Functional Ecology 1997
11, 498–507

Influence of pregnancy on the thermal biology of the lizard, *Sceloporus jarrovi*: why do pregnant females exhibit low body temperatures?

T. MATHIES and R. M. ANDREWS
Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061–0406, USA

Summary

1. Selected body temperatures of female lizards, *Sceloporus jarrovi*, were measured on a photothermal gradient during late pregnancy and again when postpartum, and pregnant females were subjected to one of three fluctuating temperature regimes that simulated body temperatures of (1) pregnant females, (2) postpartum females or (3) allowed normal thermoregulation.
2. Overall, females selected lower body temperatures when pregnant (mean = 32·0°C) than when postpartum (mean = 33·5°C).
3. Females regulated body temperature more precisely when pregnant than when postpartum as judged by their smaller variances in body temperature throughout the day.
4. When pregnant, females selected a lower mean maximum body temperature (mean: pregnant = 32·8°C; postpartum = 34·5°C) than when postpartum, but selected mean minimum body temperatures did not differ.
5. None of the experimental temperature treatments was detrimental to pregnant females. Female body length increased during pregnancy but the rate of increase did not differ among treatments. Moreover, length-adjusted body mass of postpartum females did not differ among treatments.
6. Pregnant females that experienced postpartum body temperatures produced neonates that were smaller in body mass and length than pregnant females that experienced pregnant body temperatures and females that were allowed to thermoregulate.
7. For neonates resulting from the postpartum body temperature treatment, the disparity in the body length, but not mass, was still observed at 9 days of age, although survival and growth of neonates was high and did not differ among treatments.
8. The results demonstrate that pregnant females could maintain higher postpartum body temperatures without compromising their physical condition, but select relatively low body temperatures, presumably to avoid decrements in offspring fitness.

Key-words: Embryonic development, offspring fitness, temperature, thermoregulation, viviparity
Functional Ecology (1997) **11**, 498–507

Introduction

Many reptiles regulate their body temperature within a relatively narrow range by using behavioural adjustments such as shuttling between different thermal microclimates (Cowles & Bogert 1944; Huey 1982). Regulation may include fine-grained adjustments that match body temperature to functions with physiological optima, such as digestion or sprint speed (Patterson & Davies 1978; Huey 1982; Stevenson, Peterson & Tsuji 1985). However, there may be other explanations for the association between body temperatures and physiological processes besides active temperature selection (Huey 1982). For example, shifts in body temperature could be the result of active selection of new thermal optima or the result of passive acceptance of higher or lower temperatures as the result of some ecological constraint on thermoregulation.

Temperature shifts (both upwards and downwards) associated with reproductive status are well documented among some species of lizards and snakes (Daut & Andrews 1993 and included references). A postulated benefit of an upward shift in body temperature by reproductive (gravid or pregnant) females is that developmental rates, which are temperature dependent (Muth 1980), would increase. The resultant shortened incubation period could reduce costs of reproduction (e.g. decreased survival or future fecun-

dity of females) by reducing the time over which these costs are incurred (Shine 1980, 1983; Seigel & Fitch 1984). In addition, shortened incubation periods in temperate zone environments might enhance offspring fitness by increasing the time available for growth and accumulation of energy reserves before cessation of activity in autumn. On the other hand, a postulated benefit of a downward shift in body temperature is enhanced survival of embryos; high incubation temperatures are detrimental to embryonic development (Vinegar 1974; Gutzke & Packard 1987). Thus, if normal body temperatures reduce offspring fitness, females would benefit from a shift to lower body temperatures when they become reproductive.

Are the body temperatures exhibited by reproductive females actively selected or passively accepted? Because observed shifts in body temperatures have presumptive physiological benefits, one explanation for the relatively high or low body temperatures of reproductive females is that they are actively selected. Alternatively, body temperatures may reflect ecological constraints (Hertz 1992; Hertz, Huey & Stevenson 1993). For example, if the burden of the clutch causes females to become more susceptible to predators (Shine 1980), females may compensate by adopting a more cryptic behaviour(s) (e.g. reduce the frequency and extent of movement). Such an increase in cryptic behaviours could limit a female's thermoregulatory opportunities and thereby preclude regulation of body temperatures at preferred levels. Observations on lacertid lizards support this conjecture (Braña 1993). Data from laboratory studies on the viviparous lizard, *Sceloporus jarrovi* Cope (Phrynosomatidae), were used to gain insight into why pregnant females exhibit lower body temperatures than postpartum females. *Sceloporus jarrovi* is a particularly appropriate study species because its reproductive (Goldberg 1971) and thermal biology (Beuchat 1986) are well documented, and field-active females exhibit lower mean body temperatures when pregnant than when postpartum (32·0°C and 34·5°C, respectively; Beuchat 1986).

This study addresses two complementary questions. First, do pregnant females actively select, or passively accept, low body temperatures? This question can be answered by measuring the body temperatures that females select on a thermal gradient when pregnant and postpartum. Use of a thermal gradient in a laboratory setting ensures that lizards can select body temperatures with minimal ecological costs and constraints. It was predicted that if field-active pregnant females exhibit low body temperatures because postpartum body temperatures are physiologically stressful to the female, her offspring, or both, then pregnant females on a thermal gradient would be expected to select lower body temperatures than postpartum females. Alternatively, if field-active pregnant females exhibit low body temperatures because of exogenous constraints on thermoregulation, then we would expect pregnant females on a thermal gradient to select the same high body temperatures as postpartum females.

Second, if postpartum body temperatures are physiologically stressful, do they affect the pregnant female, the embryos, or both? It was predicted that if postpartum body temperatures are stressful to pregnant females, then pregnant females maintained at postpartum body temperatures should exhibit signs of poor health or decreased survivorship. On the other hand, if postpartum body temperatures are stressful to embryos, then offspring incubated at postpartum body temperatures should exhibit features associated with low fitness.

