

## THE SCALING OF THE THERMAL INERTIA OF LIZARDS

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### SUMMARY

The thermal status of an animal is the result of a combination of physical and physiological factors. In poikilotherms, it may be possible to separate these more easily than in homeotherms, where the presence of control mechanisms can mask the processes occurring. The thermal time constant of a poikilotherm has been shown to be a useful measure of its thermal behaviour, and to vary with the physiological status of the animal. A simple model is developed to show how the thermal time constant is related to the physics of heat exchange. The derived thermal time constant is shown to scale as body mass raised to the power  $2/3$ , and this is compared with results on lizards heating and cooling in water, taken from the literature.

When heat exchange in air is considered, the concept of boundary layer resistance leads to a useful simplification. The thermal time constants in air taken from the literature show that the boundary layer resistance is approximately constant.

### I. INTRODUCTION

Although poikilotherms are normally considered incapable of maintaining a constant body temperature, it is now recognized that reptiles can and do regulate their physiology and behaviour to optimize body temperature (see reviews by Templeton, 1970; Cloudsey-Thompson, 1971; and White, 1973). Physiological control enables the animal to vary the rate at which it heats or cools in a fluctuating environment, probably by varying the blood supply to the periphery (Morgareidge & White, 1969; Grigg & Alchin, 1976). The study of this control requires that it be quantified in such a way that the index produced is easily related both to the physics of heat exchange and to the biology of the animal. Spotila *et al.* (1973) have proposed the use of the 'thermal time constant', and this is now used by most experimenters (Smith, 1976; Grigg, Drane & Courtice, 1979; Boland & Bell, 1980; Bartholomew, 1966). This concept has proved to be very useful, facilitating comparisons between experiments and between species.

Models of the thermal behaviour of lizards have been proposed which relate the thermal time constant to the physics of heat exchange (Spotila *et al.* 1973; Grigg *et al.* 1979). These models are rather complex and this can obscure the important principles which underlie thermo-regulation. This note presents a simple model based on the physics of heat conduction in solids, which still allows the derivation of a thermal

