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# CHOICE OF SUBSTRATE AND HEATING RATE IN *LACERTA VIVIPARA*

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## SUMMARY

Common lizards (*Lacerta vivipara*) in summer basked mostly on dry grass during sunny weather, but on pieces of wood when the sunshine was interspersed with periods of cloud cover (changeable weather). In order to determine whether this switch in behaviour could be interpreted as a cost-benefit situation, the effects of different substrates on heating rates at high and low irradiance were investigated. Basking times on wood were related to a number of environmental thermal variables.

Heating curves were fitted to a logistic model, which allows description of the complete curve from two basic parameters. Other parameters, such as rate of heating at any temperature, time interval for any temperature interval (or vice versa), and thermal half time, are easily derived from these.

## INTRODUCTION

The ecology of the common lizard (*Lacerta vivipara*) has been well studied, particularly its population ecology (Avery, 1975; Pilorge & Castanet, 1981; Bauwens & Thoen, 1981a) and energetics (*e.g.* Avery, 1971, 1976; Patterson & Davies, 1978a). Studies on the behaviour of wild lizards have been limited to those aspects requiring short periods of observation, such as emergence times (Avery & McArdle, 1973) and flight distances (Bauwens & Thoen, 1981b). This is largely due to their preference for densely vegetated heath and grassland (Smith, 1973) in which observation of an individual for more than a few minutes is rare. Studies of thermoregulation are limited to those on animals in enclosures (Avery, 1971) or in the laboratory (Avery, 1976; Patterson & Davies, 1978b).

The present work was prompted by seeing common lizards using habitual basking sites, which were piles of wood, and returning to these between forays into the surrounding grassland. Activity patterns of individuals were observed at these sites. It became apparent that in summer wood was only used in changeable weather; on sunny days lizards basked on small patches of dry grass. This difference in basking substrate selection was interpreted as a cost-benefit situation, and the benefits of heating on different substrates were hence investigated. A new method of describing heating rates, more applicable to ecological problems than those previously devised, was developed.

## METHODS

### FIELD OBSERVATIONS

The study area was a field of rough grassland (*Arrhenatherum* and *Anthoxanthum*) at Leavenheath, Suffolk. In 1978 and previous years lizards basked on

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small piles of old timber in the grass. These were too structurally complex to allow easy spotting of the lizards, and so all were replaced in March 1979 by two halves of an old unpainted door, each 1 m × 1 m in size, placed 25 m apart. There were no other wood sites within 50 m, and it was probable that: (a) all lizards on the wood were seen by the observer nearby; (b) lizards returning to the wood at reasonable intervals were not using other wood sites in between.

Intensive observations were made at these sites during periods of changeable weather in early July and mid August 1979. The presence and activity of each lizard was noted every 15 seconds during observation periods of 1 to 3 hours. Individuals were recognized by natural marks. Basking was defined by dorso-ventral body flattening.

Shade air temperature 30 cm above the ground ($T_A$), temperature of the upper surface of the wood ($T_W$) and temperature of a blackened probe in the sun at 30 cm ($T_{BB}$) were measured every 10 minutes with a thermistor thermometer. The meter and observer were hidden in grass 3 m from the wood, and observation from this distance had no noticeable effect on lizard behaviour provided that no sudden movements were made.

Using the same probes, $(T_{BB} - T_A)$ was calibrated against a photoelectric solarimeter under artificial light to give a measure of irradiance.

In addition to intensive observations, the area was examined daily from July to September 1979 and the pattern of lizard activity noted.

### HEATING RATES

Heating rates of a 3.45 g adult common lizard were measured on wood and straw substrates at thermal equilibrium under known irradiance. Straw was used in place of dry grass for reasons of supply, the wood was weathered timber similar to that used in the field. Irradiance was produced by a 275 W infra red reflector lamp.

Two levels of irradiance were used, 0.013 and 0.026 J $\text{cm}^{-2}\ \text{s}^{-1}$. At the lower, $T_A$ and $T_W$ were comparable to values recorded in the field. At the higher, $T_A$ was kept down to a similar level to that for low irradiance, and $T_A$ and $T_W$ were lower than those associated with high irradiance in the field. This was to separate the effect of irradiance and substrate from differences due to air temperature.

