



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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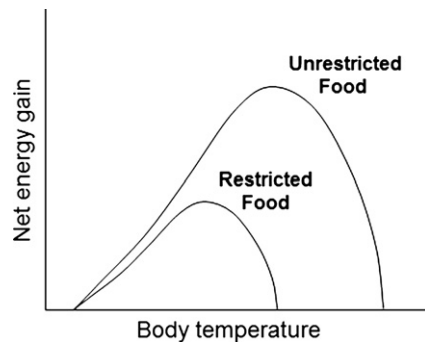


Fig. 1. Optimal body temperature for growth decreases as the food intake decreases. When food becomes restricted, a thermoregulator that maximizes net energy gain would lower its body temperature. Adapted from Huey (1982).

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*_{1,21} = 3.39, and *P* = 0.08). Time of day also had no significant effect (*MS* = 7.6, *F*_{2,144.4} = 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*_{1,21} < 0.01, and *P* = 0.98; Fig. 2). In fact, the mean body temperatures

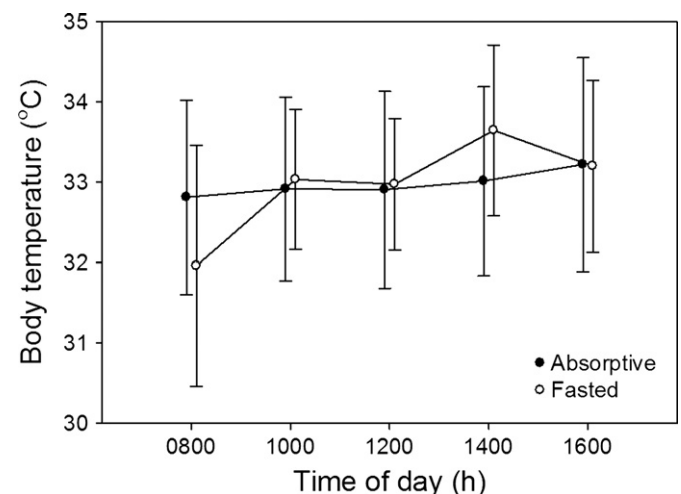


Fig. 2. At all times of day, male lizards of *S. jarrovi* selected the same body temperature when in absorptive and fasted states. Error bars are 95% confidence intervals.

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