Thermal responses to feeding in a secretive and specialized predator (Gila monster, *Heloderma suspectum*)

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**Abstract**

We investigate how a unique dietary specialist, the Gila monster (*Heloderma suspectum*), uses behavioral thermoregulation to elevate body temperature (*T*) after feeding. Lizards in a laboratory thermal gradient were fed rodent meals of three different sizes (5, 10, or 20% of body mass), or sham fed (meal of 0% body mass), and *T* values were recorded for three days before feeding and seven days after feeding. Gila monsters selected a mean *T* of 25.2°C while fasting (set-point range 23.6–27.1), and increased *T* values after feeding. The magnitude and duration of post-prandial *T* increases are positively related to meal size, and Gila monsters selected mean *T* values up to 3.0°C higher and maintain elevated *T* values for 3–6 days after feeding. Selection of *T* does not appear to differ between day and night time periods, and because the lizards are both diurnal and nocturnal (at different times of year), photoperiod may not be an important influence on *T* selection.

1. Introduction

The thermal biology of reclusive species is often difficult to evaluate because individuals are hard to observe directly engaging in thermoregulation, and because thermal trade-offs among different behaviors (e.g., foraging, refuge-site selection, predator avoidance, and reproductive activities) are usually intertwined (Blouin-Demers and Weatherhead, 2001; Downes and Shine, 1998). Reclusive lizards can often be dietary specialists (Huey et al., 2001; Pianka and Pianka, 1976) and specialized diets can lead to specific patterns of body temperature (*T*) variation (Pianka and Parker, 1975; Zimmerman and Tracy, 1989). Species that are both reclusive and dietary specialists might, therefore, be expected to have *T* patterns that are influenced by diet, as well as by the ecological and environmental factors that dictate a reclusive and specialized lifestyle.

Gila monsters (*Heloderma suspectum*) are especially reclusive lizards that spend nearly all the time hidden in underground refugia (>95% of time in some populations; Beck, 1990), even when environmental conditions are suitable for above-ground activity. They also occupy an unique dietary niche, and almost exclusively binge feed on the eggs and altricial nestlings of ground-nesting vertebrates, especially rodents and lagomorphs. Because of their specialized ‘nest-predator’ diet, meals consumed by Gila monsters can be as large as one-third of their body mass (Beck, 2005; Stahnke, 1950, 1952), and 3 to 4 large meals may fulfill an individual’s entire annual energetic needs (Beck, 1986; Beck and Lowe, 1994).

Here, we investigate how patterns of *T* selection in Gila monsters can be influenced by specialized diet and the consumption of large vertebrate prey (relative to body size). Few lizard species are able to specialize on vertebrate prey, and those that do, such as some large varanids (Losos and Greene, 1988), tend to be highly active and thermoregulate at a high and constant *T*, that allows them to actively pursue, capture, and subdue prey (Christian and Bedford, 1996; Christian and Weavers, 1996). Gila monsters are therefore unique in that they are neither highly active, nor particularly thermophilic (Beck, 2005).

However, after feeding, Gila monsters may become temporarily thermophilic and increase *T* to facilitate digestion. Feeding on in-tact vertebrate prey, such as that observed in most snakes, is often associated with a dramatic digestive response that includes increased rates of post-prandial metabolism, protein synthesis, and nutrient absorption (Secor, 2005, 2009); all of these temperature-dependent digestive processes likely function at a higher level with increased body temperature (Karasov and Martínez del Río, 2007; Wang et al., 2002). We therefore test the predictions that Gila monsters should elevate *T* after feeding, and that the magnitude and duration of elevated post-prandial *T* should be related to meal size, as larger meals likely take longer to digest and pass through the body.

2. Materials and methods

2.1. Laboratory thermal gradient

Experiments to assess *T* selection were conducted in a thigmothermal gradient. An aluminum sheet (1 cm thick) was fastened to a plywood box frame (6.1 x 1.2 x 0.6 m) from below,
and divided into four lanes by three plywood dividers (61 cm high × 1.5 cm thick). All plywood surfaces were coated with marine resin and sealed at joints with silicon sealant. A layer of sand covering the aluminum base provided a substratum that was changed between trials.

The gradient was cooled at one end by a recirculating chiller pumping a 5 °C ethylene glycol solution through 0.75 cm diameter copper tubing taped to the aluminum base along one-third of the length of the gradient. The gradient was warmed at the other end by heating strips (Omega Flexible Heaters SRFG-148/5) taped to the underside of the aluminum base and spaced at ~30 cm intervals. Each heat strip was wired to a solid-state relay and temperature was maintained at +/−0.1 °C of a given set-point by a feedback program written for a computer controller datalogger (Campbell Scientific CR10X). Temperatures ranged from 10 to 50 °C and changed linearly along the length of the gradient at ~1 °C per 16 cm.