Materials and methods

COLLECTION AND ASSIGNMENT OF FEMALES TO EXPERIMENTS

Pregnant females ($n=70$) were collected in the Chiricahua Mountains of southeastern Arizona in the vicinity of the Southwestern Research Station (SWRS) near Portal, Arizona between 30 April and 2 May 1995. Each female was given a unique toe clip and a corresponding number was painted on her back for identification. Females were randomly assigned to one of two experiments: (1) those used to measure selected body temperatures ($n = 18$) (next section) and (2) those used to determine the effect of postpartum *vs* pregnant body temperatures on pregnant females and their offspring ($n = 52$) (see Incubation experiment).

MEASUREMENT OF SELECTED BODY TEMPERATURES

Maintenance conditions

Pregnant females were housed in a $2{\cdot}5 \times 4{\cdot}0$ m^2 dirt-floored outdoor enclosure. Three $16 \times 32 \times 34$ cm^3 cinderblock cairns within the enclosure provided numerous perches and refugia. Drinking water was provided daily by running water through a shallow trench that ran alongside the bases of the cairns. Females were fed daily with crickets dusted with vitamin powder.

On 5 July, all 18 females (all postpartum) were transported to indoor facilities at Blacksburg, Virginia, where they were maintained in two $33 \times 77 \times 47$ cm^3 slate-bottomed terraria. Room temperature was maintained at ≈ 24°C and light from windows determined photoperiod. Illumination was provided by two broad spectrum fluorescent light bulbs (Vita-lite™, Duro-Light Corp., Fairfield, NJ, USA) resting on top of the terraria. One heat lamp (150 W) suspended over the end of each terraria allowed behavioural thermoregulation. Lights were turned on and off each day at 07·00 and 17·00 hours MST, respectively. Water was provided daily by squirting water into each cage to form a small temporary pool. Females were fed as above.

Testing apparatus

Selected body temperatures (see Pough & Gans 1982) of pregnant females were measured in Arizona in a room in which temperature was maintained at ≈ 24·0°C. Light from a door at each end of the room determined the photoperiod. Selected body temperatures of postpartum females were measured in Blacksburg in the same room where they were housed.

The testing apparatus consisted of a corrugated cardboard box with a 2·5-cm thick Styrofoam bottom to reduce temperature fluctuations. Cardboard strips were used to divide the box into six 37 × 200 cm^2 runways. *Sceloporus jarrovi* normally uses rock substrates and pregnant females tend to remain close to crevices where they can take refuge (Smith & Ballinger 1994). A rock surface was therefore simulated by painting the runway floors with glue and then dusting them lightly with sand. Each runway was provided with a 'continuous refugia'. This consisted of a 16-cm wide cardboard strip that ran the entire length of the runway such that the top edge of the strip rested on the runway wall and the bottom edge projected 8·5 cm away from the wall at a height of 3·5 cm above the runway floor. This arrangement allowed females to hide beneath the strip at any point along a runway. A thermal gradient was established by suspending a series of incandescent floodlamps of various wattages at various heights and spacings down the midline of each runway. Hollow aluminium probes with internal thermocouples were placed at evenly spaced intervals along the length of each runway floor and the floodlamps were adjusted so that probe temperatures ranged linearly from ≈ 29 to 41°C (Fig. 1). The average rate of temperature change in the gradient was 0·072°C cm^{-1} or 0·53°C/mean female snout–vent length (SVL). With few exceptions, females perched towards the centre of the gradient. We therefore judged that the range in available body temperatures was considerably wider then necessary for normal thermoregulation.

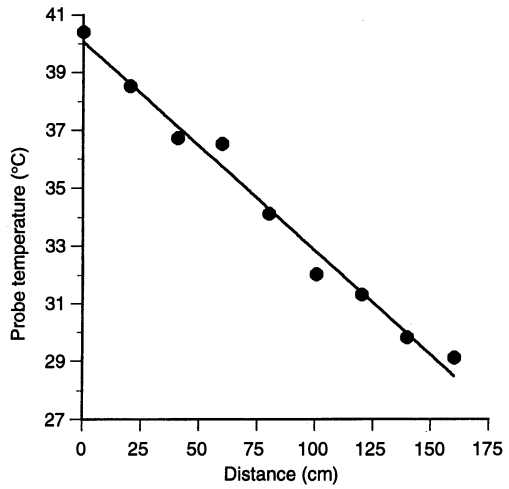

Fig. 1. Representative thermocouple probe temperatures (T_p) on the thermal gradient measured at 20-cm intervals (days). The line indicates the least-squares linear regression of probe temperature on probe position in the gradient. $T_p = 40{\cdot}06 - 0{\cdot}071$ cm, $R^2 = 0{\cdot}98$, $P < 0{\cdot}001$.

Observations

Body temperatures were measured during 15–19 May (pregnant) and 11–15 July (postpartum). Pregnant females were in their last trimester as judged by the first appearance of neonates in the field on 22 May.

The following protocol was used to measure body temperatures. On day 1 at 15·30 h, six females were placed on the gradient, each in an individual runway, where they remained for the following 35·5 h (29·5 h of acclimation and 6 h of observation). Body (cloacal) temperatures were measured at 09·00 h, 12·00 h and 15·00 hours on day 3 with a thermocouple thermometer (Physitemp digital laboratory thermometer, Model: BAT-12, Physitemp Instruments Inc., Clifton, NJ, USA). Each female was removed quickly from its runway (taking care not to disturb the female in the adjacent runway), its cloacal temperature recorded, and then returned to the gradient. This protocol was repeated for successive sets of six females. Females received no food or water while on the gradient. Gradient lights were turned on and off at 07·00 and 17·00 hours MST, respectively.

INCUBATION EXPERIMENT

Temperature treatments and maintenance conditions

During the day, field-active *Sceloporus* lizards typically exhibit a high and relatively constant body temperature, but at night, body temperatures converge on ambient temperatures. A cycling thermal regime was used that approximated the natural thermal environment of *S. jarrovi* because constant temperature regimes are stressful to squamate reptiles (Shine 1983).

