

## BODY SIZE AND THERMAL ENERGETICS: HOW SHOULD THERMAL CONDUCTANCE SCALE?

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**Abstract**—1. It is widely supposed that thermal conductance scales to body size by a power equation of the form  $C = aM^b$ .

2. It is theoretically unrealistic to expect the scaling of thermal conductance to follow a power relation, because animals exchange heat in multiple ways, each of which varies with body size in a different way.

3. I have developed models for the scaling of thermal conductance, which depart significantly from a power curve.

4. Depending upon environmental and physiological condition, the best power approximation to the "true" allometric curves for thermal conductance yields exponents ranging from 0.33 to 0.75.

5. The model's predictions are supported by a wide variety of experimental evidence.

**Key Word Index**—Thermal conductance; scaling; body size; allometry; heating and cooling rates; birds' eggs; alligators.

### BODY SIZE AND THERMAL ENERGETICS

In his recent book, *The Ecological Implications of Body Size*, Peters (1983) lists more than 1000 allometric equations, describing how numerous traits of animals vary with body size. All the allometric equations are power equations of the form:

$$y = aM^b \quad (1)$$

or, in its linearized version:

$$\log y = \log a + b \cdot \log M \quad (1a)$$

where  $y$  is a dependent variable,  $M$  is body mass (kg), and  $a$  and  $b$  are a coefficient and exponent, respectively, that make the equation explicit.

Of the more than 1000 allometric power equations, 86 describe the relation between body size and thermal energetics; 36 equations are concerned with thermal conductance, 28 with heating and cooling rates (derived from the thermal conductance and thermal capacitance), 7 with the temperature coefficient of metabolism and 15 with the limits of the thermal neutral zone of homeotherms (derived from the thermal conductance and basal metabolic rate).

This makes 79 allometric equations that deal either directly or indirectly with the scaling of thermal conductance. On the face of it, this is a significant amount of redundancy, and it raises an interesting question. Animals are all built more or less the same way, and except for some obvious differences (e.g. terrestrial vs aquatic animals), they all exchange heat in roughly the same way (e.g. Mitchell, 1976). Why, then, should 79 different equations be needed to deal with thermal conductance? Why would not one or two do?

One possible answer is that the various allometric equations each convey unique information about the diverse ways that animals cope with the challenges of body size. This argument has been most recently and explicitly put by Heusner (1982a, b) and Calder (1987) for the scaling of basal metabolic rate. The logic is roughly as follows: (1) Animals must operate under certain physical and mechanical constraints, and (2) a power equation is the appropriate mathematical description of these constraints. (3) Observed variation between taxa of the parameters of the power equation,  $a$  and  $b$ , represents, therefore, variation around the "design limitations" imposed by the mechanical and physical constraints of body size—allometric "variation on a theme", if you will. If one accepts this logic, the need for large numbers of power equations to describe the same phenomenon is self-evident—to understand a diverse phenomenon, one must first catalog and describe its variation.

Another possible answer is that the redundancy exists because we do not understand the proper way to describe the effect of body size. Suppose, for example, that the "real" physical constraints on body size do *not* manifest themselves as power equations, but come close enough so that we have been "fooled" into thinking that they do. If this is the case, measured variation of  $a$  and  $b$  do not represent "real" variation, but residual variation around a poor first approximation. Rather than allometric "variation on a theme", the myriad power equations are "noise" masking an underlying unity.

In this paper, I shall develop the latter argument as it applies to the allometry of thermal conductance. It will be my contention that a power equation is not a reasonable candidate for describing how body size affects the exchanges of heat between animals and the environment. I shall derive the equations that I consider to be more reasonable candidates, and I shall develop some of the tools needed to work with them.

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I will base my arguments on some very basic heat transfer theory. I will first show, using a simple graphical argument, that a power equation is not adequate to describe the allometric variation of thermal conductance, except in certain limited circumstances. I also will show that the "true" allometric curves, though more complex than the power equation, nevertheless are readily derived, described and analyzed, and I will develop methods to do all three. I will conclude with some practical examples of the allometric analysis of thermal conductance.

**IS THE POWER EQUATION AN APPROPRIATE MODEL FOR THE SCALING OF THERMAL CONDUCTANCE?**

It is often taken as given that a power equation is the best mathematical description for an allometric relationship. Sometimes, there is a sound theoretical reason for this assumption [e.g. the elastic similarity argument of McMahon (1973) for the scaling of basal metabolic rate]. It must be said, however, that allometricians often use a power equation because it is "traditional"—used even though it may be neither the best statistical description of the data (Smith, 1984; Hayssen and Lacy, 1985), nor even the best theoretical description (Kooijman, 1986).

The purpose of this section is to explore several questions about the scaling of thermal conductance: How reasonable an assumption is it that a power equation describes the scaling of animal heat exchange? If it is not always a reasonable assumption, are there circumstances where it would be adequate? Under what circumstances would it fail?

*Conductance, thermal resistance and equivalent circuits*

The rate that heat leaves an animal ( $\dot{q}$ ; W) is the product of (a) a temperature difference ( $\Delta T$ ; K) between the animal's interior and its surroundings, and (b) a thermal conductance ( $C$ ;  $W K^{-1}$ ; Fig. 1). We may put this another way, and replace conductance by its inverse, the total thermal resistance ( $R$ ;  $K W^{-1}$ ). This is not mere caprice: using resistance makes it easy to analyze heat flux using a so-called electrical analogy. In the electrical analogy, heat flow between two points (or nodes), separated by a temperature difference, is analogous to flow of electrical current between two points separated by a voltage difference (Fig. 1). The electrical analogy provides considerable analytical power [see Thomas (1980) and Bakken (1976) for further discussion of the

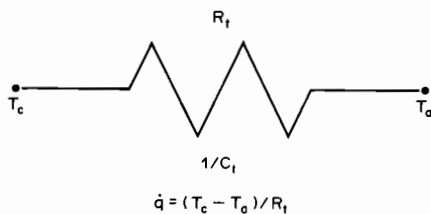


Fig. 1. An equivalent circuit for a "lumped" conductance and its relation to the total thermal resistance. Heat flows between two nodes at temperatures  $T_c$  and  $T_a$  and is facilitated by a thermal conductance  $C_t$  (or is impeded by a total thermal resistance,  $R_t$ ).

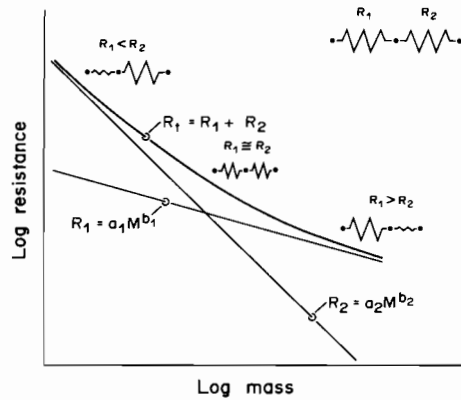


Fig. 2. Scaling of the thermal resistance for a simple equivalent circuit, comprised of two component resistors in series,  $R_1$  and  $R_2$ , that scale with body mass by different power relations. Light lines: scaling relationships of the component resistors. Heavy curve: scaling relationship of the composite resistance  $R_t$ .

electrical analogy for heat exchange], and accordingly, I will use the total thermal resistance for the model's development.

When an animal's conductance (or resistance) is measured in the laboratory, it is usually measured as a *lumped* conductance (or resistance). Put another way, the exchange of heat is assumed to be governed by a simple equivalent circuit (Fig. 1), with two nodes (the core and the surroundings) each of uniform temperature ( $T_c$  and  $T_a$ , respectively), separated by a single resistor ( $R_t$ ).

A single-resistor circuit is a gross oversimplification. It is not difficult to make the equivalent circuit more biologically realistic, expanding it into a *composite* circuit, comprised of *component* resistors (Bakken, 1976; Tracy, 1982; Turner, 1987a). I shall outline a biologically realistic equivalent circuit below. For now, I shall use a deliberately simplified circuit to explore the notion that a power equation is inappropriate for describing the scaling of thermal conductance.

*A graphical argument for the "proper" relation between body size and conductance*

Let us assume a composite equivalent circuit, comprised of two component resistors,  $R_1$  and  $R_2$ , that combine in series to form the total resistance (Fig. 2). Let us make the assumption that  $R_1$  and  $R_2$  each scale to body size by a different power equation (i.e. by equations with coefficients  $a_1$  and  $a_2$ , and exponents  $b_1$  and  $b_2$ , respectively). [We shall see later why this is a reasonable assumption.] The equation for the total resistance is:

$$R_t = R_1 + R_2 \tag{2a}$$

or

$$R_t = a_1 M^{b_1} + a_2 M^{b_2} \tag{2b}$$

Because  $R_1$  and  $R_2$  both scale by a power equation, plotting them each against body mass on a double-log plot results in a straight line for each (Fig. 2), with slopes  $b_1$  and  $b_2$ , respectively.

There is an important consequence of the different slopes for the component resistors. At extremely small size, the component with the steepest slope dominates the total resistance ( $R_1 < R_2$ ; Fig. 2). At extremely large size, the component with the shallower slope dominates the total resistance ( $R_1 > R_2$ ; Fig. 2). Near the middle of the size range, both components are roughly the same order of magnitude, and neither component can be said to dominate ( $R_1 \cong R_2$ ; Fig. 2). One consequence of this is that *the relation of  $\log R_i$  and  $\log M$  cannot be linear*. In the circumstance in Fig. 2, it is hyperbolic. In fact, there are only two circumstances where the combination of multiple components will translate into a power relation between  $R_i$  and  $M$ : (a) one resistance is so large compared to the other that reducing the circuit to a single resistor results in a negligible loss of accuracy—this means one or the other extreme body size, or (b) both  $R_1$  and  $R_2$  scale to body size by the same exponent.

