Non-universal Interspecific Allometric Scaling of Metabolism

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We extend a previously theory for the interspecific allometric scaling developed in a $d+1$-dimensional space of metabolic states. The time, which is characteristic of all biological processes, is included as an extra dimension to d biological lengths. The different metabolic rates, such as basal (BMR) and maximum (MMR), are described by supposing that the biological lengths and time are related by different transport processes of energy and mass. We consider that the metabolic rates of animals are controlled by three main transport processes: convection, diffusion and anomalous diffusion. Different transport mechanisms are related to different metabolic states, with its own values for allometric exponents. In $d=3$, we obtain that the exponent b of BMR is $b=0.71$, and that the aerobic sustained MMR upper value of the exponent is $b=0.86$ (best empirical values for mammals: $b=0.69(2)$ and $b=0.87(3)$). The 3/4-law appears as an upper limit of BMR. The MMR scaling in different conditions, other exponents related to BMR and MMR, and the metabolism of unicellular organisms are also discussed.

Keywords: Allometry, Interspecific Biological Scaling, Metabolism, Basal Metabolic Rate, Maximum Metabolic Rate, Mammals, Birds

I. INTRODUCTION

Several biological quantities change with organism size according to particular rules [1–3]. It is common to believe that these rules are related with the euclidean geometry. However, in many cases the geometric pattern is not observed because physical constraints also limit how much an organism can be modified to cope with changes in scaling. Recently, considerable effort has been invested to understand the scaling of some of these variables under certain physical and geometrical constraints: the dimensions of long bones [4, 5], the basal metabolic rate (BMR) [6–11], the maximum metabolic rate (MMR) [11–13] and the cost in food webs [14]. In this paper we are interested in the scaling of metabolic rate, which is the most studied variable in traditional allometry.

It is accepted and empirically tested that the metabolic rate B and the body mass M of almost all organisms are connected by a power law relationship $B=aM^b$, where a is a constant and b is the scaling exponent [1–3, 15]. The origin and the universality of the scaling exponent of metabolic rates is a subject of great controversies and there are several debates in the literature [16–22]. In a recent paper [11], we and a colleague proposed an unified theory for the interspecific allometric scaling of metabolism. It was developed in a $d+1$ dimensional space of metabolic states of organisms (d biological lengths and a physiological time). It is natural to include explicitly an extra temporal dimension in the analysis of allometric scaling because all biological process are time dependent. Moreover, in some cases this approach has produced a simple explanation for the problem with satisfactory results [11, 23–25]. In that paper [11], the authors supposed that each metabolic rate of organisms is characterized manly by one of two transport processes, namely, convection and diffusion. In this paper we consider the general case in which a metabolic rate of 3-dimensional organisms can be characterized by one, two or three of the transport processes: convection, diffusion and anomalous diffusion. It is well known, that the transport in large distances is done by convection and the transport in small distances is done by diffusion. A classical example is the oxygen transported from the heart until the capillaries by convection and from the capillaries to the cell by diffusion. However, the mechanism of transport of large molecules inside a cell and between the cells of a tissue is still unknown and in many cases is suggested to be an anomalous diffusion. The three kinds of transport imply also we must now deal with different characteristic times. But they are all related if the network delivery is optimal.

This work is organized as follows. We discuss the hypotheses of da Silva, Barbosa and Silva (SBS) [11] and present a new one, and derive the main equations in Sec. II. In Sec. III we re-derive the scenarios for BMR of SBS work in our present context as limiting cases. The BMR of mammals and birds is studied in Sec. IV and the scaling of capillaries and aorta are obtained in Sec. V. The approach to describe the MMR of endotherms is presented in Sec. VI and the exponents of aorta and capillaries in the MMR conditions are discussed in Sec. VII. The metabolism of unicellular organisms is discussed in Sec. VIII. We summarize our results in the last section.

II. HYPOTHESES AND MAIN RELATIONS

Following SBS [11] we use the mass density $\rho_{d+1}(L_1, L_2, \ldots, L_d, \tau)$ (mass per unit volume and unit time) and the energy density $\sigma_{d+1}(L_1, L_2, \ldots, L_d, \tau)$ (available energy per unit volume and unit time) to characterize the metabolic state of organisms. The use of energy density

is justified because in the metabolic processes ATP cannot be supplied from outside but must be synthesized within the organism (within the cells). The efficient use of substrates by cells depends on the presence of an adequate quantity of mitochondria as power house [26] and secondly on adequate supply of fuels and oxygen. The fuels, which are directly related to the available energy E, are contained inside the organism but the oxygen flux is supplied by outside the organism. So, energy content is important to characterize the state of an organism. This can also be illustrated with the MMR situation. The animal runs until it has no more available energy. Then it falls exhausted.

