermoregulate, pregnant females must shelter under thin, sun-exposed rocks, a strategy that potentially increases their chances of encountering predatory snakes. Thus, changes in thermoregulation during pregnancy could potentially influence their survival. We asked three questions: (1) Does carrying a clutch impair the locomotor performance of pregnant females? (2) Do females change their preferred body temperature when they are pregnant? (3) Does a pregnant female's thermoregulatory behaviour compensate for any impairment in maternal locomotor performance? To answer these questions, we measured the preferred body temperature of pregnant females and post-partum females in a cost-free laboratory thermal gradient. We also measured the locomotor performance of the females in a race track during late pregnancy and one week after they laid eggs at four test temperatures (20°, 25°, 30° and 35 °C). We chose these temperatures because they encompass the range of temperatures likely to be encountered by pregnant females in the wild.

2. Methods

2.1. Animal collection and husbandry

We collected pregnant female geckos (eggs were visible through the translucent venter) from rock outcrops near Nowra (160 km south of Sydney, 34°52'24.65"S, 150°21'59.28"E) and Dharawal National Park (DNP, 67 km south of Sydney, 34°14'14.59"S, 150°54'57.25"E) during October and early November, 2014. Females were placed in cloth bags and transported to the University of Technology Sydney. Upon arrival at the laboratory, females were individually housed in ventilated rectangular plastic cages (Sistema NZ 2.0 L, 220×150×60 mm) in a room (22 °C) with a 12:12 photoperiod. Each cage contained an identical shelter consisting of a plastic tube (PVC, 80×40 mm) cut in half-lengthwise, a vermiculite substrate, and a water dish. The cages were placed on racks, with one end of the cage placed on a timer-controlled heating cable (set to 32 °C) to create a thermal gradient of 22–32 °C within each cage during the day, dropping to room temperature (22 °C) at night. Females were fed live crickets twice a week and were provided with water *ad libitum*.

2.2. Measurement of preferred body temperatures

We used a laboratory thermal gradient to estimate the preferred body temperature of the geckos. The gradient consisted of four

rectangular wooden runways (120 cm long, 10 cm wide, and 60 cm high). In each runway, we placed two identical plastic tubes (120×4 cm) cut in half-lengthwise to provide a suitable shelter. This enabled geckos to move the length of the thermal gradient while still concealed, with the only difference being temperature. Heat was provided at one end of each compartment via a 250 W infrared lamp. Cooling was achieved by pumping chilled water through copper pipe affixed to the underside of the apparatus and connected to a water bath (Haake F3 K Circulating Water Bath) at the opposite end. This system provided lizards with access to a temperature gradient ranging from 10 to 50 °C.

To record female body temperatures, we taped a miniature data logger (Thermochron iButton, Dallas Semiconductor, Dallas, Texas, USA; diameter 15 mm, height 6 mm) set to record temperatures every 5 min to the dorsal surface of each gecko. Each test subject was placed in a separate runway for 24 h before trials commenced. Temperatures of 35 pregnant females (mean SVL=55.6 mm) with complete tails were recorded during late pregnancy (median time prior to oviposition=21 days, range 1–37 days) and one week after they had laid eggs. To estimate T_{set} for each individual, we used the bounds of the central 50% of the selected body temperatures (Hertz et al., 1993; Kearney and Predavec, 2000; Medina et al., 2009).

Once the pregnant females laid eggs we weighed each egg (nearest 0.01 g) with a digital balance and measured the length and diameter (to nearest 0.1 mm) with digital vernier calipers. Egg volumes were calculated using the equation given by Maritz and Douglas (1994) with $\lambda = 0.75$ (Doughty, 1997). Relative clutch mass (RCM) was calculated as clutch weight/prepartum mass and 'burden' was calculated as the mass difference between the prepartum and postpartum mass of each female (Miles et al., 2000).