Pregnant females were randomly allocated to one of three experimental temperature treatments ($n = 15$, each treatment). Two of the treatment groups were placed into controlled light and temperature chambers (Percival model I–35 L, Percival Manufacturing Co., Boone, IA, USA). Temperatures in both chambers were similar during the inactive period, falling to ≈ 15°C by 23·00 and remaining there until 07·00 the following morning. In one chamber, the temperature during the activity period (09·00–16·00 h) was 35·7°C. This temperature is higher than the observed mean body temperature of field-active postpartum females (34·5°C, Beuchat 1986), but falls within the 95% confidence interval for the mean. We used 35·7°C, as opposed to 34·5°C, because deleterious effects of temperature on physiological processes, if any, would more probably be induced by body temperatures near the extreme, rather than the mean. In the other chamber, the temperature during the activity

period (09·00–16·00 h) was 32°C, the mean field-active body temperature of pregnant females (Beuchat 1986). These two temperature regimes are hereafter referred to as the 35°C and 32°C treatments, respectively. Body temperatures (cloacal) of females in the chambers were measured to verify that females experienced the desired experimental temperature. Actual mean body temperatures of females in the 35°C and 32°C treatments were 35·4°C (n = 14, SE = 0·1°C) and 32·3°C (n = 12, SE = 0·1°C), respectively. Periodically during the experiment, ambient air temperatures in the chambers were recorded at half hour intervals for 24 h and stored in a data logger (OMEGA ® OM-550 DATALOGGER, Omega Engineering, Inc., Stamford, CT, USA). Photoperiod in each chamber was the same as that in Arizona in May (13 L:11D).

A third temperature treatment allowed females to thermoregulate behaviourally (T_{REG} treatment, hereafter). Females in this treatment were maintained in individual terraria each fitted with a 60-W incandescent light bulb over one end. Lights were turned on and off each day at 07·30 and 16·00 hours MST, respectively. These terraria were located in an open-air building where temperatures fluctuated with ambient temperatures. Thus, maintenance conditions experienced by females in the T_{REG} treatment most closely reflected those experienced by pregnant females in the field. Ambient air temperatures at the cool and hot ends of the terraria were recorded (every half hour over 24 h) periodically during the experiment and stored in temperature loggers (HOBO-TEMP-XT™, Onset Instruments, Pocasset, MA, USA) (Fig. 2; temperatures shown are from cool ends of terraria). Temperatures at the hot end of the terraria generally exceeded 37°C during the daily activity period. Direct measurements of body temperatures (cloacal) of females in the T_{REG} treatment during the activity period verified that females were able to regulate body temperatures (mean body temperature = 32·8°C; SE = 0·2°C, n = 14) similar to those of pregnant females in the field. Photoperiod was determined by ambient light from windows.

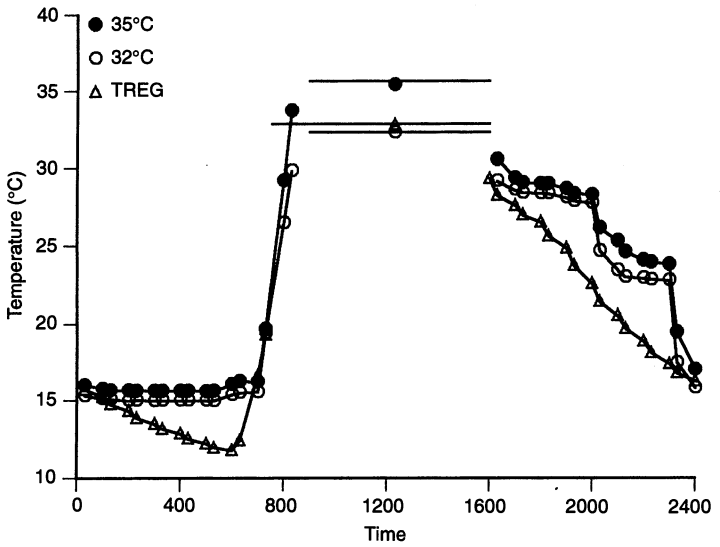

Fig. 2. Mean temperatures (air and body) in environmental chambers (35 °C and 32 °C treatments) and terraria that experienced ambient temperatures (T_{REG} treatment). Symbols connected by a line denote air temperatures for the period females were inactive. Solid horizontal bars represent average body temperatures for the period females were active. Standard errors of the mean body temperatures of females during activity in the 35 °C, 32 °C and T_{REG} treatments were ± 0·1, ± 0·1 and ± 0·2 °C, respectively.

Average body temperatures for females in each of the three treatments were calculated as the means of chamber temperatures for each half-hour interval of the inactive period and the actual mean body temperatures of females for each half-hour interval of the activity period. Temperatures for the 35°C, 32°C and T_{REG} treatments averaged (mean of the 48 means for each treatment) 26·1°C, 24·4°C and 23·7°C, respectively. Temperature profiles for the treatments are summarized in Fig. 2.

On the day that females were put under experimental conditions (3 May), all females were weighed to 0·01 g on an electronic balance (Mettler model PM200) and SVL was measured to the nearest 1 mm. At this time, the mean SVL of females in the 35°C (74·4 ± 1·5), 32°C (72·2 ± 1·4) and T_{REG} (73·1 ± 1·0) treatments did not vary among treatments ($F_{2,41} = 0·68$, $P = 0·51$, one-way ANOVA). Females were placed into individual glass terraria (28 × 22 × 31 cm^3) provided with a large piece of bark, which females could use as a perch or refuge. Terraria were rotated among positions within treatments every 3 days to minimize position effects. Crickets dusted with vitamin powder were provided once or twice each day. Water was provided twice daily by squirting water into each cage to form a small temporary pool. Females were weighed and SVL was measured every 10–12 days and immediately after parturition.

Determination of initial developmental stage

The developmental stage of embryos near (30 April–5 May) the time that females were put under experimental conditions was estimated. To do this, a small incision was made in the abdomen of each of seven females (none included in the experiments) and a section of the oviduct containing one embryo was everted. Embryos could be viewed through the oviduct and shell membrane and their developmental stage determined. Following determination of embryonic stage, embryos were put back in the body cavity, the incision closed with sutures, and the females later released. The mean developmental stage of these embryos was stage 34 and ranged from stage 33 to stage 36 (following Dufaure & Hubert 1961; range of staging sequence: 1–40; parturition at stage 40). Thus, pregnancy was presumably relatively advanced in most females at the outset of the experiment.

