On the Relationship Between Metabolism and Body Mass

In a recent paper, Blum (1977) attempts to explain the relationship between the rate of metabolism and the body mass using four-dimensional geometry. Over a century ago, in 1837 Sarrus & Rameaux (1838–1839) formulated the so-called "surface rule" according to which the rate of metabolism should increase as the power \( \frac{2}{3} \) of the body mass. This power \( \frac{2}{3} \) is obtained if one assumes that: (a) the mass is proportional to volume (constant density) which varies like the cube of a linear dimension (geometric similarity), and (b) the metabolic rate is proportional to a surface which varies like the square of a linear dimension. However, it soon became clear that in many cases this "surface rule" was not in accord with the observations; in particular for mammals the metabolic rate increases as the power \( \frac{2}{3} \) of the body mass (Schmidt-Nielsen, 1975). Blum noticed that a surface in four-dimensional space increases like the power \( \frac{2}{3} \) of a volume and that if this was significant for the relationship between body mass and metabolic rate, one should attempt to identify the fourth dimension on physical grounds. We believe that this approach is misleading and we will show below how the "surface rule" in ordinary three-dimensional space can be reinterpreted in such a way that good agreement with the observations is obtained.

In a previous paper (Derome, 1977) we stressed the importance of the search for invariants in the analysis of a system; in our case the system is a series of animals being compared, for instance mammals. The first invariant which is widely used in comparative physiology is the density of the animals. This assumption of constant density leads to the direct proportionality of body mass to total volume; this relation is very well confirmed by the observations. The second type of invariants are related to geometric similarity, i.e. it is assumed that animals in a group have the same general shape. Under this assumption the ratio of two linear dimensions (lengths) is an invariant provided the analogous lengths are measured in each species. This is clearly a strong assumption and one must be careful to use it properly. It is already being used when the body mass is supposed to increase like the cube of a linear dimension.

If one wants to relate the rate of metabolism to the body mass, one must make a further assumption: he must assume that the mechanism that governs the rate of metabolism is the same for all animals in the group. The limiting factor for the rate of metabolism is often ascribed to a surface; this surface
may vary depending on the particular group of animals or organisms which are being compared. Unfortunately it is usually assumed that the surface which controls the rate of metabolism increases as the square of a linear dimension. This assumption then leads to the "surface rule" expressing the rate of metabolism in terms of the power $\frac{2}{3}$ of the body mass. But clearly, a surface does not have to grow as the square of a linear dimension.

For instance, consider a parallelepiped in which there is a folded surface whose leaves are separated from each other by a distance small compared with a linear dimension so that the surface contains a large number of leaves. If we let the volume increase in strict geometric similarity so that $d$ increases as a linear dimension and the number of leaves is constant then the total surface increases as the power $\frac{2}{3}$ of the volume. However, if the distance between adjacent leaves is left constant and the number of leaves increases, then the surface increases like a volume. In the intermediate case, i.e. when $d$ increases but not so fast as a linear dimension the surface may increase as a power of volume with an exponent intermediate between $\frac{2}{3}$ and 1.

The mechanisms that control the rate of metabolism are quite complex and we do not wish to study them here in any detail. However, if the assumption is made that the rate of metabolism is governed by a surface and if geometric similarity does not strictly hold it is clearly possible for the rate of metabolism to depend on volume (and thence on weight) by a power other than $\frac{2}{3}$.

The "surface rule" is obtained when, in going from one animal to another in a group, it is assumed that the surface governing the rate of metabolism changes according to geometric similarity. The postulated controlling surface is often complex in form and it is not surprising that organisms or animals will depart from strict geometric similarity. If they find it possible to increase the total surface area controlling the rate of metabolism at a faster pace than $V^{\frac{2}{3}}$ they may well do so. As the volume increases, more space becomes available and a larger number of small surfaces can be generated. There is, of course, a limit to filling a given volume with small surfaces and this corresponds to letting the controlling surface increase as the volume to the power 1. It could be argued that, in a given group, the controlling surface was distributed in the available volume in such a way as to optimize the rate of metabolism, subject to the many constraints imposed by the particular mechanism governing the rate of metabolism.

The relation between the metabolic rate ($\dot{V}_{o_2}$) and the body mass ($M$) is given in the form of an allometric equation:

$$\dot{V}_{o_2} = a M^b,$$

where $a$ and $b$ are constants for a given group. The value of $b$, according to
the observations varies, for a large number of series of animals, between $\frac{3}{2}$ and 1. For mammals, as well as for other groups, $b$ is close to 0.75 which can be accounted for by a certain amount of "folding". Since it is possible to reproduce these observed allometric data by considering surfaces in ordinary three-dimensional space, it seems to us rather irrelevant to go to surfaces in a hypothetical four-dimensional space as Blum has suggested.

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REFERENCES