Lighting was provided by overhead fixtures suspended 1.2 m above the gradient surface. Ten 125 W (6400 K) full spectrum light bulbs (Hydrofarm Inc., Petaluma, CA.) were evenly spaced in two parallel rows of five bulbs. This arrangement provided an average illumination of 1894 candella (SD ± 248) on the gradient surface. Lighting was controlled to provide a 12:12 photophase: scotophase cycle, which matched the photoperiods provided to individuals in their cages between trials.

2.2. \( T_b \) sampling

Body temperatures (\( T_b \)) of 10 adult Gila monsters (mean mass = 479 ± 115 g; 8 male and 2 non-gravid female) were recorded using Thermochron ibutton dataloggers (Dallas Semiconductor). Each ibutton was calibrated against a NIST traceable standard thermometer, and was attached to the chest of the lizard directly over the heart using a 4 × 3 cm strip of 0.5 cm thick foam insulation (Frost King, Thermwell Products, Sparks, NV). The insulated datalogger package was further secured using medical tape (Nexcare Absolute Waterproof tape, 3 M, St. Paul, MN) wrapped around the circumference of the chest. The entire datalogger package had a mass of ~5 g, which was less than 2% of the mass of each lizard.

To ensure that temperatures measured by ibuttons matched internal \( T_b \), we compared ibutton recordings against cloacal temperatures. We placed one Gila monster (with attached ibutton) in each of the four lanes of the thermal gradient. A clear plastic box (inverted) was placed over each lizard and \( T_b \) was allowed to equilibrate for 15 min. We then recorded internal \( T_b \) using a Schultheis rapid-reading thermometer inserted 1.5 cm into the cloaca. This procedure was repeated at different positions in the gradient with substratum temperatures of 15, 20, 25, 30, and 35 °C. The correlation coefficient between cloacal and ibutton temperature was greater than 0.995 for each lizard (mean slope = 1.0), indicating that ibuttons attached to the chest of Gila monsters gave very close estimates of \( T_b \). In all experiments, \( T_{bS} \) were recorded every 15 min.

2.3. Feeding effects on preferred \( T_b \)

Food was withheld from lizards for two weeks prior to initiating each experiment. After introducing individuals onto the thermal gradient, they typically paced the entire length for 1–4 h before becoming settled and adopting a thermoregulatory posture in which the ventral body surface was pressed against the substrate. We considered that an individual was habituated to the gradient after it was observed either sleeping or resting for six consecutive hours without the exploratory pacing seen in newly introduced individuals.

Once lizards habituated, we logged \( T_{bS} \) for 72 h and then randomly assigned each to one of four feeding treatments that differed in meal size. Lizards were fed a meal of rat pups (Rattus norvegicus) equivalent to 5, 10, or 20% of body mass (treatment group), or were fed nothing (0% meal, sham control group). To administer meals, each lizard was removed from the gradient, placed in a clear plastic box, and fed (or sham fed) by hand. All meals were initiated at 12 pm local time and all were completed within one hour. After completing the meal (or sham), lizards were placed back on the gradient and \( T_{bS} \) continued to be recorded for seven days. Lizards were then returned to their home cages and allowed to rest for a minimum of two weeks before repeating the procedure for each of the other feeding treatments. The thermal gradient was cleaned between trials by replacing the sand substrate and by wiping down gradient wall surfaces with a dilute 5% bleach solution.

Daily means and standard deviations of selected \( T_{bS} \) were calculated for each individual in each combination of feeding period (pre and post-feeding), meal size (sham, 5, 10, or 20% of body mass), and photoperiod (photophase or scotophase). We then used the general procedures of Hertz et al. (1993) to estimate the preferred \( T_b \) set point range as the bounds of the central 50% of observed \( T_{bS} \) for each individual in each treatment combination. Thus, the lower and upper set points of the preferred \( T_b \) range are estimated by the 75% and 25% quartiles of the distribution (respectively). Typically, the framework of Hertz et al. (1993) is used to evaluate the preferred \( T_b \) of individuals in a laboratory thermal gradient where environmental constraints on thermoregulation are assumed to be absent.

2.4. Statistical analyses

Because \( T_b \) data often exhibit a skewed distribution (Dewitt and Friedman, 1979), and fail to meet the assumptions of parametric testing, we transformed data prior to analyses. We attempted several data transformations (log, square-root, inverse), but none yielded normal distributions. We, therefore, conducted analyses on untransformed data, and because the experiments were perfectly balanced (identical sample sizes among treatments), violation of the normality and homogeneity assumptions should have a small effect on the probability of Type 1 error (Refinetti, 1996). Repeated measures analysis of variance (RM ANOVA) was used to determine differences in mean \( T_b \) selection and thermoregulatory set-points as a function of feeding state (pre- or post-feeding), meal size (sham, 5, 10 or 20%), and time of day (photo- or scotophase). Post-hoc comparisons were conducted using Fisher’s LSD.