2.3. Measurement of locomotor performance

We measured the running speed of each female during late pregnancy and one week after they laid eggs. To measure running speeds of geckos we used a 1 m long and 7 cm wide wooden racetrack with a carpet substrate marked with black lines at each 20 cm interval. For each trial, we placed a gecko on the racetrack and encouraged it to run by tapping it on the tail with an artist's paintbrush. Trials were run between 10:00–15:00 h and each female was tested at four temperatures (20, 25, 30 and 35 °C), in a random sequence. The geckos were left to acclimate to the trial temperature for at least 1 h before testing, and geckos were tested at different temperatures on different days. Each trial involved chasing the gecko along the runway three times, with a 30-min rest between runs. The gecko's body temperature was recorded with a digital thermometer (Cool Tech, CT663, spot diameter=13 mm) before and immediately after each trial. A video camera (Panasonic HC-V110) placed directly above the racetrack filmed each trial. The videos were analyzed frame-by-frame (25 frames per second) using a commercial video programme (Cyberlink Power Director 10). From the video footage, we determined the geckos' maximum speed over 0.2 m and 1.0 m.

2.4. Statistical analysis

We used two way repeated-measures ANOVA to investigate the effects of temperature and reproductive status on the locomotor performance of females. A paired *t*-test was used to compare the mean, standard deviation, maximum and minimum body temperatures of females before and after they laid eggs. Regression analysis was used to examine the relationship between female SVL, RCM, clutch volume, burden and clutch mass and burst speed at four temperatures. Statistical analyses were performed using SPSS software (Version 23.0).

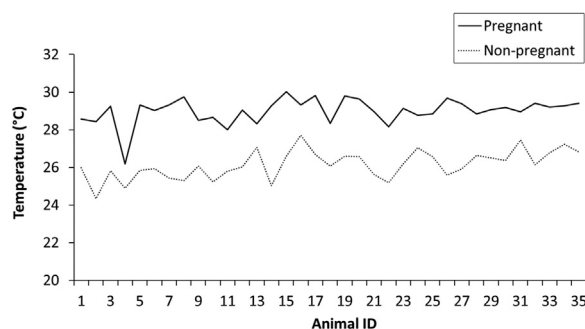


Fig. 1. Mean body temperatures selected by each female gecko in a cost free thermal gradient during late pregnancy (solid line) and one week after they laid eggs (dotted line).

3. Results

3.1. Preferred body temperatures of females during and after pregnancy

The preferred body temperature of females was higher during pregnancy (29.0 °C, SD =0.68) than after pregnancy (26.2 °C, SD =0.76) (paired *t*-test, $t_{34}=-20.26$, $p < 0.001$) (Fig. 1). During pregnancy, females maintained a narrower temperature range (27.8–30.5 °C) than when they were non-pregnant (23.8–28.7 °C). Intra-individual variance in body temperature was smaller for females when they were pregnant (mean=5.21, SD =1.51) compared to when they had laid eggs (mean=12.26, SD=3.52) (paired *t*-test, $t_{34}=11.337$, $p < 0.001$). In addition, the mean minimum temperatures maintained by females were higher when they were pregnant (22.8 °C) than non-pregnant (17.7 °C; $t_{34}=-13.86$, $p < 0.001$), and this was also true for mean maximum temperatures (34.6 °C versus 33.2 °C, $t_{34}=-5.263$, $p < 0.001$).

3.2. Effects of pregnancy on locomotor performance

Female SVL and RCM were significantly positively correlated ($r = 0.53$), as were burden ($r = 0.70$), clutch mass ($r = 0.74$), and clutch volume ($r = 0.50$). As might be expected, clutch mass was highly correlated with clutch volume ($r = 0.67$), RCM ($r = 0.80$) and burden ($r = 0.94$). SVL, RCM or burden were not significantly correlated with burst speed at any of the test temperatures (Table 1). That is, although larger females carried larger clutch mass, the physical burden of carrying eggs did not influence their burst speed during late pregnancy.