With this simple graphical argument, it is evident that a scaling relationship that is *not* a power equation may derive from an *additive* combination of scaling relationships that *are* power equations. It is important to realize that additivity of fluxes of heat is demanded by the First Law of Thermodynamics. Thus, on very simple first principle, the validity of the power equation as the best description for the scaling of heat exchange is rendered doubtful. Of course, this does not preclude admitting that a power equation may work in *some circumstances*, or may, at times, be a very good *approximation* of the “true” allometric relationship.

#### WHAT IS THE “PROPER” SCALING RELATIONSHIP FOR THERMAL CONDUCTANCE?

To explore the “proper” scaling of thermal conductance (or total resistance), a few formal tools must be developed. I first outline a simple model for the total resistance to heat exchange for animals. I then develop the formal methods for analyzing the resulting scaling relationships.

##### *What is a biologically “reasonable” equivalent circuit?*

The simplest equivalent circuit, which incorporates enough detail to be biologically reasonable, is a spherical “core-shell” model, comprised of several component resistances, each representing the important ways heat moves both inside animals, and between animals and their surroundings (Fig. 3). In a core-shell model, an animal is analogized to an isothermal core region, with radius  $r_i$ , surrounded by a concentric spherical shell of outer radius  $r_o$  (Fig. 3).

In the core-shell model, at least two resistances are assumed to govern the flow of heat between the core and surroundings. An internal resistance,  $R_i$ , impedes the flow of heat across the shell, between nodes in the core (at temperature  $T_c$ ) and the shell surface (at temperature  $T_s$ ). The internal resistance is in series with an external resistance,  $R_e$ , which impedes the flow of heat between the surface node and the surroundings (at temperature  $T_e$ ; Fig. 3).

The internal and external resistances are themselves composite resistances. Heat flows internally by conduction through the tissues, and in animals with

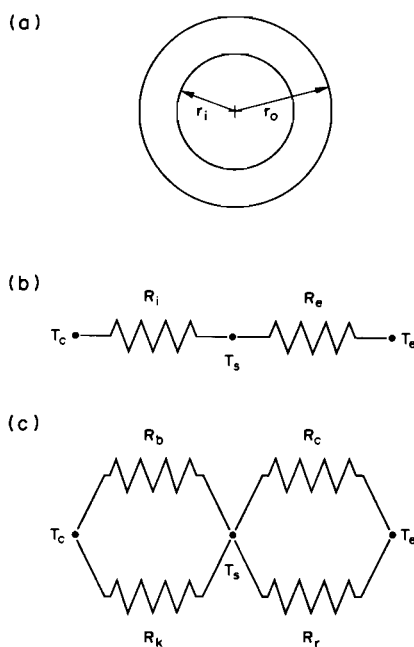


Fig. 3. Schematic diagram of the simplest, biologically reasonable equivalent circuit. Top panel: the core-shell model for a sphere. Middle panel: the internal (shell) resistance and the external resistance combine in series. Bottom panel: Resolution of the internal and external resistors into their components: blood flow resistance ( $R_b$ ) and conduction resistance ( $R_k$ ) combine in parallel to form the internal resistance; convection resistance ( $R_c$ ) and radiation resistance ( $R_r$ ) combine in parallel to form the external resistance.

a circulatory system, by transport in flowing blood. The internal resistance can therefore be described as two resistors in parallel, one for conduction ( $R_k$ ), and one for flowing blood ( $R_b$ ; Fig. 3). Similarly, the external resistance is a composite resistance. Heat leaves the surface of an animal in many different ways; by convection to the ambient fluids, by radiation, by evaporation and by conduction to a solid substrate. One could build in a resistance for each (e.g. see Bakken, 1976; Tracy, 1982; Tracy *et al.*, 1986). For this paper, I will assume there are two principal modes of external heat flux: convection to the ambient fluid and long-wave radiation. The external resistance therefore consists of the parallel resistors for convection ( $R_c$ ) and radiation ( $R_r$ ; Fig. 3).

The basic model is, therefore, a series-parallel array of four resistors. There is no reason why the model could not be more complex. For example, a “fur” resistor could be placed in series with the internal and external resistors, or more parallel resistors could be built into the external resistance, each with its own environment node (e.g. Bakken, 1976). Circuits for appendages also could be built into the model (e.g. Tracy, 1982). I shall not deal with these refinements in this paper. My purpose here is simply to illustrate how the resistances of these circuits scale and how their scaling may be analyzed. I also wish to make the point that they may provide a fruitful way to think about the scaling of heat exchange.

What are the scaling relationships for the composite resistors?

The scaling of each composite resistance is describable with its own power equation. In Appendix I, I have derived the scaling relations for each of the component resistances in Fig. 3. Their proportionalities are as follows:

$$R_k \propto M^{-1/3} \tag{3a}$$

$$R_b \propto M^{-0.75} \tag{3b}$$

$$R_c \propto M^{-0.54} \tag{3c}$$

$$R_r \propto M^{-2/3} \tag{3d}$$

Clearly, there is variation between the exponents for each composite resistor. From the graphical argument above, it is unlikely that the scaling of total resistance can be described by a power equation.

How can the “proper” scaling relation for a composite resistor be described?

There are two parts to the “proper” description of the scaling relationship for a composite resistance. First, the explicit equation for the circuit must be written. Second, a “best” power equation approximation to the “proper” scaling relationship should be derived.

The explicit equation for the circuit and hence its “proper” scaling relationship follows simply from the combining rules for arrays of resistors, in conjunction with the theoretically derived scaling relationships for each composite resistance. Resistors in circuits combine according to two basic rules. For a series array of resistors, the composite resistance is:

$$R_t = \sum_{i=1}^n R_i \tag{4a}$$

For a parallel array, the composite resistance is:

$$\frac{1}{R_t} = \sum_{j=1}^m \frac{1}{R_j} \tag{4b}$$

The actual formula for the circuit depends upon the particular ways the series and parallel arrays of resistors combine. I have derived the relations for three common types of circuits in Appendix II.

I have taken the “best” power curve approximation to the “proper” scaling relationship to be the first derivative of the relation between  $\log R_t$  and  $\log M$ . Consider a scaling relation,  $\log R_t = f(\log M)$ . Assume this relation is not linear (Fig. 4), as expected for the “proper” scaling relationship. Let us define a power equation,  $\log \Omega_t = g(\log M)$ , that is tangent to  $f(\log M)$  at  $\log M^*$ . The tangent will, of course, vary with  $\log M$ . It will be the power equation that is the best approximation to  $f(\log M)$  in the neighbourhood of a particular  $\log M$  (e.g.  $\log M^*$  in Fig. 4).

By analogy with the convention that defines the coefficient and slope of a log-transformed allometric power relation as  $\log a$  and  $b$ , respectively [eqn (1a)], the tangent also will have a coefficient and slope, which I designate as  $\log \alpha$  and  $\beta$ , respectively. In the analyses that follow, I will reserve the symbols  $a$  and  $b$ , appropriately subscripted, for power equations that describe the component resistances of a circuit.

An intuitive feeling for how the scaling parameters  $\beta$  and  $\log \alpha$  behave will be useful in following the

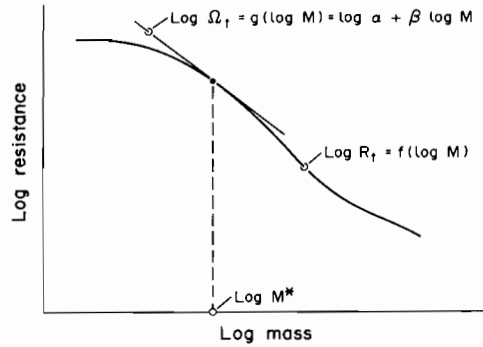


Fig. 4. Hypothetical scaling relationship,  $\log R_t = f(\log M)$ , and its relation to the best power approximation at the mass  $\log M^*$ ,  $\log \Omega = g(\log M)$ . Discussion in the text.

derivations and examples to follow. Consider again the graphical example of Fig. 2. The total resistance  $R_t$  is the sum of the two component resistors, and the function  $\log R_t = f(\log M)$  is decidedly non-linear (Fig. 5). Plotting  $\beta$  and  $\log \alpha$  vs  $\log M$  underscores this point (Fig. 5)—neither is constant with respect to  $\log M$ .

When one component is large with respect to the other,  $R_t$  approaches the value of the larger, or more generally, the dominating resistance. Thus, as  $\log M \rightarrow -\infty$  ( $M \rightarrow 0$ ),  $\log R_t \rightarrow \log R_2$ , because at small body sizes,  $R_2$  is large with respect to  $R_1$ .

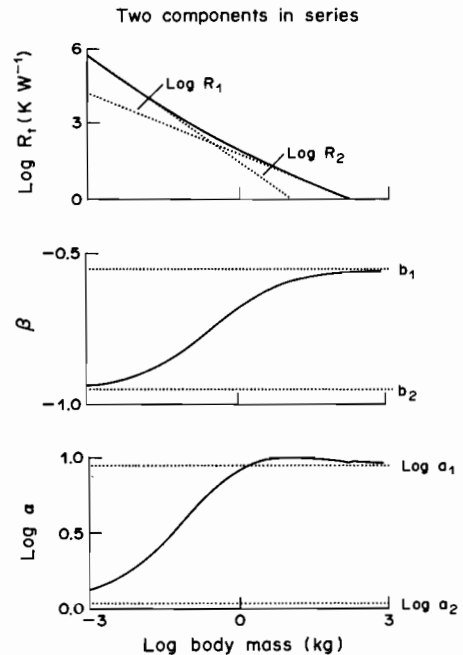


Fig. 5. The simultaneous variation of  $\log R_t$  (top panel),  $\beta$  (middle panel) and  $\log \alpha$  (bottom panel) with respect to  $\log M$  for the hypothetical composite circuit of Fig. 2. Index lines (dotted lines) show (top panel) the scaling relations for the component resistors,  $R_1$  and  $R_2$ ; (middle panel) the exponents,  $b_1$  and  $b_2$ , that describe the scaling of  $R_1$  and  $R_2$  respectively; (bottom panel) the coefficients,  $\log a_1$  and  $\log a_2$  of the scaling equations for  $R_1$  and  $R_2$  respectively.