3. Results

3.1. Effect of photoperiod on preferred \( T_b \)

Photoperiod did not affect \( T_b \) regulation of animals maintained on a 12:12 light:dark cycle. There was neither an overall effect of photoperiod as a factor on mean \( T_b \) in the full model (meal size × feeding state × photoperiod; \( F_{1.9} = 0.22, P = 0.65 \)), nor was photoperiod significant in the interactions with meal size (\( F_{1.27} = 0.29, P = 0.83 \)), with feeding state (\( F_{1.9} = 1.16, P = 0.31 \)), or with both (\( F_{1.27} = 0.60, P = 0.44 \)). Photoperiod was also not significant as a main or interaction effect for \( T_{set} \) lower or \( T_{set} \) upper, and was therefore excluded from all further analyses.
3.2. Effect of feeding and meal size on preferred $T_b$

While in a fasting (post-absorptive) state, Gila monsters on the thermal gradient selected a mean $T_b$ of $25.2 \pm 0.6$ °C and had a set-point range of $23.6 \pm 0.9$ to $27.1 \pm 0.4$ °C (mean of individual means for all lizards). There was a strong effect of both feeding and meal size on all $T_b$ metrics used to compare 72 h pre-feeding and 72 h post-feeding periods. Mean $T_b$ was significantly higher after feeding than before ($F_{1,9}=63.9, P<0.0001$; Fig. 1) and it was also significantly affected by meal size ($F_{3,27}=9.39, P<0.0001$); the results are nearly identical for $T_b$ set lower ($F_{1,9}=30.3, P<0.0001$; Fig. 1) and $T_b$ set upper ($F_{1,9}=32.2, P=0.0003; F_{3,27}=4.2, P=0.01$; Fig. 1), for tests of feeding state and meal size, respectively. The standard deviation of $T_b$ was significantly lower after feeding than before ($F_{1,9}=6.8, P=0.028$; Fig. 2) and it was also significantly affected by meal size ($F_{3,27}=5.42, P=0.005$). Interaction terms for feeding state x meal size were significant only for mean $T_b$ ($F_{3,27}=3.3, P=0.04$) and $T_{\text{set}}$ lower ($F_{3,27}=4.3, P=0.01$), but the magnitude of the interaction effect was low for both. Partial $\eta^2$, a measure of explained variance (Graham and Edwards, 2001; Keren and Lewis, 1979), was 0.068 for mean $T_b$ and 0.079 for $T_{\text{set}}$ lower, indicating that each interaction explained less than 8% of the variance in their respective models.

The duration that post-prandial Gila monsters maintained $T_b$ above the pre-feeding level varied with meal size (Fig. 3). The sham treatment (0% meal) did not elicit an elevated $T_b$ response ($F_{1,63}=1.7, P=0.13$), and mean $T_b$ actually declined to the lowest level of the experiment on day 7 post-sham, corresponding to the cumulative period of three weeks since lizards had eaten a meal. The 5% meal treatment gave a significant increase in $T_b$ overall ($F_{1,63}=3.12, P=0.007$), and $T_b$ was significantly higher for three days post-feeding. Larger meals led to longer periods of elevated $T_b$ post-feeding; both the 10% and 20% feeding treatments gave significant overall responses ($F_{1,63}=4.7, P<0.001$; $F_{1,63}=11.8, P<0.001$, respectively) and $T_b$s were significantly higher for five and six days after feeding, respectively (Fig. 3).

4. Discussion

4.1. Behavioral thermoregulation and influences on $T_b$ selection

Our goal was to investigate how the specialized feeding strategy of Gila monsters, namely binge-feeding on large meals of vertebrate prey, influences patterns of selected body temperature. After feeding,
Gila monsters selected higher and less variable Tₘs than when fasting. Presumably, selecting higher Tₘs allows lizards to improve digestion by reducing passage time of the meal through the gut (Waldschmidt et al., 1986), or by increasing digestive efficiency (Beaupre et al., 1993; Harlow et al., 1976). Digestive efficiency of Gila monsters has been reported to be 76.5% at constant Tₘ of 27 °C (Beck, 1986) and 90.6% at 29 °C (Wegscheider, 1998), suggesting that even modest increases in Tₘ, such as those observed in this study, could improve digestive performance.