The lizard was slowly cooled to 18–20°C in the light. Its body temperature ($T_B$) was measured, and it was placed in a low wire mesh arena directly under the lamp, on wood or straw. Basking usually followed; the trial was discarded if the lizard climbed from the arena or burrowed into the straw. After 5 minutes the lizard was removed, and $T_B$ measured. The lizard was then replaced, this being repeated until there was no further rise in temperature. $T_B$ was measured with a quick reading 1.5 mm diameter thermistor probe, inserted cloacally, the lizard held by the base of the tail to minimize hand warming. This took 15 seconds; time out of the arena was not included in heating time.

Heating rates under 0.026 J $\text{cm}^{-2}\ \text{s}^{-1}$ and 0.5 m $\text{s}^{-1}$ of wind from a desk fan, and cooling rates in still air and 0.5 m $\text{s}^{-1}$ of wind were also measured. For the latter the lizard was warmed in an open box under 0.5 J $\text{cm}^{-2}\ \text{s}^{-1}$ irradiance, $T_B$ measured, and the fall in $T_B$ measured every 5 minutes during activity in a large cage. Heating rates of a 6.2 g *Podarcis muralis* and a 16.6 g *Lacerta viridis* were also measured in all three conditions on both substrates.

## RESULTS

### FIELD OBSERVATIONS

The proportion of time that individual lizards spent in basking was calculated for 30 minute intervals, a time scale appropriate to that of lizard activity and of variation in cloud cover, which was the main cause of variation in the thermal conditions. The percentage of this interval spent basking (% *B*) is shown against mean $T_A$ and irradiance during the interval in Fig. 1.

Correlations between % *B* and the thermal variables are given in Table I, excluding incomplete cases or intervals when no lizards basked on the wood. Significance of correlation between % *B* and each

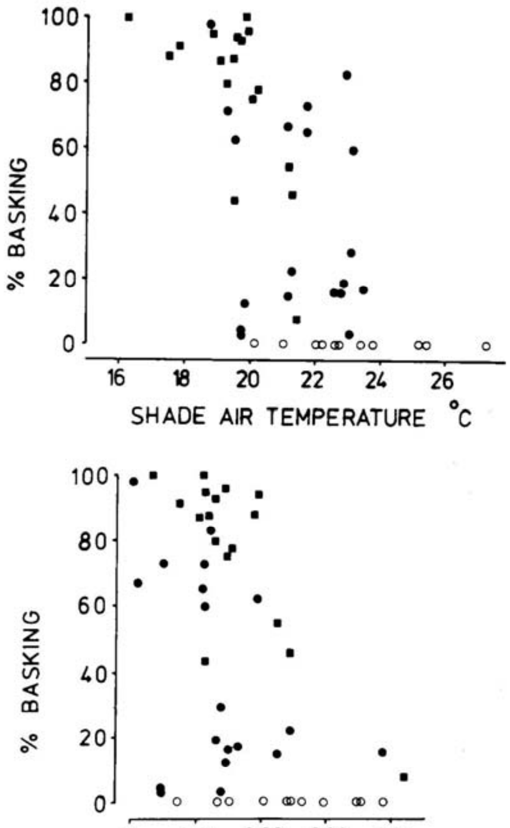

FIG. 1. Variation of percentage of time spend basking with (a) shade air temperature, and (b) irradiance. ■ juveniles, ● adults, ○ no lizards basking. Each point is one 30 minute interval.

thermal variable is investigated by Spearman rank correlation coefficient ($r_s$), as some of the variables were not normally distributed or easily transformed to normality (Sokal & Rohlf, 1969).

The coefficient of determination (proportion of total variation explained by the correlation) is also given, both for zero order correlations between % $B$ and each thermal variable, and for second order correlations between % $B$ and each variable after adjusting for the effect of the other two variables. This is the Pearson product moment correlation coefficient, squared ($r^2$) (Sokal & Rohlf, 1969). All correlations were performed using SPSS (Nie, Hull, Jenkins, Steinbrennen & Brent, 1975).