Conversely, as  $\log M \rightarrow +\infty (M \rightarrow \infty)$ ,  $\log R_t \rightarrow \log R_1$ . It follows, therefore, that the values of  $\log \beta$  and  $\log \alpha$  will track the values of  $\log a$  and  $b$  for the dominating resistance (Fig. 5). Thus, as  $\log M \rightarrow -\infty$ ,  $\beta \rightarrow b_2$  and  $\log \alpha \rightarrow \log a_2$ ; conversely, as  $\log M \rightarrow +\infty$ ,  $\beta \rightarrow b_1$  and  $\log \alpha \rightarrow \log a_1$ . Also, where one component dominates,  $\beta$  and  $\log \alpha$  will vary little with changes of body size (Fig. 5). At body sizes where neither resistance dominates,  $\beta$  and  $\log \alpha$  will assume values intermediate to the respective  $b$  and  $\log a$  for the components, and will vary rapidly with respect to body mass (Fig. 5).

We see, therefore, the crucial principle for understanding the scaling of composite resistances. When one component of an equivalent circuit dominates heat flux, the scaling of the dominating component determines both the values of  $\beta$  and  $\log \alpha$ , and makes a power equation a good approximation of the "true" scaling relationship. When more than one component dominates heat flux, a power equation is a poor approximation of the "true" scaling relationship, and the values of  $\beta$  and  $\log \alpha$  will take on values intermediate to the values of  $b$  and  $\log a$  for the dominating components.

How are the parameters  $\beta$  and  $\log \alpha$  calculated? The formulas to do this depend upon the configuration of the composite circuit: in Appendix II, I have derived them for three common types of circuits. We shall have occasion to refer to these circuits in the examples that follow. No matter what the configuration, however, there is a common method for deriving the formulas.

Once the "proper" equation for  $R_t = f(M)$  is written, the next step is to calculate  $\beta = g(\log M)$ . This is equivalent to calculating the equation for  $d(\log R_t)/d(\log M)$ . Some simple differential calculus shows that:

$$\frac{d(\log R_t)}{d(\log M)} = \frac{dR_t}{dM} \frac{d(\log R_t)}{dR_t} \frac{dM}{d(\log M)} \quad (5a)$$

and:

$$\beta = \frac{dR_t}{dM} \cdot \frac{M}{R_t} \quad (5b)$$

The value of  $\beta$  at a particular  $M$  is obtained by solving eqn (5b). Once  $\beta$  and  $R_t$  for a certain body mass is known,  $\log \alpha$  is easily calculated from the point-slope method.

$$\log \alpha = \log R_t - \beta \log M^* \quad (6)$$

To summarize this section, it is unlikely that the power equation is an appropriate model for the scaling of animals' thermal resistance (or thermal conductance, or, by extension, anything that depends directly upon thermal conductance). Even though the various means by which animals lose heat each might scale by a power equation, when they combine, the First Law of Thermodynamics demands they combine additively. A power equation does not result when power equations are added, unless all component resistances scale to the same exponent. The "proper" scaling relationships are derived from the mathematical rules governing the combining of resistances in equivalent circuits and the scaling relationship for each component in the circuit. The best power approximation to the "true" scaling

relationship at any body size is given by the first derivative of the log-transformed version of the "true" scaling relationship.

Let us now turn to some practical examples of how the scaling of total resistance (or conductance) is properly analyzed.

#### SCALING OF THERMAL RESISTANCE—SOME PRACTICAL EXAMPLES

##### Example 1—thermal resistance of infertile birds' eggs (simple series equivalent circuit)

We shall start with the simplest imaginable equivalent circuit. First, assume there is no blood flow inside the body. Then,  $R_b \rightarrow \infty$  and  $R_i \rightarrow R_k$ . Also, assume that the body has no external insulation, and loses heat from its surface by convection only. Thus,  $R_r \rightarrow \infty$  and  $R_e \rightarrow R_c$ . The equivalent circuit is, therefore, a simple series equivalent circuit, so-called because it is comprised of a series array of composite resistances (Fig. 6). This type of equivalent circuit is analyzed in detail in Appendix II.

The closest biological equivalent to this circuit is infertile birds' eggs, which have no circulatory system and no external insulation.

We shall consider the scaling of the total resistance under two extreme conditions: eggs suspended in still air, and eggs suspended in still water. Still air provides a very high external resistance. Still water, though admittedly an unnatural medium for birds' eggs, is a convenient medium for providing a very low external resistance. As shown in Appendix I, the convection resistance in still air is:

$$R_{c,air} = 4.7 M^{-0.54} \quad (7a)$$

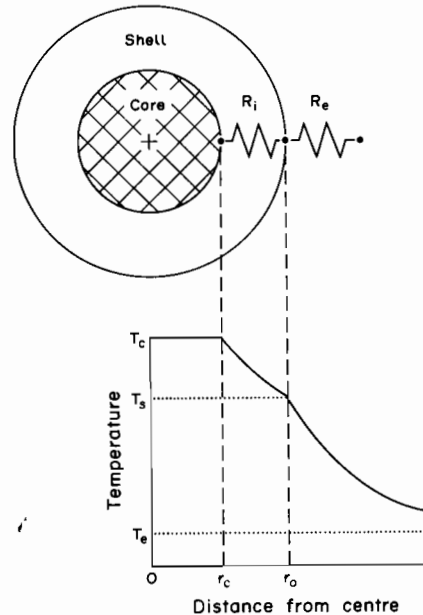


Fig. 6. The equivalent circuit for Example 1. Top panel: The core-shell model, showing the distribution of the internal and external resistors in series. Bottom panel: The expected temperature distribution in a core-shell model with an internal and external resistance in series. The temperature drop across each resistor depends upon their relative magnitudes.

In still water, the convection resistance is:

$$R_{c,water} = 0.089 M^{-0.54} \quad (7b)$$

Clearly, the resistance to convection heat loss in water is about fifty times smaller than it is in air. Note, however, that the scaling exponents are the same for both air and water (-0.54)—only the coefficients are different.

For this example, the internal resistance is equivalent to the conduction resistance. As derived in Appendix I, the scaling equation for  $R_k$  is:

$$R_k = 0.86 M^{-0.33} \quad (7c)$$

The scaling exponents for internal resistance (-0.33) and external resistance (-0.54) are different. We may judge, therefore, that  $R_i$  should not be a power function of body mass. Because  $R_c$  in air is about an order of magnitude greater than  $R_k$ , we also may judge that  $\beta$  will be close to  $b_{c,air}$ , and  $\log \alpha$  will be close to  $\log a_{c,air}$ . Both  $\beta$  and  $\log \alpha$  should vary slightly with respect to log egg mass. The simulation shows this to be the case (Fig. 7): in air,  $\beta$  ranges from about -0.52 in small (2 g) "eggs" to about -0.48 in large (1500 g) "eggs" (Fig. 7). In water, however, the situation is reversed:  $R_k$  is about an order of magnitude larger than  $R_c$ , and we expect  $\beta$  to be close to  $b_k$ , and  $\log \alpha$  to be close to  $\log a_k$ . We see (Fig. 7) that  $\beta$  ranges from about -0.40 for small "eggs" to about -0.36 for large "eggs" (Fig. 7).

The actual resistance of infertile eggs scales in ways close to that predicted (Turner, 1985). For eggs cooling in still air (Fig. 8), the approximate scaling relation is:

$$R_{i,air} \cong 2.42 M^{-0.60} \quad (8a)$$

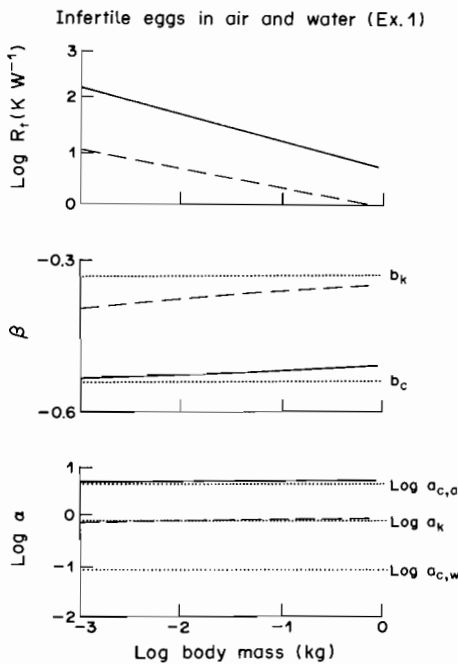


Fig. 7. Log  $R_i$ ,  $\beta$  and  $\log \alpha$  for the circuit depicted in Fig. 6. Simulations for two conditions are shown: eggs cooling in air (solid line) and eggs cooling in water (dashed line). Format as in Fig. 5.

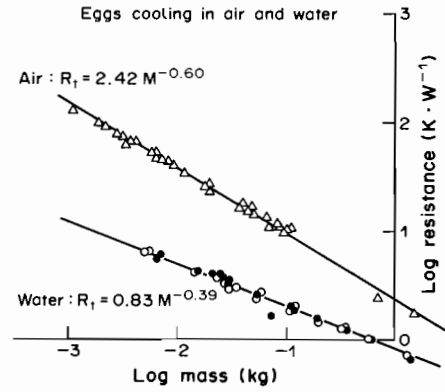


Fig. 8. Scaling of the total resistance for eggs cooling in air (open triangles) and water (circles). Data for eggs cooling in air are from Turner (1985). Data for eggs cooling in water are original to this study.

