Allometric Scaling and Central Source Systems

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Allometric scaling relations abound in nature. Examples include the power law relating the metabolic rate of animals and plants to their masses and the power law describing the dependence of the size of the drainage basin of a river on the total amount of water contained in that river. The exponent is of the form $D/D + 1$, where D is the dimension of the system. We show that this scaling exponent is simply a consequence of the source distribution of the systems considered and requires no further assumptions. To demonstrate the wide range of validity of the result we present a simple experiment that shows the predicted behavior in one dimension.

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In nature a class of remarkable laws exists which relate a wide range of inanimate as well as animate systems of a wide variety of shapes and sizes. The relations we are concerned with here are allometric scaling laws of the form

$$Y = Y_0 X^{\gamma}. \tag{1}$$

Here X and Y are two variables describing the system, γ is the scaling exponent, and Y_0 is a constant. A certain class of systems which can be described by (1) will be of special interest to us. Examples of such systems are as follows.

(i) For animals and plants the metabolic rate B is related to the mass M through a power law of the above type. One finds [1–4]

$$B = B_0 M^{3/4}. \tag{2}$$

For animals this relation is known as Kleiber's law (see Fig. 1a).

(ii) The size A of the drainage basin of a river and the total amount of water M contained in the river satisfy [5]

$$A = A_0 M^{2/3}. \tag{3}$$

(iii) To obtain an illustrative example of a one-dimensional system we performed an experiment in which we run water over a permeable tissue (see Fig. 1b). We constrained the flow of the water so that it was free to move in only one direction thus creating an essentially one-dimensional system. Because the tissue is permeable the water only manages to wet a certain length L of the tissue. This length L varies with the magnitude of the water flow into the system. One then finds that the mass M of the water on the tissue and the length L are related by the equation (see Fig. 1c)

$$L = L_0 M^{1/2}. \tag{4}$$

The scaling exponent in all of these examples is of the form $D/(D + 1)$ where D is the number of spatial dimension of the system. How can such a general relation hold for systems as different as rivers and animals?

To find an answer to this question we look at the similarities between the different systems: All systems possess a flowing medium such as water or blood that can be described by a flow $\boldsymbol{j}$. In all of the above examples this flow has one central sink (or source) and a distribution of sources (or sinks, respectively). An animal has a heart and cells that require a certain amount of nutrients per time; a river has an estuary and a drainage basin that acquires a roughly constant amount of water per time and area through rain, and the water system of Fig. 1 has a constant supply of water together with a permeable tissue that allows water to seep through at a certain rate per length. We now assert that the existence of a central sink (or source) and a distribution of sources (or sinks) is the decisive property that gives rise to the power law behavior with a scaling exponent $D/(D + 1)$.

The basic idea is straightforward and can be stated as follows. Since the central sink has to reach all of the system, the flow at any given point in the system not only accounts for the local source but has to account for all the other sources farther away from the central sink. If one then increases the size of the system, the flow at any given point increases in proportion to this size. It then follows that the overall mass of the flowing matter grows faster than the size of the system. This is the origin of the scaling exponent.

We abstract the systems above by a region V in D-dimensional Euclidean space containing the origin. On V we are given a flow $\boldsymbol{j}$ whose divergence is given by a source density σ together with a pointlike sink (or source) situated at the origin and whose transverse component vanishes on the border of V. The last assumption is saying that no flow is leaving the system. It can be regarded as following from the condition that V encompasses all of the system. We will denote by Y the volume of V. Let now ρ and $\boldsymbol{v}$ be the density and velocity of the flowing medium such that

