



Is physiological performance optimized by thermoregulatory behavior?: a case study of the eastern fence lizard, *Sceloporus undulatus*

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Abstract

Eastern fence lizards (*Sceloporus undulatus*) exhibit a distinct thermal preference that might be related to the thermal optimum for physiological performance. Sprint speed and treadmill endurance of *S. undulatus* were insensitive to body temperature in the ranges of 28–38°C and 25–36°C, respectively. Both locomotor and digestive performances are optimized at the preferred body temperature of *S. undulatus*, but thermoregulatory behavior is more closely related to the thermal sensitivity of digestive performance than that of locomotor performance. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The relationship between thermoregulatory behavior and thermal physiology has been a focus of evolutionary physiologists for several decades (see reviews by Huey, 1982, and Angilletta et al., in review). Most physiological processes proceed rapidly over a range of body temperatures, referred to as the optimal temperature range, but are retarded at body temperatures above and below this range (Huey and Stevenson, 1979). Individuals that use behavioral thermoregulation to maintain a body temperature within the optimal range will outperform those that do not. If performance is directly related to fitness, natural selection should favor the coadaptation of preferred body temperature and the thermal optimum (T_o) for physiological performance (Huey and Bennett, 1987). Therefore,

thermal sensitivities of important physiological processes can be used to understand the thermoregulatory decisions of individuals in natural populations.

Since thermal sensitivities of key physiological processes can differ (Van Damme et al., 1991; Dorcas et al., 1997; Du et al., 2000; Ojanguren et al., 2001), organisms can be faced with trade-offs resulting from thermoregulatory decisions. One solution is to temporally vary the target body temperature such that all competing processes can proceed at a maximal rate for some duration. For example, fish are known to forage at one body temperature and digest at another in order to maximize the rate of consumption and growth efficiency (Brett, 1971). Many ectotherms select higher body temperature when they are digesting (Peterson et al., 1993; Witters and Sievert, 2001). These displays of behavioral plasticity might be one solution to the dilemma posed by multiple optima. Another solution is to target a single body temperature that permits all physiological processes to proceed at a moderate rate. For example, pregnant females of the lizard *Sceloporus jarrovi* prefer a body temperature that is intermediate to

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the thermal optima for parental growth rate and embryonic development (Beuchat and Ellner, 1987). When this strategy is adopted, the relative impact of each process on fitness will determine the preferred body temperature. Comparing thermal sensitivities of physiological performance to thermoregulatory behavior observed in laboratory or natural environments can reveal the strategies that ectotherms use to ensure adequate function.

The eastern fence lizard, *Sceloporus undulatus*, exhibits a strong thermal preference that might be linked to the thermal sensitivity of physiological performance. Individuals placed in thermal gradients select body temperatures in the range of 32–34°C (Angilletta et al., 2000; Angilletta, 2001a). In natural populations, *S. undulatus* uses behavioral thermoregulation to maintain body temperatures within 1.5°C of its preference (Angilletta, 2001a). Does the thermoregulatory behavior of *S. undulatus* permit maximal performance, or is the preferred body temperature a compromise between optimizing performances with different thermal optima? To answer this question, we quantified the thermal sensitivities of sprint speed and endurance of lizards in a South Carolina population of *S. undulatus*. We combine our results with existing data on the thermal sensitivity of digestive performance and preferred body temperatures of lizards from this population, to infer the physiological consequences of thermoregulatory behavior.

2. Materials and methods

2.1. Animal collection and care

In March of 2000, we collected 14 adult males, averaging 63 mm (95% CI = 1.5 mm) in snout-vent length, from a population on the Savannah River Site (Aiken County, South Carolina). This population was the focus of previous investigations of thermoregulatory behavior and thermal physiology (Angilletta, 2001a, b). Lizards were brought to the laboratory where they were housed individually in 6 L terraria. The terraria were placed in an incubator with a light cycle of 10L:14D, with an ambient temperature of 33°C and 20°C during photophase and scotophase, respectively. Crickets and water were provided daily. Lizards were removed from their terraria only for measures of sprint speed and endurance.

