Biological scaling and physics

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Kleiber's law in biology states that the specific metabolic rate (metabolic rate per unit mass) scales as $M^{-1/4}$ in terms of the mass M of the organism. A long-standing puzzle is the $(-1/4)$ power in place of the usual expectation of $(-1/3)$ based on the surface to volume ratio in three-dimensions. While recent papers by physicists have focused exclusively on geometry in attempting to explain the puzzle, we consider here a specific law of physics that governs fluid flow to show how the $(-1/4)$ power arises under certain conditions. More generally, such a line of approach that identifies a specific physical law as involved and then examines the implications of a power law may illuminate better the role of physics in biology.

1. Introduction

There has been a recent spurt of activity by physicists to account for allometric scaling laws in biology, as highlighted in news focus (McKenzie 1999) and news feature (Whitfield 2001) articles. Most notably, there is interest in Kleiber's law (Kleiber 1932; Calder 1984) which states that the specific metabolic rate (metabolic rate per unit mass) scales as $M^{-1/4}$ in terms of the mass M of the organism. Conversely, the average life-span, which is inverse to the metabolic rate, increases with size according to $M^{1/4}$, as indeed observed over a wide range of animal species (Kleiber 1932; McKenzie 1999) from mice to elephants. The most impressive evidence is in McKenzie (1999) and in figure 1a of Dreyer (2001) which present plots of the total metabolic rate vs body mass over a wide range of these parameters for a variety of animals, covering a range from 0·1 to 1000 W(atts) in rate and 10 g to 10,000 kg in mass. All the data points fall on a single straight line in such a log–log plot as per the Kleiber law. Thus, a dove of mass 0·25 kg and metabolic rate of 1·5 W scales to a horse of mass 500 kg and rate of 500 W, the factor of 300 increase in the total metabolic rate being the 3/4 power of the factor of 2000 increase in mass. The metabolic rate per unit mass displays correspondingly the $(-1/4)$ power law. Such

universal trends point to some simple and basic underlying reason behind them.

It is natural to seek such an explanation in geometry, or in some basic physics or biology. Looking first at geometry, a long-standing puzzle is the $(-1/4)$ power in place of the usual expectation of $(-1/3)$ based on the surface to volume ratio in three-dimensions. Since absorption of nutrients, or respiration and heat dissipation, occur through surfaces while the total metabolism depends on the entire volume (and mass) of the body, the relative scaling of surface and volume would point to the $(-1/3)$ power, not the $(-1/4)$ observed. The recent papers (West *et al* 1997, 1999a; Banavar *et al* 1999, 2000; Dreyer 2001) have used different assumptions, but all based only on geometry, to arrive at the $(-1/4)$ power law. Instead, this note combines simple dimensional considerations with a specific law in physics that governs fluid flow to show how the $(-1/4)$ power arises under certain conditions. In other situations, the power may be different. Given the importance of such flows in biology, it is plausible that the physics of fluid flow has a major role in the metabolic rate of organisms, not simply geometry.

The recent papers with purported explanations of Kleiber's law fall into two main categories. One (West *et al* 1997, 1999a) argues for a fractal nature of the internal structure of biological organisms which is claimed

to make them effectively four-dimensional. Some find the catchy "life has an added dimension" (West *et al* 1999a) in itself appealing while others remain unconvinced of fractal structures, leave alone that they have precisely the requisite four-dimensions. The second set of papers (Banavar *et al* 1999, 2000; Dreyer 2001) is couched in terms of efficiency or optimality in directed transportation networks, whether discrete or continuous, and hinges on the growth in the number of sites visited and supplied in such transportation, whatever the fluid involved. Both explanations are geometrical, with little input of either biology or physics, and have attracted criticism as well, particularly from non-physicists (Haff 2000; Painter 2000). The generality of the (– 1/4) power law in biological data has itself been questioned in the past (Calder 1984, pp 358–365) and from a recent (Dodds *et al* 2001) critical examination of data: "you get all sorts of scalings" (McKenzie 1999; Whitfield 2001). The explanations are also too general, "biology's theory of everything" (Whitfield 2001), purporting to explain too much, which itself makes them suspect. Thus, the networks argument, which applies even outside biology, has been questioned, based on data from fluvial sediment transport in rivers (Haff 2000). And, while efficiency and optimality are irresistibly tempting to physicists, they may not have much relevance to the evolution of biological structures and mechanisms.

