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Can the Basal Metabolic Rate of Endotherms Be Explained by Biophysical Modeling? Response to “A New Model for the Body Size–Metabolism Relationship”

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ABSTRACT

The physiological mechanisms that determine basal metabolic rate (BMR) of endotherms have long been debated. This journal has recently presented a new model, based on biophysical principles of heat flux through the tissues of mammals, that attempts to explain the allometric relationship between BMR and body size. We offer a critique of the model and conclude that although the model may describe the physics of heat transfer through the body, it cannot explain mechanistically the level of BMR. BMR determines some of the key variables of the model, but no combination of the variables determines BMR. The model arrives at an equation relating BMR to body mass that is similar to descriptive empirical equations, but this coincidence results from the geometry of the model and the empirical values put into it.

Allometric equations of the form $Y = aM^b$ are commonly applied to biological variables (Y) in relation to the body mass (M) of plants and animals. The a value is the elevation of the curve and the b value is the exponent or power of the relationship. In general, they are descriptive; that is, they simply represent a single equation that is applied to a set of empirically obtained data by regression analysis (usually, but not always, by linear least squares regression of log-log-transformed data; Packard and Boardman 2008). One of the most basic parameters of animal physiology is the standard metabolic rate, which is the metabolic rate under standard conditions (McNab 1997;

Frappell and Butler 2004). When applied to birds and mammals—endotherms—it is called the basal metabolic rate (BMR). One of the focuses of attention for more than 170 yr has been to try to provide a mechanistic explanation of the relationship between BMR and M in endotherms because it is not linear. Typically, the relationship is allometric with an exponent less than 1, such that a 10-fold range in M is accompanied by an approximately 5-fold range in BMR.

Roberts et al. (2010) present a nice review of the descriptive and mechanistic approaches to allometry of BMR from the literature and point out some of the problems with each approach. They then go on to provide a biophysical analysis of heat generation and conduction through a three-dimensional (3-D) model of a mammal in an attempt to show that BMR is a consequence of the relationship between body size and the physics of heat transfer within the body of the animal. Their aim was to “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” (Roberts et al. 2010, pp. 398–399). In attempting to do so, they emphasize that their equation 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” (Roberts et al. 2010, p. 402).

Their central equation is a heat-transfer analytical solution for heat flux through an ellipsoid made of heat-generating tissue. The key elements of the model are net heat generation ($Q_{\text{gen}} - Q_{\text{res}}$, where Q_{gen} is metabolic heat production and Q_{res} is respiratory heat loss) and the temperature difference between the core of the model and its surface ($T_c - T_s$). It is important to realize that the model does not include insulation by the pelt, and skin temperature was taken at the base of the hairs. It also includes a value for effective thermal conductance of the tissue (h), including the roles of tissue conductivity and blood flow, but not conductance of the pelt. Finally, the volume (V) and minor radius (R) are derived from the shape of the animals to arrive at their equation (4). This equation is a special case of Newton’s law of cooling, which can be simplified to $Q = h(T_c - T_s)$.

We state the simplified version of the equation to make the point that the rate of heat generation in a body determines the temperature difference, not vice versa. For example, if one turned on a 100-W lightbulb and measured the temperature difference across the glass of the bulb after stabilization using the surface area, thickness, and thermal conductivity of glass, one could arrive at this equation. However, it would be clear

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that none of the variables describing heat loss determined the power of the bulb. If one studied bulbs of different powers and sizes, one could relate the power to the surface areas, thicknesses, and temperature differences in a meaningful way, but one could never use the size of the bulb and the temperature difference to determine, in a mechanistic way, the wattage. The only factors that determine the power of the lamp are the voltage and resistance across the filament, which are independent of the physics of heat loss from the system. In the same way, BMR is the independent variable in mammals, and the physics of heat loss are dependent.

It might be argued, however, that because animals are thermoregulating and can vary the rate of heat production, then to achieve a certain core body temperature in an environment with an ambient temperature equal to skin temperature, they would have to vary heat production according to their size. This is clearly true, according to their model, which relies on the assumption that the difference between core and skin temperatures is a constant (mean $\Delta T = 1.7^\circ\text{C}$) within the thermal neutral zone. However, the difference between core temperature and skin temperature changes within the thermoneutral zone, so at the lower critical temperature, the difference between core and skin can be about 5°C in dogs (Hammel et al. 1958), rabbits (Gonzalez et al. 1971), and squirrel monkeys (Stitt and Hardy 1971). Despite the variation in ΔT within the thermoneutral zone, BMR does not change. As Hammel et al. (1958) and others have pointed out, there are changes in perfusion to the skin under cool conditions that maintain a constant rate of heat loss despite greater temperature difference between the core and the environment. It seems unlikely that a combination of geometry and changing internal conductance determine BMR; rather, BMR is constant, and thermoregulatory mechanisms determine the temperature difference across the body.

Roberts et al. (2010) searched the literature to obtain values from 13 species to incorporate into their model, namely, Q_{gen} , Q_{res} ($T_c - T_a$), and h . They arrived at the final equation (5), $Q_{\text{gen}} = 4.9 \times \text{mass}^{0.667}$, which they said explained the scaling of BMR in mammals. Then they tested the model by calculating Q_{gen} from the body masses of the 13 species of their sample and found a close fit. All this demonstrates, however, is that the calculations of their model and test were correct, because the test is clearly circular. It does not demonstrate that the physics of heat loss determine BMR.

