INVITED PERSPECTIVES IN PHYSIOLOGICAL AND BIOCHEMICAL ZOOLOGY

A New Model for the Body Size–Metabolism Relationship

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ABSTRACT

The allometric 3/4 power relation, initially used for describing the relation between mammalian basal metabolic rate and body size, is often used as a general model for organismal design. The use of allometric regression as a model has important limitations: it is not mechanistic, it combines all physiological variables into one correlate of body size, and it combines data from several physiological states. In reassessing the use of allometric equations, we first describe problems with their use in studies of organismal design and then use a formulation for distributed net heat production and temperature distribution within the body to derive an alternative equation for the relation between basal metabolism and body size. Tests of the heat flow equation against data reported in the literature indicate that it is an accurate estimator of basal metabolism under thermoneutral conditions and suggest that the allometric equation is a special case of this mechanistic and more general model. We propose that our method is more meaningful and widely applicable for thermoneutral conditions than is a purely allometric approach.

Introduction

An important aim of biological research is understanding the principles of animal design. Because of the central importance of energetics in animal life, metabolic rate has been one of the focal points of these studies. Metabolic models fall into two main groups: (1) equations that provide purely empirical correlations between function and body size and (2) first-principles models based on physical processes (e.g., heat flow) that give mechanistic a priori predictions of physiological and physical processes.

A simple and very widely used example of the first type is the allometric equation,

$$Y = am^{b}, \qquad (1)$$

where Y is a physiological variable such as metabolic rate and a and b are empirically determined constants, assumed to be independent of both species and body mass (m). Equations of this type are also called power functions because Y varies with the mass raised to a power that is generally different from unity. Power functions have been used since the nineteenth century (Snell 1891) for two kinds of comparisons: (1) the study of relative growth rates of parts of the body (Huxley 1932; Thompson 1952, chap. 2) in one species or a group of related species (e.g., to explain the observation that antlers in large deer are proportionally larger than those in small deer) and (2) general size comparisons (Gould 1971) across many species (e.g., to explain the observation that limb bones are disproportionately thicker in elephants than in cats).

Our concern is with a very widely used equation, the “3/4 power scaling” relation, used to relate basal metabolic rate (BMR) to body mass in organisms ranging from bacteria to elephants (Brody 1945; Hemmingsen 1960). This equation has recently been extended to explain several aspects of organismal design, including ecological processes (e.g., West et al. 1997; Brown et al. 2004). However, values of the coefficient a and the exponent b differ between groups of organisms and between conditions under which the data were obtained.

We provide evidence here that the allometric equation has, in general, only a limited usefulness in understanding the relation between metabolic rate and size, for several reasons: it is a correlation and does not derive from principles of metabolism, it combines important geometric and physiological features of animals into misleadingly simple mathematical coefficients and exponents, it is derived from inconsistently obtained data from an extremely heterogeneous sample, and it uses an ill-defined “basal” metabolism that is inappropriate for ectothermic organisms. We therefore propose that there is no reason for extension of the 3/4 power relation into fundamental questions of adaptation.

Origin of Use of the 3/4 Power Relation in Endotherms

The nineteenth-century investigators (Sarrus and Rameaux, reported by Robiquet [1839]; Bergmann 1847; Rubner 1883) who first studied the relation between metabolism and body mass

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in endotherms did not explicitly describe the allometric equation; they suggested that metabolic rate maintained geometric similarity in relation to body size because basal metabolism in their experiments was a constant function of animal surface area. This translated to an allometric equation with exponent 2/3. These early studies were at least partially mechanistic in that they related metabolism to heat exchange.

In the early 1900s, additional data from a wider variety of mammals suggested that the allometric exponent was higher; it was estimated to be 3/4 by Kleiber (1932, 1961). Investigators were by this time ready to abandon the concept that metabolism depended on surface area because they could not agree on how to measure area, they did not know how much of an animal's total area actually participated in heat exchange, and they found that differences in posture and fur thickness produced differences in heat exchange that confounded simple comparisons on the basis of surface area alone. Thus, Kleiber and others took 3/4 to be a better estimate of *b* and simply replaced the "surface law" with the "3/4 power law."

Application of the 3/4 Power Law to Ectotherms

The 3/4 power law received reinforcement when data from microorganisms, invertebrates, and ectothermic vertebrates were included. Hemmingsen (1960) reported that these three groups show an exponent of 3/4 when their metabolic rates are plotted against body mass. This report was important for giving apparent credence to a general 3/4 power law because these organisms were not using energy to maintain body temperature above ambient temperature. Therefore, heat transfer could not be a major "cause" of the value of the exponent. As a result of Hemmingsen's paper, the value 3/4 was accepted as widely applicable because log-log plots of metabolic rate versus mass gave the appearance of a homogeneous data set with slope 3/4. However, the data are heterogeneous, for several reasons.

First, with regard to ectothermic organisms, Schmidt-Nielsen (1984) pointed out that published studies show much variability in regression exponents for different groups of invertebrates and ectothermic vertebrates. In addition, Prothero (1986) reanalyzed Hemmingsen's data for unicellular organisms and showed that the regression coefficient calculated by Hemmingsen was affected by an incomplete database, the inclusion of bacteria (organisms without mitochondria), and the inclusion of zygotes of multicellular animals. There is therefore little confidence that the 3/4 power relation Hemmingsen proposed for ectotherms is statistically or biologically meaningful. The metabolic rate of ectotherms increases with mass but not with a constant allometric exponent of 3/4.

