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Editorial

Scaling functions to body size: theories and facts

Knut Schmidt-Nielsen on a field trip to the Masai Mara in Kenya in 1977 with C. Richard Taylor from Harvard University and Ewald R. Weibel from the University of Berne and their collaborators working on the scaling of metabolic rate in African mammals.

This Special Issue is dedicated to Knut Schmidt-Nielsen – pioneer, mentor, friend

'Why do small animals live faster and shorter?' 'What sets the pace of life?' These are questions that have interested biologists for more than 150 years, leading to debates between theorists and experimentalists that continue today. As early as 1839, Sarrus and Rameaux (1839) realized that metabolic power cannot increase with the third power of the linear dimension or body mass, but is limited by the capacity to get rid of heat; hence, for organisms to stay in energy balance, metabolism can only vary in proportion to their surface area. Rubner (1883) found in fact that metabolic rate in dogs was in proportion to body surface area and proposed that it should scale with body mass raised to the power of 2/3. Obtaining estimates of basal metabolic rate (BMR) on a large number of species small and large, Kleiber (1932) experimentally found a (close to) 3/4 exponent to describe the relationship between BMR and body mass rather than the 2/3 exponent predicted from Rubner's 'law'. Kleiber's 'law' has been confirmed by many studies since (Schmidt-Nielsen, 1984), even though it continues to be contested.

In contrast to Rubner's surface law, Kleiber's 3/4 exponent is enigmatic, with no obvious relation to body design. A quest for explaining such an important allometric relationship fostered new theories. McMahon (1975) developed the concept of elastic similarity, stating that the likelihood of elastic failure of support structures should be kept similar in animals of all sizes. The result of this analysis indicates that legs of smaller animals can be more slender than legs of large animals. Considering elastic similarity and that the power costs of muscle work are proportional to muscle cross-sectional area, the 3/4 scaling of MR is obtained, and thus scaling theory and the experimental evidence can be brought in line. Using an entirely different intellectual approach, West et al. (1997) have more recently invoked the fractal nature of the (energy) distributing vascular network in animals, to arrive at the 3/4 scaling exponent from first principles. A similar approach, also yielding a 3/4 scaling exponent but using fewer assumptions, has been proposed by Banvar et al. (1999). Bejan's 'constructal theory' (Bejan, 2000, and p. 1677) also explains a 3/4 scaling exponent by considering that flow architectures can be deduced by a single law of maximization of access for currents.

So where do we stand today? This review volume tries to answer this question by having scientists from different areas present their theories or their experimental data. By contrasting theories with data the debate becomes transparent and the reader must make his choice – a meeting that preceded this volume was certainly spiked with numerous and heated debates, with no resolution of the conflicts. There was only one consensus that could be reached by all attending: '*there is scaling*' – but 'how' and 'why'?

On the question of principles, there are two fundamentally different approaches on which the papers presented here are based. (1) Experimentalists explore the fascinating range of variations that occur in nature, one case being the modulation of the basic blueprint of animals to accommodate the same functions in bodies of varying size, from 2 g to 5 tons in mammals; whereas (2) the theorists seek explanations from first principles for empirically established relationships, for example the scaling of metabolic rate with body size. Ideally the predictions of theory should be supported by evidence, but here the crux is that life conditions are not always simple. For example, it is important to realize that the metabolic rate of an animal will depend on many factors and can easily vary by factors of 10 or more, depending on the level of activity. Even though the 3/4 power law predicts that the mass-specific basal metabolic rate of a mouse of 20 g is five times greater than that of a 500 kg racehorse, when these two animals run as hard as they can their maximal metabolic rate per gram body mass is nearly the same. The conditions under which measurements are made must therefore be clearly defined, and the theories must account for this variation in metabolic scope. Theory and experiments must, in the end, converge.

What ultimately determines the scaling of a function with body size? An answer to this can only be found by developing mechanistic theories based on an understanding of the underlying functional principles and processes. For the case of metabolic rate, two powerful 'models' or 'theories' are presented in this issue (West et al., p. 1575 and Bejan, p. 1677), which both predict that metabolism should scale with the 3/4 power of body mass M_b on the basis of the design properties of the vascular system. For a biologist it seems hard to accept *a priori* that the rate of energy utilization in animals should be dictated by its 'fuel delivery' system: he would think of animals as systems driven by demand rather than supply of energy. The vasculature is highly malleable and molecular mechanisms have been discovered that can adjust the supply to the demand of the tissues. But maybe it is simply not as simple. A possible solution to the problem of supply *vs* demand control of metabolism is offered by the proposition of 'multi-level regulation of metabolic scaling' by Suarez and Darveau (p. 1627). They consider that supply and demand systems have co-evolved and that observed metabolic scaling is the consequence of the contribution of various steps (in an allometric cascade model) controlling both supply and demand processes relevant in setting the rate energy utilization in animals (Darveau et al., 2002). The problem here, however, is that such a model is hard to reduce to first principles and that power law scaling does not follow directly from the theory. And furthermore, if the sequential steps are all co-adjusted to an integral performance level it will be hard if not impossible to sort out primary and secondary effects.

The second caveat with modeling BMR to the 3/4 power is that BMR is only one, and quite artificial, state of living for an animal as it reflects the absolute minimum of energy needs. But energy supply must be able to accommodate a large range of different functional or metabolic states. Which of these has the strongest evolutionary effect? Maybe it would be better to consider the scaling of field metabolic rate (FMR) – the average metabolic rate effectively expended by animals over longer time periods going about their daily business of surviving (see Nagy, 1999, and p. 1621). The upper well-defined end point of the metabolic scope, maximal metabolic rate (MMR) achieved by animals running under conditions of maximal aerobic energy flow (Weibel et al., 2004; Weibel and Hoppeler, p. 1635), is also a candidate to be considered and analyzed in terms of the 'scaling laws', because it is a state that may be highly pertinent for survival and hence for selection in evolution. Looking at the three contributions in this issue of JEB dealing with BMR, FMR and MMR, we can find no convincing evidence for a general 3/4 power scaling of metabolic rate in any of these conditions. White and Seymour (2000, and p. 1611) argue that the observed 3/4 power scaling of BMR is an artifact of the inclusion of large herbivores in the published BMR datasets, as these animals take very long time periods to become post-absorptive because of fermentation of food stuffs and hence inflate the scaling exponent. They report the 'true' exponent for BMR to be 0.686, closer to the 2/3 power suggested by Rubner. For FMR, Nagy (p. 1621) reports scaling exponents ranging from <0.6 to >0.9 in 229 species of mammals, birds and reptiles. For mammals weighing 7 g to 500 kg, the scaling exponent for MMR is found to be 0.872, which is identical to the scaling of mitochondrial volume in the musculature of these animals (Weibel and Hoppeler, p. 1635). Considering all these conditions, is it then possible to find a simple universal scaling law for metabolic rate that is supported, or at least not refuted, by the experimental data?

In all this we must bear in mind that observed overall metabolic rate is the reflection of a multitude of functions of the whole body, from cell activity to locomotor performance, from the circulation of blood to digestion, respiration or reproduction, and much more. We have therefore included in this volume a number of contributions that extend beyond metabolism, in order to give a broader overview of current issues in scaling as seen by prominent comparative biologists; short resumes of these are covered in 'Inside JEB'. All these functions take place in a well-integrated system whereby some functions run in parallel while others are in series. Can such a system be simple and reducible to first principles? Or can complexity theory make a complex system simple? These questions provide food for further reflection that we hope will be fostered by the set of papers collected here.

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