



# Food consumption does not affect the preferred body temperature of Yarrow's spiny lizard (*Sceloporus jarrovi*)

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## ABSTRACT

When animals consume less food, they must reduce their body temperature to maximize growth. However, high temperatures enhance locomotion and other performances that determine survival and reproduction. Therefore, thermoregulatory behaviors during different metabolic states reveal the relative importance of conserving energy and sustaining performance. Using artificial thermal gradients, we measured preferred body temperatures of male spiny lizards (*Sceloporus jarrovi*) in fed and fasted states. Both the mean and maximal body temperatures (33° and 35 °C, respectively) were unaffected by metabolic state. This finding suggests that the benefits of foraging effectively, evading predators, and defending territory outweigh the energetic cost of a high body temperature during fasting.

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## 1. Introduction

Most organisms combine physiology and behavior to regulate their temperatures within tolerable limits (Angilletta, 2009). For ectothermic organisms, precise thermoregulation requires movements among sites that offer suitable microclimates for heating and cooling (Diaz and Cabezas-Diaz, 2004; Huey et al., 1989; Schultz, 1998; Withers and Campbell, 1985). These movements incur some energetic cost that offsets the potential benefit (Huey, 1991; Huey and Slatkin, 1976). Still, thermoregulation usually confers a net benefit because the consumption, digestion, and assimilation of food depend strongly on body temperature (Angilletta, 2001; Greenwald and Kanter, 1979; Waldschmidt et al., 1986). The extent to which an individual's temperature varies over time should depend on the costs and benefits of its thermoregulatory strategies (Herczeg et al., 2006; Huey, 1974; Blouin-Demers and Nadeau, 2005).

Food availability dramatically affects the energetic benefit of thermoregulation (Hainsworth, 1978; Huey, 1982). Animals with abundant food grow best at a relatively high temperature. If food becomes restricted, however, the optimal temperature for growth drops below that for an animal with unrestricted access to food (Brett, 1971; Elliott, 1982; Jonassen et al., 1999). In fact, the optimal temperature decreases almost linearly as a function of feeding rate

(e.g., see Elliott, 1982). This graded response stems from the thermal sensitivities of anabolic and catabolic processes, which must vary according to the amount of food that can be processed and absorbed by the gut (Fig. 1). From this information, we conclude that an ectothermic animal should adjust its body temperature according to its rate of feeding. Consistent with this prediction, many ectotherms raise their body temperatures directly after feeding, as reviewed by Angilletta (2009).

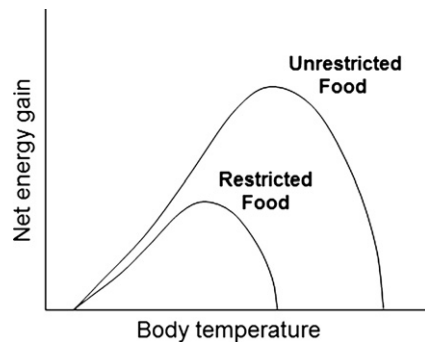
Despite the strong relationship between feeding rate and thermal physiology, models based on purely energetic benefits of thermoregulation might fail to predict the effect of food availability on body temperature. Simple energetic models do not account for the positive impact of thermoregulation on foraging success (Avery et al., 1982), predator avoidance (Cooper, 2000), and immunological defense (Pxytycz and Jozkowicz, 1994). These non-energetic benefits should favor high body temperatures even under fasted conditions. The preferred body temperature of animals during fasting should depend on the degree to which energetic and non-energetic benefits affect fitness. Thus, identifying species whose behaviors constitute exceptions to the common pattern (i.e., lower temperatures during fasting) will help to guide further investigation of the factors that influence thermoregulation.