Female sprint speed over 0.2 m was affected by both reproductive condition and temperature (two-way repeated measures ANOVA: reproductive condition $F_{1,42} = 112.65$, $p < 0.001$; temperature $F_{3,126} = 34.47$, $p < 0.001$; interaction $F_{3,126} = 10.01$, $p < 0.001$). Females ran slower at all four test temperatures when they were pregnant than non-pregnant (Fig. 2). During late pregnancy, females ran fastest at 25 °C and slowest at 35 °C (pairwise comparisons), but after they had laid eggs, females ran fastest at 30 °C and slowest at 35 °C (Fig. 2). That is, the data suggest that the optimal temperature for sprint speed over 0.2 m was 30 °C in non-pregnant females, and 25 °C in pregnant females.

Table 1

Correlations between female body size (SVL, mass) and reproductive investment (RCM, burden) and sprint speeds over 0.2 m at four test temperatures. None of the correlations was statistically significant.

	Speed 20 °C	Speed 25 °C	Speed 30 °C	Speed 35 °C
SVL	−0.097	0.046	0.093	−0.021
Mass	−0.183	−0.028	0.120	−0.095
RCM	0.024	0.020	0.175	−0.040
Burden	−0.085	−0.035	0.116	−0.029

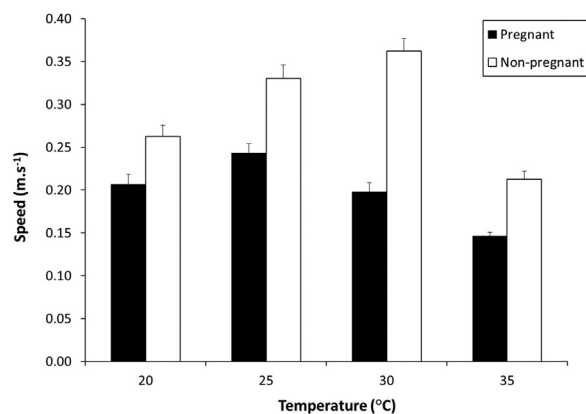


Fig. 2. The effects of reproductive status and body temperature on the sprint speed of velvet geckos over 0.2 m during pregnancy and one week after they laid eggs. Error bars denote standard errors.

Female speed over 1 m was also affected by reproductive condition and temperature (two-way repeated measures ANOVA: reproductive condition $F_{1,42} = 50.85$, $p < 0.001$; body temperature $F_{3,126} = 21.72$, $p < 0.001$; interaction $F_{3,126} = 5.87$, $p = 0.01$). As before, females ran more slowly when gravid than when not gravid, but this effect was only evident at 20, 25 and 30 °C. At 35 °C, the speed of gravid and non-gravid females was similar (Fig. 3).

The number of stops made by females over 1 m was also affected by reproductive condition and temperature (two-way repeated measures ANOVA: reproductive condition $F_{1,42} = 34.82$, $p < 0.001$; body temperature $F_{3,126} = 37.36$, $p < 0.001$; interaction $F_{3,126} = 0.11$, $p = 0.95$). Females made more stops when they were carrying eggs compared to when they were post-reproductive (Fig. 4). Not surprisingly, there were significant negative correlations between the number of stops and female body speed (Table 2). That is, females that made more stops along the runway ran slower than females that made fewer stops.