Application of the 3/4 Power Law to Endotherms

Heterogeneity

Another source of database heterogeneity is the inconsistency of the methods used to gather data used in allometric graphs. Careful investigators (e.g., Blaxter 1989; White and Seymour 2003) have stated that metabolic studies must observe three requirements: animals must be in equivalent metabolic states (e.g., adult, fasting); they must be in the same posture and activity level (e.g., resting); and they must have the same thermoregulatory demands (e.g., be at a thermoneutral temperature).

In practice, these three conditions are rarely fulfilled, as McKechnie and Wolf (2004) point out. Investigators presenting primary metabolic data for a given animal generally have not partitioned measured metabolic rate into the relative amounts allocated to thermoregulation and posture; others using the primary data for allometric modeling have simply assumed that the data are "basal" and use data from dozens of such studies, with most data collected under unreported or even unknown conditions. For large mammals such as cattle, standing metabolic rates are 30% higher than recumbent rates (Schrama et al. 1993), and for a large ruminant, even lying down requires more energy than complete repose, which is the posture in which small mammals have traditionally been studied. In addition, ambient temperatures may be below thermoneutral (Benedict 1936). This approach combines into one set data from several states—resting and active, those within the thermoneutral zone and those below it—and ignores posture, which affects both exposed surface area and metabolic rate (Porter et al. 1994, 2000). Both Benedict (1936) and Kleiber (1961) admit that larger animals in metabolic experiments are unlikely to be at BMR. In summary, the database used to generalize allometric regression equations is inconsistent. In the next section, we address the ways the data have been analyzed.

Data Analysis

Here we address some plots from commonly referenced published data sets. One of these, Brody's (1945) graph (Fig. 1*A*), is frequently reproduced and still used as evidence for wide application of the allometric equation. The second plot (Fig. 1*B*) is from a more recent review by Heusner (1991), also cited by those investigating the basis for allometry (e.g., Dodds et al. 2001). In both panels, for mammals smaller than 2.5 kg the slopes of the two regressions are not significantly different from 2/3 (two-tailed *t*-test, $P > 0.1$), while for those larger than 2.5 kg the slopes are higher than 2/3 (two-tailed *t*-test, $P < .0005$). Indeed, if data for the sedentary edentates, pangolins, and dugongs are removed from Figure 1*B* (*squares*), the slope for the mammals larger than 2.5 kg exceeds 0.9.

Most of the points on Brody's (1945) graph (Fig. 1*A*) are neither actual measured values nor values from individual animals: for many of the points he used the species' mass-metabolism equations to predict metabolism for animals of a given size. Other points are averages of measurements on several to many individuals. He also reduced measured values for the largest animals by 20%–30% because he estimated that 10% of the value was associated with standing posture and 20% was associated with feeding. Brody actually underestimated the energetic cost of standing (Vercoe 1973), which should be about three times the adjustment he made (Schrama et al. 1993). With rare exceptions (e.g., Schmidt-Nielsen 1984), investigators

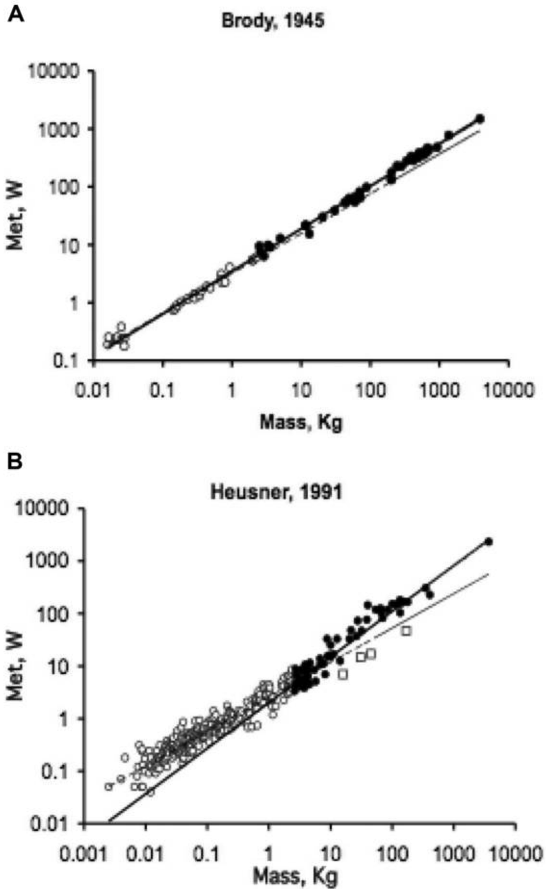

Figure 1. Replot of data from Brody (1945, *A*) and Heusner (1991, *B*), showing that the exponent of the allometric equation depends on size. In both panels, open symbols and dashed lines represent data for mammals of mass less than 2.5 kg; filled symbols and solid lines represent data for mammals of mass greater than 2.5 kg. *A*, Regression lines: for open symbols, metabolism (met) $= 3.21\text{mass}^{0.69}$; for solid symbols, met $= 3.48\text{mass}^{0.73}$. Slope for mammals <2.5 kg is not significantly different from 2/3 at the 0.05 level ($n = 29$, $P > 0.1$). Slope for mammals >2.5 kg is significantly different from 2/3 at the 0.05 level ($n = 41$, $P < 0.0005$). *B*, Regression lines: for open symbols, met $= 2.56\text{mass}^{0.66}$; for solid symbols, met $= 2.02\text{mass}^{0.87}$. Slope for mammals <2.5 kg is not significantly different from 2/3 at the 0.05 level ($n = 276$, $P > 0.1$). Slope for mammals >2.5 kg is significantly different from 2/3 at the 0.05 level ($n = 64$, $P < 0.0005$). Open squares in *B* represent data from large, relatively sedentary mammals (Pholidota, Sirenia, Edentata). Removing these species from the regression gives met $= 1.99\text{mass}^{0.90}$ for the remaining data points of mammals >2.5 kg.

using Brody's graph as evidence for the 3/4 power law have not pointed out how he manipulated his data.