To quantify the impact of feeding on thermoregulation, we compared the preferred body temperatures of male spiny lizards (*Sceloporus jarrovi*) in absorptive and fasted states. These animals typically occur on rocks and trees, where they must defend territories, capture prey, and evade predators. These activities would be enhanced by relatively high and constant body temperatures maintained via thermoregulation (Hertz et al., 1982; Van Damme et al., 1991). In this

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**Fig. 1.** Optimal body temperature for growth decreases as the food intake decreases. When food becomes restricted, a thermoregulator that maximizes net energy gain would lower its body temperature. Adapted from Huey (1982).

case, a fasted individual might face a compromise between maximizing its growth and maximizing other performances (see Huey, 1982). Given the need for these lizards to perform multiple physiological functions, we wondered whether food availability would affect an individual's preferred body temperature.

## 2. Methods

During May and June 2008, we collected 30 adult males of *S. jarrovi* (mean SVL=92 mm) in the Chiricahua Mountains of Arizona at elevations between 1500 and 2500 m. Lizards were brought to the Sevilleta Field Station of the University of New Mexico, where our experiment was conducted. Each lizard was individually housed in a plastic terrarium (25 × 43 cm) lined with paper towels. The floor of each terrarium was heated on one side, such that operative temperatures ranged from 23 to 39 °C (determined using hollow, copper models of a sceloporine lizard; Bakken and Gates, 1975). Prior to the experiment, lizards were fed adult crickets (*Acheta domestica*) and larval beetles (*Zophobas morio*) daily. Food was coated with a powder containing vitamins and minerals. Lizards were kept under these conditions for a week before the experiment began, and were returned to these conditions whenever they were not in a thermal gradient (see below).

Preferred body temperatures were measured in artificial thermal gradients. Each gradient consisted of a plastic container (36 × 91 cm) with a substrate of sand (≈ 1 cm deep). A 250 W infrared bulb (Exo-Terra, Mansfield, MA, USA), controlled by a rheostat (Exo-Terra, Mansfield, MA, USA) was suspended above one end of the container. Because the ambient temperature of the room was 21 °C, operative temperatures within the container ranged from 23 °C at one end to 45 °C at the other end. Operative temperatures decreased exponentially as one traveled from the source of heat. Such nonlinear gradients are suitable for measuring the preferred body temperatures of heliothermic lizards (e.g., see Angilletta, 2001). During measurements of body temperatures, gradients were illuminated uniformly by fluorescent lights.

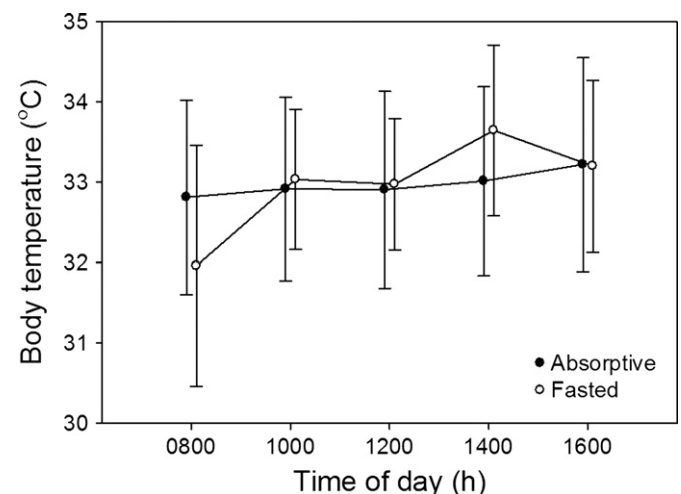
We used consecutive trials to estimate preferred body temperatures of each lizard in fed and fasted states. Fasted states were created by denying access to food for a period of 48 h prior to measurements. Studies using fluorescently labeled food have shown that closely related species of lizards pass food within 48 h of ingestion at preferred body temperatures (Angilletta, 2001; Beaupre et al., 1993; Waldschmidt et al., 1986). Thus, the small amount of food remaining in the gut lowered the thermal optimum for growth. To eliminate temporal artifacts, the order of treatments (fed and fasted) was randomized among individuals.