In still water, the approximate scaling relation is:

$$R_{i,water} \cong 0.83 M^{-0.39} \quad (8b)$$

It is important to remember that the exponents in eqns (8a, b) are equivalent to *average* values of  $\beta$ .

As predicted, the average value of  $\beta$  for eggs in air (-0.60) is larger (i.e. more negative) than it is in water (-0.139). The average  $\beta$  for eggs in water is also very close to that predicted by the model (-0.36 to -0.40; average -0.40). In air, while the average  $\beta$  (-0.60) is close to predicted (-0.52 to -0.44), it is nevertheless *larger* than the predicted values. Any error should have made the average  $\beta$  *smaller*. Explaining the discrepancy for  $\beta$  in air leads us to the next example and to another type of circuit to analyze.

*Example 2—thermal resistance of birds' eggs in air (simple parallel equivalent circuit)*

In Example 1, we saw that the external resistance in air is roughly an order of magnitude larger than the internal resistance. Thus,  $R_i \cong R_c$  and the solution to the discrepancy between the average measured  $\beta$  for eggs cooling in air and that predicted is probably in the external resistance.

In Example 1, the loss of heat from the surface was assumed to be by convection only. This is unrealistic: a body also can lose heat simultaneously by radiation. Therefore, the external resistance is actually a simple parallel array of resistors (Fig. 9), unlike the simple series array of Example 1 (Fig. 6). The simple parallel array is also analyzed in Appendix II. In this example, we shall assume the external resistance is comprised of the parallel resistors for convection ( $R_c$ ) and for radiation ( $R_r$ ; Fig. 9).

The scaling of the convection resistance in air has already been derived [Appendix I; eqn (7a)]. For radiation, the resistance scales:

$$R_r = 3.43 M^{-0.67} \quad (9)$$

(Appendix I).

Again, we see that the scaling exponents for the convection resistance (-0.54) and the radiation resistance (-0.67) are different. Consequently, we do not expect  $R_e$  to scale by a power function. Because this is a simple parallel array, the resistor that

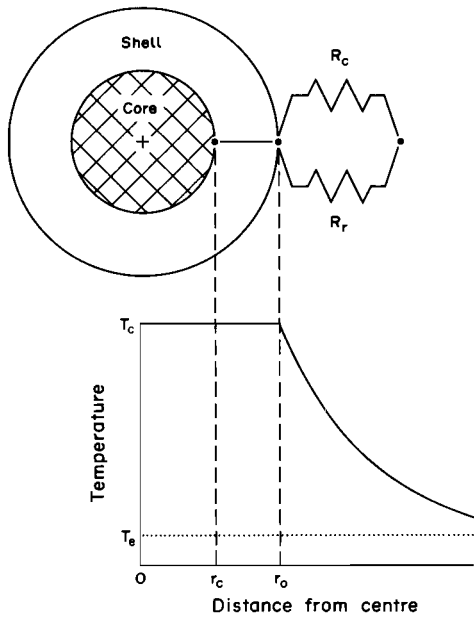


Fig. 9. The equivalent circuit for Example 2. Top panel: The core-shell model, showing the radiation and convection resistors combining in parallel to form the external resistance. Bottom panel: The expected temperature distribution in a core-shell model with a very large external resistance. Almost the entire temperature drop takes place from the surface to the surroundings and almost none in the shell. This is why the internal resistance may be ignored in certain cases.

dominates heat transfer is not the largest (as it was in Example 1), but the smallest (Appendix II). Thus,  $R_c$  for small eggs will approach  $R_c$ , while  $R_c$  for large eggs will approach  $R_r$ . The predicted value for  $\beta$  ranges from about  $-0.58$  for small (2 g) "eggs", to about  $-0.63$  for large (1500 g) "eggs" (Fig. 10), averaging about  $-0.60$  (see also Turner, 1985). This is gratifyingly close to the observed result [Fig. 8; eqn 8a].

How can we be sure the observed departure of the exponent from a value of  $-0.54$  is due to the addition of radiation heat exchange? With the model, we may predict that if radiation is much reduced, the scaling exponent for  $R_e$  should approach  $-0.54$  (Fig. 10).

Sotherland *et al.* (1987) measured the resistances to heat exchange of polished aluminum "eggs." Polished aluminum reduces the emissivity of the eggs by roughly 90%, increasing the radiation resistance by the same proportion. Their observed exponent for  $R_e$  was about  $-0.55$ . This is the predicted result (Fig. 10). It appears the average value of  $\beta$  of  $-0.60$  for the external resistance is due to the composite scaling of convection and radiation heat exchange (Turner, 1985).

*Example 3—thermal resistance of living eggs (series-parallel array)*

In Examples 1 and 2, it was assumed that no heat moved by blood flow. This is unrealistic, of course, but it served for illustration. We now turn to a more realistic model, which incorporates blood flow. In-

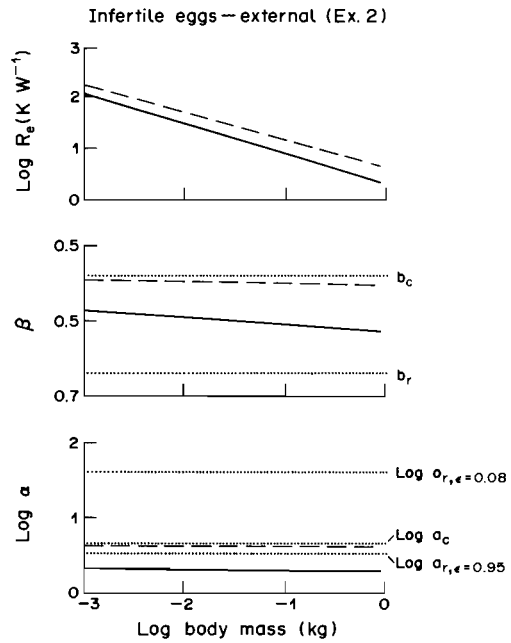


Fig. 10.  $\log R_e$ ,  $\beta$  and  $\log \alpha$  for the circuit depicted in Fig. 9. Simulations for two conditions are shown: still air, and surface emissivity = 0.95 (normal, solid line); still air, and surface emissivity = 0.08 (equivalent to polished aluminum, dashed line). Format as in Fig. 5.

side the egg, heat flows in blood simultaneously with internal conduction (Fig. 3): consequently, resistors for blood flow ( $R_b$ ) and conduction ( $R_k$ ) are in a simple parallel array (Fig. 11). When combined with the parallel array for external resistance, outlined in Example 2, this completes the series-parallel array originally proposed as the simplest biologically reasonable model (Fig. 11).

I will develop two examples using this series-parallel array. This example will consider the impact of blood flow inside developing birds' eggs. The next will consider the impact of size on blood-controlled heating and cooling rates in reptiles.

Birds' eggs begin with no circulatory system, and as they develop, a circulatory system appears and grows within the egg. Therefore, the internal resistance at the start of development is equivalent to  $R_k$ , because  $R_b \rightarrow \infty$ . As development proceeds, the blood flow resistance becomes finite and smaller as the circulatory system and the mass flow rate of blood inside the egg increases (Tazawa, 1980; Turner, 1987b, c). Before considering how this developing blood flow affects the egg's total resistance, let us turn first to how it affects the internal resistance. Because the internal resistance is a simple parallel array, the methods developed in Example 2 to analyze  $R_e$  can be used in this example to analyze  $R_i$ .

Scaling equations are needed for both  $R_k$  and  $R_b$ . There already is an expression for  $R_k$  [eqn (7c)]. In Appendix I, the scaling equations for  $R_b$  in developing birds' eggs have been derived. Obviously, there is not a single expression for  $R_b$ —the expression varies with age of the egg:

$$R_b \rightarrow \infty \tag{10a}$$

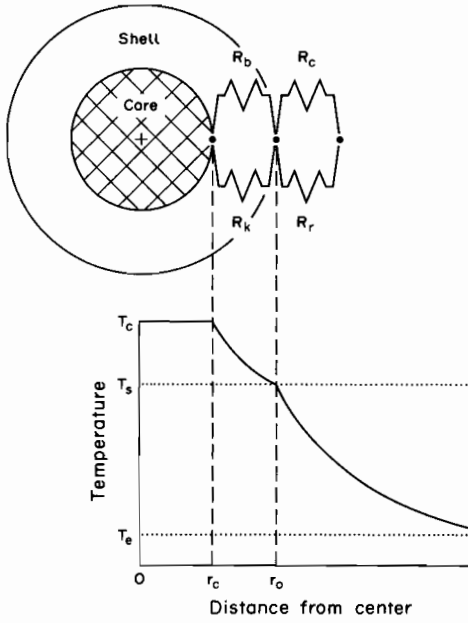


Fig. 11. The equivalent circuit for Examples 3 and 4. Top panel: The core-shell model, showing the distribution of the four component resistors that comprise the simplest biologically reasonable equivalent circuit (Fig. 3). Bottom panel: The expected temperature distribution in a core-shell model with an internal and external resistance in series. The steepness of the temperature drop across each resistor depends upon their relative magnitudes.

at day 0 of incubation

$$R_b = 2.8 M^{-0.75} \tag{10b}$$

midway through incubation, and

$$R_b = 0.30 M^{-0.75} \tag{10c}$$

near the end of incubation.

Note that the exponent is assumed to be constant through incubation, and increases of blood flow with development are reflected as a reduction of the coefficient. Note also that the exponent for  $R_b$  ( $-0.75$ ) parallels that for metabolism of eggs, and that it is much different from the exponent for  $R_k$  ( $-0.33$ ). Finally, note that the coefficient for the conduction resistance [0.86; eqn (7c)] is at first much smaller than the coefficient for  $R_b$  [2.8; eqn (10b)], but by the end of incubation, the coefficients are similar [0.86 vs 0.30; eqns (7c) and (10c) respectively].

