Feeding causes thermophily in the woodhouse’s toad (Bufo woodhousii)

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Abstract

(1) We placed 12 toads (Bufo woodhousii) in linear thermal gradients with floor temperatures ranging from 10 to 40°C and monitored body temperatures (Tb's) with chromega-omega thermocouples interfaced with a datalogger. (2) We measured Tb's at 10 min intervals over a 24 h period in toads that had eaten an equivalent of 5% of their body mass or had fasted for 5 days. (3) The mean 24 h Tb did not differ significantly between the fed and fasted groups. (4) Hourly mean Tb’s of fed toads differed significantly over the 24 h, but those of fasted toads did not. Fed toads selected highest Tb’s during late afternoon and evening. © 2001 Elsevier Science Ltd. All rights reserved.

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Behavioral thermoregulation has been well studied in reptiles, but much less is known about thermoregulation in amphibians. Several factors contribute to the paucity of information regarding amphibian thermoregulation. (1) There are potential conflicts between thermoregulation and hydroreagulation since amphibians need to maintain a moist skin for cutaneous respiration (Hutchison and Dupré, 1992). Unlike reptiles, anurans abandon thermoregulation in dry environments (Williams and Wygoda, 1993; Tracy et al., 1993). (2) Many anurans spend time both in water and on land, and duplicating both hydric and thermal gradients simultaneously in the laboratory is difficult. (3) Many anuran species show no temperature preference (Brattstrom, 1963).

Anurans can thrive with a feast-or-famine lifestyle because they rely on behavioral rather than physiological thermoregulation. Because they are not forced to seek food on a continuous basis to fuel a high metabolic rate, they can be selective in when they are active thereby avoiding adverse environmental conditions and predators. If they sequester themselves in cool retreats metabolic rate is further reduced and anurans can extend the amount of time they are inactive (Pough, 1983). Although seeking low body temperatures (Tb's) allows energy conservation and a decrease in water loss (Williams and Wygoda, 1993), some anuran species or life stages intentionally elevate Tb’s at appropriate times. Benefits of elevated Tb’s include increased digestive rate and digestive clearance which allows anurans to ingest more per time and grow faster or store more energy than anurans which cannot warm up (Freed, 1980; Lillywhite et al., 1973). Elevated Tb’s also increase sprint speed (Tracy et al., 1993) which could be important in catching prey and evading predators.

Larval anurans thermoregulate in both the laboratory (Tracy et al., 1993) and the field (Bradford, 1984). By selecting warm water temperatures larvae can decrease the time until they metamorphose and lower the likelihood of being predared or dying of dehydration if the pool evaporates (Dupré and Petranka, 1985). Many juvenile anurans are diurnal and readily bask (Lillywhite et al., 1973; Freed, 1980; Tracy et al., 1993). For nocturnal adults, finding warm microhabitats during activity can be problematic, but, they can shuttle
between water and land, or seek thermally appropriate microhabitats (Bradford, 1984). Thermoregulation may be the most important in newly metamorphosed anurans that need to maximize growth rather than in larger adults (Lillywhite et al., 1973; Tracy et al., 1993), yet, many adult anurans, such as the bufonids, readily thermoregulate in both laboratory and field situations (Freed, 1980; Bradford, 1984; Tracy et al., 1993).

*Bufo woodhousii* lives in the Great Plains and SW portion of the United States where it inhabits areas near temporary breeding pools and is encountered in undisturbed areas, agricultural land, and back yards (Conant and Collins, 1991). *B. woodhousii* is nocturnal and spends days in small mammal burrows (Collins, 1993) or buried in loose soil. We have observed captive individuals basking under incandescent lights and since adults readily eat in the laboratory, we felt *B. woodhousii* would be a good organism for studying thermoregulatory behavior.

Our purpose was to determine: (1) if feeding influences heat seeking in *B. woodhousii* and (2) if feeding modifies diel cycles of thermoregulation. We predicted that fasted toads would select lower *Tb*’s than fed individuals and that both groups would display diel cycles in temperature preference. To test our predictions we measured *Tb*’s of 12 toads in a laboratory thermal gradient over a 24 h period.