4. Discussion

Pregnancy affected the preferred body temperatures selected by female velvet geckos. During late pregnancy, females in a cost-free thermal gradient selected higher mean temperatures (29.0 °C vs 26.2 °C) and thermoregulated more precisely than they did one week after they had laid eggs. Females also shifted their set-point temperatures upwards during pregnancy, and selected a higher, narrower range of temperatures when pregnant (27.8–30.5 °C) than when they were non-pregnant (23.7–28.7 °C). Similar shifts in thermoregulation, with females maintaining higher or more stable temperatures during pregnancy, have been documented in both egg laying and viviparous

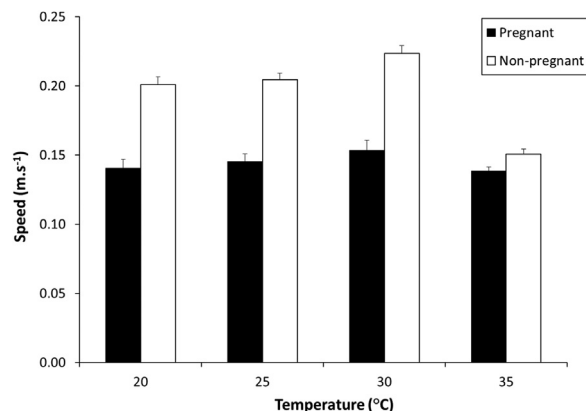


Fig. 3. The effects of reproductive status and body temperature on the maximum speed of velvet geckos over 1 m. Error bars denote standard errors.

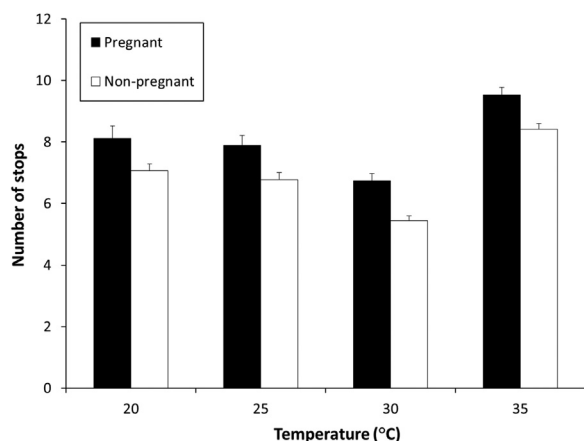


Fig. 4. The effects of reproductive status and body temperature on the number of stops made by female velvet geckos over 1 m. Error bars denote standard errors.

Table 2

Correlations between the mean number of stops made by females along the race track and their mean running speed over the distance of 1 m.

	20 °C	25 °C	30 °C	35 °C
pregnant	−0.760**	−0.726**	−0.333*	−0.578**
Non-pregnant	−0.740**	−0.684**	−0.770**	−0.739**

All correlations were significant at the $P=0.01$ level** or $P=0.05$ * level.

squamates (Peterson et al., 1993; Shine, 2006). One unanswered question is whether females shift their preferred body temperatures to a lower set-point shortly after laying eggs, as could occur if females were anorexic due to depletion of energy stores (Peterson et al., 1993). We could not address this question as we measured the thermal preferences of female one week after oviposition. Another question we could not address is whether non-gravid adult females maintain similar preferred body temperatures to adult males. This was beyond the scope of our study.

Why do female geckos select higher, more stable temperatures during late gestation? According to the maternal manipulation hypothesis, such changes could enhance offspring fitness by providing ‘optimal’ temperatures for developing embryos. Studies on egg laying squamates have provided support for this hypothesis. For example, gravid childrens pythons (*Antaresia childreni*) that were maintained at set-point temperatures selected by females during pregnancy (31.5 °C) produced faster offspring than females that were placed in chambers that mimicked thermoregulation by non-reproductive females (Lorion et al., 2012). In the skink *Bassiana duperreyi*, pregnant females were maintained at three temperature regimes (cold: 17 ± 5 °C, warm: 22 ± 5 °C, hot: 27 ± 5 °C) inside incubators for two weeks, and eggs were then incubated under the same conditions simulating nest temperatures. Offspring from the hot treatment, which mimicked maternal thermoregulation, ran faster than offspring from the other two treatments (Shine, 2006).

