



Does behavioural thermoregulation help pregnant *Sceloporus adleri* lizards in dealing with fast environmental temperature rise?

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The physiological performance of reptiles is subject to specific body temperature ranges, which are frequently similar between closely-related species even when they inhabit sites with different thermal conditions. Pregnant females should be particularly efficient for thermoregulation because healthy embryos develop at a narrow temperature range, a potential problem in the context of current global warming. To test the idea that pregnant lizards adjust their thermoregulatory behaviour to rising temperatures, we set up an experiment with 40 pregnant *Sceloporus adleri* and measured daily activity and basking time at different treatments (22, 24, 26 and 28°C) for six consecutive days. Basking time significantly decreased with increasing temperature. Lizards were more active in the earliest two time periods of the day (0800–1030 and 1030–1300 hours) when compared to later hours (1530–1800) for all treatments, although the trend was less pronounced at 24 and 26°C. Unexpectedly, the probability of activity for lizards increased at 28°C. All lizards maintained a body temperature without significant differences across treatments. These results suggest that pregnant *S. adleri* females are able to adjust their behavioural thermoregulation to different thermal environments in a short period of time to maintain an adequate body temperature for key physiological processes such as development and growth of their offspring.

Key words: climate change, ectotherms, laboratory, reptiles, thermal treatments

INTRODUCTION

In closely related species of reptiles, basic biological and ecological mechanisms such as feeding, water balance and breeding usually occur at similar ranges of field body temperature (T_b) regardless of deviating ambient temperatures (“conservative thermal physiology”, Bogert, 1949; Bowker, 1993; Seebacher & Shine 2004; Glanville & Seebacher, 2006). *Sceloporus* lizards are a good example for this phenomenon, and exhibit similar T_b ranges through diverse ecological and geographic conditions via adaptive thermoregulatory behaviour (Avery, 1982; Huey, 1982; Crowley, 1985; Crowley, 1987; Mathies & Andrews, 1997; Andrews, 1998). Gravid females need to be particularly efficient for thermoregulation because healthy embryos develop at a relative narrow temperature range (28–34°C; Beuchat & Ellner, 1987; Beuchat, 1988). Thus, pregnant females should display a variety of behavioural mechanisms such as adjustment of daily activity time, microhabitat selection or shuttling between sun and shade to ensure an adequate thermal environment for their offspring (Andrews, et al., 1999; Angilletta, 2000; Angilletta, 2009; Webb et al., 2006).

The fast environmental warming episode we are experiencing (Berteaux et al., 2004) may pose a challenge for suitable thermoregulation in lizards, potentially affecting their physiological performance and, ultimately, their survival (Deutsch et al., 2008; Sinervo et al., 2010). In this context, effective thermoregulation of pregnant *Sceloporus* females would be key for maintaining their body temperature within the preferred range for physiological performance and offspring development (Beuchat 1986; Qualls & Andrews, 1999; Mathies & Andrews, 1997; Andrews et al., 2000). Individuals should exhibit simple changes in behavioural traits that appear to be the most critical in determining T_b , such as adjustments in daily activity time and basking frequency as a way to contend with warm environmental temperatures (Stevenson, 1985; Adolph, 1990; Bauwens et al., 1996; Kearney, 2002; Huey et al., 2003).

Here we hypothesise that pregnant *Sceloporus* females are able to rapidly change their behavioural thermoregulation to counteract potential negative effects of warmer temperatures on themselves and their developing offspring (Angilletta et al., 2002). We evaluated the ability of pregnant *S. adleri* females to

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reach and maintain their preferred T_b range under experimental thermal conditions projected for the future in tropical regions by climate models. We focused on activity time and basking time (BT) in four different controlled thermal treatments, and predicted that, as temperature rises, activity time becomes reduced and basking time becomes shortened.

MATERIALS AND METHODS

Fieldwork

We collected 40 pregnant individuals in good physical condition (within 50–54 mm of snout-vent length SVL, Smith & Savitzky, 1974) from Carrizal de Bravos, in the State of Guerrero, Mexico (17.6° N, 99.8° W at 2400m elevation). Lizards were noosed, and their field body temperature (T_b) was immediately measured with a Miller and Weber® quick-reading cloacal thermometer. We detected pregnant lizards by gently palpating the abdomen to feel for embryos and avoiding impairment (Gartrell et al., 2002). Lizards were then transported to the laboratory for experimental procedures. After the experiments, all lizards gave birth. Fieldwork was conducted in December, when neurulation, organogenesis and embryo growth occurs (Guillette & Sullivan, 1985), and when females of the *S. formosus* species group (to which *S. adleri* belongs) are highly sensitive to temperatures above 34°C (Beuchat, 1988).