Despite the problems with collection and interpretation of data, Kleiber's and Brody's ideas were enthusiastically embraced. There were three effects of this acceptance of the 3/4 law following their work: first, it furthered the use of purely empirical approaches to the study of animal design; second, emphasis on a single value of *b* made it appear that all mammals, regardless of size, have the same value of the variable *a*; third, it drew attention away from understanding the physiological basis for *a* and from thinking that metabolic rate is related to the processes involved in regulation of heat transfer. We deal with these issues in the remainder of this article.

Attempts to Generalize 3/4-Power Scaling Models

Several investigators (McMahon 1973; Blum 1977; Sernetz et al. 1982; West et al. 1997; Banavar et al. 1999) have considered the apparent 3/4 power slope of the metabolism–body mass relation as a mechanistic feature that required explanation. These explanations use several formats.

Elastic Similarity

Because of the combined stresses of gravity and movement, bones of large mammals must be proportionally thicker than those of small mammals. The allometry of bone and body size has been modeled on the principle of "elastic similarity" by McMahon (1973), who based his analysis on two concepts: (1) the bone sizes needed to counteract buckling under self-loading and (2) the power output of muscles. He derived an allometric equation for muscle output as a function of body mass in which the exponent of the mass term is 3/4. This result has led to elastic similarity being accepted as "a model that predicts the 3/4 exponent [for metabolism] directly" (Calder 1984, p. 81). However, neither buckling under load nor muscular activity applies to resting conditions. The projection of elastic-similarity theory to the resting situation was originally made because the allometric slopes of basal metabolism in the early literature appeared to be the same as those for maximal metabolism during exercise. However, this view has been revised recently (Bishop 1999; Darveau et al. 2002), and it is now clear that large animals have proportionally higher maximal metabolic rates (MMRs) than do small animals; it is thus difficult to see how the elastic-similarity model can be an explanation for the BMRs of resting animals.

Distribution Networks

The development of fractal mathematics in the 1970s led to attempts to apply it to organismal function (see Blum 1977). One result of this work has been explanations of the 3/4 power scaling exponent by Sernetz et al. (1982) and West et al. (1997, 1999). These investigators assumed the correctness of the allometric equation and of the 3/4 exponent and then used fractal mathematics and nutrient supply network theory to explain why 3/4 is a reasonable estimate for the scaling of basal metabolism. Banavar et al. (1999) came to similar conclusions, although they did not consider organisms as fractal structures.

All these models share the disadvantage of modeling basal metabolism with processes typical of active animals. Darveau et al. (2002) emphasize that nutrient supply is limiting at the MMR, not at the basal levels that West et al. modeled. Further, large animals have greater capacity than small animals to increase supply of fuel and oxygen during exercise and hence achieve greater MMR as a proportion of their BMR. This ability emerges as an apparently higher exponent (0.88 vs. 0.75) of

MMR as compared to BMR. The critique of Darveau et al. applies as well to the models of Sernetz et al. (1982) and to Banavar et al. (1999), who also model basal metabolism using processes characteristic of active animals.

The analysis of West et al. has also been criticized by Dodds et al. (2001) and White and Seymour (2003), who used additional statistical tests to reevaluate the original metabolic data on which the 3/4 power law was based. Dodds et al. showed that in metabolic studies, the value of the exponent *b* depends on the mass of the animal concerned, and they came to several conclusions: that 3/4 is not a better estimate of *b* than is 2/3, that it is misleading to apply a single estimate of the coefficient or the exponent to all animals, and that there may not exist a simple scaling law for metabolism. White and Seymour extended Dodds et al.'s critique of standard methods of measuring the value of *b*: they reanalyzed data on mammals for which body temperatures were available from the original studies and used Q_{10}, the temperature coefficient of metabolism, to normalize metabolism to a standard rate based on a body temperature of 36.2°C. They also eliminated mammals whose gut fermentation would likely have raised metabolism above resting. These authors have therefore accounted for two of the factors that had most troubled earlier attempts at metabolic scaling. Their statistical analysis indicates that the metabolic rate–mass equation has a slope 0.68, and they state that this result challenges the theory of 3/4 power scaling. They conclude that it is necessary to seek other explanations for the relation between metabolism and mass. Agutter and Wheatley (2004) also call for more inclusive modeling of metabolism, noting that a proper understanding of the relation between metabolism and size may reside not at the cellular level but at higher levels of physiological organization.

Hollow-Cored Model

Ahlborn and Blake (1999) used heat transfer principles to deduce the components of the metabolism–body size relation for aquatic mammals. They used a standard heated-pipe model with insulation that has two distinct regions: the core of undefined composition but uniform temperature and the wall of insulation. The core is assumed to be at a constant temperature but has no metabolic mechanism for generating that temperature; that is, it does not reflect the distributed heat production due to metabolic activity of all tissues. Further, all heat is transferred by conduction. As a result of these two assumptions, the model predicts a concave logarithmic temperature profile, which is not observed in endotherms.