1. Materials and methods

*B. woodhousii* (mean mass = 68.5 ± SE 10.4 g; range = 34.4–156.8 g) was collected in June 1998 in Chase and Lyon Counties, KS, USA. Toads were maintained in the laboratory at 21°C with a LD 12:12 photoperiod with photophase starting at 0600. Groups of no more than three toads were housed in 50 × 50 × 22 cm plastic containers with ventilated lids. PVC pipe retreats and water were available as well as a basking light with a 25 W incandescent bulb. Toads were offered crickets (*Acheta*) and/or mealworm larvae (*Tenebrio*) three times each week and were acclimated in the laboratory for a minimum of 14 days before testing began. Toads were not fed for 5 days prior to the experiment.

Toads were induced to urinate and weighed the day before data were recorded. An individual toad was then placed in a linear thermal gradient and left to habituate. The thermal gradients were located in an 8°C environmental walk-in chamber on the same LD 24:00 photoperiod to which the toad was acclimated. The thermal gradient had floor temperatures ranging from 10 to 40°C. A subsurface heat pad maintained the warm end of the floor of the thermal gradient at 40°C. Water bowls were placed at either end of the gradient behind a styrofoam partition and cloth disposable towels sewn together sat on the floor of the thermal gradient. The ends of the towels rested in the water bowls. This wicked the water into the towels and kept the gradient floor moist throughout the time the toad was in the thermal gradient.

Each toad participated as both a fed and fasted individual, allowing each animal to act as its own control. Half of the animals served as fed individuals initially and the other half were fasted. After at least 14 days toads had *Tb*’s monitored again. This time the previously fed toads were fasted and the previously fasted toads were fed. An hour before temperatures were recorded, toads in the fed group were given crickets equivalent to 5% of their body mass. For both groups, a thermocouple was inserted 1–2 cm into the large intestine. The exiting wire was affixed with surgical staples to the toad’s dorsum and interfaced with a Kane May data logger (KM1242). The toads were replaced in the thermal gradient and allowed 30 min before we started measuring *Tb*’s. We recorded temperatures at 10 min intervals for 24 h and calculated the mean temperature for each toad for each hour.

We compared *Tb*’s between the two groups and compared changes in selected temperature over time with a two-way repeated measures Analysis of Variance (ANOVA). The interaction term allowed us to compare the pattern of temperature selection over time between the two groups. A one-way repeated measures ANOVA compared *Tb*’s over time within each group over the 24 h period. A Student–Newman–Keuls (S–N–K) pairwise comparison test compared which hourly temperature values differed over time. We compared fed and fasted *Tb*’s measured at the same hour with a *t*-test. Mean values were considered significant at *P* ≤ 0.05. All values are given as mean ± SE.

2. Results

*Tb*’s of the two groups were not significantly different over the entire 24 h period (*P* = 0.56). Mean *Tb*’s of the fed toads were 26.0 ± 0.7°C and those of fasted toads were 25.6 ± 0.7°C. Temperature selection over time differed significantly (*P* = 0.022) as did the interaction term (*P* < 0.001) indicating a difference in the shapes of the time–temperature curves between the two groups (Fig. 1).

There was no significant difference in *Tb*’s between any of the hours over the 24 h period (*P* = 0.98) in the fasted group. The fed group showed a significant difference in *Tb*’s over time (*P* < 0.001). The fed toads selected highest temperatures from 2200 to 2400 and lowest temperatures from 0400 to 1600 h (Fig. 1). Specifically, hours 0400–1600 were significantly lower than hour 2200 (*P* < 0.05), hours 0600–1400 were significantly lower than hour 2300 (*P* < 0.05), and hours 0600, 0800, and 1000–1300 were significantly lower than
hour 2400 (P < 0.05). Significantly higher temperatures were chosen by fed toads than by fasted toads at 1900, 2100, and 2300 h.