The same procedure was used for measurements of preferred body temperatures under fed and fasted conditions. Two days before the first trial, lizards assigned to the fasted treatment were denied food, while lizards assigned to the fed treatment continued to consume as many as five crickets per day. On the evening before the measurements, lizards were placed in the gradient and were left undisturbed. During this period, no artificial source of light was available. On the following morning (≈ 0700 h), fluorescent lights were turned on to stimulate activity. Between 0800 and 1600 h, body temperatures were recorded every 2 h with a cloacal thermometer (T-4000, Miller & Weber, Inc., Queens, NY). Although lizards were not disturbed between measurements, we examined diel variation in body temperature for potential signs of handling stress. If repeated handling had affected thermoregulatory behaviors, we should have detected a significant pattern of variation throughout the day, particularly on the first day of measurements. After the first trial, lizards were returned to their terraria and given several days to rest before the second trial. During this period, all lizards were provided food on a daily basis. Two days before the second trial, the order of treatments was reversed for each lizard and the entire procedure was repeated. After both trials, we measured the snout–vent length and body mass of each lizard; lizards were fasted for 48 h before measurements of mass to minimize artifacts caused by food in the gut.

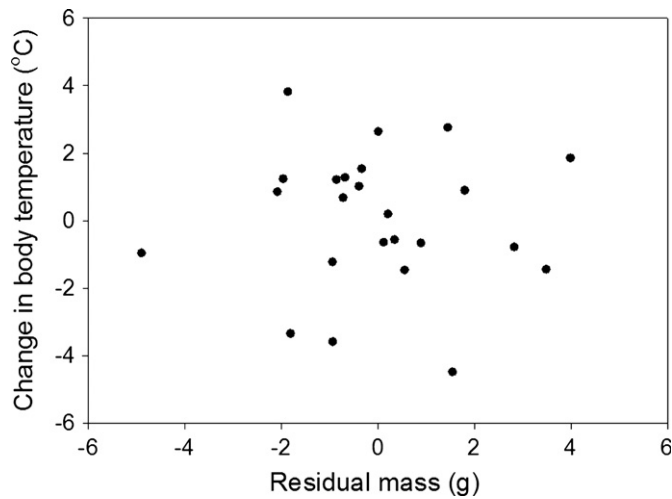
We used an ANCOVA for repeated measures to estimate the effects of physiological state (fed or fasted), treatment order (fed or fasted during trail 1), and time of day on preferred body temperature. Body condition, defined as the residual of mass regressed onto snout–vent length, was used as a covariate. Since the data did not meet the assumption of compound sphericity, we used *P* values adjusted according to Greenhouse and Geisser (1959). Descriptive statistics are reported as mean ± 95% confidence interval. Analyses were performed with Statistica 6.0 (StatSoft, 2003).

## 3. Results

Our analysis indicated no significant interactive effects on the preferred body temperature of spiny lizards (all *P* > 0.40), which greatly simplified our interpretation of the data. Preferred body temperature was unaffected by the order in which the treatments were administered (*MS* = 69.3, *F*<sub>1,21</sub> = 3.39, and *P* = 0.08). Time of day also had no significant effect (*MS* = 7.6, *F*<sub>2,1,44.4</sub> = 0.86, and *P* = 0.44). Most importantly, physiological state did not significantly affect the preferred body temperatures of male spiny lizards (*MS* < 0.1, *F*<sub>1,21</sub> < 0.01, and *P* = 0.98; Fig. 2). In fact, the mean body temperatures



**Fig. 2.** At all times of day, male lizards of *S. jarrovi* selected the same body temperature when in absorptive and fasted states. Error bars are 95% confidence intervals.



**Fig. 3.** Difference in preferred body temperature between fed and fasted states was unrelated to the body condition, defined as the residual of mass regressed onto snout–vent length ( $\beta=0.02$ ,  $r^2 < 0.001$ ,  $F_{1,22}=0.01$ , and  $P=0.91$ ).

during fed and fasted states were remarkably similar:  $33.0 \pm 1.6$  and  $33.0 \pm 1.4$  °C, respectively. Likewise, the minimal and maximal temperatures (averaged among lizards) were similar; mean minima were 27.3 and 28.8 °C and mean maxima were 35.5 and 35.2 °C during fed and fasted states, respectively. Consequently, the central 80% of preferred body temperatures (Bauwens et al., 1995), pooled among individuals, was similar for fed and fasted states (30.7–34.5 °C and 31.2–34.7 °C, respectively). Among individuals, the difference in preferred body temperature between physiological states was unrelated to body condition (Fig. 3).