2.2. Trials of sprint speed

We began measuring sprint speed of lizards within two weeks of capture. Each lizard was raced at seven temperatures in an order that was determined randomly (33°C, 20°C, 27.5°C, 30°C, 38°C, 25°C, 36°C). Lizards

were raced at one temperature per day and were given 48 h to rest between temperatures. Thus, the entire series of measures were made over three weeks. At the end of this series, lizards were raced again at the initial temperature (33°C) to determine if individual performance changed during the course of the study. Additionally, we measured body mass of lizards on each day of sprinting. Of the 14 lizards, two were eliminated because they failed to maintain their body mass throughout the trials.

Sprint speed was measured by chasing lizards down the length of a 2-m racetrack, consisting of a plywood base and sidewalls of clear acrylic. The substrate was fine sand, similar to that encountered by *S. undulatus* in its natural habitat. Eight pairs of infrared photocells (Banner Engineering Corp. Mini-Beam SM31EQD/SM31RQD) were evenly spaced along the length of the racetrack. These photocells were interfaced with a data logger (Onset Computer Corp., Tattletale Model 8 Data Logger/Controller Engine) by using a TxBasic program run in MS-DOS. Sprint speed (cm s^{-1}) was recorded as a split for each consecutive pairs of lights, such that each sprint down the length of the racetrack produced seven splits.

Lizards were raced four times at each body temperature, using the same protocol for all body temperatures. One hour prior to racing, lizards were placed in cloth bags and were put in an incubator set at the race temperature. As lizards were removed for racing, we used a cloacal thermometer to determine body temperature. Individuals were heated or cooled slightly as needed to reach the desired temperature. When body temperature was within 0.2°C of the target, the lizard was placed at the start of the track and was physically provoked to sprint by tapping the lizards hindquarters and striking the substrate behind the lizard. Immediately after the first race, body temperature was checked and the lizard was raced a second time. Between the second and third races, lizards were returned to the incubator and given 2 h to rest. The third and fourth races were performed exactly as the first two.

Since we raced each individual at all temperatures, we used a repeated measures design to analyze the data. Each of the four races at a given temperature produced seven splits, so a total of 28 estimates of sprint speed were generated for each individual at each temperature. We used the fastest of the 28 estimates of sprint speed as a measure of the maximum sprint speed. The analysis of maximum sprint speed has become a standard because it avoids consideration of low sprint speeds that can reflect an individual's unwillingness to run faster rather than its inability to run faster (Garland and Losos, 1994). Analysis of Variance with repeated measures was used to determine the within-subjects effect of body temperature on sprint speed. Because our primary goal was to determine the optimal range of body temperatures for

sprint speed, we used Tukey's honest significant difference test to determine significant differences in sprint speed among body temperatures. A paired *t*-test was used to compare sprint speed at 33°C at the beginning and end of the study because this comparison was planned. To facilitate comparison of our data with those reported by other investigators, we also used the minimum convex polygon method of van Berkum (1986) to compute the thermal optimum and performance breadths for sprint speed and endurance. All descriptive statistics are mean \pm 95% confidence interval.

2.3. Trials of endurance

After all sprinting trials were completed, we measured the thermal sensitivity of endurance for all lizards except the two lizards that failed to maintain mass throughout the sprinting trials. Endurance was measured by running individuals on a motorized treadmill at 0.5 km/h until a loss of righting response occurred. Like sprint speed, we measured endurance at seven temperatures, in an order that was randomly determined (33°C, 30°C, 36°C, 25°C, 38°C, 27.5°C, 20°C). Because treadmill endurance of lizards is highly repeatable (Robson and Miles, 2000), it was measured once at each temperature. Lizards were given 48 h between successive endurance trials. After endurance was measured at all temperatures, we measured endurance at 33°C a second time to determine if individual performance changed during the course of the study.