$$\boldsymbol{j} = \rho \boldsymbol{v}. \tag{5}$$

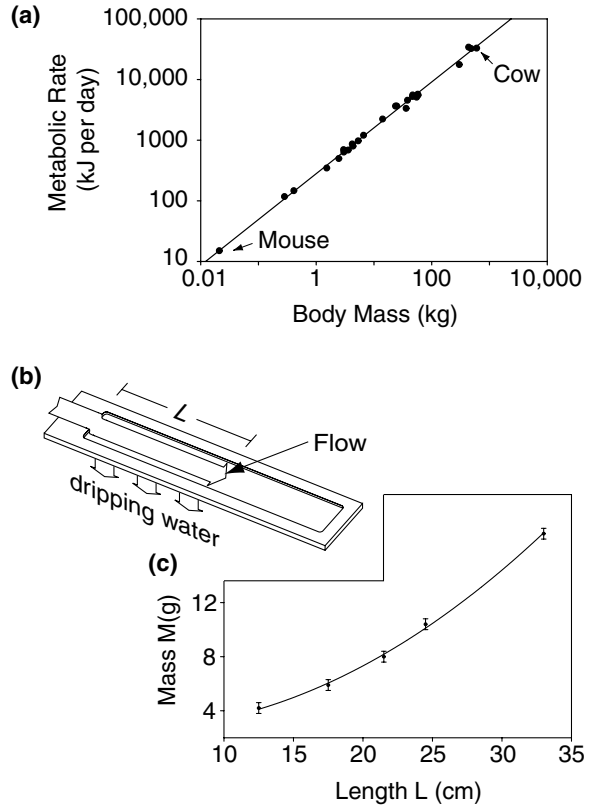

FIG. 1. Examples of allometric scaling. (a) This graph shows a double logarithmic plot of the metabolic rate vs the mass for several mammals. The slope of the straight line is three-fourths. The data for the plot are taken from Kleiber [2]. (b) An example of a one-dimensional central source system: Water running over a permeable tissue. The flow of the water is constrained in one direction so that the system is essentially one dimensional. Since water is dripping through the tissue a water layer of length L is forming. (c) Plotting the mass M of the water on the tissue vs the length L of the water layer gives a parabola in agreement with Eq. (4) which gives $M \propto L^2$. An existing linear term is due to water clinging onto the surface of the tissue before dripping off.

We then define X to be the integral of the density ρ over the volume V. Our goal is to establish the following relation between the quantities X and Y:

$$Y = Y_0 X^{D/(D+1)}, \tag{6}$$

for some constant Y_0. We will then discuss in detail how X and Y are related to the quantities found in our examples.

For the sake of concreteness we will assume in the rest of the paper that we have a central sink and a distribution of sources inside of V. The situation then resembles that of a river.

Before dealing with the general case we look at the instructive but purely academic example of a ball V of radius R. To facilitate the discussion even more we will assume that we have a constant distribution of sources inside the ball, that the magnitude of the velocity $\boldsymbol{v}$ is constant, and that the situation is spherically symmetric. In this highly idealized case the flow j can be easily found. Since we assume a constant source density the amount of medium acquired inside two spheres of radius r and R, $r < R$, is proportional to the volume contained within these spheres. It then follows from the assumption that j vanishes on the border of V that this amount of medium has to flow entirely through the inner sphere of radius r (see Fig. 2a). If we thus denote by $j(r)$ the flow through the sphere of radius r we find

$$j(r) \propto (R^D - r^D). \tag{7}$$

Since we assume that the magnitude of the velocity is constant we infer from Eq. (5) that the quantity X is proportional to the integral of $j(r)$ over the whole ball. We thus find

$$X \propto R^{D+1}. \tag{8}$$

Since Y is proportional to R^D we obtain the desired equation (6) if we eliminate R.

We now turn to the general case, i.e., the case in which there is no constant distribution of sources, no constant

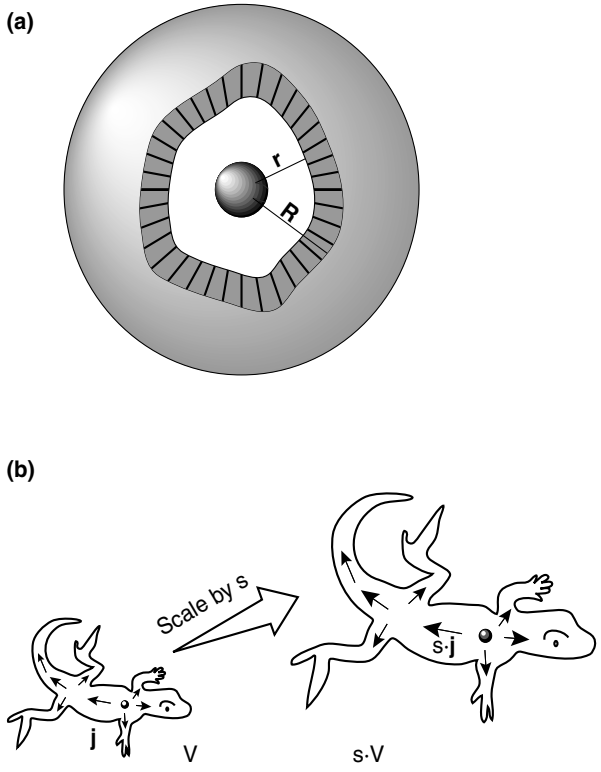

FIG. 2. The origin of the scaling exponent of $D/(D+1)$ for central source systems. (a) For a spherical system the flow $j(r)$ through a shell of radius r is proportional to the volume within the spheres of radius r and R, i.e., to $(R^D - r^D)$; (b) the key observation for the general situation is that if $\boldsymbol{j}(\boldsymbol{r})$ is the flow for the unscaled system then $s \cdot \boldsymbol{j}(\boldsymbol{r}/s)$ is the flow for a system scaled by a factor s.