In contrast, the distributed-heat-generation model to be developed below (Porter et al. 1994, 2000) recognizes that each finite, differential, concentric "envelope" of tissue not only conducts heat but also generates additional heat of its own that will be conducted through the next-outermost layer. All distributed-heat-generation solutions for geometries of slabs, cylinders, spheres, and ellipsoids have the same general form: a central-core maximal temperature at the geometric center and a convex parabolic temperature distribution from core to skin, unlike conduction models (Porter et al. 1994).

Empirical versus Mechanistic Models

Empirical models such as the allometric equation are based on data rather than on principles, so they are difficult to test without using the data from which they were derived (Lewontin 2000). They can be tested for internal consistency but cannot be extrapolated to data outside the original set. In contrast, physical or mechanistic models can be tested by using any data from actual animals.

The primary features missing from earlier models involving allometric approaches are (1) a meaningful index of body size; body mass has traditionally been the most convenient measure of body size, but because two animals of the same mass may have very different shapes, mass alone is not a good predictor of the features that influence metabolic rate; and (2) an understanding of the mechanisms of heat flow within the body and from the body to the environment. Allometric models do not explicitly invoke any of the natural processes known to influence heat exchange and hence the metabolic rate required to keep an animal alive.

In the early 1980s, other investigators attempted to apply geometrical analysis and heat transfer theory to the study of metabolic scaling. Gates (1980) argued that Kleiber had erred in denying that heat loss through the surface was an important feature determining metabolic rates. Metabolism is a source of internal heat production; the heat thus produced must be lost through a surface, so the role of the surface in heat exchange should not be ignored. Gates pointed out that body size and shape are prominent factors determining heat exchange and should be used for derivation of general models relating mass, metabolic rate, and body temperature.

A few investigators recognized that a more mechanistic approach to understanding allometry was needed. Heusner (1982) concluded that previous authors had improperly constrained the allometric variable *a* to be constant for all mammals, and he reanalyzed their data by performing regressions with smaller size ranges. He found that 2/3 was the best estimate of *b* for all mammals of the same shape but that the value of *a* was different for mammals of different sizes and shapes. McNab (1988) and Agutter and Wheatley (2004) have also remarked on the interdependence of *a* and *b*, and Lovegrove (2000) showed that *b* depends on size, with small mammals having *b* values below 3/4 and large mammals having values close to unity.

Blaxter (1989) listed other early attempts to explain why *b* appeared to equal 3/4. Some of these proposed 3/4 as a mean of area-based and mass-based scaling, others saw it as a statistical artifact, and yet others as the expression of differential mitochondrial activity in large and small animals. None of these models invoked energy exchanges as causal agents. Below, we propose a model that incorporates the suggestions of recent authors (Gates 1980; White and Seymour 2003; Agutter and Wheatley 2004). We develop a predictive equation based on heat transfer theory and animal physiology to estimate the minimum value an endotherm's metabolism should take in the thermoneutral ambient temperature range.

A Predictive Equation for Basal Metabolism

We begin with the equation for the steady state temperature gradient in the thermoneutral zone within an object with a distributed average internal heat generation per unit volume of uniform material. The governing equation is consistent for all geometries (Porter et al. 1994, 2000; Bird et al. 2002):

$$T_c - T_s = \frac{gL^2}{nk}, \tag{2}$$

where T_c and T_s are the core and surface temperatures, respectively, of the object, L is the distance through which heat flows, g is the average heat production per unit volume, k is the effective thermal conductivity of object, and n is 2 for a slab, 4 for a cylinder, between 4 and 6 for an ellipsoid, and 6 for a sphere; see appendix A.

We consider that an endotherm, such as a mammal, may be modeled as an ellipsoid, as in equation (3). This geometry represents an animal in a thermoneutral posture rather than a posture associated with cold, such as a curled up into a sphere. Further, as animals at rest generally sit with legs under the body, we did not include appendages here, although appendage heat transfer is present in Niche Mapper numerical solution programs for ectotherms and endotherms (Porter and Mitchell 2006):

$$T_c - T_s = \frac{g \times R^2}{4.28 \times k}, \tag{3}$$

where R is the radius of a cylinder and the coefficient 4.28 represents the value of n for the ellipsoid shape modeled in this article; see appendix A. Equation (3) predicts that the temperature gradient across an endotherm will be directly proportional to the rate of heat production and inversely proportional to the conductivity of the material and that it will vary in a parabolic manner with R.

To our knowledge, temperatures have not been measured across the entire body wall of mammals, but Bazett et al. (1948) and Pennes (1948) reported the temperature distribution from center to surface of cylindrical human limbs with heat production uniformly generated in muscle. Reader and Whyte (1951) presented similar measurements from other parts of the body. Both sets of data show a clear parabolic temperature distribution.