Laboratory procedures and experimental design

Lizards were randomly housed into four experimental plastic containers (150 cm x 100 cm x 25 cm) in equal numbers in a room with a stable temperature regime ($\bar{X}=19.7\pm 0.39^\circ\text{C}$) and large windows that provided natural daylight periods (0800–1800). Lizards were marked on their back with epoxy paint, using consecutive numbers from 1 to 10 for convenient identification within each treatment. Containers were disinfected with a 5% dilution of sodium hypochlorite prior to treatment, and lizards remained isolated from other organisms during the captivity period (Pasmans et al., 2008). Containers were filled with a 2 cm mixture of soil, sand and leaf litter collected in the field and divided lengthwise into two equal sections: one for basking with a heat source at treatment-specific temperatures, and the other for retreating and shelter with small rocks and wood. To control temperature of the basking area, two 75W incandescent reflectors (Phillips BR25 125V

E26 ES) were suspended 30 cm above substrate. The irradiated temperature produced by the reflectors in each basking section was regulated by a programmed digital pyrometer (TERMACRON JK-999-UR) plugged into a power relay (OMROM MGN2A-AC120), and a type J thermocouple with $\pm 1^\circ\text{C}$ accuracy (Honeywell SCTC-TCJ100). The thermocouple worked as a temperature sensor and was set 1 cm above the substrate. Prior to this, we measured the temperature along the basking section every 15 cm to verify that temperature was uniform. When temperature decreased or increased beyond the treatment temperature, the system regulated the reflectors.

Control treatment was maintained at 22°C, with an operative temperature range of $\bar{X}=22.07\pm 0.02^\circ\text{C}$ and $\bar{X}=19.3\pm 0.60^\circ\text{C}$ between basking and retreating areas. We chose this baseline temperature because it represented the recorded mean daytime environmental temperature in the field ($\bar{X}=22.1\pm 2.8^\circ\text{C}$) during the first stages of the reproductive period. Thus, in order to represent the gradual temperature increase of 6°C predicted at high altitudes in tropical regions under the A2 emissions scenario by the end of the century (IPCC 2007), experimental treatments were fixed at 24°C [$\bar{X}=24.05\pm 0.13^\circ\text{C}$ (basking) and $\bar{X}=19.2\pm 0.86^\circ\text{C}$ (retreat)], 26°C [$\bar{X}=26.09\pm 0.04^\circ\text{C}$ (basking) and $\bar{X}=19.3\pm 0.44^\circ\text{C}$ (retreat)] and 28°C [$\bar{X}=28.07\pm 0.02^\circ\text{C}$ (basking) and $\bar{X}=19.5\pm 0.44^\circ\text{C}$ (retreat)]. The thermal treatments operated from 0800 to 1800 hours and remained inactive at night.

Lizards were acclimated at captivity conditions in a thermal regime of 22°C in all treatments for ten days prior to experimentation (Kelley et al., 2006). No aggressive or competitive behaviour between females was detected in the field or during acclimation (but see Ruby, 1977; Ruby, 1978; Davies & Ford, 1983; Contreras-Lozano et al. 2011 for other *Sceloporus* species). The basking area was wide enough to allow several small lizards to thermoregulate simultaneously. Thus, we have no evidence that captive conditions influenced the thermoregulatory behaviour of individuals (Carrascal et al. 1992; Bulova, 1994; Mathies & Andrews, 1997).

We measured the following behavioural traits: (i) the number of active lizards and (ii) basking time (in seconds) of each active lizard (BT) that remained directly exposed to the experimental temperature in its designated basking area. In each treatment we recorded behavioural traits from 0800 to 1800 divided into four bins of two and

Table 1. Descriptive statistics for basking time (BT) and active body temperature (T_b) observed for *Sceloporus adleri* at different temperature treatments. Ten individuals were used for each treatment, but since the number of active lizards at a given time varied over six days and four times of day, the number of observations (n) in each treatment is not constant.