Although Gila monsters likely elevate Tₘ following feeding to improve digestion, they can also regulate digestive function without changing Tₘ. While being maintained at a constant Tₘ of 30 °C, Gila monsters increase metabolism up to 4.9 times basal levels after consuming rat meals equivalent to 10% of body mass (Christel et al., 2007). Selecting elevated Tₘs, therefore, could work interactively with physiological processes to optimize digestion (Dorcas et al., 1997; Tracy et al., 2005). However, the benefit of elevating Tₘ to up-regulate digestive machinery after feeding is likely governed by the size of the meal. A large meal (either 10 or 20% of body mass) was generally required to evoke a significant increase in upper or lower thermoregulatory set-points (Fig. 1). This suggests that selecting higher Tₘs after eating small meals may not be necessary, because digestion can take place effectively in the absence of a post-prandial Tₘ increase, or that the metabolic costs of elevating Tₘ (Q₁₀ effects), may be more than the value of the meal.

Digestive costs for Gila monsters, calculated as specific dynamic action (SDA; Secor et al., 1994), are roughly 18% of the energetic value of a meal when meal size is equivalent to 10% of body mass (Christel et al., 2007). Research from other carnivorous reptiles has shown that digestive costs can be considerable even for small meals, and that digestive costs increase with meal size (Secor and Diamond, 1997a, b). To process a meal, the digestive organs and cellular machinery must be up-regulated from a quiescent state when the gut is empty to a functioning state when the gut is full. If the metabolic costs of a post-prandial Tₘ increase are added to the SDA costs, along with the pre-feeding costs of prey pursuit and consumption (Cruz-Neto et al., 2001; Pough and Andrews, 1985), it could mean that eating small meals would yield little net energy gain. This may partially explain why Gila monsters are adapted to consume large meals, such as the entire contents of prey nests. By consuming large meals, the energetic return to Gila monsters may be large relative to the digestive costs.

The Tₘ selection of Gila monsters did not appear to be influenced by time of day. Photoperiod is an important factor influencing temperature selection in other lizard species (Ballinger et al., 1969; Sievert and Hutchison, 1991; Tracy et al., 2005), and this is likely related to voluntary ‘hypothermia’ (Regal, 1967). To save energy, some lizards seek cooler Tₘs at night when predation risk is putatively lower, and there is less need to maintain a high and constant Tₘ for predator avoidance or escape (Dawson, 1975). Digestion likely poses a limit to any voluntary reduction in Tₘ (Tracy et al., 2005), and with large meals, the benefit of increasing digestive function by selecting warmer Tₘs may outweigh the potential energy savings of reducing Tₘ during the night.

An alternative explanation might be that photoperiod is simply not a strong environmental cue for temperature regulation in nocturnal and secretive species, such as Gila monsters. Some species of nocturnal geckos have little or no diel variation in preferred Tₘ (Angilletta and Werner, 1998), yet other diurnal species routinely show strong day and night differences (Firth and Belan, 1998; Firth et al., 1989; Tracy et al., 2005). While diurnal species may translate photoperiodic cues using the pineal complex and its regulatory effects on melatonin production and Tₘ selection (Lutterschmidt et al., 2003; Ralph et al., 1979), nocturnal and crepuscular species may not be as sensitive to cues from photoperiod in regulating circadian processes (Ellis et al., 2006; Hyde and Underwood, 2000). This hypothesis is supported by the observation that Gila monsters are “poor time-keepers” (referring to their circadian patterns) and show no differences in activity under constant light or constant dark conditions (Lowe et al., 1967).

While Gila monsters select higher Tₘs after feeding, many reptiles do not. Preliminary reviews by Sievert (1989) and Touzeau and Sievert (1993) suggest that only about half of the species tested show significant elevation of Tₘ after feeding. Many factors may obfuscate the ability to detect a significant post-prandial thermophilic response, including meal size, meal composition, and feeding frequency. Clearly, more work is needed to

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**Fig. 3.** Mean body temperatures (Tₘ) of Heloderma suspectum prior to (day 0) and following feeding for each of four meal size treatments; meals equal to 0 (sham treatment), 5, 10, or 20% of lizard body mass. Values are mean of individual means (± 1 SE) for each combination of meal size and day post-feeding. N=10 individuals for all. Dashed line is grand mean of pre-feeding Tₘ. Stars indicate days in which Tₘ was significantly elevated (Fisher’s LSD) above the pre-feeding baseline.
explain patterns of postprandial thermophily in the context of variation in species’ diets.

We have shown how the specialized feeding strategy of Gila monsters, binge-feeding on large meals of vertebrate prey, can lead to shifts in patterns of preferred \( T_b \). Gila monsters use behavioral thermoregulation to regulate \( T_b \) and preferred \( T_b \) changes with digestive state and meal size. By selecting higher \( T_b \) after feeding, both gut passage rate and digestive efficiency could be increased, thereby reducing the time in which Gila monsters would be physically encumbered by a digestive tract full of food and more vulnerable to predation.

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