TABLE I. Correlation of percentage of time spent basking with thermal variables

| Total (n = 33) | Shade air temperature | Substrate (wood) temperature | Irradiance |
|---|---|---|---|
| $r_s$ | −0.520 | −0.633 | −0.305 |
| $P$ | 0.001 | 0.001 | 0.042 |
| Zero order $r^2$ | 0.276 | 0.331 | 0.126 |
| Second order $r^2$ | 0.003 | 0.081 | 0.053 |
| Adults (n = 19) | | | |
| $r_s$ | −0.142 | −0.248 | −0.370 |
| $P$ | 0.281 | 0.153 | 0.059 |
| Zero order $r^2$ | 0.056 | 0.132 | 0.160 |
| Second order $r^2$ | 0.021 | 0.068 | 0.096 |
| Juveniles (n = 14) | | | |
| $r_s$ | −0.504 | −0.508 | −0.511 |
| $P$ | 0.033 | 0.032 | 0.031 |
| Zero order $r^2$ | 0.552 | 0.619 | 0.645 |
| Second order $r^2$ | 0.026 | 0.169 | 0.121 |

$r_s$ is the Spearman rank correlation coefficient; $r^2$ (coefficient of determination) is the Pearson product-moment correlation coefficient, squared.

Basking period was calculated as the duration of a period of uninterrupted basking. Variation of this is shown with mean irradiance and $T_W$ during the period in Fig. 2. Short basking periods occurred in all conditions, long periods only when it was cooler.

The three thermal variables were mutually correlated, and related by the equations

$$\text{irradiance in J cm}^{-2}\,\text{s}^{-1} = 0.00253T_A - 0.037 \quad (r^2 = 0.302)$$

$$T_W = 1.82T_A - 8.3 \quad (r^2 = 0.706).$$

Most basking on wood was at $T_A$ below 24°C, irradiance below 0.025 J cm$^{-2}$ s$^{-1}$, and $T_W$ below 36°C (Figs. 1 and 2). These conditions were exceeded, often considerably, on sunny summer days, and extensive observations indicated that lizards used small patches of dead grass in hot weather. They moved through the area of grassland, apparently not returning to any particular place habitually.

## HEATING RATES

Heating curves of a 3.45 g common lizard under high and low irradiance on wood and straw substrates are shown in Fig. 3. The means of several trials are fitted to a curve with a logistic limitation to the rate of heating, such that at any temperature, $T$°C;

$$r_T = r_0 \frac{(K - T)}{K} \tag{1}$$

where $r_T$ is the rate of increase of temperature per unit time ($dT/dt$) at $T$°C, $r_0$ is the rate at 0°C, and $K$ is the equilibrium body temperature under the conditions. The assumptions of this model are noted in the discussion.

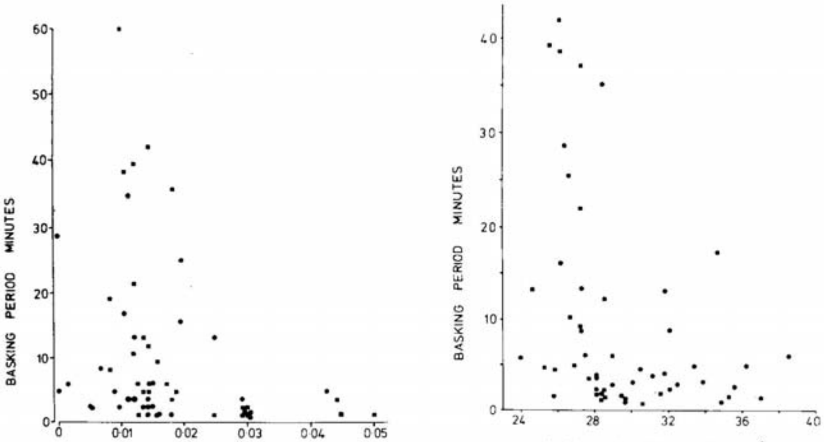

FIG. 2. Variation of length of basking period on wood with (a) mean irradiance and (b) mean substrate temperature during the period. ■ juveniles, ● adults.