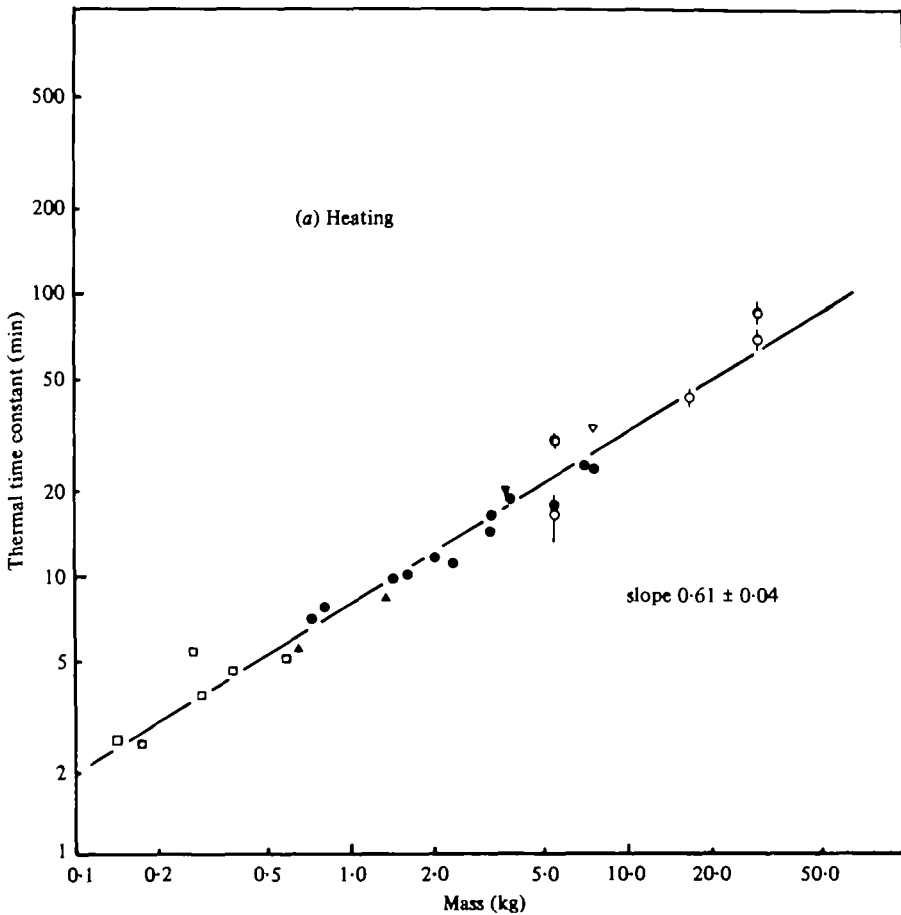


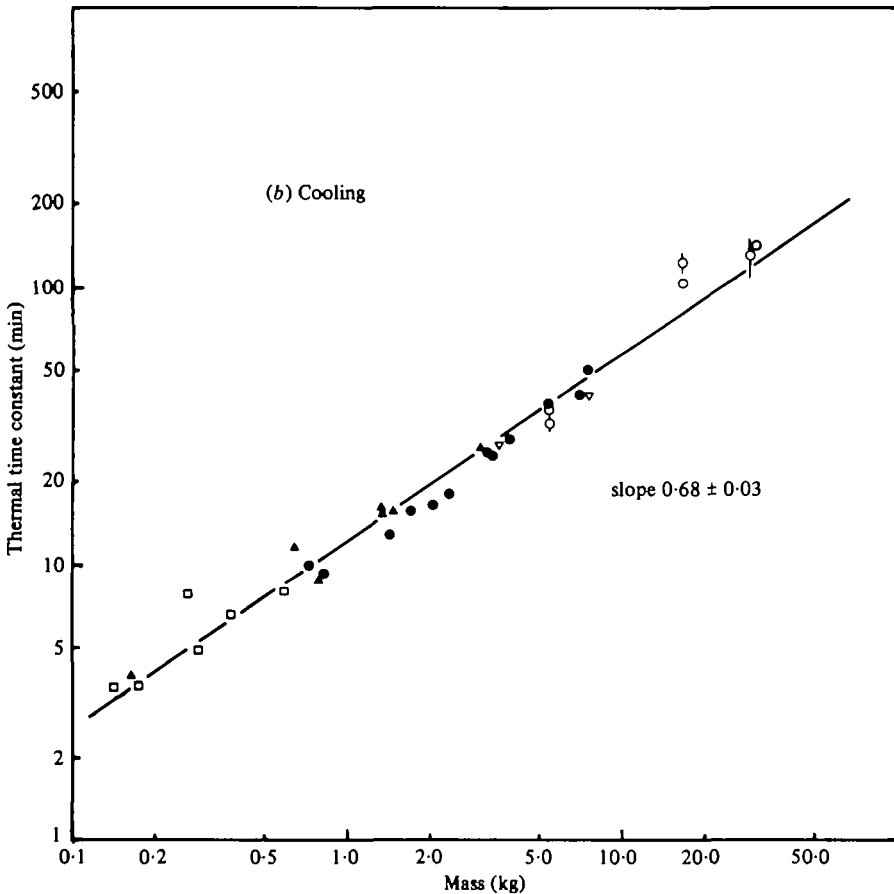
Fig. 1. Log-log plots of thermal time constant against mass for various lizards heating and cooling in water. The data have been taken from the literature, and in many cases have been calculated from the rates measured at the midpoint of the heating or cooling curve.

time constant that has a scaling law very similar to that observed for lizards. The mathematical details of this model will be presented elsewhere.

## 2. THE MODEL

The simplest possible thermal model for an animal which cannot use metabolic heat to control its temperature consists of an isothermal core surrounded by a uniform, thin insulating layer of negligible heat capacity. The rate of change of core temperature may then be regulated by changing the conductance of the insulating layer. If the environment is assumed to be isothermal with infinite heat capacity, the amount of heat transferred from the surroundings per unit time is given by,

$$\frac{dQ}{dt} = hA(T_a - T_c), \quad (1)$$



The species involved are:  $\nabla$ , *Crocodylus johnstoni* (Grigg & Alchin, 1976);  $\bullet$ , *Alligator mississippiensis* (Smith, 1976);  $\square$ , *Physignathus lesueurii* (Grigg *et al.* 1979);  $\circ$ , *Crocodylus porosus* (Boland & Bell, 1980);  $\blacktriangle$ , *Amblyrhynchus cristatus* (Bartholomew, 1966; Bartholomew & Lasiewski, 1965). The lines are the least squares regression lines of log time constant on log mass. The uncertainties given are the 95% confidence limits. The theoretical value of this slope is 0.67.

where  $h$  is the thermal conductance of the insulating layer,  $T_a$  is the ambient temperature,  $T_c$  is the temperature of the core and  $A$  is the surface area of the body. The temperature of the core will change by  $1/C \, dQ/dt$  per unit time, where  $C$  is the heat capacity of the body. We can then write this as a differential equation,

$$\frac{dT_c}{dt} = \frac{hA}{C} (T_a - T_c), \quad (2)$$

which can be solved for any particular set of initial conditions. The solution will have a term of the form  $f(T_a) \cdot \exp(-t/\tau)$ , where  $\tau$  is equal to  $C/hA$ . This is then the thermal time constant in this simple model.

This model is basically a simplification of those of Spotila *et al.* (1973) and Grigg *et al.* (1979). It is equivalent to a single layer of insulating fat with no heat storage in the former, and letting the heat capacity of the insulating layer go to zero in the latter paper.

