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Original Article

A model for allometric scaling of mammalian metabolism with ambient heat loss

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ABSTRACT

Background: Allometric scaling, which represents the dependence of biological traits or processes on body size, is a long-standing subject in biological science. However, there has been no study to consider heat loss to the ambient and an insulation layer representing mammalian skin and fur for the derivation of the scaling law of metabolism.
Methods: A simple heat transfer model is proposed to analyze the allometry of mammalian metabolism. The present model extends existing studies by incorporating various external heat transfer parameters and additional insulation layers. The model equations were solved numerically and by an analytic heat balance approach.
Results: A general observation is that the present heat transfer model predicted the 2/3 surface scaling law, which is primarily attributed to the dependence of the surface area on the body mass. External heat transfer effects introduced deviations in the scaling law, mainly due to natural convection heat transfer, which becomes more prominent at smaller mass. These deviations resulted in a slight modification of the scaling exponent to a value < 2/3.
Conclusion: The finding that additional radiative heat loss and the consideration of an outer insulation fur layer attenuate these deviation effects and render the scaling law closer to 2/3 provides in silico evidence for a functional impact of heat transfer mode on the allometric scaling law in mammalian metabolism.

1. Introduction

Allometric scaling, which represents the dependence of biological traits or processes on body size, is a long-standing subject in biological science. Extensive review articles[1–5] indicate that the relevance of this subject spans a wide spectrum of biological fields, such as the principles of animal design and evolution of life.

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Allometric scaling describes the basal metabolic rate (BMR) as a power function of body mass (m), i.e., BMR = am^b, where a is a proportionality constant and b is the scaling exponent. Sarrus and Rameaux[6] first presented the hypothesis that metabolic rate is limited by heat loss and linearly proportional to the surface area. An experimental study by Rubner[7] confirmed a linear relationship in dogs. Considering that the surface area is proportional to $m^{2/3}$, this implies that $b = 2/3$, which is referred to as the surface scaling law. A later study by Kleiber[8] estimated BMR in a number of mammalian species and found that b is actually > 2/3 and closer to 3/4 which is now well-known as the 3/4 power scaling. Brody[9] and Hemmingsen[10] further claimed the validity of the 3/4 power scaling for a variety of organisms ranging from bacteria to elephants, including ectotherms and microorganisms. The empirical and theoretical basis for the 3/4-power law was extensively reviewed by Glazier.[11]

Theoretical investigations have attempted to provide a physical explanation for the empirical 3/4 power scaling. Among them, the fractal network theory (FNT)[12] has attracted significant attention. FNT assumes that the resource distribution system in an organism has a self-similar fractal structure that is independent of body size. An optimal cascade path is sought for fluid transporting nutrients from the central reservoir to the finest tubes (e.g., capillaries). A detailed mathematical analysis yielded $b = 3/4$. Similar approaches[13,14] employing simpler assumptions have predicted the same scaling exponent. Consequently, FNT has been considered a reasonable explanation for a large number of empirical relationships found in the entire range of organisms including plants.

The universal 3/4 power scaling law, however, has been subjected to critical scrutiny. For example, the reliability of the data and interpretation was questioned, and it was argued that the basic assumptions behind the theoretical analysis may pose substantial limitations in generalizing the results.[2,15–19] In particular, a major concern was that a large amount of empirical data yielded significant scatters in the scaling exponent between 1/2 and 1. These discrepancies have eventually led to a suspicion as to whether the metabolism of the entire organism can be correlated with a simple two-variable power relationship. As a result, alternative models of metabolic scaling have been proposed.[11,15,20]

Another strategy to reconcile the observed discrepancies in the scaling exponent is to narrow down the analysis to a smaller group of species that share some specific features of physics, geometry or biology. For example, White and Seymour[17] considered only mammalian metabolism and reprocessed the existing BMR data to account for variations associated with body temperature, digestive state, and phylogeny. The refined data clearly showed that $b = 2/3$ rather than 3/4. These results are consistent with the findings of Heusner[18] who performed a statistical analysis focusing on intraspecific comparisons. The revival of the surface scaling law demonstrates the important role of heat dissipation in mammalian metabolism.

Recently, there have been several papers to model and explain these phenomena effectively.[20–22] In particular, Roberts et al[22] proposed a new conceptual model (hereinafter, the RLP model) of mammalian metabolism based on the macroscopic energy balance in a body with heat generation. Experimental data from 10 mammalian species were carefully collected from the literature, so as to satisfy the requirements to be *basal*. Utilizing the physiological variables derived from collected data, a closed-form equation was derived for allometric scaling. The model, which was verified by the experimental data, showed that BMR is proportional to the surface-to-volume ratio (i.e., $b = 2/3$) and identified factors affecting the proportionality constant. This simple and informative model, however, had a few limitations. In particular, the assumption that the temperature difference between the core and surface is constant, aside from verifying its validity with the experimental data, poses several logical limitations. Specifically, since the surface temperature, which is the only external factor in the model, is constant, heat balance is determined by only internal factors. The neglect of variations in external factors, such as convective heat loss (possibly a strong function of length), inherently rules out size-dependence from the model.

In this study, we develop a new theoretical model of metabolism that is based on the RLP model, but considers two additional factors: heat loss to the ambient and an insulation layer representing mammalian skin and fur. Allometric scaling in mammals is examined numerically solving the full heat transport equation as well as by an analytic investigation of a simplified heat flow circuit. The results for mammalian metabolism are compared with those obtained by Roberts et al[22] and the biological implications are discussed. Particular attention is paid to the significance of external heat transfer properties in the prediction of the allometric scaling law.

2. Methods

2.1. *Physical and mathematical model*

A simple conceptual model for allometric scaling of mammalian metabolism was developed. The original RLP model[22] was modified to incorporate the interactions between BMR and external environmental factors. The major modifications were: (1) the geometry was changed from an ellipsoid to a cylinder with spherical ends; (2) an additional passive layer covering the main body was considered; and (3) heat loss to the ambient, which was not included in the RLP model, was considered.

Fig. 1 depicts the configuration of a mammal in a thermoneutral state. Roberts et al[22] chose a horizontally aligned prolate spheroid with an aspect ratio 5.4 as the best geometrical representation of animals in a thermoneutral posture. Unfortunately, no correlations of natural convection are available for this geometry in the literature. Therefore, an alternative geometry of a cylinder with spherical ends was adopted, for which a correlation for the heat transfer coefficient can be determined with good accuracy.[23] For geometrical similarity, however, the ratio of volume V to surface area A is chosen to be identical to that of the ellipsoid, $V/A = 0.2017D$, where D is the diameter. This yields a fixed value of the length-to-diameter ratio, $L/D = 1.724$.

The body is assumed to have a duplex structure: an inner core of tissue and an outer insulation layer representing