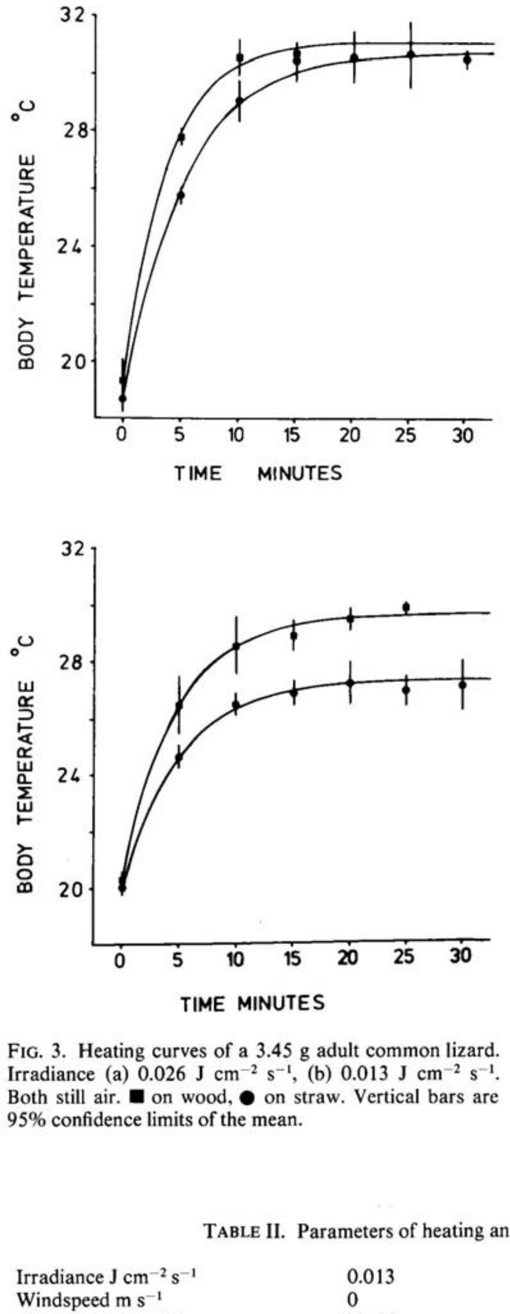

FIG. 3. Heating curves of a 3.45 g adult common lizard. Irradiance (a) 0.026 J cm$^{-2}$ s$^{-1}$, (b) 0.013 J cm$^{-2}$ s$^{-1}$. Both still air. ■ on wood, ● on straw. Vertical bars are 95% confidence limits of the mean.

The fitted curves are equation 1 integrated with respect to time ($t$)

$$T_t = K - (K - T_0)\, e^{(-r_0/K)t} \qquad (2)$$

where $T_0$ is the starting temperature in °C, $t$ the time from the start in minutes, and $e$ the base of natural logarithms.

Where data are in the form of a series of temperatures at a fixed time interval (in this case, five minutes), the parameters $K$ and $r_0$ may be estimated by linear regression (a) of $(T_{t+5} - T_t)$ on $T_t$ gives $K$ as the intercept on the abscissa; (b) of ln $(K - T)$ on $t$, where ln is the logarithm to the base $e$, gives $r_0$ as ($-$ slope) $K$ for temperatures below equilibrium (modified from Caughley 1977: 182). Small errors in measurement of $T$ or estimation of $K$ will cause large errors where $(K - T)$ is small, and only values of $(K - T)$ over 2°C were used.

A FORTRAN program was developed to calculate $K$ and $r_0$ by performing these regressions in turn on data supplied as a series of body temperatures at a given fixed time interval. This simple fitting method is unreliable where few points are involved, but produces starting values which may be modified to improve the fit.

Cooling curves were fitted from a baseline of 40°C, defining $\overline{T}_t = 40 - T_t$, $\overline{K} = 40 - K$, and $r_{40}$ as the rate of cooling at 40°C. The curves were then fitted as above, replacing $T_t$, $K$ and $r_0$ by $\overline{T}_t$, $\overline{K}$ and $r_{40}$. The cooling curve is then described by

$$T_t = K + (T_0 - K)\, e^{(-r_{40}/\overline{K})t} \qquad (3)$$

Table II shows the parameters $K$ and $r$ for all the heating and cooling conditions, together with some secondary parameters.