To apply equation (3) to endotherms, we have made two modifications. First, we considered that the term g, volume-specific heat production, can be replaced by $(Q_{gen} - Q_{res})/V$, where $Q_{gen} - Q_{res}$ is net core heat production in watts and V is animal volume in cubic meters. The term Q_{gen} is what physiologists call "metabolic rate" and is based on measurements of oxygen consumption converted to units of power. The term Q_{res} is respiratory heat loss, from measurements of respiratory evaporative water loss. The subtraction of Q_{res} is required by the fact that respiratory heat is lost directly from the body without passing through the skin (Kolka and Elizondo 1983). Equation (3) can thus be modified to solve for $Q_{gen} - Q_{res}$:

$$Q_{gen} - Q_{res} = \frac{4.28 \times k \times (T_c - T_s) \times V}{R^2}. \tag{3a}$$

Second, equation (3a) consists of four sets of terms: $(Q_{gen} - Q_{res})$, k, $(T_c - T_s)$, and V/R^2. As our overall purpose is to model the metabolism–body size relation, we wished to determine whether Q_{res}, k, or $(T_c - T_s)$ varies with body mass. To do this, we needed measurements of metabolic rate, respiratory water loss, core and skin temperatures, and dimensions for mammals that were resting at thermoneutral conditions. We searched the literature of mammalian metabolic rate and found a small number of studies that measured all these variables and for which the animals were postabsorptive and not using energy to maintain posture. The data are shown in Table 1 as measurements of T_c, T_s, Q_{gen}, and Q_{res} occurring at air temperatures that allow basal metabolic heat production. We cover each of these in turn.

Thermal conductivity. The effective thermal conductivity k (in W/m/°C, hereafter W/mC) is fixed in inanimate objects but can vary in animals, as it can be increased by core-to-skin blood flow. We propose that k can be modeled as the sum of two terms: a basal conductivity, here called k_b, and B, representing the additional heat transfer achieved by blood flow from core to skin. The pure conductive component k_b is nearly constant for animal tissues. Cohen (1977) and Valvano et al. (1985) showed that for all hydrated tissues (thus excluding dry skin and fat), k_b is $0.5 \pm .02$ (SD) W/mC, with no tendency to increase or decrease from core to skin. The additional blood flow component B is minimal at air temperatures below thermoneutrality, where endotherms limit heat loss; thus, at cool temperatures, k is dominated by k_b. At thermoneutral temperatures and higher, however, B is high compared to k_b (Buettner 1936). Thus,

$$k = k_b + B, \tag{3b}$$

and equation (3a) can be modified to

$$Q_{gen} - Q_{res} = \frac{4.28 \times (k_b + B) \times (T_c - T_s) \times V}{R^2}. \tag{3c}$$

For further analysis, we factored the R^2 term, so

$$Q_{gen} - Q_{res} = \frac{4.28 \times (k_b + B) \times (T_c - T_s)}{R} \times \frac{V}{R}. \tag{3d}$$

Factoring provides two advantages: (1) we can express animal size in terms of surface area (V/R is m^3/m and has units of m^2). This is consistent with the analytical approach of Gates (1980) and Porter et al. (1994, 2000); and (2) we can introduce thermal conductance, a dimensionalized conductivity. Heat transfer specialists (e.g., Ede 1967) define thermal conductance

Table 1: Thermal characteristics of 10 mammalian species and prediction of basal metabolic rate

Species	Mass (kg)	T_c (°C)	T_s (°C)	Q_{res} (W)	Q_{gen} (W)	Eq. (5) (W)	Sources
Peromyscus maniculatus	.016	39.2	38.2	.08	.3	.31	Conley 1985; Conley and Porter 1985
Mesocricetus auratus	.13	37.4	36.7	.08	.6	1.26	Jones et al. 1976
Rattus rattus, normotensive	.38	38.7	36.6	.6	2.3	*2.57*	Collins et al. 1987
R. rattus, hypertensive	.30	39.5	36.8	.62	2.3	2.20	Collins et al. 1987
Saimiri sciureus	.95	39.3	36.2	.82	5.5	4.74	Stitt and Hardy 1971
Felis domesticus	2.6	39.9	39	3.6	9.6	9.27	Adams et al. 1970
Oryctolagus cuniculus	3.0	39.1	37.1	2.2	9.3	10.20	Gonzalez et al. 1971
Rhynchotragus kirki	4.6	38.2	36	2.6	11.6	13.56	Kamau 1988
Erythrocebus patas	4.9	38.1	36.5	2.9	23.6	14.14	Kolka and Elizondo 1983
Canis familiaris	8.5	38.8	37.2	5.9	16.1	20.42	Hammel et al. 1958
C. familiaris	10.5	38.7	37.2	9.8	18.1	24.95	Hammel et al. 1958
C. familiaris	10	38.5	37.5	9.3	23.7	22.76	Hammel et al. 1958
Homo sapiens	70	36.9	34.5	11.2	95	83.34	Caldwell et al. 1969; Hardy et al. 1971[a]

[a] Hardy et al. (1971) provided all needed data except Q_{res}. Caldwell et al. (1969) provided the ratio Q_{res}/Q_{gen}. Thus, the table combines data from these two sources only for Q_{res}.

(h) as conductivity over a distance (k/R in our use; app. B). Because both thermal conductivity and thermal conductance are concerned with core-skin blood flow, we combine them:

$$h = \frac{k_b + B}{R}. \tag{3e}$$

Core-skin thermal conductance, also called tissue thermal conductance for use in whole-animal thermal physiology (Gordon 1993), is given as

$$h = \frac{Q_{gen} - Q_{res}}{(T_c - T_s) \times A}. \tag{3f}$$

Our use of h is consistent with the above and is explained in appendix B. We determined values for h for the mammals in Table 1 and found that h showed no tendency to increase or decrease across a wide range of body sizes (Fig. 2*A*). If conductance (W/m^{2}C) does not change with R, then thermal conductivity ($k_b + B$; [W/mC]) must be proportional to R. This is demonstrated as follows.