Treatments	BT (mean) \pm SD (min–max) (n)	T_b (mean) \pm SD (min–max) (n)
22°C	256.7 \pm 82.3 (105.0–576.0) (130)	28.6 \pm 1.9 (24.8–32.1) (44)
24°C	142.4 \pm 43.7 (57.0–280.0) (96)	28.6 \pm 2.0 (24.6–32.1) (46)
26°C	115.3 \pm 35.7 (45.7–197.0) (60)	28.4 \pm 2.3 (24.1–32.5) (20)
28°C	56.9 \pm 22.9 (10.0–152.0) (105)	29.4 \pm 1.5 (25.9–32.5) (43)

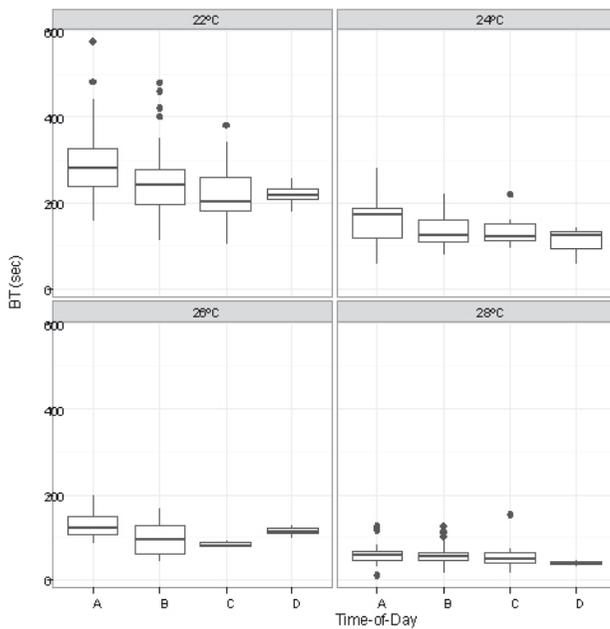


Fig. 1. Box plots for BT [not \sqrt{BT} , for ease of interpretation] exhibited by active *Sceloporus adleri*, grouped by time and treatment.

half hours (following Martin & Bateson, 1993): morning (0800–1030), midday (1030–1300), afternoon (1300–1530), and evening (1530–1800). These time periods are henceforth denoted by letters A, B, C and D, respectively.

We simultaneously surveyed the lizards' behaviour in the four treatments at a distance of 2.5 m, which was the tolerated distance before hiding as observed in the field. We recorded body temperature (T_b) of active lizards with a Miller & Webber® cloacal thermometer once a day only during period B after recording the corresponding behavioural observations. The rationale of measuring T_b in period B was to allow lizards enough time to raise and achieve their preferred body temperature after emerging from their shelters. Measurements were recorded for six consecutive days; these measures were compared across time-of-day, days and treatments (Zar, 1999). Lizards were fed daily with crickets (*Acheta domestica*) and meal worms (*Tenebrio molitor*), and supplied with water *ad libitum*; organic debris (food and faeces) were

removed after the six-day trials. The hatchlings born in captivity showed a healthy condition and survived until their release in the field. At the end of the experiments all lizards were released at their locality of capture.

Data analysis

To account for the effect of measuring the observations in the same lizards along time (and thus a possible dependence structure in the response variables), we used repeated measures models (Laird & Ware, 1982; Pinheiro & Bates, 2000). Two main specific models were considered: linear models for continuous responses, and logistic regression for analysing the binary state of being active or not. Hypotheses are tested with standard ordinary linear models and ANOVA (such as F tests, t -tests, or normal approximation z -tests), but making technical allowances in order to conserve validity in the results even under repeated measurements on the same subjects. See Appendix for further details and rationale regarding the statistical models and procedures. All statistical computations were performed with R software v.2.12.1 (R Development Core Team, 2012). Discussion of results assumes the standard $\alpha=0.05$ unless specified otherwise. Some of the graphical displays were produced with the ggplot2 R package (Wickham, 2009).

RESULTS

Basking time (BT)

We observed progressively lower values of BT with increasing temperature (Fig. A1 and Table 1). Activity and the rate of activity between treatments changed with respect to time-of-day. Lizards that were only sporadically active however did not appear to show any correlation between activity and time of day (95% confidence interval for the autoregressive parameter: -0.26 – 0.47). Temperature (ANOVA tests in mixed-effects models $F_{3,213}=356.3$, $p<0.01$) and time-of-day ($F_{3,213}=11.4$, $p<0.01$) significantly explained the BT exhibited by lizards. Day was not significant $F_{5,213}=1.7$, $p=0.117$, which was expected under constant experimental conditions. We found no clear evidence for treatment-time interaction ($F_{9,157}=1.9$, $p=0.045$).

Table 2. Parameter estimates and end points of 95% confidence intervals for fitted mixed-effects linear model for studying \sqrt{BT} . Interactions are not displayed because they were not significant. These intervals are plotted in Figure A2.