At the start of incubation,  $R_i$  is coincident with  $R_k$ , for the simple reason that  $R_b \rightarrow \infty$ . At this age,  $R_i$  is a power function of size, with  $\beta = -0.33$  for eggs of all sizes (Fig. 12)—no surprise, since it has been defined that way. As incubation proceeds and blood flow increases,  $R_b$  becomes finite, and, in parallel with  $R_k$ , lowers  $R_i$  and forces its scaling to deviate from a simple power curve (Fig. 12). Midway through incubation,  $\beta$  ranges from  $-0.34$  for small “eggs”, to  $-0.43$  for large “eggs” (Fig. 12), signifying that conduction is still very important for heat flow relative to transport in blood. At the end of incubation,  $\beta$  ranges from  $-0.38$  for small “eggs”, to about  $-0.62$  in large “eggs” (Fig. 12), signifying that circulation has become a more important medium of

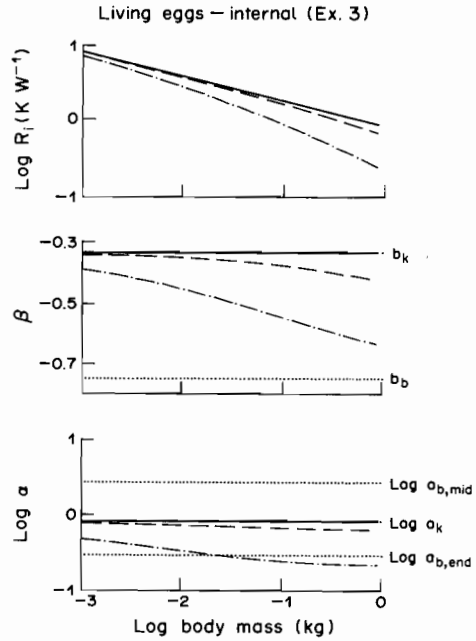


Fig. 12.  $\log R_i$ ,  $\beta$  and  $\log \alpha$  for the internal resistance of Fig. 11, comprised of the parallel resistors for conduction and blood flow. These simulations are for developing birds' eggs (Example 3). Simulations for three conditions are shown: eggs at the start of incubation (solid line), eggs at the middle of incubation (dashed line), and eggs at the end of incubation (dashed and dotted line). Format as in Fig. 5.

heat flow. Because the exponent for  $R_b$  is larger than for  $R_k$ , the developing circulation reduces internal resistance more for large eggs than for small eggs (Fig. 12; Table 1).

Now that the effect of blood flow on internal resistance is clarified, we may turn to its effect in combination with the eggs' external resistance. We shall use the same scaling equations for external resistance as were used in Examples 1 and 2 [eqns (7a, b, 9)].

The external resistance for an egg in still air is large relative to its internal resistance (Examples 1 and 2). In still air, then, we would expect the developing blood flow to have little effect on the egg's total resistance, regardless of how much it lowers the egg's internal resistance (Fig. 13a). If the egg is in still water, however, the internal resistance now dominates the egg's heat exchange, and any change in  $R_i$

Table 1. Proportional change of internal resistance ( $R_i/R_k$ ) as a result of increasing blood flow in eggs of various sizes

Egg mass (g)	$R_i/R_k$		
	Start of incubation	Middle of incubation	End of incubation
2	1	0.98	0.84
10	1	0.96	0.73
60	1	0.92	0.56
150	1	0.89	0.47
1500	1	0.76	0.26

As development proceeds (start  $\rightarrow$  middle  $\rightarrow$  end of incubation) and blood flow increases, the internal resistance is lowered. The effect of blood flow at any age is greater in larger eggs than it is in smaller eggs.

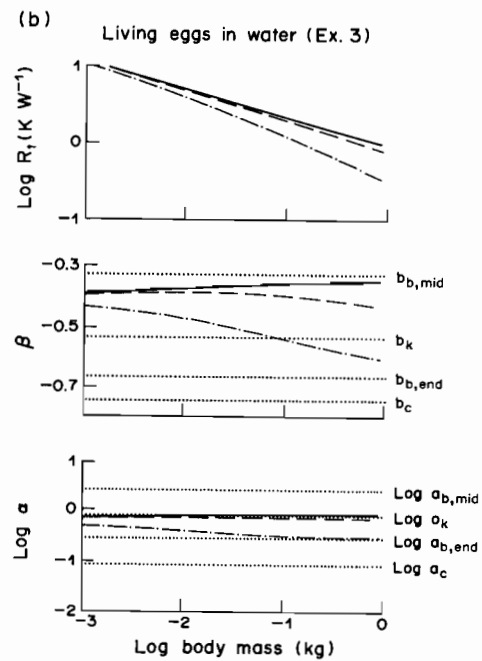
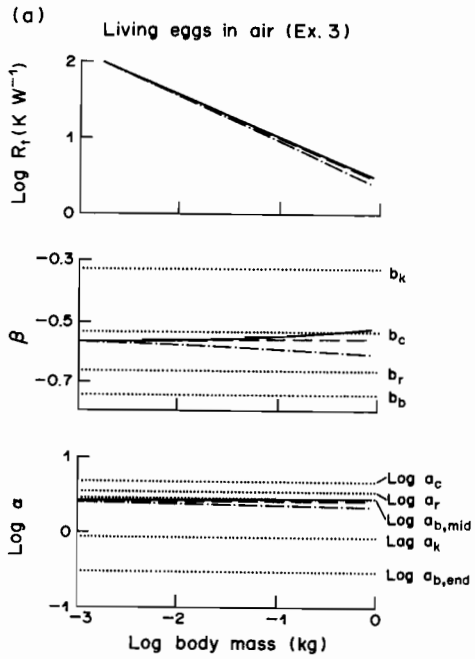


Fig. 13a.  $\text{Log } R_t$ ,  $\beta$  and  $\text{log } \alpha$  for the core-shell model depicted in Fig. 11, incorporating the external resistance in air. Simulations for three incubation ages are shown: start of incubation (solid line), middle of incubation (dashed line) and end of incubation (dashed and dotted line). Format as in Fig. 5.

Fig. 13b.  $\text{Log } R_t$ ,  $\beta$  and  $\text{log } \alpha$  for the core-shell model depicted in Fig. 11, incorporating the external resistance in water. Simulations for three incubation ages are shown: start of incubation (solid line), middle of incubation (dashed line) and end of incubation (dashed and dotted line). Formats as in Fig. 5. The index lines for  $\text{log } \alpha$  are off the scale.

brought about by the developing circulation should also change  $R_t$ . Because circulation is more important to the internal resistance of large eggs than it is to small eggs, the effect of circulation on total resistance will be greater for large eggs (Fig. 13b). This point is effectively made in Table 2, which calculates the expected changes of resistance. Expressing these results as a proportional change of the total resistance through incubation (Table 3), the point is made even more dramatically.

For eggs of domestic chickens (egg mass of about 60 g), and eggs of bobwhite quail (egg mass about 10 g), these predictions are effectively upheld (Table 4; Turner, 1987b, c).

*Example 4—heating and cooling rates of reptiles (series—parallel array)*

Many reptiles vary blood flow to alter their rates

of temperature change (Smith, 1979; Bartholomew, 1982; Turner, 1987a). Most often, peripheral blood flow is elevated during warming, making the body heat faster, and is depressed during cooling, making the body cool more slowly. We may use the array in Example 3 to explore the problem of body size and the control of heating and cooling rates of reptiles (Turner, 1987a). In Example 3, variations of blood flow came about as a consequence of development. In this example, variation of blood flow comes about as a result of active control on the part of the animal.

Some different scaling equations must be used because the conditions are somewhat different for reptiles. The specific equations are derived in Appendix I. The most important difference is in the equations for  $R_b$ . The rate of cutaneous blood flow in alligators appears to be directly related to body size (Smith *et al.*, 1978). Consequently, the scaling ex-

Table 2. Estimated resistances ( $\text{K W}^{-1}$ ) for eggs at the start and end of incubation

Egg mass (g)	Air		Water					
	$R_{i, \text{start}}$	$R_{i, \text{end}}$	$R_c$	$R_{t, \text{start}}$	$R_{t, \text{end}}$	$R_c$	$R_{t, \text{start}}$	$R_{t, \text{end}}$
2	6.0	5.1	100.7	106.7	105.8	2.2	8.2	7.3
10	3.5	2.6	38.4	41.9	41.0	0.9	4.4	3.5
60	2.0	1.1	13.4	15.4	14.5	0.4	2.4	1.5
150	1.4	0.7	7.6	9.0	8.3	0.2	1.6	0.9
1500	0.7	0.2	1.9	2.6	2.1	0.1	0.8	0.3

Internal resistances are calculated as the composite parallel resistances of blood flow [eqns (10a), (10c)] and conduction [eqn (7c)]. External resistances are calculated as the composite parallel resistances for radiation [eqn (9)] and convection, either in still air [eqn (7a)] or still water [eqn (7b)]. Total resistance is the composite series resistance of the internal and external resistances.