For mammalian tissues, basal conductivity k_b has the mean value 0.5 W/mC (Cohen 1977; Valvano et al. 1985). In addition, h has the mean value 21.8 W/m^{2}C (Fig. 2*A*). Thus, giving values to the variables in equation (3e),

$$21.8 = \frac{0.5 + B}{R}, \tag{3g}$$

from which we obtain

$$B = 21.8 \times R - 0.5. \tag{3h}$$

Equation (3h) predicts that at thermoneutrality, skin blood flow in mammals will be proportional to the animal's radius R. Actual measurements of the relation between skin blood flow and size have not been made for mammals in general; however, Buettner (1936) measured thermal conductivity ($k_b + B$) in the warm skin of human subjects and found it to be 3.6 W/mC, close to the value (3.4 W/mC) predicted for humans (mass = 70 kg, radius = 0.18 m) by equation (3h). This analysis supports our prediction that the constancy of h over a wide range of mammal sizes (Fig. 2*A*) is a result of B increasing in proportion to R. In addition, it supports our use of thermal conductance as a separate term in equation (4). These ideas have not, to our knowledge, been proposed previously in this form. From this analysis, we can rewrite equation (3d) as

$$Q_{gen} - Q_{res} = \frac{4.28 \times h \times (T_c - T_s) \times V}{R}. \tag{4}$$

The core-skin temperature gradient ($T_c - T_s$), *or* ΔT. A plot of ΔT versus mass (Fig. 2*B*) shows that mean ΔT for the mammals in Table 1 is 1.7° ± 0.2°C (SE, $n = 13$) and that it appears not to change in a regular way with mass.

Respiratory heat loss Q_{res}. To determine how Q_{res} varies with size, we found the ratios Q_{res}/Q_{gen} for the mammals in Table 1 and plotted them against mass (Fig. 2*C*). The value of Q_{res} is approximately 0.27 ± 0.03 (SE, $n = 13$) times Q_{gen}, and it appears not to change in a regular way with mass. This consistency allows us to rewrite equation (4) as

$$Q_{gen} - 0.27Q_{gen} = \frac{4.28 \times h \times (T_c - T_s) \times V}{R}, \tag{4a}$$

which becomes

$$Q_{gen} = \frac{(1/.73) \times 4.28 \times h \times (T_c - T_s) \times V}{R}. \tag{4b}$$

Animal shape. Finally, with respect to the relation between volume and radius, the ratio of V to R depends on the shape

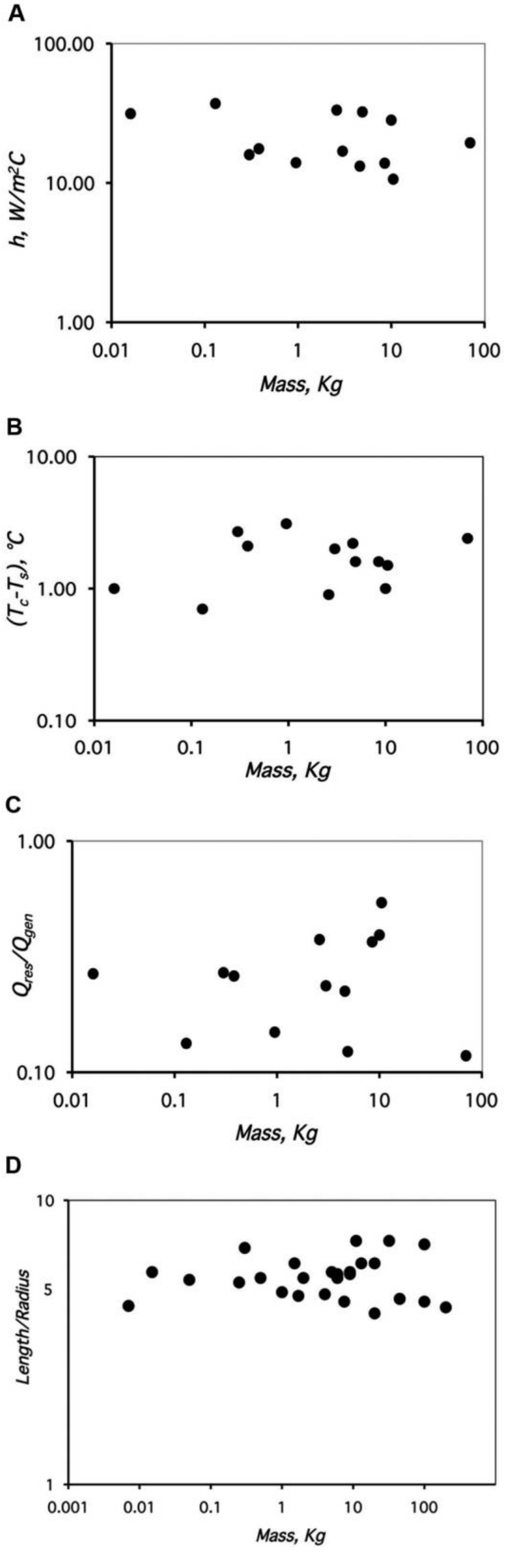

Figure 2. Physiological variables derived from mammals used to test equation (5). All data come from references in Table 1. *A*, Thermal conductance versus mass; mean value 21.8 ± 2.5 (SE) W/m^2C. Slope not significantly different from 0: $F_{1,11} = 0.197$, $P = 0.67$. *B*, Core-skin thermal gradient versus mass; mean value 1.7° ± 0.2°C. Slope not significantly different from 0: $F_{1,11} = 0.510$, $P = 0.49$. *C*, Q_{res}/Q_{gen} versus mass; mean value 0.27 ± 0.03. Slope not significantly different from 0: $F_{1,11} = 0.527$, $P = 0.48$. *D*, Ratio of length to radius versus mass; mean value 5.4 ± 0.2. Slope not significantly different from 0: $F_{1,24} = 0.525$, $P = 0.48$.