We found the model interesting because it apparently refuted 0.75 power scaling and supported 0.67 power scaling, something we had empirically demonstrated on 469 species of mammal (White and Seymour 2003). However on careful examination, the exponent emerges as merely a geometric consequence of the model. Any simple 3-D model that invokes a constant temperature difference between the core and the surface will scale with $M^{0.67}$. To be specific, in the model of Roberts et al. (2010), the value of b is based on the mass independence of the ratio of length to radius of 27 species of mammal (5.4 ± 0.2 SE) and that Q_{gen} is proportional to V/R . Incorporation of the relation between R and V of an ellipsoid ($4/3[\pi xyz]$, where in the model, y and z are each equal to R

and $x = 0.5 \text{ length} = 2.7R$, so $V = 11.31R^3$) leads to $Q_{\text{gen}} \propto V/V^{1/3}$, and because $M \propto V$, $Q_{\text{gen}} \propto M^{2/3}$. Similarly, given that the surface area (A) of a prolate spheroid (an ellipsoid where $y = z$ and $x > z$) is given by

$$A = 2\pi \left(z^2 + \frac{xz \arcsin(\sqrt{x^2 - z^2}/x)}{\sqrt{x^2 - z^2}/x} \right),$$

and that in the model $x = 2.7y = 2.7z$, it follows that $A \propto R^2$. Thus, because $V \propto R^3$ and $Q_{\text{gen}} \propto V^{2/3}$, $Q_{\text{gen}} \propto (R^3)^{2/3} \propto R^2 \propto A$.

Because the model predicts that $Q_{\text{gen}} \propto A$, species with relatively high A (or high ratios of length to R) should have relatively high BMR. However, residuals of the relationship between \log BMR and $\log M$ are not significantly correlated with residuals of the relationship between $\log A$ and $\log M$ (White and Seymour 2004), suggesting that this is not the case. It can be concluded that while A (or V/R , which is proportional to A) and BMR all scale with similar exponents, there is no evidence that they are mechanistically related. That BMR should be proportional to A was first suggested by Sarrus and Rameaux in 1838 (cited by Brody 1945) and later supported by Rubner (1883). The surface law was comprehensively rejected by the 1980s (e.g., Kleiber 1961; Peters 1983; Schmidt-Nielsen 1984).

In fact, the scaling exponent of mammalian BMR is not equal to 0.67. Recent independently conducted, phylogenetically informed analyses of the exponent for nearly 700 species of mammal reveals a b value between 0.67 and 0.75, statistically excluding both of these values (Duncan et al. 2007; Sieg et al. 2009; White et al. 2009; Capellini et al. 2010). Moreover, even if the scaling exponent of mammalian BMR were equal to 0.67, parallel scaling between the model and data would not demonstrate that the former predicts the latter.

While heat dissipation may limit the duration of high intensity exercise (Fuller et al. 1998; González-Alonso et al. 1999) and restrict sustained metabolic rate (Speakman and Król 2010), the capacity of some resting endotherms to vary the insulation of their fur or feathers by up to 11-fold and maintain body temperature and BMR independent of ambient temperature over a range of at least 70°C in the thermoneutral zone (Scholander et al. 1950) suggests that heat dissipation does not determine BMR. Similarly, increasing heat loss by substitution of He for N_2 leads to a significant increase in thermal conductance within the thermoneutral zone but no change in BMR (Holloway and Geiser 2001), further suggesting that basal energy expenditure is not related to heat loss.

The model of Roberts et al. (2010) is noteworthy because it ostensibly makes a quantitative prediction for the a value of the allometric equation, while other mechanistic analyses consider only the b value (West et al. 1999; Brown et al. 2004; West and Brown 2005) or predict the boundary constraints on b and the relationships between a and b (Glazier 2010). While the value of a predicted by Roberts et al. (2010) agrees fairly well with that of larger data sets (e.g., White et al. 2009), this arises only as a consequence of the circularity of their model. They parameterize a model of heat loss in endotherms using a range

of measured values. Given that all heat produced by metabolic processes must ultimately be lost to the environment, it is not surprising that they are able to "predict" BMR with reasonable accuracy. This does not demonstrate that they are able to explain allometric variation in BMR in a mechanistic sense; it only demonstrates that the model approximates reality.

Despite this apparent agreement with empirical data sets, there are other problems with the assumptions of the model, especially that heat moves essentially radially by what amounts to a conductive mechanism. Although heat convection by blood is recognized, the model lumps conduction (k_i) and convection (B) as both being "driven" by a temperature difference; k_i and B therefore have the same units. The convective component is proposed to be proportional to the radius of the animal. Thus, convection would scale with $M^{0.33}$. Because skin mass scales to approximately $M^{0.92}$ (Pace et al. 1979; Lindstedt and Calder 1981), one would need a mass-specific skin respiration rate to scale with $M^{-0.59}$. However, the exponent is much shallower in mice $M^{-0.37}$ (Fuhrman and Fuhrman 1957) and is consistent with the mass-specific scaling of tissue metabolism of most organs (Wang et al. 2001). Lumping conduction and convection into a single constant ignores that convection may not only change allometrically between species but also in one species at different points within the thermal neutral zone.

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