

Null models and the thermal biology of the anguid lizard *Anguis fragilis*; evidence for thermoregulation?

Roger Meek

Abstract. Observations were made on the behaviour and body temperatures of the legless lizard *Anguis fragilis* when active above ground in outdoor enclosures. The lizards were most frequently observed in partially shaded locations followed by fully shaded areas; full basking and locomotory movement were minor activities irrespective of weather conditions. Weather conditions had no significant influence on behaviour. Tests for thermoregulation using null models indicated that the main reason for movement above ground was thermoregulatory. Body temperatures were significantly higher than shade operative temperatures but lower than operative temperatures in open locations whatever the weather. Standard deviations in body temperature, employed as a measure of thermoregulatory precision, were lower than standard deviations of operative temperatures in sunny weather but not significantly different from operative temperatures during overcast weather or shaded operative temperatures during sunny weather. The limited amount of locomotory movement suggests thermoregulation was achieved through selection of appropriate microenvironments.

Introduction

The thermal biology of the anguid lizards is of interest because they contain species that are either limbed or limbless, are usually eurythermic operating at body temperatures that are lower than those found in other sympatric lizards and have irregular activity patterns (Avery, 1982; Hailey, 1984). The species with limbs are known to bask, although among the limbless forms, extensive basking has so far only been documented in the genus *Ophisaurus* (Johnson and Voigt, 1978; Meek, 1986). The legless form *Anguis fragilis* is in several respects a paradigm of the fossorial forms. It is secretive and partly fossorial, is known to bask occasionally and is active over a wide range of body temperatures. Field studies of thermoregulation have been problematical, mainly due to the secretive nature of the species, which makes it difficult to detect (Street, 1979; Frazer, 1983). Spot measurements (Patterson, 1990; Platenberg, 1999) confirmed the wide ranges in body temperature found in earlier laboratory studies (e.g. Speller-

berg, 1976; Gregory, 1980) but, because of the difficulty of locating animals in the open, the measurements were mainly confined to individuals under refugia.

The comment by Frazer (1983) about the lizards being observed in partially concealed locations is of interest, since it may indicate that above ground activity does indeed have a thermoregulatory basis, but if so how is thermoregulation achieved? This question is at present largely unanswered, mainly because of their secretive behavioural history. One solution is to employ natural enclosures that minimise animal location difficulties and which have been demonstrated as a way of providing useful insight into reptilian thermoregulation under a range of conditions (Lee, 1996; Lee and Mills, 2000). The present study attempts to answer the question of whether *A. fragilis* thermoregulates when it is above ground by employing such enclosures and using comparisons of the temperatures of non-thermoregulating lizard models with the body temperatures of real lizards; the temperatures of the null models are assumed to be indicators of non-thermoregulation (Bakken and Gates, 1975; Grant and Dunham, 1988) and extent of divergence of body temperatures from model temperatures, a measure of the extent of thermoregulation. Additionally, by measur-

The Herpetological Unit, Huddersfield Technical College, Huddersfield, UK
Present address: 7 Rue Georges Clemenceau, Chasnais 85400, France
e-mail: Rogermeek85@aol.com

ing body temperature non-invasively with an infrared detector the method has allowed a minimum disruption of behaviour patterns.

Materials and methods

Study animals and enclosure. The observations were made in outdoor enclosures in Huddersfield, UK between 2000 and 2002. Two enclosures were used, both designed to provide typical *A. fragilis* habitat. The first measured 2.6 m by 1 m into which four adult male and four adult females had lived and hibernated for a minimum of one year before data collection began. The sides were constructed of bricks with an aluminium frame with glass sides situated on top of the brick base. The top was covered with 20 mm wire mesh to deter domestic cats from entering. The second enclosure, used during the summer of 2002, measured 6.2 by 6.2 m with walls constructed of wood but with metal attached to the inside verticals to prevent escapes. Constructed in 1992 six individuals (three males, three females) were introduced. Small shrubs provided a mosaic of shaded and open areas. Several refuge sites, using flat stones and pieces of plastic, were also provided. Animals were fed on a regular diet of slugs and earthworms.