## DISCUSSION

### SUBSTRATE CHOICE

During changeable weather when lizards were basking on wood, the percentage of time spent basking was significantly negatively correlated with all three thermal variables (Table I). Correlations for juveniles were higher than for adults, indeed for the latter only

TABLE II. Parameters of heating and cooling curves for an adult common lizard

| Irradiance J cm$^{-2}$ s$^{-1}$ | 0.013 | | 0.026 | | 0.026 | | 0 | |
|---|---|---|---|---|---|---|---|---|
| Windspeed m s$^{-1}$ | 0 | | 0 | | 0.5 | | 0 | 0.5 |
| Air temperature °C | 22–23 | | 20–21 | | 22–23 | | 21–22 | |
| Substrate | wood | straw | wood | straw | wood | straw | wood | straw |
| n | 5 | 5 | 5 | 5 | 10 | 10 | 10 | 10 |
| Substrate temperature °C | 26–27 | 23–25 | 28–30 | 23–25 | 28–30 | 26–28 | 21– 22 | |
| $r_0$ or $r_{40}$°C minute$^{-1}$ | 6.25 | 5.47 | 8.14 | 5.53 | 8.88 | 7.00 | 4.50 | 4.97 |
| $K$°C | 29.7 | 27.4 | 31.2 | 31.2 | 31.9 | 31.3 | 22.2 | 21.3 |
| $\Delta t_{21-25}$ minutes | 2.9 | 4.9 | 1.9 | 2.8 | 1.6 | 2.2 | — | — |
| $r_{15}$°C minute$^{-1}$ | 3.1 | 2.5 | 4.2 | 2.9 | 4.7 | 3.6 | — | — |
| $\Delta t_{15-25}$ minutes | 5.4 | 8.2 | 3.7 | 5.4 | 3.2 | 4.3 | — | — |
| Half time minutes | 3.3 | 3.5 | 2.7 | 3.9 | 2.5 | 3.1 | 2.7 | 2.6 |

$r_x$ is the rate of change of temperature per unit time at $x$°C; $tx - y$ is the time to heat or cool from $x$°C to $y$°C. Lizard used for cooling was slightly smaller than the one used for heating.

irradiance had an effect approaching significance. Zero order correlations do not show a clear pattern of which variables have the greatest effect. Second order partial correlations show that air temperature has a much smaller effect than irradiance or substrate temperature, for adults, juveniles, and the combined results.

Extensive observations produced only occasional sighting of lizards basking on grass in changeable weather; most were on wood. On sunny days they were on patches of dry grass and none were seen basking on wood. This was interpreted in terms of the costs and benefits of moving to and basking on different substrates. Wood sites were much less numerous, and would involve greater movement costs (time and energy) to lizards returning to them, and restriction to a relatively limited foraging area (central place foraging—see Orians & Pearson, 1979).

The proposed benefit was increased rate of heating, thus reducing the time spent basking. The substrate selected should switch where the extra cost of moving to wood is the same as the benefit of less time basking once there. The transition from changeable to sunny weather was thought to cause this switch, with the benefit of wood being greater in low or fluctuating irradiance.

The cost will depend on the $T_B$ at which return to the basking site occurs (and the lizard's performance at that $T_B$), and the distance moved to reach the basking site. On sunny days lizards will reach a higher $T_B$, and as a result may go further while foraging. They will also start back at a higher $T_B$ (as they are cooling to a higher ambient temperature), and so the cost of moving back to the basking site is probably relatively independent of the weather.

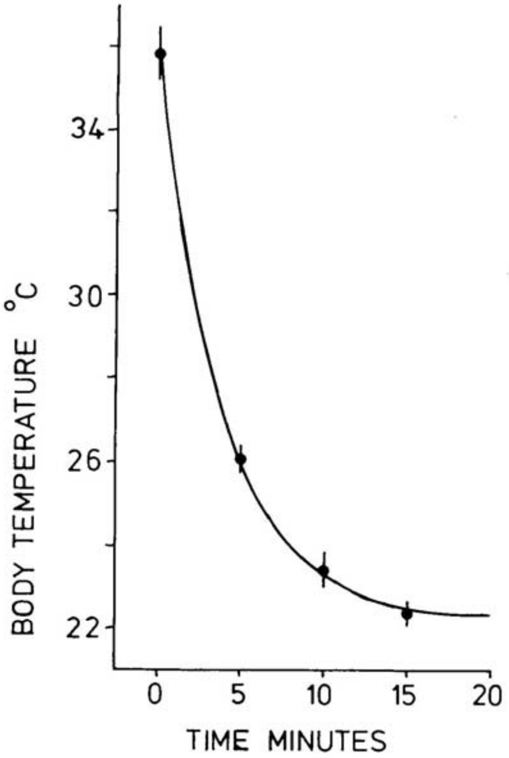

FIG. 4. Cooling curve of an adult common lizard in still air. $T_A$ 21–22°C. Vertical bars are 95% confidence limits of the mean.

