

Feeding state and selected body temperatures in the slow-worm (*Anguis fragilis*)

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Lizards may select higher body temperatures after feeding, but rigorous experimental evidence of this is confined to a small number of lineages. Here it was examined in an anguid lizard, namely the slow-worm *Anguis fragilis*, which is a semi-fossorial cool temperate species that exhibits relatively low field body temperatures. Body temperatures selected by slow-worms in a thermal gradient were low compared with many other lizards (means ranged from 25.3 to 26.4 °C). This indicates that low field body temperatures described previously are not due to thermoconformity in a cool environment. More significantly, selected body temperatures differed between fed and three-day fasted treatments, with an increase of 0.4–1.2 °C being observed after feeding. The magnitude of this increase is similar to that reported for two iguanid lizards, and shows that a postprandial response is also present in this ecologically and phylogenetically distant species.

Key words: Anguidae, fasting, food, temperature selection, thermoregulation

INTRODUCTION

There is evidence that squamates select higher body temperatures after feeding. To date, detailed studies have been largely confined to several snake species (e.g. Blouin-Demers & Weatherhead, 2001; Sievert & Andreadis, 1999; Sievert et al., 2005) and a small number of lizards. These include two iguanids, *Anolis* (Brown & Griffin, 2005) and *Crotaphytus* (Sievert, 1989), the gekkonid *Eublepharis* (Autumn & De Nardo, 1995) and a pyropodid, *Lialis* (Bradshaw et al., 1980). The iguanids and the pyropodid both showed evidence of an increase in selected body temperature after feeding, although the gekkonid did not. Studies of other reptiles and amphibia have also indicated postprandial thermophily (e.g. Witters & Sievert, 2001; Gvoždík, 2003), although not all studies have detected a significant effect (Brown & Brooks, 1991; Mullens & Hutchison, 1992; Brown & Weatherhead, 2000). A question that has received little attention is whether it is more pronounced in Squamata that show low daytime activity temperatures, due to a potentially greater impact on digestion (although see Tosini et al., 1994). This paper tests for a postprandial thermophilic response in a cool habitat species that shows low field activity temperatures.

The European lizard, *Anguis fragilis*, belongs to the Anguinae clade within the Anguidae, which it shares with several *Ophisaurus* species (Macey et al., 1999). It is a relatively small (adults usually 120–200 mm) cool temperate member of the group with a distribution that extends to near the Arctic circle. Scientific interest in the Anguinae stems largely from the fact that they comprise mainly legless species, and appear ecologically quite distinct from other anguid clades. The Anguinae have been described as surface-dwelling grass-swimmers (Wiens & Slingluff, 2001). Anecdotal field observations suggest that this is not an appropriate ecomorph label for *A.*

fragilis because, despite regular surface activity, it also appears semi-fossorial (e.g. Simms, 1970). Fossorial lizards often show lower field body temperatures (T_b) than surface-dwelling species (e.g. López et al., 2002), which may, in part, be attributed to lower thermal preferences (e.g. Bury & Balgooyen, 1976). Field studies of *A. fragilis* seem to support this: body temperatures recorded by Patterson (1990) under “optimal” temperature conditions ranged from 14.5 to 28 °C (Patterson, 1990), with a mean of 22.1 °C under sunny conditions being described by Meek (2005). There have been no detailed studies of selected body temperatures under controlled conditions (although see Spellerberg, 1976, and Gregory, 1980, for preliminary data), so it is not yet possible to robustly assess how much of this is due to thermoconformity within a cool environment, and how much is due to low temperature preferences. This report provides the first detailed analysis of body temperatures selected by *A. fragilis* in a thermal gradient.

MATERIALS AND METHODS

Specimens and maintenance

Slow-worms were obtained from an enclosed part of a garden in Wareham, Dorset, UK (an area in which they also occur naturally). They were returned to the same site following this project. A total of 30 individuals were housed in two glass aquarium tanks (60cm × 30cm × 35cm and 101cm × 31cm × 46cm). A commercially available “Forest bed” substrate (manufacturer: T-Rex) on one side of the tank, of depth 5–7 cm, allowed burrowing. It was partially covered with bark and sphagnum moss and kept moist by daily spraying. Thermoregulation was facilitated by a single 60 W bulb (12:12 LD) suspended above gravel substrate at the opposite end of each tank. Minimum night temperatures were approximately 18–20 °C, while day temperatures in the tanks were generally around 25–

Table 1. Mean selected body temperatures (\pm S.E.) of 20 *Anguis fragilis* at different times of the day under fed (FEED) and food-deprived (FAST) treatments.