Data collection

Terraria were checked daily for the appearance of neonates. On the day of parturition, we recorded the

mass and SVL of the postpartum female and each neonate. Neonates were examined for morphological and behavioural (i.e. movement) abnormalities. One randomly selected neonate from each litter was killed and dried at 50°C for 24 h and weighed to 0·01 g. Another randomly selected neonate was killed and preserved in 70% ethanol for later determination of residual yolk mass. After ≈ 240 days, the residual yolk was removed from neonates, dried and weighed to 0·01 mg. Up to five of the remaining neonates in each litter were used to measure growth rate (additional neonates were released). These neonates were first housed by litter in $40 \times 25 \times 26$ cm^3 terraria under similar conditions as females in the T_{REG} group (above). At 3 days of age, each neonate was reweighed, remeasured and transferred to a common outdoor enclosure identical to that described above, except that it contained numerous rocks scattered about the bases of the cairns. At 9 days of age, each neonate was reweighed and measured for a third time and then released. Neonates were fed *ad libitum* with live insects collected by sweep net and with 2–4 mm crickets dusted with vitamin powder. Water was provided once or twice each day by misting the sides of the terraria and by running water through a trench that ran alongside the bases of the cairns.

STATISTICAL ANALYSES

All analyses were performed using SAS statistical packages (SAS Institute Inc. 1985). Means or least-squared means and their standard errors are presented as mean ± 1 SE. Differences were considered significant at $P < 0{\cdot}05$ unless stated otherwise.

A repeated-measures ANOVA (repeated across the three times of day and between reproductive conditions) was used to compare selected body temperatures of females when pregnant and when postpartum. Tukey's least significant differences was used to identify pairwise differences in the means for each time of day.

Variance in body temperature was used as an index of thermoregulatory precision (Sievert & Hutchison 1988; Hertz *et al.* 1993). Variances were calculated for pregnant and postpartum females at 09·00, 12·00 and 15·00 hours. F_{max} tests were used to test for differences in thermoregulatory precision between pregnant and postpartum females at each of these three times of day. For this analysis and the above analysis of selected body temperatures, the alpha level (0·05) was Bonferroni corrected for the number of tests (three) in each analysis and differences were thus considered significant at $P < 0{\cdot}017$.

The physical condition of females was assessed in two ways: by determining growth rate (change in SVL) and body condition (length-adjusted body mass; Bradshaw 1986) at parturition. Size-specific growth rate of pregnant females was calculated as

$$\text{Size-specific growth rate} = [\ln(SVL_2) - \ln(SVL_1)]/(t_2 - t_1),$$

where SVL_1 and SVL_2 denote the SVL on the day females were placed under experimental conditions and the last measurement of SVL before parturition, respectively, and $t_2 - t_1$ denotes the time in days elapsed between the two measurements of SVL.

Treatment effects on body condition of postpartum females were determined with ANCOVA, using postpartum body mass (measured on the day of parturition) as the dependent variable and SVL at parturition as the covariate.

All analyses involving neonates were based on litter means except those for neonate dry mass, neonate water content and dry residual yolk mass. Neonate water content was determined as the difference between neonate live and dry masses. One-way analyses of variance (ANOVA) were used to determine whether treatment affected date of parturition, neonate mass, neonate SVL and neonate dry mass. Tukey's least significant differences tests were used to identify pairwise differences among the treatment means.

Analysis of covariance (ANCOVA) was used to determine whether treatment affected neonate 'robustness'; that is, how heavy a neonate was relative to its SVL. Treatment effects on neonate water content and residual yolk mass were determined similarly using neonate dry mass as the covariate.

ANCOVAs were used to determine whether body mass and SVL of neonates differed among treatments at the end of each growth period (i.e. days 1–3 and days 3–9). For each analysis, the size measurement (averaged for each litter) immediately preceding the following size measurement was used as the covariate. For example, for the period day 3 to day 9, litter means for SVL on days 9 and 3 were used as the dependent variable and the covariate, respectively.

Results

SELECTED BODY TEMPERATURES OF FEMALES WHEN PREGNANT *VS* POSTPARTUM

Females had significantly lower body temperatures when pregnant than when postpartum (Fig. 3; $F_{1,17} = 12{\cdot}4$, $P = 0{\cdot}001$, repeated-measures ANOVA). Body temperature did not differ among the measurement times during the day for females in either reproductive condition ($P = 0{\cdot}57$). Mean body temperatures of pregnant females were lower than those of postpartum females at 09·00 hours and 12·00 hours (P-values $< 0{\cdot}017$), but not at 15·00 hours ($P > 0{\cdot}017$). The overall mean body temperatures of females when pregnant and postpartum were 32·1 ± 0·1°C and 33·5 ± 0·5°C, respectively.

Females also regulated their body temperatures more precisely when pregnant than when postpartum (Fig. 3). Variance in body temperature when pregnant (09·00 h, 1·1; 12·00 h, 0·8; 15·00 h, 0·4) was lower than when postpartum (09·00 h, 4·9; 12·00 h, 3·0;

15·00 h, 4·0) at all three times of day (P-values < 0·017). Mean minimum body temperatures did not differ between pregnant (31·3 ± 0·2°C) and postpartum (32·4 ± 0·5°C) females (paired t-test; t = 1·8, P = 0·10). However, the mean maximum body temperature of pregnant females (32·8 ± 0·1°C) was lower than that of postpartum (34·5 ± 0·3°C) females (paired t-test; t = 5·1, P < 0·001).

INCUBATION EXPERIMENT

Females gave birth between 20 and 50 days after being placed under experimental conditions. The time to parturition varied among treatments ($F_{2,41}$ = 3·7, P = 0·03). The mean time to parturition was 32·7 ± 1·9 days, 37·3 ± 1·9 days and 40·0 ± 2·0 days for the 35°C, 32°C and T_{REG} treatments, respectively. Time to parturition for females in the 35°C treatment was shorter than that of females in the T_{REG} treatment (P < 0·05). However, time to parturition did not differ between the 35°C and 32°C treatments or between the 32°C and T_{REG} treatments (P-values > 0·05).