of the animal. To estimate this ratio, we measured the lengths and radii of a large variety of terrestrial mammals from photographs in Walker (1964). In collecting these data, we used only animals whose long axes were parallel to the plane of the photo, and we did not include animals with long necks. We realize that the use of photographs is not an ideal way to make such measurements, but the ratio length : radius is a general geometric concept needed for an understanding of mammalian metabolic physiology, and no one has made the necessary measurements on live mammals. We found that for mammals from 12 g to 200 kg, the average ratio of length to radius is 5.4 ± 0.2 (SE, $n = 27$) and does not change with body mass (Fig. 2*D*). We therefore used this value to compute a value for R from the published value for mass of each mammal (Table 1).

The previous paragraphs suggest that h, Q_{res}/Q_{gen}, $(T_c - T_s)$, and L/R have fairly constant values for mammals at rest in thermoneutral conditions. Our analysis is empirical in the sense that we do not yet know what geometric or physiological principles constrain these values; it is theoretical in the sense that the variables themselves were derived from heat transfer analysis. The apparent constancy of these values at thermoneutrality is an important demonstration, as it provides for the first time a basis for understanding the coefficient a in the allometric equation (eq. [1]). It would be important for future studies to determine whether these terms continue to be fairly constant over an even wider range of mammal sizes; in any event, our analysis allows construction of the overall relation between Q_{gen} and body mass.

The values described above ($h = 21.8$ W/m^2C; $\Delta T = 1.7°C$; $Q_{res}/Q_{gen} = 0.27$; $L/R = 5.4$) allowed us to obtain

$$Q_{gen} = \frac{(1/0.73) \times 4.28 \times 21.8 \times 1.7 \times V}{R} = 217.3\frac{V}{R}. \tag{4c}$$

When equation (4c) is combined with the relation between radius and volume of an ellipsoid (app. C), the result is our final equation:

$$Q_{gen} = 4.9 \times \text{mass}^{0.667}. \tag{5}$$

We then used equation (5) to predict Q_{gen} from body mass from each study listed in Table 1. The results are shown in Figure 3. The points and dashed line represent the metabolism measured in each study; the solid line represents the predicted metabolism based on equation (5). The results show that equation (5) is a good predictor of net heat production for the range of mammals illustrated, implying that it is possible to derive a relationship for BMR from principles of heat transfer, given a small number of geometric and physiological features of the animals involved.

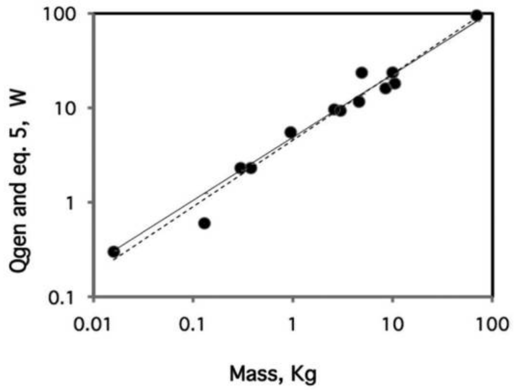

Figure 3. Comparison of basal metabolism Q_{gen} predicted from equation (5) with actual data from mammals (Table 1). Filled symbols and solid line show predictions from equation (5) ($Q_{gen} = 4.9\text{mass}^{0.67}$). The dotted line ($Q_{gen} = 4.53\text{mass}^{0.70}$) illustrates actual data for basal heat production.

The similarity of equations (4c) and (5) to the allometric equation (eq. [1]) is shown by the V/R term, which is proportional to the surface area, or $m^{2/3}$. However, equation (4c) specifies the individual components of what earlier investigators had combined into the single expression am^b. For example, the coefficient a is a complex term involving Q_{res}, h, and $(T_c - T_s)$. Equation (5), therefore, has a form similar to that of the allometric equation, and we propose that it is a mechanistic version of that equation.

It is important to emphasize that equation (5) is not a new formulation. It simply uses established principles in a novel manner, and it is, to our knowledge, the first attempt using meaningful variables to predict BMR for endotherms. It will be important to test the generality of the equation over a much larger size range, but such a test will have to await additional studies in which metabolism, respiratory heat loss, and both core and skin temperatures are measured in larger mammals that are at actual basal metabolism. It may be difficult to obtain truly resting metabolism in large mammals, but our analysis strongly suggests that to understand the relation of basal metabolism to size, new approaches are necessary.

The equation further amplifies our earlier discussion of allometry to suggest that a realistic estimate of basal metabolism must incorporate thermally significant variables. Our analysis separates these thermally important components, so it is possible to see what determines an endotherm's need to produce heat. That "need" is not simply its mass raised to some power; rather, it is set by conditions influencing heat exchange.