	Time			
	1200	1400	1600	1800
FEED	26.3 \pm 0.48 °C	26.3 \pm 0.41 °C	26.4 \pm 0.31 °C	26.2 \pm 0.34 °C
FAST	25.6 \pm 0.43 °C	25.4 \pm 0.33 °C	25.3 \pm 0.40 °C	25.8 \pm 0.33 °C

30 °C. Small common earthworms (*Lumbricus* spp. and *Aporrectodea* spp.) were provided as food on alternate days. Prior to the experiments, the slow-worms were housed in pairs in plastic cages (23 cm \times 15 cm \times 18 cm) to allow restriction/monitoring of food intake. Temperature gradients were also created in these smaller cages, via a 60 W bulb above one end (connected to a thermostat to avoid overheating). The substrates described for the larger tanks were replicated in these smaller cages.

Measurement of selected body temperature

A thermal gradient of size 122cm \times 62 cm was constructed from chipboard. Three longitudinal wooden partitions divided the gradient into four lanes, each 15 cm wide. Overhead ceiling lights provided uniform illumination along the gradient. "Forest Bed" substrate was applied to a depth of about 1 cm. A floor made from copper sheet enhanced heat conduction, with a thermal gradient maintained by two 150 W bulbs sited below the hot end, and an ice-filled container below the cold end. Temperatures measured on top of the substrate ranged from approximately 20 to 45 °C between the ends of the gradient, although this range was greater on the copper floor. Cardboard strips with a single fold running down them extended the length of each compartment, to provide additional shelter for the slow-worms during the experiment. Slow-worms were placed individually in each lane at 1000 (GMT) and left undisturbed for two hours. Body temperatures selected in the gradient (SBT) were recorded four times at two-hourly intervals before the slow-worms were returned to their cages. Individuals were removed using rubber gloves (to reduce possible heat transfer) and cloacal temperatures taken by insertion of a thermocouple approximately 5 mm into the cloaca. All readings were taken within 20 seconds of removing the slow-worm, which was then immediately returned to the same position on the gradient. Handling was kept to a minimum to reduce the possible effects of stress. Cloacal body temperatures were taken because it was felt that they better reflected core body temperatures and were more repeatable than body temperatures obtained by other methods.

Experimental design and statistical analyses

A total of 20 adult animals that were in good condition and feeding well were selected for the experiments. Two treatments were applied to each individual prior to measurement of SBT. Under the FEED treatment, individuals were offered food as normal (2–3 small earthworms every other day), although we also checked that all individuals had fed within one day of the start of the experiment. Un-

der the FAST treatment, food was withheld for three days prior to the start of the experiment. This was a relatively short period and may have led to relatively low power in detecting a difference between feeding treatments, but was chosen because it appeared ecologically relevant, i.e. it is reasonable to expect that these animals often undergo similar periods without feeding in the wild. It was also unlikely to lead to the major physiological changes that begin after longer periods of fasting (e.g. Gist, 1972), and was comparable with food-deprivation periods used in previous studies. The order in which the feeding treatments were applied to each individual was assigned randomly, with ten individuals tested under the FAST treatment first, and the remaining ten tested under the FEED treatment first.

Time and feeding treatment were the within-subject factors in this repeated measures design, i.e. four SBTs were recorded in each individual under each of the two feeding treatments. The data were analysed using a repeated measures analysis of variance in SPSS (ver. 14).

RESULTS

Minimum and maximum SBTs recorded under the FEED treatment were 21.4 °C and 30.1 °C, respectively, while corresponding values under the FAST treatment were 21.7 °C and 29.9 °C. Mean SBTs within time-treatment combinations are given in Table 1 and ranged from 25.3 to 26.4 °C. Within-individual deviations between feeding treatments were calculated for each of the four measurement times and are shown graphically in Figure 1. The positive mean deviations of FEED–FAST SBTs are repeated across all four measurement times. The significance of this was confirmed by the repeated measures ANOVA. Feeding state was significant at the 5% significance level ($F_{1,19}=5.32$, $P=0.03$), but measurement time was not ($F_{3,57}=0.27$, $P=0.94$). There was no interaction between feeding state and time ($F_{3,57}=0.45$, $P=0.72$). Note that neither Mauchly's test nor Kolmogorov–Smirnov tests of normality were significant for any of these within-subjects effects ($P>0.05$), and so sphericity and normality (respectively) were assumed.