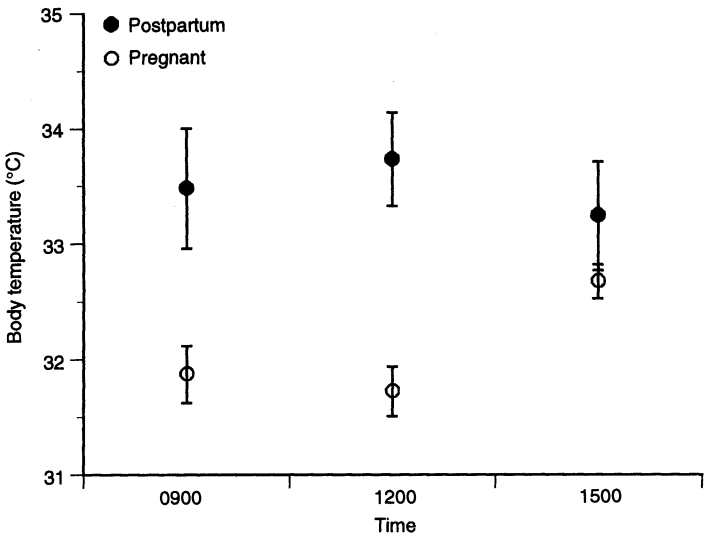

Fig. 3. Mean selected body temperatures (± 1 SE) of female *Sceloporus jarrovi* (n = 18) when pregnant and postpartum measured at three times during the main portion of the daily activity period.

Table 1. Condition of offspring from females that produced at least one abnormal/dead embryo or neonate

		Neonate/embryo condition at parturition		
Treatment	Female no.	Normal (n)	Abnormal (n)	Dead (n)
35 °C	19	0	1	6 (Stage 40)
	33	10	0	1 (Stage 33)
	30	9	1	0
	15	0	1	5 (Stage 40:2; Stage 33–36:3*)
32 °C	29	4	0	1 (Stage 33)

Number following the colon indicates the number of embryos dead at that developmental stage. *Embryos too decomposed to stage precisely.

All females survived to the end of the experiment. On average, females in all treatments increased in SVL over the duration of the experiment. However, growth rates of females did not differ among treatments (ANOVA $F_{2,41}$ = 2·69, P = 0·08). The mean size-specific growth rates of females were 0·0035 ± 0·0007, 0·0044 ± 0·0007 and 0·0060 ± 0·0008 mm day^{-1} for the 35°C, 32°C and T_{REG} treatments, respectively.

Treatment effects on female body condition, if any, should be most apparent at parturition. None was detected; the length-adjusted postpartum body mass of females did not differ significantly among treatments (ANCOVA $F_{2,39}$ = 1·4, P = 0·25). At the grand covariate mean SVL (74·4 mm), the adjusted mean postpartum body masses of females were 11·5 ± 0·2, 11·3 ± 0·2 and 11·8 ± 0·2 g for the 35°C, 32°C and T_{REG} treatments, respectively.

Five females produced dead or abnormal offspring (Table 1). Abnormal neonates were weak and did not move normally. For the four females in the 35°C treatment that produced dead offspring, mortality varied within litters. Nearly all the offspring produced by two females were born dead whereas nearly all of those produced by the other two females were born alive and seemed normal. Of the three live, but abnormal, neonates born to females in the 35°C treatment, only one survived to day 9. All other neonates in the experiment survived, and seemed healthy on day 9.

Neonate mass (live) at parturition and maternal SVL were unrelated (linear regressions; P-values > 0·05), so female size was not used as a covariate in the following analyses. At parturition, neonates from the 35°C treatment were smaller in mass and SVL than neonates from the 32°C and T_{REG} treatments (Table 2). Neonate size did not differ between the 32°C and T_{REG} treatments. Neonates from the 35°C treatment were also smaller in dry mass although this difference was not significant. Neonates from the 35°C treatment had lower water content than neonates from the 32°C and T_{REG} treatments. The small size of neonates from the 35°C treatment was not due to them being born 'prematurely' (i.e. with a relatively large amount of internalized residual yolk); the least-squares means for dry mass of residual yolk did not differ significantly among treatments. While neonates from the 35°C treatment were relatively small, SVL-adjusted neonate mass at parturition did not differ among treatments. Thus, neonates from the 35°C treatment were just as 'robust' for their SVL as neonates from the other treatments.

Differences in neonate size among treatments persisted over time. At 9 days of age, neonates from the 35°C treatment were still significantly smaller in SVL than those from the 32°C and T_{REG} treatments. Mean body mass of neonates from the 35°C treatment was also still less than that of neonates from the other treatments, but the difference was not significant. As was true at parturition, length-adjusted neonate mass at 9 days of age did not differ among treatments.

Neonates from all treatments increased in mass and SVL over the observation period at similar rates (Table 2). Neonate mass (adjusted for masses at the previous weighing) did not differ among treatments on days 3 and 9 (Table 2). Likewise, neonate SVL (adjusted for SVLs at the previous measuring) did not differ among treatments on these days.

Discussion

SELECTED BODY TEMPERATURES

Female *S. jarrovi* in the laboratory selected lower body temperatures when pregnant than when postpartum even though higher body temperatures would have been easily attainable. Furthermore, the mean selected body temperature of pregnant females in this study (32·1°C) was virtually identical to the mean body temperature of field-active pregnant females (Beuchat 1986: 32·0°C). These data suggest that field-active pregnant females select low body temperatures and that ecological constraints (e.g. the encumbrance of the clutch) do not affect thermoregulatory behaviour. However, without information on the operative field temperatures (see Hertz 1992; Hertz *et al.* 1993) available to pregnant and postpartum females, we cannot be certain as to how difficult it would be for pregnant females to maintain body temperatures as high as those of postpartum females. But since the difference in mean field-active body temperatures of postpartum and pregnant females is small, it seems likely that pregnant females could maintain higher field-active body temperatures if they wanted to. We also do not know the extent to which our estimates of selected body temperatures might have been affected by seasonal variation in selected body temperature as body temperatures of postpartum and pregnant females were measured at different times. However, selected body temperatures of *Sceloporus occidentalis* do not vary seasonally (McGinnis 1966).