To show how the thermal time constant scales with body size, we make the further assumption that the series of animals is allotropic. Then, for any given shape, the volume scales as the linear dimension ( $d$ ) cubed, while surface area scales as  $d^2$ . The thickness of the insulating layer will scale as the linear dimension, implying that the thermal conductance  $h$  will scale inversely with  $d$ . Now the heat capacity  $C$  will be proportional to the mass for a homogeneous body, and this in turn is proportional to the volume:

$$C \propto V \propto d^3.$$

The thermal time constant is given by:

$$\tau = \frac{C}{hA} \propto \frac{d^3}{d^{-1}d^2} = d^2.$$

Thus the thermal time constant should scale as  $d^2$ , and so be proportional to mass to the power 2/3, if this simple geometrical model is valid.

### 3. RESULTS

This prediction can be tested by comparing thermal time constants measured for lizards heating and cooling in water, a close approximation to an isothermal environment. Fig. 1 shows published values of  $\tau$  plotted on a log-log scale against the corresponding body mass for lizards between 150 g and 30 kg. The differences between heating and cooling time constants are quite marked. The slope of the regression line fitted to the data for cooling agrees well with the prediction, but that for heating is significantly different at the 95% level.

It thus appears that this simple model can account for the increase in the thermal inertia of lizards with increasing mass, but that in order to get full quantitative agreement, a greater understanding of the physiology and a correspondingly more complex model may be needed.

The literature also contains many values for the time constant for heating and cooling in air. In this case, the boundary layer of air adjacent to the animal provides an additional insulating layer. Analysis is facilitated by using the concept of 'resistance' advocated by Clark, Cena & Monteith (1973). They define the resistance to heat flow as:

$$r = \frac{\rho C_p A (T_a - T_c)}{dQ/dt} \quad (3)$$

where  $\rho$  and  $C_p$  are the density and specific heat of air, and  $A$  is the area. Defined in this way,  $r$  has dimensions of time divided by length (e.g. s m<sup>-1</sup>), and can easily be compared with other heat or mass transfer resistances.

We can now think of the insulating layers as two resistors in series, those of the body and the boundary layer. If we call these resistances  $r_B$  and  $r_s$  respectively, then the total resistance  $r_H = r_s + r_B$ . Comparing eqn (1) with eqn (3), it is seen that the thermal conductance is inversely proportional to  $r_H$ ,