DISCUSSION

Several early studies suggested thermophily after feeding, while others indicated no significant effect. However, the design and analysis of these has been criticized (see Sievert, 1989), and many can best be considered as providing only anecdotal contributions. Hence, apart from studies of snakes and those that address the effects of food composition (e.g. Geiser & Learmonth, 1994), only a

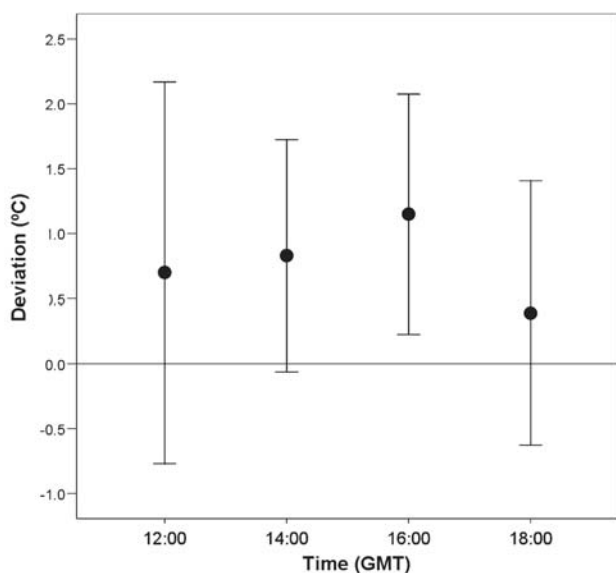


Figure 1. Mean deviations and their 95% confidence intervals obtained as the differences between FEED and FAST body temperatures within individuals (a positive deviation indicates a higher FEED body temperature).

small number of detailed experiments have been carried out on feeding-state related changes in SBT in squamates (e.g. Sievert, 1989; Tosini et al., 1994; Brown & Griffin, 2005). Here, the increase in post-prandial increase was small (0.39–1.15 °C) relative to the three-day food deprivation treatment, but was significant and was observed consistently across the four measurement times. Two previous studies on SBT in squamates showed similar increases: mean changes in *Anolis carolinensis* ranged from 0.4 to 0.7 °C in females and from 0.6 to 2.1 °C in males (Brown & Griffin, 2005), while an overall increase of 1.6 °C over 24 h was reported for *Crotaphytus collaris* (reaching 4.1 °C in the scotophase) (Sievert, 1989). These two species have high selected body temperatures (around 30 and 34 °C, respectively). Another lizard (*Lialis burtonis*) with a high selected body temperature shows large differences between fed and starved states (approximately 5 °C), although this latter experiment was based on only a small number of individuals (Bradshaw et al., 1980). The current evidence does not point to a greater difference between pre- and postprandial states in lizards that have lower active body temperatures, but a larger number of studies on species from a wide range of lineages are required to show this conclusively.

The hypothesis of a greater postprandial effect in species with lower selected body temperatures is largely based on the assumption that higher body temperatures after feeding represent an adaptive behavioural response that enhances digestion (e.g. van Marken Lichtenbelt, 1992) and/or conserves energy during periods of low food availability. This is not necessarily the case. First, Brown & Griffin (2005) have argued that the magnitude of the effect is probably too small to represent a significant energy saving to “low-cost” ectotherms such as reptiles. Second, non-thermoregulating *Varanus* monitor lizards show increased body temperatures after feeding by a

similar magnitude (approximately 0.5 °C) to those described for thermoregulating reptiles, and are associated with a 3–4-fold increase in metabolic rate (Bennett et al., 2000). This suggests that specific dynamic action of food leads to at least part of the observed increase in body temperature. Future studies should assess how much of this increase could be accounted for by specific dynamic action, before concluding that it is exclusively a behavioural response to enhance digestion. This could broaden the perspective from which ecophysiological studies consider the effects of digestion on body temperature.

Selected body temperatures in slow-worms are low (around 25–26 °C on average), relative to many non-snake squamates which typically have mean values in the 28–37 °C range (e.g. Brattstrom, 1965; Arad et al., 1989; Huey & Bennett, 1987; Bauwens et al., 1995). This suggests that the low field temperatures in this species (Meek, 2005) may be at least partially explained by thermoregulation with low thermal preferences, rather than thermoconformity. Selected body temperatures tend to be lower, on average, in some lineages, such as the Xantusiidae and the Anguidae. Within the Anguidae, both the closely-related legless *Ophisaurus apodus* and the more distantly-related legless *Anniella puchra* select low body temperatures (approximately 28 °C and 24–25 °C) (Bury and Balgooyen, 1976; Hailey, 1984), with values for the latter species being similar to, or slightly lower than, those recorded here. Interestingly, the former is a heliothermic species while *A. puchra* appears considerably more fossorial than *Anguis fragilis* (Miller, 1944).

In summary, the semi-fossorial *Anguis fragilis*, one of the few European squamata found at latitudes higher than 60° N, selects low body temperatures in a thermal gradient. It is one of a small number of lizards now shown to exhibit a significant increase in body temperature after feeding, although the magnitude of this effect does not appear greater than that observed in other Squamata that select higher body temperatures.

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