On days of endurance trials, lizards were treated in the same manner that they were for sprinting trials. However, endurance trials required a special effort to control body temperature because they were of longer duration than sprint speed trials. We used a heat lamp to maintain the body temperature of a lizard throughout the trial. A ceramic heat lamp (60 W) was positioned above the treadmill. The height of the bulb was adjusted so that an operative temperature model (Bakken and Gates, 1975) of a fence lizard was at the appropriate experimental temperature. To be certain that this design was effective, we measured body temperatures of lizards before and after each endurance trial. The heat lamp was fairly effective at maintaining the desired temperature during endurance trials. On average, body temperature at the end of an endurance trial deviated 0.7°C (range = 0.1–1.9°C) from that at the start.

We measured treadmill endurance by following the protocol of Robson and Miles (2000). Lizards were placed on the treadmill and were prompted to run by gently tapping the posterior region of the body repeatedly. Endurance was defined as the duration for which lizards could maintain the speed of the treadmill. When lizards began to fall below this speed, they were inverted and righting response was checked. If a lizard was able to right itself it was prompted to maintain

speed by increasing the frequency of stimulation. The endurance trial was ended when a loss of righting response was achieved.

Endurance was analyzed with a multivariate ANOVA instead of a univariate ANOVA with repeated measures, because the assumption of sphericity made by the univariate test was not met ($W = 0.00$, $\chi^2 = 41.06$, $df = 20$, $P < 0.01$). The multivariate analysis makes fewer assumptions about the form of the variance–covariance matrix, and is more appropriate than the univariate analysis when successive measures within individuals are correlated (Potvin et al., 1990).

2.4. Critical thermal limits

After all locomotor trials were completed, critical thermal minimum (CTMin) and maximum (CTMax) were determined for each individual. To determine CTMax, we placed lizards in an incubator at 35°C for an hour. We used an operative temperature model to design environments in which a lizard would heat up or cool down at a known rate. We raised the body temperature of each lizard at a rate of 1°C per minute and assessed the lizards righting response several times per minute (Bauwens et al., 1995). If a lizard could not right itself on two successive assessments, we considered its body temperature to be the CTMax. We used a similar protocol for determining the CTMin. Lizards were initially brought to a body temperature of 15°C. Body temperature was lowered by approximately 1°C per minute and the body temperature at which righting response was lost was considered to be the CTMin. Critical thermal limits were used to bound performance curves for sprint speed and endurance.

3. Results

Both sprint speed and endurance were relatively insensitive to body temperature over a broad range (Fig. 1; Table 1). Although body temperature had a significant effect on maximum sprint speed ($MS = 15,628$, $F_{6,66} = 16.4$, $P < 0.00001$), lizards sprinted equally fast at body temperatures of 27.5–38°C. Body temperature had a more pronounced effect on endurance (Wilk's $\lambda = 0.02$, $F_{6,3} = 22.56$, $P = 0.01$), but endurance was not sensitive to body temperatures in the range of 30–36°C. Endurance at body temperatures of 30–36°C was significantly greater than that at 20–27.5°C and 38°C. Neither sprint speed ($t = -0.85$, $df = 11$, $P = 0.42$) nor endurance ($t = 1.96$, $df = 8$, $P = 0.08$) at 33°C changed significantly during the course of the study. Locomotor performance was measured within 10°C of the CTMin (11.4°C \pm 0.6°C) and within 2.5°C of the CTMax (40.4°C \pm 0.6°C).