Variances and ranges of selected body temperatures provided additional insights into the nature of the shift to low body temperatures by pregnant females. Females selected body temperatures that were less variable during pregnancy than when postpartum at each of the three measurement times during the day. Increased precision of thermoregulation by reproductive females (both in laboratory and field studies) is well documented (Stewart 1984; Beuchat 1986; Gier, Wallace & Ingerman 1989; Charland & Gregory 1990) although not always observed (Schwarzkopf & Shine 1991; Daut & Andrews 1993).

One explanation why females increase their precision of thermoregulation when reproductive is that offspring fitness is optimized at a species-specific temperature (Beuchat 1986). Therefore, reproductive females should regulate body temperatures closely around this temperature. However, a statistical (unintentional on the female's part) 'increase in precision' could result if offspring fitness is adversely affected

Table 2. Means and standard errors of dry mass, water content, dry residual yolk mass, morphology and growth of offspring in the viviparous lizard *Sceloporus jarrovi* maintained under three incubation regimes

Trait	35°C treatment	32°C treatment	Treg treatment	Statistical test
Neonate dry mass at parturition (mg)	85·63 ± 2·36 a	91·63 ± 2·28 a	92·31 ± 2·36 a	ANOVA $F = 2·45$, df = 2,40 $P = 0·10$
Neonate water content (adjusted for neonate dry mass) at parturition (g)	0·52 ± 0·01 a	0·58 ± 0·01 b	0·57 ± 0·01 b	ANCOVA $F = 5·35$, df = 2,38 $P = 0·009$
Neonate dry residual yolk mass (adjusted for neonate dry mass) at parturition (μg)	6·18 ± 1·92 a	6·93 ± 1·78 a	6·35 ± 1·90 a	ANCOVA $F = 0·05$, df = 2, 30 $P = 0·95$
Neonate mass (g)				
At parturition	0·59 ± 0·02 a	0·66 ± 0·02 b	0·66 ± 0·02 b	ANOVA $F = 7·37$, df = 2,41 $P = 0·002$
At 9 days of age	0·89 ± 0·03 a	0·98 ± 0·03 a	0·96 ± 0·03 a	ANOVA $F = 2·63$, df = 2,39 $P = 0·08$
Neonate SVL (mm)				
At parturition	25·83 ± 0·19 a	26·85 ± 0·19 b	26·72 ± 0·20 b	ANOVA $F = 8·56$, df = 2,41 $P < 0·001$
At 9 days of age	29·45 ± 0·28 a	30·66 ± 0·28 b	30·33 ± 0·28 b	ANOVA $F = 4·96$, df = 2,39 $P = 0·012$
SVL-adjusted neonate mass (g)				
At parturition	0·63 ± 0·01 a	0·64 ± 0·01 a	0·64 ± 0·01 a	ANCOVA $F = 0·11$, df = 2,40 $P = 0·90$
At 9 days of age	0·96 ± 0·01 a	0·93 ± 0·01 a	0·94 ± 0·01 a	ANCOVA $F = 1·19$, df = 2,38 $P = 0·31$
Mass-adjusted (previous) neonate mass (g)				
At 3 days of age	0·66 ± 0·01 a	0·67 ± 0·01 a	0·66 ± 0·01 a	ANCOVA $F = 0·35$, df = 2,40 $P = 0·71$
At 9 days of age	0·94 ± 0·19 a	0·93 ± 0·02 a	0·95 ± 0·02 a	ANCOVA $F = 0·19$, df = 2,38 $P = 0·83$
SVL-adjusted (previous) neonate SVL (mm)				
At 3 days of age	26·94 ± 0·10 a	26·92 ± 0·10 a	26·81 ± 0·10 a	ANCOVA $F = 0·51$, df = 2,40 $P = 0·61$
At 9 days of age	30·02 ± 0·19 a	30·21 ± 0·19 a	30·21 ± 0·18 a	ANCOVA $F = 0·31$, df = 2,38 $P = 0·74$

Table shows least-squares means ± SE; mean value ± SE are given for neonate dry mass at parturition, neonate mass and neonate SVL. Interaction terms were not significant in any of the ANCOVAs. Means followed by the same letters were not significantly different ($P > 0·05$). Treg treatment denotes pregnant females that were allowed to thermoregulate.

by a particular temperature extreme and females that are otherwise thermoregulating normally simply avoid temperatures approaching this extreme. Lizards do seem to thermoregulate between upper and lower set-point temperatures, rather than around a single body temperature (Berk & Heath 1975; Barber & Crawford 1977). Furthermore, set-points may vary with reproductive state (Patterson & Davies 1978; Sievert & Hutchison 1988). The maximum and minimum body temperatures selected by pregnant and postpartum *S. jarrovi* females on the thermal gradient were used to estimate these set-points. The upper set-point was lowered during pregnancy; the mean maximum body temperature females when pregnant was lower than when postpartum. However, pregnancy did not influence the position of the lower set-point; there was no difference in the mean minimum body temperature of females when pregnant and when postpartum. Indeed, a lowering of the lower set-point temperature would not be expected if the length of gestation is related to costs of reproduction. Thus, pregnant females exhibit low mean body temperatures because they avoid upper temperature extremes that are tolerated when postpartum. Consequently, the relatively low variance in body temperatures exhibited by pregnant females may be the inevitable result of lowering the upper set-point temperature against a stationary lower set-point temperature rather than a reduction in variance about a single optimal temperature for development.