Figure 3 shows that the benefit of a wood substrate appears greater at low irradiance. This benefit may be expressed in two ways:

(1) The time saved in heating over a specified temperature range. The time saved heating from $T_A$ (about 21°C) to 25°C is 2 minutes at 0.013 J cm$^{-2}$ s$^{-1}$, 1 minute at 0.026 J cm$^{-2}$ s$^{-1}$ (Table II, $\Delta t_{21-25}$). At higher irradiance the absolute size of this saving will be reduced still further as heating rates increase on both substrates.

(2) A higher temperature may be reached. This may be particularly important at low irradiance during prolonged basking (see below). At higher irradiances, lizards will resume activity before $K$ is reached (on sunny days, $T_W$ was over 40°C).

Adult common lizards were studied in a large cage under combinations of irradiance and basking site availability thought to favour a basking substrate switch. However, inability to provide both a sufficiently large area (costs of moving to the wood too low), and sufficient numbers of small prey to stimulate continued foraging, produced activity/basking patterns which could not be considered normal (Hailey, 1980). Demonstration of a change in basking substrate choice with irradiance in controlled conditions is therefore lacking.

### BASKING PERIODS

The pattern of basking period decreasing exponentially with increasing irradiance (Fig. 2) is similar to that for the time to heat over a given temperature interval (see Avery & McArdle, 1973; Avery, 1976). In practice the temperature interval over which a lizard basks will change with conditions, lizards returning to bask and reaching a higher temperature in hot weather.

Avery (1971) found that daily food consumption of *L. vivipara* in changeable weather was only about half that in sunny weather, and later implied (Avery, 1976: 252) that this was due to limitation of foraging time. This is apparently contradicted by the long basking periods (over 20 minutes) observed in changeable weather during this study (Fig. 2). At these times, little increase in $T_B$ can be expected as $K$ is approached, and any small rise will be lost rapidly on activity (Fig. 4). This apparent waste of time when time is limiting could have several possible explanations:

(1) Lizards are waiting for irradiance to increase. Such an increase may be rapid during changeable weather in summer, and can be taken advantage of immediately. Bauwens & Thoen (1981b) found that stationary common lizards face little risk of predation.

(2) Lizards switch from active foraging to sentinel predation. Continued basking will enable lizards to maintain a high $T_B$ to respond efficiently to prey passing near (this was seen twice). Continued basking thus allows high $T_B$ to be saved for pursuit and not lost while searching for prey.

(3) Basking may increase the amount of food that can be processed on changeable days. Avery (1971) found that on sunny days, food intake was limited by the ability to process rather than catch prey. Food through-put rate is temperature-dependent in Lacertids (McClelland, pers. comm.) as in other reptiles (Skoczylas, 1978). It is possible that lizards still feed maximally on changeable days but processing limits this to half that on sunny days. Under such conditions, further basking would be more advantageous than further foraging.

These possibilities are not mutually exclusive. Use of substrates which enable a higher $K$ to be maintained and also act as heat stores in fluctuating conditions will be particularly advantageous in changeable weather. Demonstration of long basking periods when time is thought to be limiting highlights the importance of studying behaviour of individuals—this would not be suspected from studying what the population generally is doing at any time.

## DESCRIPTION OF HEATING RATES

Description of heating rates has a complex literature. Three parameters have been used previously:

(1) The time taken to heat over a specified temperature interval, $\Delta t_{T1-T2}$ (*e.g.* Avery & McArdle, 1973; Hailey, 1980). This is unsatisfactory where the upper limit approaches $K$, as a small change in the value chosen (usually somewhat arbitrarily) will cause a large, non linear change in $\Delta t$.

(2) The rate of heating at a specified temperature (*e.g.* Bartholomew & Tucker, 1963; Avery & McArdle, 1973; Claussen & Art, 1981). This rate will depend on the temperature chosen as well as the conditions.