The first and second hypotheses are that natural selection enforces the constraints of *scaling-invariant* (independent of body mass) ρ_{d+1} and σ_{d+1}, during evolution. The third hypothesis is that the scaling of the metabolic states is determined by the *dominant dynamical transport processes of nutrients*. Moreover, these processes are characterized by scaling-invariant quantities (diffusion coefficient, average velocity, etc.).

Although we have d biological lengths, each one with its characteristic time t_i ($i = 1, 2 \ldots, d$), we suppose that only one time τ is relevant to describe the metabolic states. It means that the resources rates of all these processes must be matched (($1/t_1) \propto (1/t_2) \ldots (1/t_d) \propto (1/\tau)$) (symmorphosis principle proposed by Taylor and Weibel [12]). Therefore we are considering optimal transportation networks (the new fourth hypothesis).

It follows from the second hypothesis that $E = \sigma_{d+1} \tau V_d$. Here, we have that τV_d is the $(d+1)$-volume and $V_d = L_1 L_2 \ldots L_d$. Using the power definition ($P = dE/dt$), the energy can be written in terms of the metabolic rate B, the power averaged over the time scale τ, as $E = B\tau$. Therefore from the first and second hypotheses we obtain an equation for the organism's mass, namely

$$M = \rho_{d+1} \, \tau V_d \, , \tag{1}$$

and the following expression for the metabolic rate

$$B = \sigma_{d+1} \, V_d \, . \tag{2}$$

Note that Eqs. (1) and (2) are valid for all metabolic regimes. Different metabolic scaling regimes will appear because there are different ways to transport nutrients.

III. LIMIT SCENARIOS FOR THE BASAL METABOLIC SCALING

III.1. The BMR-3 scenario

We discuss in this section some limit cases for the basal metabolic rate scaling. Let us first study the BMR-3 scenario, a lower bound for all metabolic scaling. We suppose that all the transportation occurs via diffusion, implying that

$$L_i = D_i t_i^{1/2} \, , \text{ with } \, i = 1, \, 2 \ldots, \, d \, ,$$

where D_i^2 are the scaling-invariant diffusion coefficients and t_i are characteristic times. Since the resource supply rates

must be matched ($1/t_1 \propto 1/t_2 \ldots 1/t_d \propto 1/\tau$), we have only one time scale (τ) and only one relevant length, namely

$$L_1 \propto L_2 \propto \ldots \propto L_d \propto L \, .$$

Note that the biological volume is given by $V_d \propto L^d$. Since $L_i = D_i \tau^{1/2}$, we obtain from Eq. (1) that $\tau \propto M^{2/(d+2)}$. This relation furnishes how L depends on M, namely $L \propto M^{1/(d+2)}$, and we can use Eq. (2) to obtain that

$$L \propto M^{\frac{1}{2+d}} \, ,$$
$$\tau \propto M^{\frac{2}{2+d}} \, ,$$
$$B \propto M^{\frac{d}{2+d}} \, .$$

In $d = 3$, the metabolic exponent is $b = 3/5$. Since these transportation processes are the slowest ones, this value is a lower bound for the exponent b for all metabolic situations. Note that this scenario can, in principle, describe the metabolic rate of very small organisms because diffusion over short distances is fast.

III.2. The BMR-2 scenario

For larger organisms, transport by convection is utilized on large length scales because diffusion is slow. In the cardiovascular system of mammals, for example, blood circulates in a ballistic regime until the capillaries, where diffusion plays the main role. Therefore we consider first that the BMR is driven by *ballistic transport*, namely

$$L = v_0 \tau \, ,$$

where the velocity v_0 is scaling-invariant. Then we must taken in account the other metabolic steps. In a "cylindrical" symmetry we have $L_1 \propto L = v_0 t_1$ (ballistic term) and $d - 1$ lengths $R_i = D_i t_i^{1/2}$ (diffusion terms). v_0 and all D_i ($i = 2, 3, \ldots, d$) are scaling-invariant. Since the delivery of the network is optimal ($t_1 \propto t_2 \ldots \propto \tau$), it follows that $R_i \propto D_i \tau^{1/2}$. From Eq. (1) we obtain that $\tau \propto M^{2/(3+d)}$, implying that $L_1 \propto M^{2/(3+d)}$ and $R_i \propto M^{1/(3+d)}$. Since the biological volume is $V_d \propto R^{d-1} L_1$, we obtain from Eq. (2) that

$$L_1 \propto \tau \propto M^{\frac{2}{3+d}} \, ,$$
$$R \propto M^{\frac{1}{3+d}} \, ,$$
$$B \propto M^{\frac{1+d}{3+d}} \, .$$

Then in $d = 3$, we obtain the 2/3 law. Note that this result was obtained without mention of the area/volume ratio.