Table 3. Proportional change of resistance for eggs in air and in water. Values calculated from figures in Table 2

Egg mass (g)	$R_{t,end}/R_{t,start}$			
	Air		Water	
	Upper limit ( $R_t \rightarrow R_c$ )	Lower limit ( $R_t = R_c + R_i$ )	Lower limit ( $R_t \rightarrow R_i$ )	Upper limit ( $R_t = R_i + R_c$ )
2	1	0.99	0.84	0.88
10	1	0.97	0.73	0.78
60	1	0.94	0.56	0.63
150	1	0.91	0.47	0.54
1500	1	0.77	0.26	0.32

In air or in water, an upper limit and a lower limit are given. For eggs in air, the upper limit is where total resistance is very close to the external resistance. The lower limit is where total resistance is the sum of the internal and external resistances. For eggs in water, the lower limit is where total resistance is very close to the internal resistance. The upper limit is where total resistance is the sum of the internal and external resistances.

ponent is unity for  $R_b$  during both heating and cooling. For cooling reptiles, the blood flow resistance scales:

$$R_{b,c} = 1.91 M^{-1.0} \tag{11a}$$

and for reptiles warming:

$$R_{b,w} = 0.62 M^{-1.0} \tag{11b}$$

The scaling equation for conduction is assumed to be the same as for eggs [eqn (7c)].

For external resistance, we shall assume the scaling equation for radiation is identical to that for eggs [eqn (9)] in the previous three examples. We shall also assume that the convection resistance is for forced convection, with a wind speed of  $5 \text{ m s}^{-1}$ . (This equation is derived in detail in Appendix I). The scaling relation for convection resistance is:

$$R_{c,s} = 0.75 M^{-0.52} \tag{12}$$

It is clear from the model calculations (Fig. 14) that there is a body size at which the difference between  $\log R_t$  during cooling and warming is maximized. At this size, of course, this difference (equivalent to the ratio of heating and cooling rates) also is maximized.

When the heating and cooling rates of living alligators are measured, the qualitative result (Fig. 15) conforms to the predictions (Turner and Tracy, 1985; Turner, 1987a): there is a clear optimum body size (about 5 kg) for control of heating and cooling rates in alligators.

**WHY NOT USE POWER EQUATIONS FOR THE SCALING OF THERMAL CONDUCTANCE?**

In this paper, I have attempted to show, through theoretical argument and experimental demonstration, that there is no *a priori* reason to presume that

Table 4. Ratios of resistances at day 18 ( $R_{t,18}$ ) and day 0 ( $R_{t,0}$ ) for bobwhite and chicken eggs, cooling in still air and still water

Cooling in:	$R_{t,18}/R_{t,0}$			
	Bobwhite		Chicken	
	Predicted	Observed	Predicted	Observed
Still air	1.00-0.97	0.96	1.00-0.94	0.98
Still water	0.78-0.73	0.75	0.63-0.56	0.58

Predicted ranges are from figures in Table 3. Observed values are from Turner (1987b, c).

thermal conductance (or resistance) scales by a power equation. There are several lines of argument that lead to this conclusion. The first Law of Thermodynamics, in combination with elementary physics of heat transfer, demands it. It can be shown with simple calculations and graphical arguments. Verifiable predictions about body size and thermal energetics can be made without the *a priori* presumption of a power law.

Nevertheless, the argument can be (and has been) made that, irrespective of what the physics might say, power equations "work." The power equation model clearly provides a "good fit"—explained variances are quite high for data described using a least-squares estimate of the "best" power equation, usually in excess of 80% (Peters, 1983). Power equations are good for making rough estimates of the

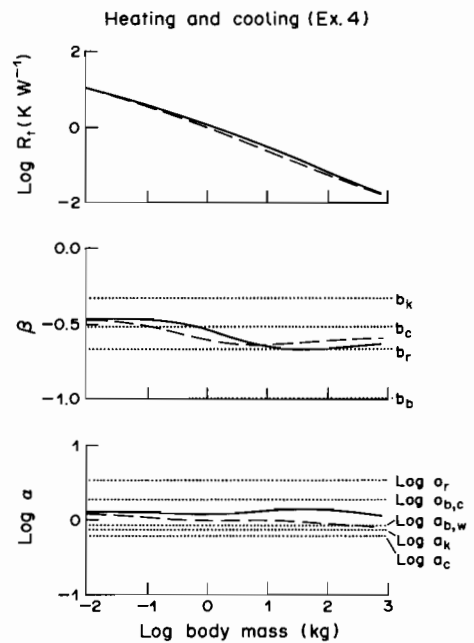


Fig. 14.  $\log R_t$ ,  $\beta$  and  $\log \alpha$  for the core-shell model depicted in Fig. 11, incorporating the external resistance in air at a windspeed of  $5 \text{ m s}^{-1}$ . This simulation is for reptiles cooling (solid line) and warming (dashed line).

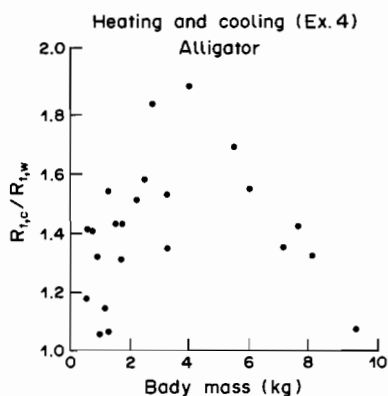


Fig. 15. The ratio of heating and cooling rates for alligators ranging from 600 g to nearly 10 kg body mass. An optimum ratio of heating and cooling rates is evident at about 5 kg body mass. After Turner and Tracy (1985) and Turner (1987b).

consequences of body size on animal energetics. They are useful as “benchmarks” for comparing animals against each other. They are easily understood mathematically, readily worked with and capable of generating robust predictions. Why *not* use them?

I wish to suggest at least two reasons. They are not unique to this problem, but in fact are common to any scientific endeavor. First, prevailing dogmas always channel one’s thinking so that certain, perhaps fertile, ways of thinking about a problem are precluded. If the prevailing dogma is physically erroneous, misconceptions can arise and persist with remarkable tenacity, sometimes even becoming entrenched to the point that data contrary to ‘dogma’ are rendered effectively “invisible.” Second, unless a description of a phenomenon has a firm theoretical foundation, one can never be confident about predictions or comparisons one may make using it.

Perhaps the most widespread and deeply entrenched misconception about body size and heat exchange is that surface area, or the surface–volume ratio, effectively determines the rate of heat loss from an animal.

The fortunes of this idea over the past several decades are discussed admirably by Schmidt-Nielsen (1984). The logic behind this idea is compellingly simple. Heat must leave an animal through its surface, and the rate of heat loss must therefore be proportional to the animal’s surface area. Isomorphic objects will always have surface areas that scale to the  $2/3$  power of mass, and so heat loss from isomorphic objects should always scale to the  $2/3$  power of mass. The measured heat loss of real animals does not scale in this way, but to  $M^{0.5}$ – $M^{0.6}$ , and basal metabolic rate scales to  $M^{3/4}$  (Kleiber 1975; Schmidt-Nielsen, 1984, but see Heusner 1982a, b, 1987). Why these discrepancies exist in the scaling exponents has been a persistent problem in the allometry of animal energetics.

The discrepancy between “theory” and “result” has been resolved in at least two ways. One resolution might be characterized as one of despair. This argument accepts that surface area limits heat loss, but goes on to argue that the complex shapes of animals,

as well as uncertainties about what the “true” surface area of an animal is, renders making any generalization based on surface area hopeless (Schmidt-Nielsen, 1984). The other resolution argues that animals are not isomorphic—that is, their surface areas do not really scale to  $M^{2/3}$ , but to some other exponent (Bartholomew, 1977; McMahon, 1973). The most sophisticated argument of this type is McMahon’s, who suggests that animals are not geometrically similar (in which case,  $A \propto M^{2/3}$ ), but are *elastically* similar (in which case,  $A \propto M^{0.63}$ ). From this presumption, one can derive both the result that basal metabolic rate scales to  $M^{3/4}$ , and the result that conductance scales to some exponent *smaller* than  $2/3$ .

It is not my intention to suggest these resolutions of the problem are incorrect. Rather, I wish to make the point that one hypothesis—namely that animal heat loss is *not* proportional to surface area—has been precluded altogether, even in “animals” (like birds’ eggs) where there is no uncertainty about what the true surface area is. This is surprising, because, as we have seen, it is only radiation heat exchange that scales with surface area [eqns (3a–d); Appendix I]; all other modes of heat loss scale to some other exponent. Depending upon which mode dominates, or how they combine, scaling of heat exchange may scale closer to metabolic rate, or directly to volume, or more closely to the linear dimension than to surface area, even for isomorphic objects like birds’ eggs (Turner, 1985). Nevertheless, most previous research has been directed toward understanding the ways that animals *might not be isomorphic*, rather than discovering ways that heat loss from *isomorphic animals properly scales*. This has sometimes led to conclusions about the scaling of heat loss that are plainly at variance with data, but are accepted because there is no way to explain their deviation from expectation. Two examples of this might be illuminating.

The first example relates to the problem of conductance of birds’ eggs. In a study of the problem of incubation energetics, Kendeigh (1963) measured the cooling rates of eggs, and obtained the result that conductance scaled to  $M^{0.60}$ , identical to later, similar experiments (Turner, 1985). From this result, Kendeigh concluded that heat loss scaled to surface area of the egg, because an exponent of 0.60 is very close to the “expected” value of  $2/3$ . As shown in Example 2 and elsewhere (Turner, 1985; Sotherland *et al.*, 1987), when the problem is properly analyzed, 0.6 is the “expected” result, and one the data support strongly. Clearly, the expectation of a scaling exponent of  $2/3$  is very powerful.

A second example of “invisible data” relates to the problem of heating and cooling rates of reptiles (Example 4; Turner, 1987a). Several authors have been led to the conclusion that the ratio of heating and cooling rates is a monotonically increasing function of size (Smith, 1976, 1979; Grigg *et al.*, 1979; Bell, 1980). In fact, if one assumes that conductance scales to body size by a power equation, no other conclusion is possible (Turner, 1987a). As we have seen, an analysis from first principles leads to the conclusion that conductance does *not* scale to a power equation, one consequence being that there is

an optimum size for the control of heating and cooling rates of reptiles (Example 4; Turner, 1987a), a prediction borne out by the data (Fig. 15; Turner and Tracy, 1985; Turner, 1987a). Curiously, this result was observed, but ignored at least a decade ago (Smith, 1976; Turner, 1987a), another example of the powerful influence of the power equation on thinking about the biology of body size.