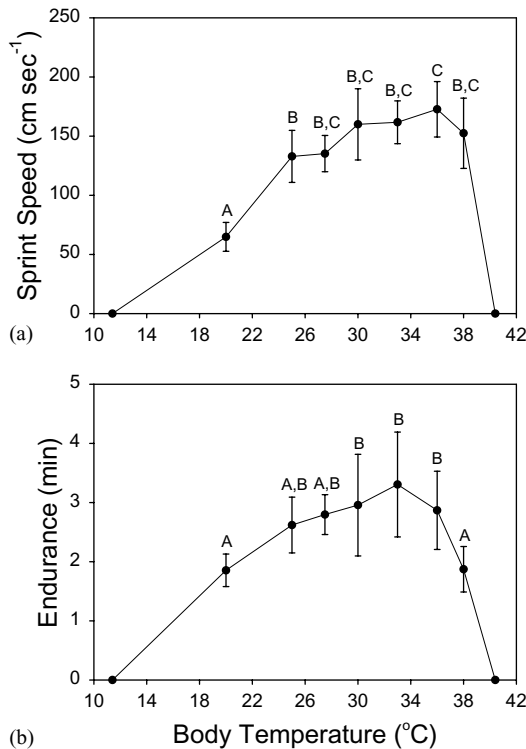


Fig. 1. Both maximum sprint speed (A) and treadmill endurance (B) were relatively insensitive to body temperature in the eastern fence lizard, *Sceloporus undulatus*. Critical thermal minimum and maximum were used to bound the curves. Error bars represent 95% confidence intervals, and letters denote temperatures at which performance did not differ significantly (Tukey's test, $P < 0.05$).

We found no evidence of phenotypic trade-offs within or between locomotor performances. Individuals that ran quickly at one temperature were very likely to run quickly at another temperature (Kendall's coefficient of concordance = 0.54; average Spearman rank $r = 0.50$). This result was not driven by differences in snout-vent length or mass among individuals. Both measures of body size varied little among subjects (coefficients of variation were 4% and 10% for SVL and mass, respectively), and neither was significantly related

to sprint speed at any temperature. Likewise, the endurance of individuals was substantially correlated among temperatures (Kendall's coefficient of concordance = 0.53; average Spearman rank $r = 0.47$). Finally, there was no significant correlation between maximum sprint speed and endurance at any temperature (all $P > 0.05$), indicating that there is no trade-off between these two locomotor performances.

4. Discussion

As with other species of lizards (Bennett, 1980; Hertz et al., 1983; van Berkum, 1986; Huey et al., 1989), locomotor performance of *S. undulatus* is relatively insensitive to body temperature. Rather than a single body temperature that maximizes sprint speed or endurance, there appears to be a range of body temperatures over which locomotor performance is maximal. For physiological performances that are largely insensitive to temperature, such as locomotor performance, it is best to describe the optimal temperature range (Huey and Stevenson, 1979). Unlike the performance breadth, which is based on an arbitrary selection of a performance criterion, the optimal temperature range is discovered by statistical analysis of repeated measures of performance. If performance does not differ significantly between two consecutive body temperatures, it is optimal in the range bounded by those temperatures. The optimal temperature ranges for sprint speed and endurance in *S. undulatus* are quite broad (see Fig. 1). *S. undulatus* sprints maximally over the range of 28–38°C. Similarly, endurance was maximal at body temperatures ranging from 25–36°C. Therefore, a fence lizard could maintain any body temperature between 28°C and 36°C, and maximize both sprint speed and endurance capacity. Our results are consistent with previous estimates of optimal temperature ranges for the locomotor performance of lizards, which range from 6°C to 14°C in breadth (Ji et al., 1995, 1996; Du et al., 2000).

Neither sprint speed nor endurance was sensitive to body temperature in the range that is normally experienced by *S. undulatus* during activity. The preferred body temperature of *S. undulatus* is highly

Table 1

Parameters of performance functions for maximum sprint speed and endurance in *Sceloporus undulatus*. Maximum performance, the thermal optimum (T_0), and 95% and 80% performance breadths (B_{95} and B_{80} , respectively) are reported as mean \pm 95% confidence interval. To facilitate comparison with previous studies of locomotor performance, the thermal optimum was estimated from the midpoint of the 95% performance breadth

	Maximum	T_0 (°C)	B_{95} (°C)	B_{80} (°C)	N
Speed (m/s)	1.72 (± 0.21)	34.1 (± 0.6)	31.3 (± 1.4)–37.0 (± 0.6)	27.1 (± 1.1)–37.8 (± 0.4)	12
Endurance (s)	199 (± 33)	31.3 (± 1.3)	29.2 (± 1.8)–33.3 (± 1.2)	25.1 (± 1.8)–35.6 (± 0.7)	11

conserved among populations; fence lizards from Ohio, Nebraska, New Jersey, and South Carolina select an average body temperature of 33°C when placed in thermal gradients while in an absorptive state (Angilletta et al., 2000; Angilletta, 2001a; Niewiarowski, pers. comm.). During activity, fence lizards in South Carolina typically have a body temperature within 1.5°C of the preferred body temperature (Angilletta, 2001a). Although the thermoregulatory behavior of *S. undulatus* clearly enables maximal locomotor performance, the precision of thermoregulation observed in this species is somewhat puzzling. If fence lizards maintained a lower body temperature, they could reduce their daily energy expenditure and still be well within the optimal temperature range for locomotor performance (Angilletta, 2001b).