III.3. The BMR-1 scenario

In this scenario all metabolic relevant lengths are related to the ballistic transport, namely $L_i = v_i t_i$ ($i = 1, \ldots, d$). Using that all characteristic times are proportional to τ (fourth hypothesis), we find that $L_i \propto \tau$. In other words, there is only *a single metabolic relevant length* $L \propto v_0 \tau$ and *a single time*

τ, both related to the ballistic transport. This scenario represents an upper bound for BMR. Since that $V_d \propto L^d$, we find from Eq. (2)that

$$L \propto \tau \propto M^{\frac{1}{d+1}} \ ,$$
$$B \propto M^{\frac{d}{d+1}} \ .$$

Therefore we find the 3/4-law for $d = 3$, namely $B \propto M^{3/4}$. This upper bound value is the same as those of West, Brown and Enquist [6] and Banavar et al. [7, 8]. It is worth mentioning that Demetrius [10] found that the b exponent of BMR should be in the interval $[2/3, 3/4]$. His work is based in the integration of the chemiosmotic theory of energy transduction with the methods of quantum statistics.

IV.   BMR OF MAMMALS AND BIRDS

From now on we use $d = 3$ because cells and organisms are three dimensional objects. We also use a single time (τ) for all transportation processes because all characteristic times are proportional to it. In order to study the BMR scaling of mammals and birds, let us discuss the nutrient transport inside an eukaryotic cell and between different cells of a tissue. The first biological length L_1 is related to the transport of oxygen and small molecules by diffusion, namely

$$L_1 = D\tau^{1/2} \ .$$

On the other hand, large molecules can also be trapped in vesicles by macropinocytoses and pinocytoses and transported in direction of the nucleus. Note that a vesicle can carry a relatively large quantity of fuel. Although the exact description of vesicular transport is still unknown, we suppose it as an anomalous diffusion process [27, 28], namely

$$L_2 = D_x\tau^{(1/2)+x} \ .$$

The normal diffusion and ballistic transport processes occur when $x = 0$ and $x = 1/2$, respectively. This description is supported by works [29, 30] about the movement of engulfed particles on eukaryotic cells. Beads placed on the peripheral lamella of giant human fibroblasts are engulfed into the cytoplasm and move in direction of the nuclear region. In the lamella region the beads move ballistically with an average velocity of $v \approx 1 \ \mu m/min$ ($L \propto vt$). In the perinuclear region they move randomly within a restricted space and the authors have determined that $L \propto t^{3/4}$. Moreover, in a recent work of Neto and Mesquita [31] of optical microscopy, the authors conclude that the movement of a macro pinosome inside a macrophage is ballistic ($L \propto vt$). The average velocity v varies from $0.5 \ \mu/min$ to $2.0 \ \mu m/min$ depending on the radius of the macro pinosome. Therefore is quite probable that $x \approx 1/2$. We emphasize that a fuel vesicle is transported not only inside a cell but also from one cell to other one of the tissue.

In the case of the BMR of mammals and birds, there is also a biological length

$$L_3 = v_0\tau$$

TABLE I: Allometric exponents related to the basal metabolism for mammals and birds. Under parenthesis is the error in the last significative of the observed quantities.