Body temperatures and behaviour definitions. Total number of body temperature records during sunny weather, i.e. clear skies and with the enclosure exposed to the sun, was 568 and in overcast weather 606. Due to location problems, sample sizes varied for individual lizards, ranging from 24-52 ($\bar{x} = 40.3$) during sunny weather and 18-66 ($\bar{x} = 48.5$) during overcast days. Temperatures were recorded with a Digitron Pyrometer which measures infra-red energy by focusing onto a germanium filter. The default error is 1.0°C, although increased proximity to the skin surface increases the accuracy, so measurements were usually taken at distances less than 5 cm. Every effort was made to measure temperature at the central area of the body although this was not always possible due to the lizards' position in vegetation and hence the region of the body closest to the centre was measured.

Behaviour and lizard position in relation to sunlight was recorded. Position/behaviour definitions were: (i) *open*, positioned in full sunlight or in a site with no cover; (ii) *partial open*, the animal was located in a mosaic of light and dark areas; (iii) *shade*, no part of the body was exposed to the sun; (iv) *locomotory activity* is self explanatory. The observations were made from May to August between 2000 and 2002. Days with sunshine and overcast weather were selected to provide environmental contrast, although sunny days may have had some cloud from time to time and cloudy weather the occasional hazy sunshine.

Null models. Four copper models 10 mm in diameter and 20 cm in length were painted black and filled with water and used to measure operative temperatures (Bakken, 1992). Black was used in preference to models painted grey which had heating rates less in agreement with lizard temperatures

— they had slightly slower heating rates. The models were placed in selected areas designed to replicate potential lizard locations — basking in full sunlight, partial basking in dappled sunlight and in a fully shaded area and thus represented the temperatures potentially attainable to the lizards. Two models were employed to measure dappled sunlight operative temperatures, but the one closest to each lizard's position was used in the analysis. By selecting appropriate microhabitats, it was assumed that the lizards could achieve any body temperature between the temperature extremes recorded by the models; for example potentially a lizard could track operative temperatures in dappled sunlight by either spending 50% of time in sun or shade or by positioning half in sun and half in shade (Christian et al., 1983). Model temperatures (overcast $n = 2424$; sunny $n = 2272$) were measured in the same way as the real lizards by directing the infrared detector at the central area of the model and recorded simultaneously with lizard body temperatures.

Rates of heating of one of the operative models was compared with the heating rates of a real lizard (male) by placing both in an empty open container at 9°C which was then moved into sunlight until the body temperature of the lizard reached 26°C. Thirteen paired measurements were made and the relationship between the heating rate of the lizard (T_b) and the model (T_0) defined by the regression,

$$T_b - T_0 = 1.23T_0 - 3.6 (r^2 = 0.9) \quad (1)$$

The equation shows that the lizard (T_b) heated slightly faster than the model (T_0) but that the models provided good estimates of lizard body temperature. This is in agreement with earlier work indicating that the low heat capacity of copper models respond readily to changes in radiation levels (Vitt and Sartorius, 1999; Shine and Kearney, 2001). Furthermore, Shine and Kearney (2001) demonstrated that differences in model size, colour, amount of contact with the substrate and orientation have little effect on model temperatures.

Statistical analysis. The Central Limit Theorem determines that the mean of the sample means will be the mean of the population. Employing the properties of this theorem for statistical analysis avoids pseudoreplication and inflating the degrees of freedom (Lombardi and Hulbert, 1996). Therefore analyses are based on the means or medians of 7 males and 7 females and tested against the means of corresponding operative temperatures. However, during overcast weather two of the lizards were never located above ground reducing the sample size to 12 lizards. Parametric two-sample *t*-tests were used to test for mean equality and for equality of standard deviations and non-parametric Mann-Whitney *U*-tests for the equality of medians with associated 95% confidence intervals.