2. Poiseuille's law for fluid flow

We proceed differently here, tying a few simple dimensional considerations with a specific physical result on streamline flow to show how the (– 1/4) power can arise in certain situations. Where applicable for transport of nutrients, blood, or other fluids in biology and elsewhere, it accounts for this power law while also pointing to other powers when circumstances vary. The key result is the well-known Poiseuille formula (Calder 1984, p. 95) for q, the volume transport per unit time, in a streamline flow through a cylinder,

$$q = (p/8) \, R^4 \, P/hL, \tag{1}$$

where R is the radius and L the length of the cylinder, P the pressure drop across it, and h the viscosity of the fluid. The high (fourth) power dependence on R is crucial and will be related below to the (– 1/4) power in Kleiber's law. The Poiseuille formula was noted (although not the specific scaling arguments developed here) in some of the earlier literature on biological scaling (West *et al* 1997, 1999b) but its significance does not seem to have been fully appreciated, the authors themselves later abandoning hydrodynamics for a purely static, geometrical argument in terms of fractal structures in part in their

quest for a more general explanation for the (– 1/4) power law (McKenzie 1999; Whitfield 2001).

Let us model fluid transport, whether in blood vessels of animals or in channels in plants and trees, by cylindrical tubes and consider how different physical quantities scale with size. We also introduce N parallel tubes, such parallelism being observed widely (see Calder 1984, p. 95 for branching of blood vessels). The high power dependence on R in eq. (1) itself argues for the advantage of the parallel arrangement, the growth in q kept lower by adding several tubes N rather than just increasing R. Thus, we will focus on the flow Q in such a network: $Q = Nq$. We will also take from observation on such flows that P is roughly constant (Calder 1984, p. 98) and assume that h is also constant.

These assumptions hide various subtleties, for instance, that blood is not a simple, uniform, Newtonian fluid. Its viscosity changes with speed v, being lower in capillaries (Breuer 1975, p. 128) as red blood cells collect in the middle thus lowering resistance to flow. Remarkably, however, for the range of speeds involved, blood viscosity is indeed sensibly constant (Sparks and Rooke 1987) even though blood is more a suspension than a simple fluid. Similarly, although the Poiseuille law holds only for streamline flow, turbulence in the blood stream seems to be restricted (except in the case of pathologies) only to the largest arteries like the aorta in the region just beyond the aortic valve, so that the assumption of smooth flow is generally valid (Nave and Nave 1975, p. 88). The greatest departures from the Poiseuille law are due to pulsatile rather than continuous flow, the elasticity and non-rigidity of blood vessels, and departures from the assumed parabolic velocity profile within the flow tube. But, while all these may lead to departures of a few ten percent (Milnor 1982), detailed studies of blood flow show that "the relationships stated by Poiseuille's equation are qualitatively correct" and this law is "indispensable for hemodynamics" (Milnor 1982). In particular, the dominant dependence through the fourth power of the radius R, which will be our focus, is the most crucial element.

3. Scaling

Let us consider a scale factor l; for example, $l = 2$ means doubling. Allowing for possibly different scalings of linear and transverse dimensions, let lengths L scale as l^a and radii R as l^b. Indeed, such different scalings often arise, not all lengths having the same power. For example, the physics of stability of vertical columns against bending due to gravity requires diameters to grow more rapidly than heights; typically, $a = 1$, $b = 3/2$ (Calder 1984, p. 57). This accounts in part for the stockier appea-

rance of tall trees or the legs of elephants when contrasted with the more slender look of their smaller counterparts. Let us also scale time as l^c. With these scalings of distances and time, it follows from dimensional considerations that volumes (whether the amount of blood or other fluids or of the organism as a whole, these expected to be in proportion) and masses (density being approximately constant) scale as $M \propto Nl^{a+2b}$, speeds as $v \propto l^{a-c}$, and from eq. (1), $Q \propto Nl^{4b-a}$. The metabolic rate W, which is an energy flow per unit time, scales similarly to Q under our assumption of constant pressure, energy being the product of volume and pressure. Now, the flow Q is also given by a second expression, namely NAv, where A is the area of cross-section of the tubes and thereby Av the amount flowing per unit time through each tube, so that we have a second relation, Q, $W \propto Nl^{a+2b-c}$. The specific metabolic rate, W/M, thereby scales as l^{-c} as expected, this being inverse to the scaling of time.