EFFECTS OF INCUBATION TEMPERATURE ON FEMALES AND OFFSPRING

Do female *S. jarrovi* select lower body temperatures when pregnant than when postpartum because postpartum body temperatures are detrimental to the female, to the embryos, or both? In general, the physical condition of pregnant females was found to be unaffected by any of the experimental temperature treatments. However, the fitness of neonates that had been exposed to the 35°C treatment during embryogenesis was reduced.

The growth and survival of females did not differ among treatments. Growth (in SVL) of females in the 35°C treatment was the same as that of females in the other treatments. In concordance with this result, treatment temperature had no effect on body condition (size-adjusted body mass). Postpartum females in the 35°C treatment had virtually the same body mass for their SVL as postpartum females in the other two treatments. Moreover, all females in our study survived to the end of the experiment. These results differ markedly from those of a parallel study on the effects of temperature during the gestation period of *S. jarrovi* (Beuchat 1988). Beuchat (1988) observed ≈ 40% mortality of females in her 36°C and 32°C temperature treatments, and surviving lizards in her 36°C temperature treatment lost weight during the experiment. Unlike the present study, however, lizards in Beuchat's (1988) study were maintained under constant temperature regimes. Constant high temperatures are particularly stressful to squamates, and cause high mortality (Licht 1965; Shine 1983) suggesting why Beuchat's (1988) results differ so much from those reported in this paper.

In contrast to the absence of treatment effects on the physical condition of females, temperature treatment had a strong affect on embryonic development. Neonates produced by pregnant females from the 35°C treatment were smaller in live body mass and in SVL than those produced by pregnant females in the 32°C and T_{REG} treatments. At parturition, neonates from the 35°C treatment were ≈ 10·6% lighter in mass and 3·6% shorter in SVL than neonates from the other treatments. Beuchat (1988) also observed a decrease in the body size of neonates that were exposed high incubation temperatures.

Mean incubation temperature was related to the mean time to parturition. Females in the 35°C treatment gave birth an average of 4 and 7 days, respectively, before females in the 32°C and T_{REG} treatments. Thus, pregnant females could conceivably reduce costs of reproduction and increase offspring fitness by selecting high body temperatures. However, the detrimental effects of high body temperatures on neonate size probably outweigh these advantages. Indeed, the 4-day difference (not significant) in mean time to parturition for females in the 35°C and 32°C treatments seems trivial compared with the lasting effects of high incubation temperature on offspring body size.

Very few dead or abnormal offspring were observed overall. However, four of the five litters with dead and or abnormal neonates were in the 35°C treatment, suggesting that embryos were subjected to some level of thermal stress during gestation. In contrast, Beuchat (1988) observed a large number of dead or abnormal offspring (> 60% in some treatments). Such high morbidities are even more striking considering females in Beuchat's (1988) study were field-collected and placed under experimental conditions much later in the season (≈ 1 month later) than the females in our study; hence, these embryos were only under experimental conditions for a few weeks before parturition. These results presumably also reflect high levels of experimentally induced stress on pregnant females and their embryos caused by constant high temperatures.

The relatively low body mass of neonates from the 35°C treatment was not entirely because of their shorter SVL; these neonates also had relatively low water contents. In accord, neonates exhibited greater similarity in dry mass than wet mass among treatments (dry mass was, however, lowest for neonates in the 35°C treatment). The most likely site for the observed water deficiency is the urinary bladder. At parturition, the bladder of neonatal *S. jarrovi* contains dilute urine that constitutes ≈ 13·6% of its total body mass (Beuchat, Vleck & Braun 1986). Using this value and

the mean body mass of neonates in the 32°C and T_{REG} treatments (0·66 g, Table 2), it was predicted that the bladder of a fully hydrated neonate would contain a fluid content of 0·09 g. Actual body water content of neonates from the 35°C treatment was ≈ 0·06 g less than that of neonates from the other two treatments. Thus, the deficiency in body water content exhibited by neonates from the 35°C treatment could have been because of an incompletely filled (≈ 33·3% full) urinary bladder. Such a reduction in fluid content of the bladder could adversely affect neonate survival because the bladder may serve as a reserve of reabsorbable water that is used to buffer body tissues against osmotic perturbation during the first few days following parturition (Beuchat *et al.* 1986).

Differences in SVL between neonates from the 35°C treatment and neonates from the 32°C and T_{REG} treatments persisted until at least 9 days of age. The effect of treatment on body mass was lessened through time; body mass of neonates did not differ significantly among treatments at 9 days although neonates from the 35°C treatment were still lighter on average than neonates from the other treatments. However, despite their smaller body size, neonates from the 35°C treatment were no less robust than neonates from the other treatments. Thus, for the traits measured, the overall effect of high incubation temperature (35°C treatment) on offspring phenotype was a reduction in body size (particularly SVL) of otherwise normally proportioned offspring.

Variation in body size of the magnitude reported here can affect neonate survival and fitness. Large juvenile lizards have been shown to survive better than small juveniles (Fox 1978; Ferguson & Fox 1984), occupy more optimal habitat (Fox 1978) and be socially dominant over conspecifics (Fox & Rostker 1982). Differential survival between smaller and larger juveniles can be amplified when competition for resources is increased (Ferguson & Fox 1984). Thus, it is possible that differences in growth among neonates from the different temperature treatments were not observed because food was always available in excess.

Our results demonstrate that while temperatures near the upper set-point for postpartum females are not detrimental to pregnant females, pregnant females actively select relatively low body temperatures. Observations on the effect of relatively high body temperature on embryonic development indicate that pregnant females avoid high temperatures during pregnancy because such temperatures are deleterious to their offspring. Specifically, high temperature during gestation results in relatively small, and presumably less fit, offspring.

Acknowledgements

We would like to thank the staff at the Southwestern Research Station of the American Museum of Natural History for their logistical support and P. E. Hertz, J. R. Cranford, M. D. Denbow, A. G. Heath, P. B. Siegel, C. P. Qualls and an anonymous reviewer for their comments on the manuscript. This research was supported by NSF grant no. BSR-9022425 to R.M.A. and grants to T.M. from Sigma Xi and the Theodore Roosevelt Memorial Fund of the American Museum of Natural History.