Results

Behaviour. The lizards were most frequently observed in partially covered locations whatever

the weather; overcast, *median* = 69% (15.6-81.4%), sun, *median* = 59.2% (32.2-71.9%). However the difference in median values were not significant (Mann-Whitney *U*-test, $w = 186.5$, $P = 0.92$). Lizards in full shade was the second most frequently observed behaviour; overcast *median* = 37.4% (7.9-70.0%), sun *median* = 16.8% (5.5-55.9%) but again no significant differences between weather conditions were detected ($w = 208.5$, $P = 0.33$). Lizards in fully exposed locations was the least frequently observed activity and no difference was detected between overcast, *median* = 1.8% (0-6.2%), and sunny days, *median* = 0% (0-22.2%; $w = 183.0$, $P = 0.76$). Furthermore, no difference in locomotory activity was detected between overcast, *median* = 4.2% (0-5.7%), and sunny days *median* = 2.9% (0-17.5%; $w = 177.5$, $P = 0.55$).

Body temperatures. There was no significant difference in male and female body temperatures during overcast or sunny days (overcast: males $15.2 \pm 2.6^\circ\text{C}$, females $14.3 \pm 2.7^\circ\text{C}$; $t = 0.68$, $P = 0.5$, $df = 11$; sunny days: males $22.2 \pm 2.7^\circ\text{C}$, females = $22.0 \pm 2.8^\circ\text{C}$; $t = 0.12$, $P = 0.91$, $df = 9$). Male and female body temperatures were therefore pooled and not surprisingly showed significantly lower means during overcast weather; pooled overcast $\bar{x} = 14.7^\circ\text{C}$, pooled sunny $\bar{x} = 22.1^\circ\text{C}$, $t = 7.2$, $P < 0.0001$.

Body temperatures and operative temperatures. During overcast weather mean body temperatures were significantly lower than mean $T_{0(\text{open})}$, significantly higher than $T_{0(\text{shade})}$ but not significantly different from $T_{0(\text{dapple})}$. When the weather was sunny mean body temperatures were significantly lower than both $T_{0(\text{open})}$ and $T_{0(\text{dapple})}$ but significantly higher than $T_{0(\text{shade})}$. The statistical tests that these statements are based on are shown in table 1.

Comparisons with null models using regression. Applying regression analysis to the combined overcast and sunny weather data sets for each

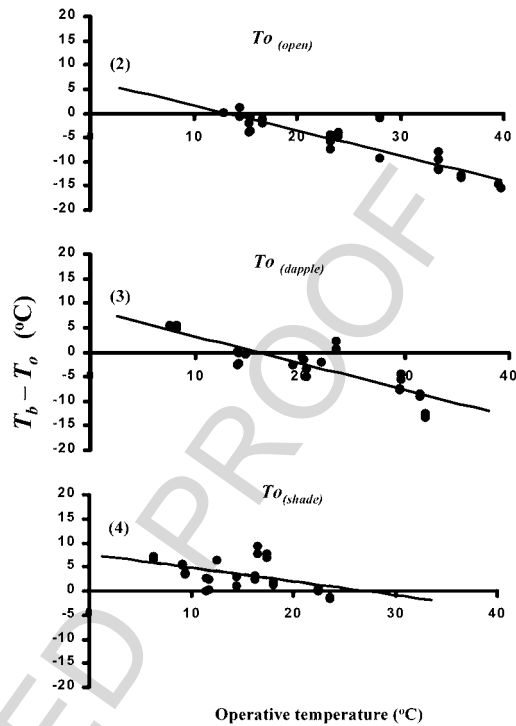


Figure 1. Graphs of mean body temperatures plotted against mean operative temperatures either in shade dappled or open areas. The lines taken through the data were fitted using the equations (numbered) given in the text.