velocity v, and no spherical symmetry. We assume that we have calculated the quantities X and Y for a region V and we ask how these quantities change if we scale the region by a factor $s > 0$, i.e., if we replace V by $s \cdot V$, and replace the source density $\sigma(\boldsymbol{r})$ by $\sigma(\boldsymbol{r}/s)$ (see Fig. 2b). The values of X and Y for the scaled region will be denoted by $X(s)$ and $Y(s)$, respectively. The key observation here is that if $\boldsymbol{j}(\boldsymbol{r})$ is a flow for the unscaled region, then $s \cdot \boldsymbol{j}(\boldsymbol{r}/s)$ is the corresponding flow for the scaled region. This can be seen as follows. The flow for the unscaled region satisfies $\nabla \cdot \boldsymbol{j}(\boldsymbol{r}) = \sigma(\boldsymbol{r})$. We require the corresponding relation to be true for the scaled region also. The flow must then be $s \cdot \boldsymbol{j}(\boldsymbol{r}/s)$ since $\nabla \cdot s\boldsymbol{j}(\boldsymbol{r}/s) = (\nabla \cdot \boldsymbol{j})(\boldsymbol{r}/s) = \sigma(\boldsymbol{r}/s)$. The flow thus scales with the factor s. The quantity $X(s)$ can now be calculated if we furthermore assume that the velocity for the scaled region is given by $\boldsymbol{v}(\boldsymbol{r}/s)$. Since the volume scales as s^D we then find

$$X(s) = s^{D+1} X\,, \tag{9}$$

$$Y(s) = s^D Y\,. \tag{10}$$

After eliminating s in these formulas we obtain Eq. (6).

We now want to relate our result to the examples given in the introduction. We have to identify the two quantities X and Y in our formula (6) with the quantities introduced there.

We start with our first example of animals and plants. Let V be the part of the animal or plant that contributes to the metabolism and that is supplied with nutrients. The metabolism B is then proportional to the volume of V, i.e., to our quantity Y. It is important to note here that Y is generally smaller than the total volume of the animal or plant.

Next we have to identify the quantity X. It is known that the mass M of an animal is proportional to the amount of blood contained in the animal [4]. Our quantity X, which is the integral of ρ over V, is exactly the mass of the blood. X is thus proportional to the mass M of the animal.

It is important here to realize that for our derivation of the scaling law to be valid we needed to assume that the velocity of the blood is approximately independent of the scale. This means that blood does not move faster in a whale then it does in a lizard. This assumption has been shown experimentally to be true for mammals [6]. These arguments then show that our Eq. (6) entails Eq. (2) for $D = 3$.

For a river the size A of the drainage basin is the volume of the system and thus equals our quantity Y. By an argument similar to the one given for animals and plants we see that X corresponds to the amount of water contained within the river. The assumption that the velocity of the water within the basin is independent of the size of the basin has been checked experimentally [7,8]. Setting $D = 2$ in Eq. (6) then gives Eq. (3).

In our one-dimensional water system Y corresponds to the length L of the water layer on the tissue and X is the mass M of the water in the system. We recover (4) from (6) for $D = 1$.

Our results show that very few assumptions have to be made to account for the class of allometric scaling laws discussed here. If a system is a central source system it will show this type of scaling with the characteristic $D/(D + 1)$ scaling exponent. The generality of the result resonates well with the wide validity of the power law.

Our explanation of the allometric scaling law is very much in the spirit of the one given by Banavar *et al.* [5] which deals with discrete transportation networks. A difference lies in the fact that our continuous approach excludes certain flows from the outset. A spiral-like configuration, e.g., which connects every node of the network through one string of links does not have an admissible counterpart in our framework. This is why our assumptions are sufficient to arrive at the correct scaling law. Our result furthermore provides insight into the case of unicellular organisms where no transportation network exists.

The result given here casts some shadows of doubt on explanations given recently by West *et al.* [9] in terms of special properties of transportation networks such as their fractal character. The simple assumptions made here show that fractality may not be the fundamental principle underlying allometric scaling.

It is remarkable that the rather complicated reasoning given by McMahon [10] in terms of elastic criteria leads to the same result as our reasoning in terms of central source systems. It is tempting to speculate what nature would look like if these two considerations lead to different results.

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