References

Barber, B.J. & Crawford, E.C. (1977) A stochastic dual-limit hypothesis for behavioral thermoregulation in lizards. *Physiological Zoology* **50,** 53–60.

Berk, M.L. & Heath, J.E. (1975) An analysis of behavioral thermoregulation in the lizard *Dipsosaurus dorsalis*. *Journal of Thermal Biology* **1,** 15–22.

Beuchat, C.A. (1986) Reproduction influences on the thermoregulation behavior of a live-bearing lizard. *Copeia* **1986,** 971–979.

Beuchat, C.A. (1988) Temperature effects during gestation in a viviparous lizard. *Journal of Thermal Biology* **13,** 135–142.

Beuchat, C.A., Vleck, D. & Braun, E.J. (1986) Role of the urinary bladder in osmotic regulation of neonatal lizards. *Physiological Zoology* **59,** 539- 551.

Bradshaw, S.D. (1986) *Ecophysiology of Desert Reptiles*. Academic Press, Sydney.

Braña, F. (1993) Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. *Oikos* **66,** 216–222.

Charland, M.B. & Gregory, P.T. (1990) The influence of female reproductive status on thermoregulation in a viviparous snake, *Crotalus virdis*. *Copeia* **1990,** 1089–1098.

Cowles, R.B. & Bogert, C.M. (1944) A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History* **83,** 261–296.

Daut, E.F. & Andrews, R.M. (1993) The effect of pregnancy on the thermoregulatory behavior of the viviparous lizard *Chalcides ocellatus*. *Journal of Herpetology* **27,** 6–13.

Dufaure, J.P. & Hubert, J. (1961) Table de développement du lézard vivipare: *Lacerta* (Zootoca) *vivipara* Jacquin. *Archives d' Anatomie Microscopique et de Morphologie Experimentale* **50,** 309–328.

Ferguson, G.W. & Fox, S.F. (1984) Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: Its causes and evolutionary significance. *Evolution* **38,** 342–349.

Fox, S.F. (1978) Natural selection on behavioral phenotypes of the lizard *Uta stansburiana*. *Ecology* **59,** 834–847.

Fox, S.F. & Rostker, M.A. (1982) Social cost of tail loss in *Uta stansburiana*. *Science* **218,** 692–693.

Gier, P.J., Wallace, R.L. & Ingerman, R.L. (1989) Influence of pregnancy on behavioral thermoregulation in the northern Pacific rattlesnake *Crotalus virdis oreganus*. *Journal of Experimental Biology* **145,** 465–469.

Goldberg, S.R. (1971) Reproductive cycle of the ovoviviparous iguanid lizard *Sceloporus jarrovi* Cope. *Herpetologica* **27,** 123–131.

Gutzke, W.H.N. & Packard, G.C. (1987) Influence of the hydric and thermal environments on eggs and hatchlings of bull snakes *Pituophis melanoleucus*. *Physiological Zoology* **60,** 9–17.

Hertz, P.E. (1992) Evaluating thermal resource partitioning by sympatric *Anolis cooki* and *A. cristatellus*: A field test using null hypotheses. *Oecologia (Berlin)* **90,** 127–136.

Hertz, P.E., Huey, R.B. & Stevenson, R.D. (1993) Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. *American Naturalist* **142,** 798–818.

Huey, R.B. (1982) Temperature, physiology, and the ecology of reptiles. *Biology of the Reptilia* (*Physiology C: Physiological Ecology*), Vol. 12 (eds C. Gans & F. H. Pough), pp. 25–92, Academic Press, New York.

Licht, P. (1965) The relation between preferred body temperature and testicular heat sensitivity in lizards. *Copeia* **1965**, 428–436.

McGinnis, S.M. (1966) *Sceloporus occidentalis*: Preferred body temperature of the western fence lizard. *Science* **152,** 1090–1091.

Muth, A. (1980) Physiological ecology of desert iguana (*Dipsosaurus dorsalis*) eggs: Temperature and water relations. *Ecology* **61,** 1335–1343.

Patterson, J.W. & Davies, P.M. (1978) Preferred body temperature: seasonal and sexual differences in the lizard *Lacerta vivipara. Journal Thermal Biology* **3,** 39–41.

Pough, H.F. & Gans, C. (1982) The vocabulary of reptilian thermoregulation. *Biology of the Reptilia* (*Physiology C: Physiological Ecology*), Vol. 12 (eds C. Gans & F. H. Pough), pp. 17–23, Academic Press, New York.

SAS Institute Inc. (1985) *SAS Users Guide: Statistics*, Version 5. Cary, NC, USA.

Schwarzkopf, L. & Shine, R. (1991) Thermal biology of reproduction in viviparous skinks, *Eulamprus tympanum*: Why do gravid females bask more? *Oecologia* **88,** 562–569.

Seigel, R.A. & Fitch, H.S. (1984) Ecological patterns of relative clutch mass in snakes. *Oecologia* **61,** 293–301.

Shine, R. (1980) 'Costs' of reproduction in reptiles. *Oecologia* **46,** 92–100.

Shine, R. (1983) Reptilian viviparity in cold climates: Testing the assumptions of an evolutionary hypothesis. *Oecologia* **57,** 397–405.

Sievert, L.M. & Hutchison, V.H. (1988) Light vs. heat: Thermoregulatory behavior in a nocturnal lizard (*Gecko gecko*). *Herpetologica* **44,** 266–273.

Smith, G.R. & Ballinger, R.E. (1994) Temperature relationships in the high- altitude viviparous lizard, *Sceloporus jarrovi. American Midland Naturalist* **131,** 181–189.

Stevenson, R.D., Peterson, C.R. & Tsuji, J.S. (1985) The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. *Physiological Zoology* **58,** 46–57.

Stewart, G.R. (1984) Thermal biology of the live bearing lizard *Gerrhonotus coeruleus. Herpetologica* **40,** 349–355.

Vinegar, A. (1974) Evolutionary implications of temperature induced anomalies of development in snake embryos. *Herpetologica* **30,** 72–74.

Received 4 June 1996; revised 7 November 1996; accepted 21 November 1996