We turn now to the second problem, that of using allometric equations as "benchmark equations."

A benchmark equation often is used to compare an individual with a "baseline" set of data, to compare scaling between different taxa of animals or between animals of very different body size. At times they are used to estimate a trait for an animal that is extinct, or is impossible to obtain meaningful data from. The benchmark may be derived from a theoretical argument, but in allometry it is most often an empirical equation, like the famous "mouse-to-elephant" curve.

Needless to say, the strength of such comparisons and estimates depends upon the validity of the benchmark equation. Clearly, one can have no confidence in the size of a residual from a benchmark if one has no confidence in the benchmark itself. An animal judged to be statistically "off" a widely accepted, but nevertheless erroneous benchmark, may be judged to be "on" if it is compared with the "true" benchmark. I wish to emphasize that a benchmark based purely on empirical measurements is likely to be inadequate. To be useful, a benchmark must also be physically intelligible. For describing the scaling of heat exchange, the power equation fails this test.

For example, what should one make of the observed variation of  $b$  for the scaling of thermal conductance? The scaling exponent for conductance, as measured by various investigators, ranges from 0.33 to 0.63 (Peters, 1983). If one presumes there is a single "expected" result (i.e. that conductance scales to the  $2/3$  power of mass), variation of  $b$  must be construed as variation in shape of the animals that departs from isomorphic scaling, or as the result of some special adaptation, say longer appendages or thicker fur.

It is noteworthy that the range of observed variation of  $b$  coincides almost exactly with the variation of  $\beta$  estimated from the models developed here. However, the variation of  $\beta$  cannot result from deviations from isomorphy, or from special adaptations, because these explanations were defined away in the models—the model "animals" were isomorphic, and were given no special adaptations. Rather, variation of  $\beta$  results from: variation of environmental condition (e.g. still air or still water—Example 1, or the balance between radiation and convection—Example 2), variation of physiological state (e.g. level of blood flow—Examples 3 and 4), and, most importantly, from variation of body size itself (because  $\beta$  is not constant with respect to mass—all examples).

To conclude, there is no good reason to suppose a power equation is an appropriate description for the allometry of heat exchange. Allometric equations derived from first principles of heat transfer are not power equations. Nevertheless, they are capable of making robust predictions about body size and ther-

mal energetics. In some cases, these models provide a more sound interpretive base for interpreting the constraints of body size on the thermal energetics of animals.

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Tracy *et al.* (1980) have found that a core radius of 3/4 the outer radius works well for modelling the heat exchanges of lizards. I have chosen this convention for my predictions. When  $r_i = 3r_o/4$ , eqn (1.3) simplifies to:

$$R_k = 1/(12\pi r_o k) \tag{1.4}$$

For spheres of constant density,  $r_o \propto M^{1/3}$ . Therefore,  $R_k \propto M^{-1/3}$ .

*Resistance to convection heat loss from the surface*

In a still fluid, convection heat loss from an object's surface is driven by temperature-induced density variations near the surface. This free convection is described by the dimensionless Nusselt–Rayleigh (Nu–Ra) relation:

$$Nu = A + BRa^m \tag{1.5}$$

The Rayleigh number is itself the product of two other dimensionless numbers, the Prandtl number (Pr) and the Grashof number (Gr). These dimensionless numbers are:

$$Nu = h_c D/k \tag{1.5a}$$

$$Pr = \mu c/k \tag{1.5b}$$

$$Gr = g\beta D^3(T_s - T_f)/\nu^2 \tag{1.5c}$$

where  $k$  = thermal conductivity of the fluid ( $W m^{-1} K^{-1}$ ),  $h_c$  = convection coefficient ( $W m^{-1} K^{-1}$ ),  $D$  = diameter (m),  $\mu$  = dynamic viscosity of the fluid ( $kg m^{-1} s^{-1}$ ),  $c$  = specific heat of the fluid ( $J kg^{-1} K^{-1}$ ),  $g$  = gravitational acceleration ( $m s^{-2}$ ),  $\beta$  = coefficient of thermal expansion ( $K^{-1}$ ),  $T_{s,f}$  = temperature of the surface and fluid, respectively ( $K$ ) and  $\nu$  = kinematic viscosity of the fluid ( $m^2 s^{-1}$ ).

The Nusselt number describes the transfer of heat, the Prandtl number describes how effectively heat is conducted away, and the Grashof number describes the temperature-induced movements of fluid around the object.

For a sphere, the constants in eqn (1.3) are  $A = 2$ ,  $B = 0.43$  and  $m = 0.25$ . Once the Nusselt number is calculated, the convection coefficient may be estimated from the equation for the Nusselt number. Convection heat loss ( $W$ ) is then given by the equation:

$$\dot{q} = h_c A (T_s - T_f) \tag{1.6}$$

and the resistance to convection heat transfer is:

$$R_c = 1/h_c A \tag{1.7}$$

In this resistance equation, two terms scale with size. Area obviously will scale with body size, but a look at eqns (1.5a)–(1.5c) should convince that  $h_c$  also will scale with body size. As Turner (1985) and Sotherland *et al.* (1987) have shown,  $R_c \propto M^{-0.54}$ .

The resistance to forced convection is calculated in a way similar to that for free convection. Rather than using Nusselt–Rayleigh number to calculate a convection coefficient [eqn (1.5)], forced convection uses a Nusselt–Reynolds correlation. The Reynolds number is defined:

$$Re = U D/\nu \tag{1.8}$$

where  $U$  = wind speed ( $m s^{-1}$ ). The Nusselt–Reynolds correlation recommended for spheres by Thomas (1980) is:

$$Nu = 2 + (0.4 Re^{0.5} + 0.06 Re^{0.67}) Pr^{0.4} \tag{1.8a}$$

Solving this equation for the convection coefficient and the convection resistance, as described above [eqns (1.6), (1.7)], and for dry air at  $5 m s^{-1}$ , the convection resistance scales:

$$R_c = 0.75 M^{-0.52} \tag{1.9}$$

*Resistance to radiation heat loss from the surface*

Radiation heat loss from a surface is governed by the Stefan–Boltzmann Law:

$$\dot{q} = A\epsilon\sigma F(T_s^4 - T_c^4) \tag{1.10}$$

**APPENDIX I**

*Scaling Equations for Component Resistances*

I shall derive the scaling equations for four component resistors that, in various combinations, make up the composite resistances in the examples. These are: resistance to conduction inside the shell, resistance to convection heat loss from the surface of a sphere, resistance to radiation heat loss from the surface of the sphere and resistance to heat transport by blood flow across the shell.

*Resistance to conduction inside the shell*

The one-dimensional form of the Fourier law of conduction for spherical coordinates is:

$$\dot{q} = -kA_r \frac{dT}{dr} \tag{1.1}$$

where  $A_r$  is the area of a spherical shell of radius  $r$  ( $m^2$ ) and  $k$  is the thermal conductivity ( $W m^{-1} K^{-1}$ ). For conduction of heat through a spherical shell with outer radius  $r_o$  and inner radius  $r_i$ , eqn (1.1) is:

$$\dot{q} = \frac{4\pi r_o r_i k}{r_o - r_i} (T_i - T_o) \tag{1.2}$$

which yields the conduction resistance  $[(T_i - T_o)/\dot{q}]$ :

$$R_k = \frac{r_o - r_i}{4\pi r_o r_i k} \tag{1.3}$$

where  $\epsilon$  = emissivity (about 0.95 for most surfaces),  $\sigma$  = Stefan-Boltzmann constant ( $5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$ ) and  $F$  = shape factor. For a sphere losing heat to enclosing walls very far away,  $F$  is close to unity. Because my experiments involved eggs enclosed in very large chambers, I have assumed that  $F$  is unity.

Calculating thermal resistance ( $\Delta T/q$ ) means factoring out a temperature difference from the difference in temperatures to the 4th power in eqn (I.10). Doing this results in the equation:

$$R_r = 1/A\epsilon\sigma F(T_s + T_e)(T_s^2 + T_e^2) \quad (\text{I.11})$$

The only factor that depends upon size in this equation is  $A$ . Therefore,  $R_r \propto M^{-2/3}$ .

