Allometric Scaling Laws in Biology

In their report "A general model for the origin of allometric scaling laws in biology" (4 Apr., p. 122), Geoffrey B. West *et al.* explore the ubiquity of quarter-power scaling relationships in biology. They (p. 122)

> propose that a common mechanism underlies these laws: Living things are sustained by the transport of materials through linear networks that branch to supply all parts of the organism.

They go on to develop a model of the mammalian circulatory system as a space-filling, self-similar fractal, and they show that the model results in predicted allometric exponents for structural and functional features of the circulatory system that are in good agreement with published values. They state that their model is generalizable, with comparable predictive ability, to other branching transport systems such as the mammalian lung and the tracheal systems in plants and insects.

I concur that (p. 126) "allometric scaling is perhaps the single most pervasive theme underlying all biological diversity." Its very pervasiveness, however, is compelling evidence that the underlying mechanistic basis must surely be common to all living things, and therein lies a difficulty. A good fraction of the earth's organisms do not have structural tubular systems, fractal or otherwise, for the transport of nutrients, gases, and wastes, yet they obey the same scaling relationships as those that do (*1*). Furthermore, the statement by West *et al.* of a three-quarter power scaling law belies the intensity of the debate about the "true" value that has been ongoing for decades. There seem to be different exponents for intra- and interspecific allometries (b = 0.66 and 0.75, respectively, where b is the scaling exponent), for ontogenetic and static allometries (b = 0.66 and 0.75, respectively), and among groups of species over different ranges of adult body size (for example, b = 0.65 in mammals with much less than 20 kilograms of body mass and b = 0.77 in mammals heavier than 20 kilograms) (*2*, *3*).

The explanations of scaling relationships offered by West *et al.*, based as they are on simple physical principles, are compelling; form and function cannot escape the laws of physics. The challenges now are to determine if and how this model can be applied to organisms lacking tubular transport systems, and to reconcile, within the conceptual framework of the model, the presence of both two-thirds and three-quarters power scaling relationships.

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West *et al.* emphasize that their model for the origin of allometric scaling laws predicts, among other things, structural and functional properties of vertebrate cardiovascular and respiratory systems. This model, a fine addition to biology, could serve as well to explain mammalian physionome. The energy minimization principle, however, partly constrains the quar-

ter-power model because substances diffuse across capillary walls, and the capillaries themselves obey the cubic law in their branching. High regional heterogeneity of perfusion, metabolism, and receptor density is necessary for an organism to acclimate to daily life. For example, in the pulmonary vascular bed of mammals, the relative spatial dispersion, *RD*, which can be used to measure regional heterogeneity of blood flow, is not constant (*1*). Lung capillaries have low compliance, and high perfusion pressure opens some (previously closed) pathways as total blood flow increases. Although each individual pathway of the lung has a constant relative dispersion equivalent to a single vessel system ($RD \cong 0.19$, which obeys the quarter-power model), the total heterogeneity of these pathways is threefold at rest (*1*, *2*). As pulmonary blood flow increases, *RD* decreases along with the cubic law (*2*), which allows more homogeneous distribution of blood flow during exercise.

In short, with a minor variant, the model presented by West *et al.* can be used to describe mammalian physiometry.

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Response: Kuikka suggests an important extension of our model. During maximal aerobic activity the metabolic rates of a mammal can increase sevenfold. To deliver more oxygen and nutrients to the cells entails many changes in the resource distribution networks, including increases in respiratory and heart rate and blood flow through the capillaries. Kuikka finds that the quantitative changes in capillary perfusion show quarter-power scaling relationships, as predicted by our model.

Beuchat writes that organisms which lack tubular resource distribution networks show the same allometric scaling relationships as those which have them. We regard this as a testable hypothesis rather than an established fact. We question whether any organisms rely on simple diffusion through a uniform medium for transporting resources. For example, even unicellular organisms have a complicated internal structure of organelles and microtubules, although its role in the distribution of materials is not well understood. Sponges and cnidarians are far from simple, and some have elaborate branching architecture. Further, there have been few allometric studies of these organisms. Additional anatomical and physiological studies are needed to determine whether or not they have the characteristics predicted by our model.

Beuchat correctly points out that empirically measured allometric exponents sometimes deviate from the quarter powers predicted by our model. Exponents less than 3/4 have been reported, especially for variation in metabolic rate among individuals of the same or closely related species. We offer several responses.

First, in many of these cases, the range of body masses is less than several orders of magnitude. Consequently, if there is size-independent variation in the dependent variable, regression procedures tend to underestimate the value of the scaling exponent (*1*). In most cases, 3/4 is within the statistical confidence intervals.

Second, the deviations from quarter-power exponents referred to by Beuchat are primarily in metabolic rate. Our model accurately predicts the observed scaling of other anatomical and physiological variables (see our table 1), which can be measured more precisely than whole-organism metabolism.

Third, our model implies that as organisms vary in size, they must redesign their resource distribution networks in order to comply precisely to the predicted quarter-power scaling. For example, as mammals vary in mass over more than seven orders of magnitude, they change the branching architecture of the circulatory and respiratory systems, the exchange surface between these systems in the lungs, the oxygen affinity of hemoglobin, the density of capillaries in the tissues, and the genetic code and developmental program that direct these changes. When the variation in mass is not too large, organisms may be able to "get away" without making all of these changes, causing the observed exponents to deviate from those predicted by our model.

Fourth, several of the references cited by Beuchat (*2*) conclude that quarter-power scaling is widespread in biology and discuss at length its possible mechanistic basis. There is little discussion of third-power scaling.

Fifth, the deviant values mentioned by Beuchat were obtained empirically. She offers no theoretical explanation for them. Our model develops a theoretical and mechanistic basis for the ubiquitous quarter-power scaling in biology. It also predicts some departures from these values, such as the small deviations from quarter-power scaling observed in the smallest mammals.

Finally, our model is not intended to account for all observed variation in biological allometry. Like any model, it is a deliberate oversimplification that can serve as a point of departure for understanding a much more complicated reality. It should be useful if it captures the essence of the mechanisms that underlie biological scaling and if, by making theoretical predictions, it helps to explain observed deviations from these values.

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Corrections and Clarifications

The News article "NIH case ends with mysteries unsolved" by Jocelyn Kaiser (26 Sept., p. 1920) should have indicated that the refrigerator mentioned was in a conference room, not in a laboratory.

In the Table of Contents for the issue of 5 September (p. 1411), the title of the report by K.-C. Yeh *et al.* (p. 1505) was incorrect. The title should have been "A cyanobacterial phytochrome two-component light sensory system."

In reference 41 (p. 725) of the article "Exploitation of mammalian host cell functions by bacterial pathogens," by B. B. Finlay and P. Cossart (2 May, p. 718), the page number for the article cited should have been "712," not "5313."

Letters to the Editor

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