Main effects	Lower	Est.	Upper
22°C (Intercept)	16.199	16.967	17.736
24°C	-5.360	-4.483	-3.605
26°C	-6.369	-5.553	-4.737
28°C	-10.083	-9.300	-8.516
TimeB	-2.173	-1.274	-0.374
TimeC	-3.203	-2.151	-1.100
TimeD	-4.016	-2.027	-0.038

Table 2 displays numerical values of parameter estimates for significant main effects and corresponding 95% confidence intervals for the fitted mixed-effects linear model for \sqrt{BT} (see also Fig. A2). Time-of-day had a less dramatic effect on BT than treatment. For all treatments we found that Times B-D were not significantly different from each other but significantly smaller than Time A. Moreover, BT was significantly shorter between 24–28°C, but did not differ between 24°C and 26°C. Basking time was overall shorter at 24°C, 26°C and 28°C as well as during periods B, C and D (Fig. 2).

Activity of lizards and probability

Parameter estimates for population effects for the state of being active or not are shown in Table 3. As before, treatment and time-of-day had significant effects on a lizard's probability of being active (except for Time B). Probability values (denoted by P in the appendix) specified by the fitted logistic regression model implicitly for the condition of being active are plotted in Fig. 2. The highest estimated probabilities for lizards to be active occurred at 22°C through most of the day, albeit it decreased at interval D. In upper thermal regimes (24 and 26°C) this probability was higher during the intervals A and B than during C and D. Surprisingly, the probability of lizards being active increased at 28°C during Times A–D. This suggests that *S. adleri* can separately or simultaneously adjust the extent of daily activity and BT in response to the available temperature within treatments.

Body temperature (T_b) of lizards

Mean T_b attained by lizards did not change significantly between treatments ($F_{3,36}=0.516$, $p=0.6742$) and days ($F_{5,108}=0.395$, $p=0.851$; Table 1 and Fig. 3). The same statistical modelling also provided a 95% confidence interval for the mean T_b in the laboratory, given by (27.4°C, 29.8°C) with a point estimate of 28.6°C. Data obtained in the field ($\bar{X}=28.2\pm 2.64^\circ\text{C}$) yields almost the same the interval (27.4°C, 29.0°C).

DISCUSSION

Species are expected to respond to changing climate behaviourally (Kearney et al., 2009), physiologically (Bradshaw & Holzapfel, 2010), by adjusting the timing of biological processes such as reproduction (Parmesan, 2006), or by migration (Pounds et al., 2005). When such response strategies fail, populations are predicted

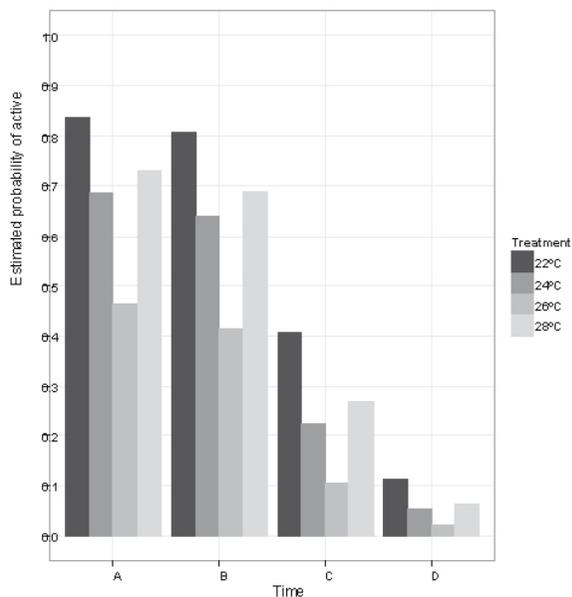


Fig. 2. Estimated probabilities of *Scleroporus adleri* being active, as a function of time-of-day (0800–1030, 1030–1300, 1300–1530 and 1530–1800 represented by letters A, B, C and D on the horizontal axis) and treatment, as computed by logistic regression with random effects for lizards.

to decline and population may collapse (Sinervo et al., 2010). It is therefore key to understand how behavioural traits are fine-tuned under warming temperatures.