At present, we have no data on optimal temperatures for embryonic development in *A. lesueuri*. However, the set point temperatures selected by pregnant females are significantly higher than the inter-quartile range of temperatures (19.8–25.3 °C) recorded inside natural nests (Pike & Webb, unpubl. data). Thus, we doubt that the higher temperatures selected by females enhance offspring fitness, for two reasons. First, incubation experiments revealed that eggs incubated at higher temperatures (mean = 27.0 °C, 14–37 °C) produced smaller hatchlings than eggs incubated at lower temperatures (mean = 23.2 °C, 10–33 °C) (Dayananda et al., 2016). Second, maintenance of high maternal temperatures during pregnancy is likely to accelerate embryogenesis leading to earlier hatching (Shine, 2006). While earlier

hatching may benefit hatchlings in cold climates due to the short time period available for growth prior to hibernation (Burger, 1998; Olsson and Shine, 1997), it could be a handicap for other species that encounter high summer temperatures. In exposed rock outcrops, hatchling velvet geckos which are born earlier in summer will encounter lethally high temperatures under rocks (Dayananda et al., 2016; Webb and Shine, 1998b). In such circumstances, hatchlings will have to shuttle between thermally suitable microsites, thereby increasing their risk of predation on exposed rock outcrops (Webb and Whiting, 2005). Interestingly, in the lizard *Psammotromus algeris*, hatchlings emerged from eggs early in summer at cooler high-elevation sites, but emerged later in summer at hotter low-elevation sites. This suggests that the timing of birth matches environmental conditions, thereby allowing hatchlings to avoid high temperatures that restrict activity (Zamora-Camacho et al., 2013).

Plausibly, females might select higher temperatures during pregnancy to enhance their ability to flee from predators. However, we found no evidence to support this. On average, females ran 31% more slowly during late pregnancy, and selection of higher temperatures did not offset this decrease in sprinting ability (Figs. 2 and 3). This decrement in speed is similar to that reported for oviparous and viviparous squamates (Bauwens and Thoen, 1981; Olsson et al., 2000; Shine, 1980; Webb, 2004). In oviparous species, the decrement in speed may result from the increased mass coupled with the reduced stride length that results from the distension of the abdomen (Miles et al., 2000). Alternatively, locomotor impairment could be associated with physiological changes associated with pregnancy (Olsson et al., 2000). Notably, we found no correlations between measures of reproductive investment and sprint speed (Table 1), suggesting that the physical burden was not responsible for the decrement in speed during pregnancy in geckos. Future manipulative studies are necessary to determine the mechanical and physiological pathways associated with loss of speed in pregnant lizards (Miles et al., 2000).

Interestingly, females also modified their behaviour during pregnancy. At all test temperatures, females made more stops along the runway when they were carrying eggs compared to when they were non-pregnant. Such changes in behaviour have been reported in other lizards and might reflect either difficulties associated with running and/or a lack of motivation to run (Miles et al., 2000), and reliance on crypsis during encounters with predators (Bauwens and Thoen, 1981). In the field, hatchling and adult geckos often run and stop, and human observers have difficulty spotting motionless geckos as they are well camouflaged. Thus, crypsis might be an effective means of avoiding predation in this species. Because both pregnant and non-pregnant females rely on crypsis, it is probable pregnant females made more stops along the racetrack due to difficulties associated with running. Irrespective of why they made more stops on the runway, pregnant females were slower sprinters over short and longer distances.

Overall, our results are consistent with the hypothesis that females select higher temperatures during pregnancy to speed up embryogenesis and reduce the period during which they have reduced performance (Schwarzkopf and Andrews, 2012a). Our data suggest that females prioritise survival, rather than short-term thermal benefits for developing offspring, as is predicted for a long-lived species (Schwarzkopf and Andrews, 2012b). Selection of stable temperatures by pregnant females might provide positive benefits to embryos, but manipulative experiments, similar to those carried out on other taxa (Lorion et al., 2012; Shine, 2006; Webb et al., 2006), are necessary to test this hypothesis.

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