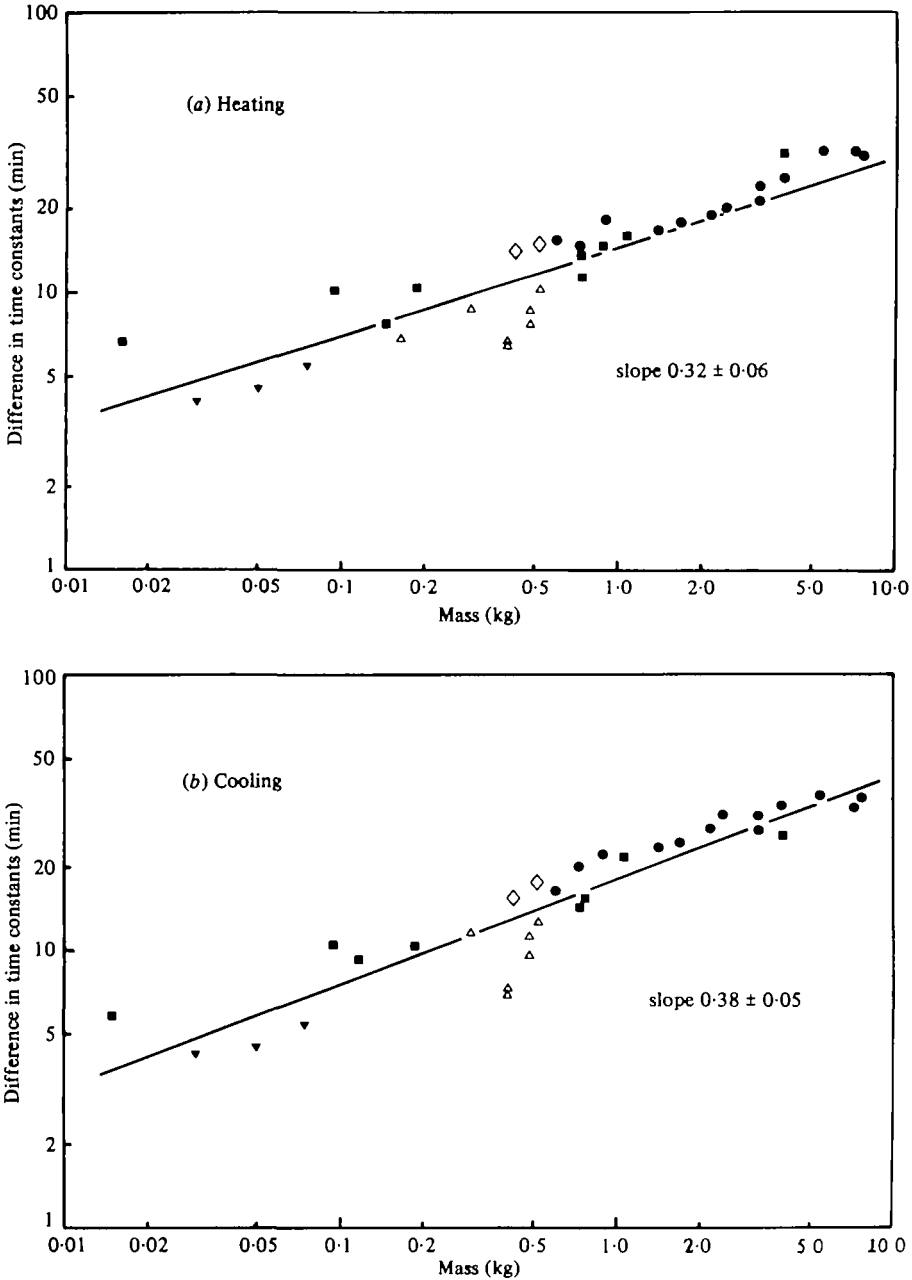


Fig. 2. Log-log plots of the component of the thermal time constant in air due to the boundary layer, against mass for both heating and cooling. This component has been calculated by subtracting the time constant in water derived from the regression equations found previously from the value of the time constant in air in the literature. This difference was then normalized to an air velocity of  $3 \text{ m s}^{-1}$  using a correction proportional to the square root of the air velocity in the particular experiment (Monteith, 1973). Only experiments where the air velocity was greater than  $1.5 \text{ m s}^{-1}$  have been used. The species are: ●, *Alligator mississippiensis* (Smith, 1976); ■, *Varanus* spp. (Bartholomew & Tucker, 1964); ▼, *Disposaurus dorsalis* (Weathers, 1970); △, *Amphibolurus barbatus* (Bartholomew & Tucker, 1963); ◇, *Tiliqua scincoides* (Bartholomew *et al.* 1965). The regression lines shown do not differ significantly from lines of slope 0.33, indicating that heat loss in air is proportional to the area to volume ratio, and that the boundary layer resistance is constant.

$$h = \frac{K}{r_H},$$

where  $K$  is a proportionality constant involving only the arbitrarily selected parameters of the density and specific heat of air. The thermal time constant is given by,

$$\tau = \frac{C}{hA} = \frac{Cr_H}{KA} \propto \frac{d^3}{d^2} r_H;$$

or

$$\tau \propto dr_H = d(r_B + r_s).$$

If we ignore the boundary layer for a moment, we can see that the first term is just the thermal time constant in water and so can be removed by subtracting the fitted time constants for heating and cooling in water. We are then left with the contribution due to the boundary layer which should scale as  $dr_s$ , or as  $M^{\frac{1}{3}} r_s$ .

Fig. 2 shows that  $r_s$  appears to be constant, and approximately the same for heating and cooling. As  $r_s$  is proportional to the Nusselt number, it could be expected to vary with the linear dimension of the animal, and so vary with mass (Monteith, 1973). However, at the high air velocities used in these experiments (typically 2–3 m s<sup>-1</sup>), the boundary layer will have a thickness of only a fraction of a millimetre, probably of the same order as the surface roughness of the skin. In this case the overall dimension of the animal will be unimportant, and the surface roughness will maintain  $r_s$  above that predicted for a smooth surface.

#### 4. DISCUSSION

For smaller lizards heating and cooling in air, the boundary layer resistance is much larger than that of the insulating layer. As mass increases, the former becomes less important, and the resistances become equal at a mass of about 7 kg for heating and 4 kg for cooling. For masses much larger than these, the boundary layer resistance can be ignored, and lizards will heat and cool equally in air or water.

The largest animals appearing in these results are small crocodiles of around 20 kg mass. These had time constants for cooling of about 2 h, thus allowing considerable freedom of movement in adverse environments before basking would be necessary. If we extrapolate the results presented here, we can predict that a large crocodile of mass 400 kg will have a thermal time constant for cooling of about 12 h. It will therefore have a high degree of thermal stability, its body temperature varying by only a few kelvins between night and day. If we extrapolate even further, it can be seen that larger lizards such as dinosaurs would have even greater thermal stability. For instance, a 2000 kg lizard is predicted to have a thermal time constant of almost 48 h. As has been pointed out by Spotila *et al.* (1973) and others, such a massive creature would feel little effect of the diurnal cycle in ambient temperature, and be able to remain quite active during cool periods for some time.

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