lizard has enabled more general tests for thermoregulation possible. Here the means of operative temperatures in either open, dappled sunlight or shaded areas have been treated as the independent variables (T_0), and the differences between mean operative temperatures and mean body temperatures (T_b) as the dependent variables. This gives an equation of the form,

$$T_b - T_0 = mT_0 + b$$

where m is the regression coefficient and b the y -intercept. In this test, no thermoregulation is indicated when $T_b - T_0 = 0$ and $m = 0$, and can be evaluated by comparison against a hypothetical regression coefficient of 0 using a t -test at $n - 2$ degrees of freedom (Bailey, 1981) with the assumption that 0 = no thermoregulation. Significant departures from 0 therefore provide evidence of thermoregulation. Figure 1 shows a series of graphs of $T_b - T_0$ plotted against

Table 1. Comparisons of *A. fragilis* mean and standard deviations in body temperature (T_b) with mean or standard deviations of operative temperatures in open ($T_{0(\text{open})}$), dappled ($T_{0(\text{dapple})}$) and shaded ($T_{0(\text{shade})}$) locations. Statistical comparisons are based on two sample t -tests.

	T_b	$T_{0(\text{open})}$	t	df	$T_{0(\text{dapple})}$	t	df	$T_{0(\text{shade})}$	t	df
Overcast mean	14.7	17.4	2.04*	21	14.5	0.15 ^{n.s.}	18	11.5	2.68**	23
Sunny mean	22.1	32.4	5.75*	15	27.7	3.79*	17	18.1	2.89**	18
Overcast Std. Dev.	3.2	4.1	1.48 ^{n.s.}	25	3.1	0.20 ^{n.s.}	22	2.7	0.90 ^{n.s.}	22
Sunny Std. Dev.	4.4	6.8	2.28*	14	5.7	2.12*	21	4.0	0.56 ^{n.s.}	21

* , mean body temperatures or standard deviations of body temperature significantly lower.

** , mean body temperatures or standard deviations of body temperature significantly higher.

No significant difference between means or standard deviations is shown as *n.s.*

mean T_0 's for both overcast and sunny weather; the lines running through the data were derived from the equation in open areas ($T_{0(\text{open})}$),

$$T_b - T_{0(\text{open})} = -0.53 \pm 0.04T_{0(\text{open})} + 6.3, \\ r^2 = 84.3\% \quad (2)$$

in dappled sunlight ($T_{0(\text{dapple})}$)

$$T_b - T_{0(\text{dapple})} = -0.55 \pm 0.06T_{0(\text{dapple})} + 8.7, \\ r^2 = 76.0\% \quad (3)$$

and in shaded areas ($T_{0(\text{shade})}$),

$$T_b - T_{0(\text{shade})} = -0.29 \pm 0.11T_{0(\text{shade})} + 7.7, \\ r^2 = 21.5\% \quad (4)$$

Where r^2 are the adjusted values and the \pm values the standard errors on the regression coefficients. The negative regression coefficients are significantly different from 0 in all equations: (2) $t = 17.02$, $P < 0.0001$, $df = 24$; (3) $t = 8.93$, $P < 0.0001$, $df = 24$; (4) $t = 2.56$, $P = 0.02$, $df = 24$. The equations, hence, provide evidence for thermoregulation by demonstrating increasing departures of body temperatures from operative temperatures as the latter increased.

Precision of thermoregulation. The standard deviations around the means have been used as a measure of thermoregulatory precision with the assumption that the higher the standard deviation the less the degree of thermoregulatory precision. Mean standard deviation was significantly smaller during overcast

than sunny weather (3.2°C and 4.4°C respectively; $t = 2.08$, $P = 0.05$, $df = 23$). When the weather was overcast mean standard deviation of body temperatures was not significantly different from mean standard deviations of any operative temperature. However, sunny weather mean standard deviations of body temperatures were significantly smaller than either those of $T_{0(\text{open})}$ or $T_{0(\text{dapple})}$ but not significantly different from $T_{0(\text{shade})}$. The statistical tests on which these statements are based are given in table 1.