The two different scalings of Q or W, the first from the Poiseuille formula and the second purely from three-dimensional geometry, must of course coincide, which leads to

$$2a - c = 2b. \tag{2}$$

For many flows, including of blood, the speed v is roughly constant (Calder 1984, p. 96, Dreyer 2001) so that $a = c$ and, upon combination with eq. (2), we have

$$a = c = 2b. \tag{3}$$

One more relation is needed to link the specific metabolic rate's scaling exponent c with any of the quantities M, Q or W, all of which involve N. We need to know how N scales, $N \propto l^n$. Requiring that Q or W scale just as they would were all linear dimensions to be simply scaled together in the same way as per $L \propto l^a$, that is Q, $W \propto l^{3a}$, leads to $n = 2a$ and thereby $M \propto l^{4a}$, $t \propto l^a$, so that $t \propto M^{1/4}$ and, correspondingly, the specific metabolic rate shows the Kleiber ($-1/4$) scaling with mass.

While accounting for the ($-1/4$) power, the thread of the above argument also shows how other scaling laws may arise. Thus, along with eq. (3), if it is the total mass or volume rather than Q or W that is required to scale by simple uniform dimensional scaling, that is, $M \propto l^{3a}$, then we get $n = a$ and $t \propto M^{1/3}$. This argument of different powers depending on whether M or W is subjected to uniform scaling provides additional perspective on the ($-1/4$) power law. That law, therefore, accommodates a faster than simple scaling growth of mass while holding the increase in metabolic rate reasonable. A numerical example may help to reinforce this point. Consider Poiseuille flow through a cylinder and imagine doubling all linear dimensions, that is, $a = b = 1$, $l = 2$. In this case,

eq. (3) no longer holds, but from eq. (2) we have $c = 0$ so that the speed also doubles. The volume and M increase by a factor of 8 as does the metabolic rate q in eq. (1). Instead, the considerations of the previous paragraph replace the single cylinder by 4 similar cylinders of twice the length and $\sqrt{2}$ times larger radius, as per $a = 1$, $b = 1/2$, $n = 2$, $l = 2$. As a result, Q increases by the same factor of 8 while accommodating a much larger increase in M by a factor of 16. Thereby, as M increases, the Kleiber scaling in the previous paragraph has the growth in Q kept smaller in spite of the high power dependence on R in eq. (1).

4. Conclusions

The arguments that have been advanced so far by previous authors swing to extremes at either end. Thus, the rich variety and diversity in biology, including of scaling exponents, has been used to dismiss the search for underlying causes simply as physicists' hubris. This stance is untenable because, notwithstanding the diversity, there is far too much evidence as already noted from widely disparate biological systems for scaling laws, many of them with the ($-1/4$) power. On the other side, it is also an overreach to argue too generally, claiming the same power law for "everything". This is not how physics fits into biology. Rather, physics comes in especially "at the edges" in constraining the limits into which biological organisms fit since they too are subject to the laws of physics.

What is remarkable about the biological world is that within such limits set by physics, most niches in between seem to have been explored, if not occupied, during the course of biological evolution. A more modest approach, therefore, and the spirit in which this note is advanced, is to see what constraints are set by geometry and by physical laws that are expected to be relevant, and then see what some of the observed biological scalings further imply. We have examined here one such, the Poiseuille law governing fluid flow under certain conditions. This leads to constraints such as eq. (3) but even there permits alternative scaling laws including the ($-1/4$) power law depending on further assumptions as explored above.

Finally, our discussion also makes a pleasing historical contact because Jean Louis Marie Poiseuille (1799–1869) was a French medical doctor who contributed to the theory of blood circulation while providing a law of physics. He was the first to use mercury for blood pressure measurements and, in trying to understand blood flow in capillaries, he conducted experiments with narrow tubes, thus developing the basic principles of both hemodynamics and hydrodynamics (Sparks and Rooke 1987).

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