Pregnant *S. adleri* lizards in four temperature treatments did not show significant differences in T_b during the six days of experiment, suggesting that they achieve similar body temperatures by regulating their activity and basking times (two of the main behavioural thermoregulatory mechanisms in ectotherms, Stevenson, 1985; Adolph, 1990). Individuals spent significantly more time out of their shelters throughout the day at the lowest temperature (22°C). That the effect was higher at intervals A and B is in line with our first prediction regarding the restriction of activity out of refuges to specific times of the day. Furthermore, lizards at 24°C and 26°C significantly reduced their BT . This supports our second prediction and suggests that lizards in raise their preferred T_b equally fast across treatments, with less basking required at warmer temperatures. Both results suggest that lizards evade long exposure at warmer environmental temperatures to prevent overheating.

Table 3. Summary of estimated parameter results for logistic regressions with random effects applied to lizards' (*Scleroporus adleri*) state of being active or not.

Main effects	Estimate	Std Error	z value	p
22°C (Intercept)	1.641	0.215	7.616	<0.001
24°C	-0.865	0.229	-3.768	<0.001
26°C	-1.789	0.241	-7.438	<0.001
28°C	-0.640	0.229	-2.800	<0.001
TimeB	-0.203	0.202	-1.007	0.314
TimeC	-2.017	0.216	-9.356	<0.001
TimeD	-3.691	0.312	-11.851	<0.001

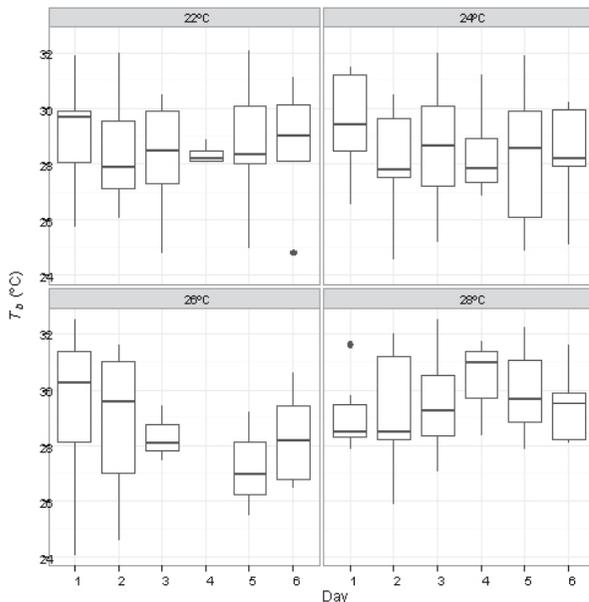


Fig. 3. Box plots for T_b raw data recorded to active *Sceloporus adleri*, grouped by day and treatment (see also Table 1).

The activity levels of lizards at 28°C was more similar to the 22°C treatment than to the 24°C and 26°C treatments. Lizards at higher temperatures are expected to reduce their activity time until remaining hidden in shelters, leading to restricted foraging and reproduction (Huey & Tewksbury, 2009; Angilletta, 2009; Sinervo et al., 2010). Pregnant *S. adleri* females at 28°C did not restrict their activity time by hiding in the last periods of the day, and reduced their BT using a mechanism known as shuttling, i.e., moving constantly between warm areas and shade, which allowed them to be active for feeding and exploration reducing the effective time they were directly exposed to warmer temperatures (Carrascal et al., 1992).

In sum, pregnant females of *S. adleri* showed similar preferred body temperature across thermal treatments, and T_b was almost identical to the temperature recorded in the field for other viviparous *Sceloporus* species (Beuchat, 1988; Mathies & Andrews, 1997). Our results suggest that pregnant *S. adleri* females achieved their preferred body temperature through behavioural thermoregulation even when temperatures rose by 6°C (as observed by Hertz 1981; Stevenson, 1985; Van Damme et al., 1987; Adolph 1990; Bauwens et al., 1996; Díaz, 1997; see also Beuchat & Ellner, 1987 for pregnant *S. jarrovi*). Experimental temperatures to which lizards were exposed did not exceed the maximum temperatures reported for *Sceloporus* embryo development (Beuchat, 1988), and *S. adleri* may therefore be able to counteract rising temperatures without compromising their physiological condition or the viability of offspring at sites which offer a mosaic of sun and shade (Huey et al., 2003; Herczeg et al., 2008; Huey & Tewksbury, 2009). In cooler sites at the upper distributional limits, populations may even benefit from a moderate warming (Chamaillé-Jammes et al., 2007). This study represents a step forward towards an understanding of potential

behavioural responses of a tropical lizard to a local environmental temperature increase.

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Please note that the APPENDIX containing Figures A1–A3 and supporting information for this article is available online via the Herpetological Journal website (http://http://www.thebhs.org/pubs_journal_online_appendices.html)