Given the broad optimal temperature range for locomotor performance, why does *S. undulatus* thermoregulate with such precision? A comparison of thermal sensitivities of multiple physiological processes yields a better understanding of the thermoregulatory behavior of this species. Although the optimal temperature ranges for sprint speed and endurance are quite broad, the digestive performance of lizards is far more sensitive to body temperature than locomotor performance (Angilletta, 2001a). The preferred body temperature of *S. undulatus* is one that simultaneously maximizes sprint speed, endurance, and the rate of metabolizable energy intake (Fig. 2). Thus, the precision of thermoregulation by *S. undulatus* is more closely related to the narrow optimal temperature range for energy assimilation than the wider optimal temperature ranges for sprinting and endurance. The thermoregulatory behavior of other

reptiles appears to be influenced by the thermal sensitivity of digestive performance (Huey, 1982; Dorcas et al., 1997; van Marken Lichtenbelt et al., 1997), suggesting that there is some generality to our conclusion. Other physiological performances that have narrower optimal temperature ranges than locomotor performance (e.g., sensory perception; Werner, 1976) probably exert some influence on the thermoregulatory behavior of lizards. Expanding the suite of traits for which thermal sensitivities are known will increase our understanding of the causes and consequences of thermoregulation.

Although locomotor performances of *S. undulatus* were relatively insensitive to body temperature, thermal sensitivity does vary among populations. Previously, Crowley (1985) evaluated the sprint performance of fence lizards from New Mexico and Colorado. Like lizards from South Carolina, lizards from Colorado and New Mexico sprinted at greater than 95% of their maximum speed over a wide range of body temperatures (28–40°C). However, the T_o for sprinting was 40°C and the CTMax was 43°C for lizards from both populations. Because Crowley detected no differences in the thermal sensitivity of performance between populations, he concluded that the thermal physiology of *S. undulatus* is conservative. However, a comparison of Crowley's data and our data leads to a different conclusion. We estimated that the sprint speed of lizards from South Carolina is maximized at 34.1°C ($\pm 0.6^\circ\text{C}$), which is considerably lower than the T_o reported for lizards from Colorado and New Mexico. In fact, the T_o for sprint speed in lizards from Colorado and New Mexico is roughly equivalent to the CTMax of lizards from South Carolina! Clearly, there is variation in thermal physiology among populations that is due to either acclimatization or adaptation to local environments. Though intraspecific studies often support a conservative view of thermal physiology, there is no doubt that the thermal sensitivity of physiological performance can evolve within species (Angilletta et al., in press). We expect that the thermal sensitivity of sprint speed and endurance will differ primarily at extreme body temperatures, because locomotor performance is insensitive to body temperature in the intermediate range.

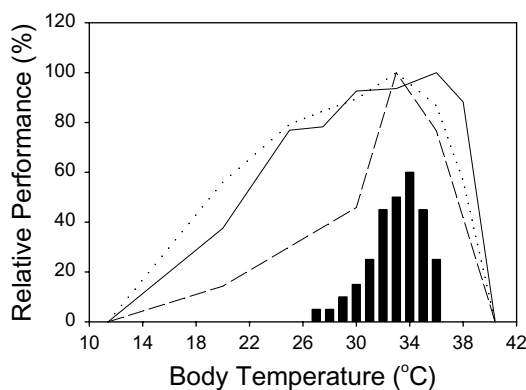


Fig. 2. Thermal sensitivities of sprint speed (solid line), endurance (dotted line), and metabolizable energy intake (dashed line) in the eastern fence lizard, *Sceloporus undulatus*. The distribution of preferred body temperature in this species is depicted by the solid bars (scale is relative). Data for metabolizable energy intake and preferred body temperature are from Angilletta (2001a).

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