Discussion

The present study provided evidence that *A. fragilis* thermoregulates when above ground. The absence of major shuttling behaviour, as indicated by the limited amounts of locomotory activity, logically suggests that thermoregulation was achieved by microhabitat selection. This enabled the maintenance of body temperatures that were largely independent from operative temperatures particularly when the latter were very low or high. Nevertheless, the body temperatures reported here are in general lower than those recorded in the zero cost ecological conditions of laboratory heat gradients (Spellerberg, 1976; Gregory, 1980). However, this is probably explained by *A. fragilis* operating in thermally unfavourable conditions that are adaptive in terms of prey capture. Low levels of locomotory activity presumably reduce the risk of detection by predators and suggest the evolution of a compromise between precise thermoreg-

ulation and predator avoidance since shuttling and full basking are conspicuous behaviours. Predators on *A. fragilis* are birds, snakes and mammals (Frazer, 1983), species that often rely on movement of prey as a method of location and hence a basking strategy in partial concealment that reduces the need for extensive shuttling may be adaptive — although this may not be effective against predators that detect prey by olfactory means. In contrast sympatric species, such as *Lacerta vivipara*, shuttle extensively to maintain activity temperatures of 30-33°C (Patterson and Davies, 1978; Avery, 1982). However, *L. vivipara* is an agile species relying on its speed to avoid predators.

The body temperatures of *A. fragilis* during sunny weather in the present study were in approximate agreement with those measured by Platenberg (1999) under refugia. The latter must represent less vulnerable locations than those above ground — so why are the lizards active above ground? It may be that low growing vegetation is employed when suitable underground locations with the appropriate thermal conditions are limited. Beebee and Griffiths (2000) suggested that underground retreats increase the time taken to achieve preferred body temperatures but there is also the possibility of increased chance of prey capture above ground — molluscs, earthworms and slugs (Luiselli, 1992), by operating as a sentinel predator, particularly when the weather is overcast. This contrasts with the large anguid *Ophisaurus apodus* a cruising forager that may operate conspicuously in open clearings when the weather is overcast and cool and at much lower body temperatures than is normal when the weather is sunny (Meek, 1986). However, defence is essentially passive and reliant on large size and dermal armour (Hailey, 1984; Hailey and Theophilidis, 1987) features that are lacking in *A. fragilis*. The body temperatures and lack of thermoregulatory precision reported in the present study are generally in good agreement with those found in other fossorial reptiles includ-

ing the Anniellidae and Amphisbaenidae (Hailey, 1995).

Stumpel (1985) could find no correlation between above ground presence in *A. fragilis* and air temperatures, number of sunshine hours or rainfall, although he suggested that the activity has a thermoregulatory basis. Smith (1999) observed that the distribution of *A. fragilis* is limited in the north of its range by low temperatures, which limits activity, and in the south by excessive heat, which may restrict food availability. Reproduction is also known to influence the body temperatures of gravid females, that are often higher than those that are not gravid (Capula and Luiselli, 1993) — there was no indication that any of the females used in the present study were gravid.

In summary, the present study has shown that *A. fragilis* does thermoregulate but not to the extent observed in many other reptiles. The statistical departures from operative temperatures found in most instances, provide evidence for thermoregulation and observations of behaviour, which showed low levels of locomotory movement, an indication that thermoregulation is achieved through microhabitat selection. Additionally, the positive relationship between body temperatures and $T_{0(\text{shade})}$ (fig. 1, equation (4)) suggests that background levels of infra-red energy, which are not particularly relevant for thermoregulation in heliothermic reptiles, are an important source of heat for *A. fragilis*. These factors combined enable moderate but effective thermoregulation and indicate that above ground activity is an example of opportunistic thermoregulation representing a compromise between thermoregulation and predator avoidance but with the added possibility of increased food availability.

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