Discussion

We have revisited the fundamentals of heat exchange to develop a general relation between metabolism and the body size of an endotherm. Our analysis provides two important advances over previous approaches based on allometry: first, we show that basal metabolism is proportional to the animal's volume per unit radius (b is therefore 2/3); next, we suggest that a, the coefficient of the area term, combines the important variables respiratory heat loss, thermal conductance, and core-skin thermal gradient. Our analysis suggests that published allometric graphs are simply special cases of graphs of the heat transfer–based equation.

Finally, we suggest reasons that data reported in the literature have appeared to give an allometric slope of 3/4. Small mammals have a 2/3 slope because they have a simple geometry under test conditions and because little extra metabolism is associated with posture or thermoregulation. Large mammals have a slope closer to 1 because they have complex geometries and, under test conditions, use energy for nonmaintenance functions (posture and thermoregulation). Thus, the published metabolic rates for large mammals combine basal rates with additional energy expenditures. If combined into a single graph, the lower slope for small mammals and the higher slope for large mammals (Fig. 1*B*) give an apparent 3/4 slope overall on a log-log plot. We therefore conclude that there is no 3/4 power relation for investigators to explain by invoking distribution networks (West et al. 1997).

The allometric relation is a good starting point for studies of animal design. As long as it is used for purely descriptive purposes, it is an adequate approximation. However, because approximation and description are not mechanistic, we suggest that to give an understanding of whole-body metabolism under any conditions (including previously unstudied conditions), it is best to use a mechanistic model that is based on realistic physical and physiological measures.

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Appendix A

Fundamental Heat Transfer Equation and Shape Factors for Different Geometries

The fundamental heat transfer equation is derived by Bird et al. (2002) and is given as equation (2). Its form for any geometry is

$$T_c - T_s = \frac{g \times F^2}{2n \times k},$$

where T_c and T_s are core and skin temperature (°C), respectively, g is volume-specific heat production (W/m^3), F is the distance through which heat flows (m), and k is the effective thermal conductivity of the material (W/mC).

There are several possible geometries for heat flow. Each has its characteristic shape factor, the product $2n$ in the denominator, where $n = 1, 2$, or 3 for a slab, a cylinder, or a sphere, respectively. This coefficient reflects the one, two, or three dimensions for heat flow in the derivation of the respective equations.

In the case of ellipsoids, shape varies from spherical to extended, so F^2 varies as well. The general equation for F^2 for an ellipsoid (Porter et al. 1994) is

$$F^2 = \frac{a^2b^2c^2}{a^2b^2 + a^2c^2 + b^2c^2}.$$

The more elongated an ellipsoid is, the more its shape factor approaches that of a cylinder. However, the ellipsoid formulation includes three-dimensional "end effects," which are not included in the two-dimensional cylinder solution. As indicated in Figure 2*D*, mammals are elongated ellipsoids with $L = 5.4 \times R$. Thus, if the semiminor ellipsoid axes are symmetric, then

$$b = c = R,$$

$$2a = 5.4 \times R,$$

$$a = 2.7 \times R,$$

From this it follows that

$$F^2 = \frac{(2.7^2 \times R^2 \times R^2 \times R^2)}{(2.7^2 \times R^2 \times R^2 + 2.7^2 \times R^2 \times R^2 + R^2 \times R^2)} = \frac{R^2}{2.14}.$$

The heat transfer equation becomes

$$(T_c - T_s) = \frac{g \times R^2}{2 \times 2.14 \times k}, = \frac{g \times R^2}{4.28 \times k}.$$

For a mammal-shaped ellipsoid, the shape factor is 4.28.

Appendix B

Definitions of Thermal Conductivity and Thermal Conductance

Ede (1967) defines thermal conductivity as the "ratio of heat flow across a unit cube of the material when two opposite faces are maintained at temperatures differing by one degree" (p. 40) and thermal conductance as the "ratio of heat flux (heat flow per unit area) to the difference between the temperatures of the inner and outer faces" (p. 136). In practical terms, Ede (p. 43) defines conductance as conductivity divided by the distance through which the heat flows.

In this article, we use "thermal conductance" in a slightly different way: heat flows radially in an endotherm, and thus there are not two equal entry and exit "faces" of the material through which heat flows. Nonetheless, an endotherm is made of material with measurable conductivity; it has measurable core and skin temperatures, and heat flows to the surroundings through a surface area. That is the context of our use of the term "thermal conductance."

Appendix C

Conversion of Equation (4c) to Equation (5)

For an ellipsoid, $V = (4/3)\pi \times abc$. For mammals, b and c are equal and are considered to be equal to the radius R. Half the length is a, and $a = 2.7 \times R$ (Fig. 2*D*). Thus, for a mammal-shaped ellipsoid,

$$V = \frac{4}{3}\pi \times abc = 11.31 \times R^3,$$

and the radius can be computed as

$$R = \left(\frac{V}{11.31}\right)^{0.333},$$

where V (in m^3) = mass (kg)/1,000 (kg/m^3). Thus,

$$R = \left(\frac{1}{11{,}310}\right)^{0.333} \times \text{mass}^{0.333} = 0.447 \times \text{mass}^{0.333}.$$

From equation (4c),

$$Q_{\text{gen}} = 217.3 \times \frac{V}{R}$$

$$= 217.3 \times \frac{\text{mass}}{1{,}000} \times \frac{1}{0.0447 \times \text{mass}^{0.333}}$$

$$= \frac{217.3}{44.7} \times \text{mass}^{(1-0.333)},$$

yielding equation (5):

$$Q_{\text{gen}} = 4.9 \times \text{mass}^{0.667}.$$

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