#### 4. Discussion

A model of optimal thermoregulation based on energetic costs and benefits predicts that animals will decrease their body temperature when food becomes restricted (Huey, 1982). In contrast to this prediction, male spiny lizards selected essentially the same mean body temperature during fed and fasted states. This result implies that these lizards tune their thermoregulatory behavior to non-energetic benefits as well as energetic ones. Other squamates tend to decrease their body temperature during fasting, as predicted by optimal energetics (see Table 4.2 in Angilletta, 2009). By maintaining high body temperatures during periods of fasting, spiny lizards defend the capacity to perform critical functions, such as locomotion, even though growth probably suffers as a consequence. We might expect such a strategy to be more pronounced in individuals that possess greater energy reserves (e.g., see Geiser et al., 1998). Nonetheless, we did not observe any relationship between the body condition of a lizard and its tendency to maintain a high temperature during fasting (see Fig. 3).

Non-energetic benefits of thermoregulation, such as development, immunity, and locomotion, are well documented among ectotherms (Angilletta, 2009). In particular, the need to capture prey and avoid predators provides a strong incentive to maintain body temperatures that enhance locomotion. Physiologists have long known that the locomotor performances of ectotherms depend strongly on body temperature (Bennett, 1980; Huey and Stevenson, 1979). When an animal cools below its optimal or preferred temperature, its ability to locate and subdue prey lessens (Diaz, 1994; Greenwald, 1974; Van Damme et al., 1991). To make matters worse, cold animals cannot escape predators effectively by running (Christian and Tracy, 1981; Cooper, 2000), and must detect

predators earlier or adopt alternative defenses (Goode and Duvall, 1989; Hertz et al., 1982; Passek and Gillingham, 1997; Rand, 1964; Shine et al., 2000). When a lizard maintains a high body temperature during periods of fasting, it trades current energy reserves for the possibility of future energy gain and reduced predation risk.

Thermal depression of locomotion could also impair a lizard's ability to defend resources against conspecifics (Garland et al., 1990; Robson and Miles, 2000). These thermal constraints seem especially important because fasted animals need to forage more often than do nourished animals. *S. jarrovi* breeds during September and October, but territoriality and aggression begin in the spring and intensify as the year progresses (Ruby, 1978; Ruby and Baird, 1994; Simon, 1975). During the non-breeding season, when our study was conducted, the territories of males are largely driven by the abundance and distribution of food rather than females. In fact, males will even display aggression towards females at this time. Both correlative and experimental lines of evidences indicate that lower densities of food result in larger home ranges (Simon, 1975). Therefore, a fasted male should benefit by maintaining a body temperature that enhances its ability to patrol a larger home range, even if this temperature exceeds the optimal one for growth.

A general theory of thermoregulation would enable one to predict changes in body temperature during transitions in metabolic state. Such a theory must weigh both the energetic and the non-energetic benefits of thermoregulation against the costs (Angilletta, 2009; Huey, 1982). By considering non-energetic factors, unexpected patterns of thermoregulation might become more intuitive. For example, green tree vipers (*Trimeresurus stejnegeri*) lowered their temperature by 5 °C during fasting when provided access to refugia, but did not lower their temperature when denied access to refugia (Tsai and Tu, 2005). Possibly, these distinct responses occurred because snakes perceived a potential need for evasive locomotion in the absence of refugia. Similarly, common roaches (*Rutilus rutilus*) lowered their nighttime temperature during fasting, but maintained a high daytime temperature (van Dijk et al., 2002). This diel variation in thermoregulation might have reflected different perceptions of foraging opportunities or predation risks during the night and the day. One could test these hypotheses more rigorously by considering the thermal sensitivities of diverse performances and the relative impact of these performances on fitness (Angilletta et al., 2002; Huey, 1982). A model that considers these factors would predict the direction (and magnitude) of thermoregulatory responses to fasting and should tell us how fluctuations in resources would affect the evolution of body temperature.

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