(3) The half time or time constant. The half time is that for the elimination of 50% of the $\Delta T$ between body and ambient temperature (Spigarelli, Romberg, Prepejchal & Thommes, 1974; McKenna & Packard, 1975; Glidewell, Beitinger & Fitzpatrick, 1981). The time constant (Spotila, Lommen, Bakken & Gates, 1973; Smith, 1976), is a similar measure, using 63% of the $\Delta T$, and is equal to the half time × 1.44 (Glidewell *et al.*, 1981). These parameters are useful in step transfer conditions (where $K$ is fixed) and in the study of the scaling of heat change with body mass (see also alternative time constant of Bell, 1980). They are less useful in ecological discussion, however, as a lizard of given size will have approximately constant half time, independent of conditions (see below).

The logistic model proposed here has the major advantage that the *complete curve* is described by two parameters, $K$ and $r_0$. Given these, it is simple to calculate any of the other parameters, though the reverse is not possible.

The time interval for a given temperature interval is calculated from equation 2, or the modified form:

$$\Delta t_{T_U} - T_L = \left[ -\ln \frac{(K - T_U)}{(K - T_L)} \right] . \frac{K}{r_0} \qquad (4)$$

where $T_U$ and $T_L$ are the upper and lower limits. For cooling curves, $K$, $T_U$, $T_L$ and $r_0$ are replaced by $\bar{K}$, $\bar{T}_U$, $\bar{T}_L$ and $r_{40}$.

The rate of heating at a given temperature, $r_T$, is calculated from equation 1.

The half time is calculated from equation 4 modified as:

$$\text{half time} = -\ln 0.5 . \frac{K}{r_0} \qquad (5)$$

replacing $K$ and $r_0$ by $\bar{K}$ and $r_{40}$ for cooling.

As with its use in population ecology (*e.g.* Caughley, 1977), the logistic model assumes that the rate of change is directly proportional to $(K - T)$. This is also assumed for half times and time constants, and is approximately valid over small (in physicist's terms) temperature ranges (Whelan & Hodgson, 1971). Table III shows the mean fit of 180 heating curves calculated using the double regression method by computer. There is a significant departure at 10 minutes, but this is extremely small (less than the accuracy of the thermistor used), and may be an artifact of the periodic handling experimental technique or fitting by regression.

The half time varies with body mass—mean half times of the three lizards used were:

| | | |
|---|---|---|
| *L. vivipara* | (3.45 g) | 3.2 minutes |
| *P. muralis* | (6.21 g) | 4.6 minutes |
| *L. viridia* | (16.6 g) | 6.9 minutes |

It also varies with the means of heat exchange, being reduced by the extra conduction component from wood (Table 2) [see also Bell's (1980) comparison of temperature change in air and water]. However, in conditions differing only by the size or position of the temperature interval ($T_0$ to $K$) it will be constant.

It is hoped that the economy with which the logistic model described heating curves and the ease with which other parameters may be calculated from it will prove useful in the study of reptile thermal ecology.

## SUBSTRATE AND MORNING EMERGENCE

$r_{15}$ for *L. vivipara* is higher, and $\Delta t_{15-25}$ lower, (Table II) than that found by Avery & McArdle (1973) at the same irradiance, though their lizards were slightly smaller. There are two obvious reasons for this:

(1) Their lizards were strapped to a block of wood at 5°C, here the lizard was on a warm substrate at equilibrium under the irradiance.

TABLE III. Goodness of fit of the logistic model fitted by double linear regression for 180 heating curves

| Time minutes | 5 | 10 | 15 | 20 |
|---|---|---|---|---|
| Mean (observed-calculated) °C | −0.072 | +0.083 | +0.060 | +0.063 |
| ±1.96 standard errors | ±0.106 | ±0.056 | ±0.064 | ±0.065 |

(2) Air temperature was 15°C in their experiments, 21–22°C here.

In the early morning conditions approximate to those of Avery & McArdle (1973), *i.e.* cold air and cold substrates. Later on, conditions will approach those used here as the air and substrates warm up under increasing irradiance. $\Delta t_{15-25}$ will fall below that shown in Fig. 3 of Avery & McArdle (1973) as the morning progresses, and the point of levelling off may be later, as substrate heating will lag behind rises of irradiance due to thermal inertia. This may explain the observation that emergence was later than predicted from heating due to irradiance alone.

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