3. Discussion

We fed our toads at noon which is not the normal foraging time for toads, but instead of seeking heat immediately, our toads selected highest $T_b$'s during the time they would normally be away from their burrows. Nocturnal animals cannot thermoregulate by basking in the sun, but there are many thermally buffered microhabitats, such as rocks and paved roads, that retain heat long after sundown. At night burrows can provide warmer temperatures and humidity than exposed sites above ground (Moore and Moore, 1980). Therefore, during both activity and inactivity toads can easily find warm places with comparable temperatures to those chosen by our fed toads. Aside from accelerating digestion rate, elevated $T_b$'s enhance locomotion and therefore agility, alertness, and hearing in ectotherms (Stevenson et al., 1985; Werner, 1972; Xiang et al., 1996). All of these are important for procuring food without being predated.

The ability of amphibians to select lower temperatures during inactivity is probably a highly adaptive mechanism to conserve energy (Hutchison and Dupre, 1992) rather than an inability to find warm temperatures. Burrows can provide protection from predators, cooler temperatures, and higher humidity during the day than exposed sites. Conversely, at night burrows provide warmer temperatures and higher humidity than exposed sites. The latter was observed with B. punctatus where higher $T_b$'s were attained while the toads were in burrows after feeding than when they were active outside the burrow (Moore and Moore, 1980). By exerting very little effort, toads can thermoregulate by spending activity time on readily accessible warm substrates, escape predators and dessication by returning to a warm, humid burrow, and can spend days in a relatively cool, humid burrow. Occupying a burrow is important for hydroregulation, but also allows a toad to passively maintain $T_b$'s that accelerate digestion at night and conserve energy during the day.

Seeking heat during the day would accelerate digestion, but it also elevates metabolic rate during a time when toads are normally inactive and hidden, and thereby expends energy needlessly. By seeking warm temperatures during the normal activity period rather than any time there is food in the gut, B. woodhousii can maximize the amount of energy it consumes relative to that which it expends.

Our prediction that fasted animals would select lower $T_b$'s than fed toads was only true for some of the hours during the activity period. Toads normally spend their summer days in burrows. This behavior protects them from the high temperatures and dry conditions associated with summer in Kansas. The situation at night during the normal activity period is much different. During the summer in Kansas toads are exposed to a thermal mosaic where paved roads and rocks retain heat and vegetated areas do not. Thus, with very little effort a toad can thermoregulate. The normal activity time was the only time during which we observed differences in thermoregulatory behavior between the fed and fasted toads.

We predicted that both fasted and fed toads would display diel cycles, however, the results show that only the fed toads had temperature variation in their daily cycles. The fasted toads remained at their cool, daytime $T_b$'s all the time which kept metabolic rate low. Fed toads elevated $T_b$'s and metabolic rates presumably because of food in the gut. Not all amphibians have diel cycles of $T_b$ (Mullens and Hutchison, 1992) and some amphibians only maintain a diel cycle at certain times of the year (Hutchison and Dupre, 1992). Our results suggest that feeding may play an important role in the expression of a diel cycle of temperature selection.

The thermal gradients were set up in a manner that maintained high humidity. This removed moisture level as a potentially confounding variable (Williams and Wygoda, 1993) in our experiment. Because amphibians are prone to dehydration, seeking elevated temperatures is often thought to be dependent on the presence of water. However, Hyla cinerea was observed basking without the presence of water (Freed, 1980) and Lillywhite et al. (1973) found that basking behavior in B. boreas was decreased but not eliminated when the substrate was dry.
There is a lack of data on many aspects of amphibian thermoregulation (Hutchison and Dupre, 1992). Field $T_b$'s of fed and fasted *B. woodhousii* over a 24 h period have not been measured. Our results suggest that it should be possible for *B. woodhousii* to exert control over $T_b$ in the field and that digestion may be a causative factor in whether a toad seeks heat.

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**References**