*Resistance to heat flow in blood across the shell*

The transport of heat by a fluid between two points of temperatures  $T_c$  and  $T_s$  is:

$$\dot{q} = \dot{m} c (T_c - T_s) \quad (\text{I.12})$$

where  $\dot{m}$  = mass flow rate of the fluid ( $\text{kg s}^{-1}$ ) and  $c$  = specific heat of the fluid ( $\text{J kg}^{-1} \text{ K}^{-1}$ ). The resistance is therefore:

$$R_b = 1/\dot{m}c \quad (\text{I.13})$$

Obviously resistance will scale to the inverse of whatever  $\dot{m}$  scales to. I have assumed that  $\dot{m}$  scales to the 0.75 power of egg mass, paralleling the scaling of metabolic rate for eggs seen by Rahn *et al.* (1974) and Hoyt and Rahn (1980). The coefficient will vary with age, i.e. as the circulation develops. If the scaling exponent is set at 3/4, and if a measurement of blood flow in an egg of a single mass is known at any age  $A$ , then the point-slope method may be used to write a scaling equation for  $\dot{m}_A$ . Tazawa (1980) has measured chorioallantoic blood flow for hens' eggs from about midway through incubation (day 9 out of day 20) to near the end of incubation (day 18 out of 20). With these data, one may now write a series of scaling equations for  $\dot{m}_A$ . For midway through incubation:

$$\dot{m}_{\text{mid}} = 8.8 \times 10^{-5} M^{3/4} \quad (\text{I.14a})$$

and near the end of incubation:

$$\dot{m}_{\text{end}} = 7.8 \times 10^{-4} M^{3/4} \quad (\text{I.14b})$$

Assuming the specific heat of blood is  $4.2 \text{ kJ kg}^{-1} \text{ K}^{-1}$ , we may use eqns (I.14a) and (I.14b) to write two scaling

equations for  $R_b$ , one at midway through incubation, and one at the end of incubation. For midway through incubation:

$$R_{b,\text{mid}} = 2.8 M^{-3/4} \quad (\text{I.15a})$$

and for near the end of incubation:

$$R_{b,\text{end}} = 0.30 M^{-3/4} \quad (\text{I.15b})$$

For the blood flow resistances of warming and cooling alligators, I used the data on blood flow in the peripheral tissues of alligators, measured by Smith *et al.* (1978). These authors found that skin blood flow was directly proportional to size. Therefore, the scaling exponent is unity. The cutaneous blood flow during cooling was  $0.092 \text{ ml cm}^{-3} \text{ min}^{-1}$  and during warming, cutaneous blood flow was  $0.030 \text{ ml cm}^{-3} \text{ min}^{-1}$ . Applying the requisite conversion factors, the blood flow resistance may be calculated. During cooling, the blood flow resistance scales:

$$R_{b,c} = 1.91 M^{1.0} \quad (\text{I.16a})$$

and for warming:

$$R_{b,w} = 0.62 M^{1.0} \quad (\text{I.16b})$$

**APPENDIX II**

*Scaling Formulae for Composite Circuits*

In this section, I derive formulae for  $R_t$  and  $\beta$  for three common equivalent circuits: a simple series circuit, a simple parallel circuit and one type of series-parallel array. A diagram of each type of circuit is provided in Fig. A1. I do not derive the specific formulae for log  $\alpha$ . As explained in the main body of text, this is derived readily from  $R_t$  and  $\beta$ , using the point-slope method.

*Case A—simple series circuit*

Consider a simple series equivalent circuit of  $n$  composite resistors in series (Fig. A1; Panel a). The equation for the total resistance of this circuit is:

$$R_t = R_1 + R_2 + \dots + R_n = \sum_{i=1}^n R_i \quad (\text{II.1})$$

Each composite resistor,  $R_i$ , scales by its own power equation:

$$R_i = a_i M^{b_i} \quad (\text{II.2})$$

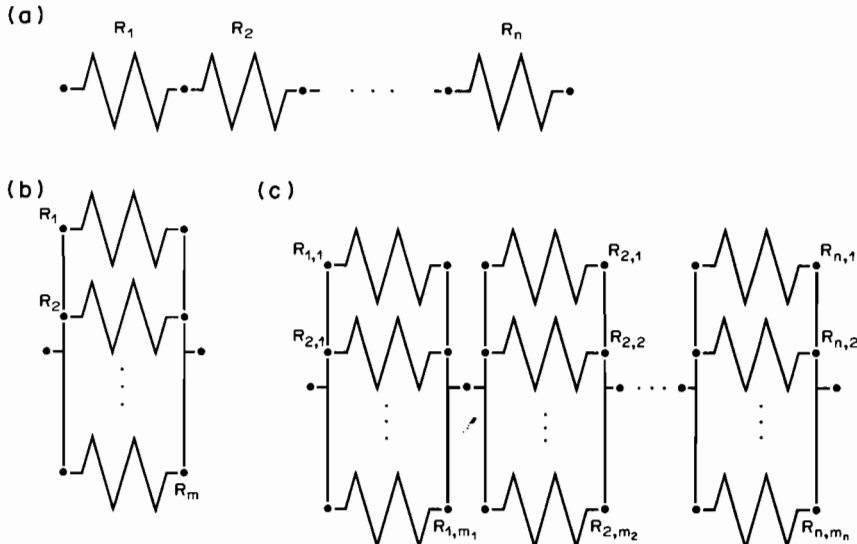


Fig. A1. Examples of general types of equivalent circuits. Panel a: simple series circuit. Panel b: simple parallel circuit. Panel c: series-parallel array.

Therefore,

$$R_t = \sum_{i=1}^n a_i M^{b_i} \quad (II.3)$$

Differentiating  $R_t$  with respect to  $M$  and multiplying by  $M/R_t$  yields the formula for  $\beta$ :

$$\beta = \frac{\sum_{i=1}^n b_i R_i}{\sum_{i=1}^n R_i} = \frac{\sum_{i=1}^n a_i b_i M^{b_i}}{\sum_{i=1}^n a_i M^{b_i}} \quad (II.4)$$

*Case B—simple parallel circuit*

Consider a composite circuit of  $m$  resistors in parallel (Fig. A1, panel b). The equation for  $1/R_t$  of this circuit is:

$$1/R_t = \sum_{j=1}^m 1/R_j \quad (II.5)$$

As in the simple series circuit [eqn (II.2)], each composite resistor scales by its own power equation. Therefore:

$$R_t = 1 / \left[ \sum_{j=1}^m (1/R_j) \right] = 1 / \left[ \sum_{j=1}^m (M^{-b_j}/a_j) \right] \quad (II.6)$$

Again, when eqn (II.6) is differentiated and multiplied by  $M/R_t$ , the equation for  $\beta$  is:

$$\beta = \frac{\sum_{j=1}^m (b_j M^{-b_j}/a_j)}{\sum_{j=1}^m (M^{-b_j}/a_j)} \quad (II.7)$$

*Case C—circuit in a series-parallel array*

Consider a circuit like that depicted in Fig. A1, panel c. This circuit is comprised of  $n$  arrays of resistors in series. Each array has the composite resistance  $R_i$ . Each array is comprised of  $m_i$  resistors in parallel, each with the component resistance  $R_{i,j}$ . The total resistance of this type of circuit is:

$$R_t = \sum_{i=1}^n R_i \quad (II.8)$$

Each resistance  $R_i$  is:

$$R_i = 1 / \left[ \sum_{j=1}^{m_i} (1/R_{i,j}) \right] \quad (II.9)$$

and the total resistance is therefore:

$$R_t = \sum_{i=1}^n \left\{ 1 / \left[ \sum_{j=1}^{m_i} (1/R_{i,j}) \right] \right\} \quad (II.10)$$

Once again, each resistor,  $R_{i,j}$  scales by its own power equation, with coefficient  $a_{i,j}$  and exponent  $b_{i,j}$ . Therefore, in terms of body mass,  $R_t$  is:

$$R_t = \sum_{i=1}^n \left\{ 1 / \left[ \sum_{j=1}^{m_i} (M^{-b_{i,j}}/a_{i,j}) \right] \right\} \quad (II.11)$$

Differentiating eqn (II.11) and multiplying by  $M/R_t$  yields the equation for  $\beta$ :

$$\beta = \sum_{i=1}^n \left\{ \frac{\sum_{j=1}^{m_i} (b_{i,j} M^{-b_{i,j}}/a_{i,j})}{R_t \cdot \left[ \sum_{j=1}^{m_i} (M^{-b_{i,j}}/a_{i,j}) \right]} \right\} \quad (II.12)$$

NOMENCLATURE

*Italic symbols*

<i>A</i>	area (m <sup>2</sup> ), coefficient in Nusselt–Reynolds relation, incubation age
<i>B</i>	coefficient in Nusselt–Reynolds relation
<i>C</i>	thermal conductance (W K <sup>-1</sup> )
<i>D</i>	diameter (m)
<i>F</i>	shape factor
<i>M</i>	body mass (kg)
<i>R</i>	thermal resistance, component resistance (K W <sup>-1</sup> )
<i>T</i>	temperature (K)
<i>U</i>	wind speed (m s <sup>-1</sup> )
<i>a</i>	the coefficient of an allometric power equation
<i>b</i>	the exponent of an allometric power equation
<i>c</i>	specific heat (J kg <sup>-1</sup> K <sup>-1</sup> )
<i>g</i>	gravitational acceleration (m <sup>2</sup> s <sup>-1</sup> )
<i>h</i>	convection coefficient (W m <sup>-2</sup> K <sup>-1</sup> )
<i>k</i>	thermal conductivity (W m <sup>-1</sup> K <sup>-1</sup> )
<i>m</i>	exponent in Nusselt–Reynolds relation
<i>ṁ</i>	mass flow rate (kg s <sup>-1</sup> )
<i>q̇</i>	heat flow rate (W)
<i>r</i>	radius (m)
<i>y</i>	a dependent variable in the allometric equation

*Greek symbols*

log Ω	first derivative of log $R_t = f(\log M)$
log α	coefficient for log Ω = $g(\log M)$
β	exponent for log Ω = $g(\log M)$ , coefficient of thermal expansion (K <sup>-1</sup> )
ε	emissivity
μ	dynamic viscosity (kg m <sup>-1</sup> s <sup>-1</sup> )
ν	kinematic viscosity (m <sup>2</sup> s <sup>-1</sup> )
π	pi (3.1416 . . .)
σ	Stefan–Boltzmann constant (5.67 × 10 <sup>-8</sup> W m <sup>-2</sup> K <sup>-4</sup> )

*Dimensionless groups*

Gr	Grashof number
Nu	Nusselt number
Pr	Prandtl number
Re	Reynolds number

*Subscripts*

air	in air
b	blood flow
c	core, convection, cooling
e	external, environmental
end	end of incubation
f	fluid
<i>i, i</i>	internal, <i>i</i> th component in the series array
<i>j</i>	<i>j</i> th component in the parallel array
k	conduction
mid	midway through incubation
o	outer
r	radiation
s	surface
start	start of incubation
t	total
w	warming
water	in water