Predicted	Observed	Comment	Ref.
	Basal metabolic rate		
0.714	0.712(13)	mammals	[17]
[0.667, 0.714]	0.737(26)	binning data	[17]
0.666 (BMR-2)	0.668(25)	small mammals	[16]
0.750 (BMR-1)	0.710(21)	mammals	[16]
	0.664(15)	birds	[16]
	0.686(14)	large mammals excluded	[19]
	0.669	birds	[42]
	Heart rate		
−0.286	−0.25(2)	mammals, unknown data	[34]
[−0.333, −0.286]	−0.25	mammals	[43]
−0.333 (BMR-2)	−0.27	mammals	[33, 44, 45]
−0.250 (BMR-1)	−0.25(3)	mammals, binning data of [33]	[17]
	−0.26	mammals	[46]
	−0.27	mammals	[47]
	−0.23	birds	[48]
	−0.209	birds	[49]
	−0.33(6)	birds	[50]
	Respiration rate		
−0.286	−0.260(5)	mammals	[34]
[−0.333, −0.286]	−0.28	mammals	[45]
−0.333 (BMR-2)	−0.28	mammals	[51]
−0.250 (BMR-1)	−0.25	mammals	[52]
	−0.26(6)	mammals, binning data of [53]	[17]
	−0.31	birds	[48]
	−0.20	birds	[49]
	−0.33	passerines	[43]
	−0.28	nonpasserines	[43]

related to the transport by convection utilized on large length scales. For example, we find in mammals the cardiovascular system that transports blood to the capillaries.

To obtain the exponent b we first evaluate V_3 in terms of τ, namely $V_3 \propto DD_xv_0\tau^{2+x}$. Then, we use the relation between mass and τ (Eq. 1) to find how τ depends on M ($\tau \propto M^{1/(3+x)}$). Finally, we use Eq. (2) to obtain how B depends on M. It follows that

$$B \propto M^{\frac{2+x}{3+x}} \ ,$$
$$\tau \propto M^{\frac{1}{3+x}} \ .$$

The case $x = 0$ give-us $b = 2/3$ and correspond to the BMR-2 scenario, where we have two lengths related to diffusion and one related to convection. This scenario yields the 2/3 law. When $x = 1/2$ the vesicular transport within a cell is ballistic and we have that $b = 5/7 \approx 0.714$. Since it is quite probable that $x \approx 1/2$, the BMR exponent of mammals and birds is close to $b = 5/7$.

The empirical and predicted values of the BMR exponent b of mammals and birds are shown in Tab. I. This is the most analyzed and discussed allometric scaling in the last years. Note that all empirical values for b are in the predicted range, except the one $(0.737(26))$ obtained by Savage et al. [17] with a data "binning" procedure. In such procedure the log-transformed data were averaged into equally spaced data points in order to achieve equal weight to all body size intervals and prevents phylogenetic relatedness. However, the error bars do not exclude the upper value of the range 0.714. Since their procedure has been criticized by Glazier [20], we note that the same data set without the binning procedure furnishes $b = 0.712(13)$, a value in good agreement with our prediction. Perhaps the more rigorous

and complete study of the mammalian BMR exponent is the work of White and Seymour [19](see also [32]). The authors excluded large herbivores of the data due to their long fast duration required to reach the post-absorptive state of BMR and obtained $b = 0.686(14)$. They note that such animals are typically fasted for less than $72\,h$ before the measurement of O_2 consumption, while the post-absorptive state of ruminants may require 7 days to be reached. We think that large mammals must be included in the data. Perhaps the BMR value can be obtained by a time extrapolation procedure, in which some measurements are realized periodically after the initial fasting. It is quite possible that this procedure will slightly raise the estimation of b. Interesting, the avian BMR exponent values are close to the lowest value of the predicted range.

Since the heart rate scaling is obtained by using that $F \propto M^{-f} \propto 1/\tau \propto M^{-1/(3+x)}$, the predicted range for f is $[-0.333, -0.286]$. There is not a recent comprehensive analyze of this exponent for mammals. In Tab. I we also shown the data for the pulse rate and respiration rate of mammals and birds measured in basal conditions. Savage et al. [17] obtained -0.25 by binning the data of Brody [33] (original exponent $b = -0.27$). Stahl [34] claims that $f = -0.25$ but he has not published its data. The empirical value for birds is more scattered and there is a report of an empirical value near the lower value of the predicted range. Although the pulse rate is more easy to measure than BMR, it is hard to achieve any conclusion about the empirical value of f. Note that the value -0.27 is out of the predicted range but is also different from -0.25. In fact, it is equidistant from -0.25 and -0.286. It is worth mentioning that -0.27 was also predicted by other recent analysis of Bishop [35]. On the other hand, the respiration rate empirical exponents of mammals and birds have the majority of values within the predicted range.

V.   OTHER EXPONENTS OF BASAL METABOLISM FOR MAMMALS AND BIRDS

In order to obtain other exponents, let us now characterize the network by "aorta" and "capillaries". We define L_a, R_a and v_a as the aorta length, radius and fluid velocity, respectively. The capillaries can be described by the capillary number N_c, length l_c, radius r_c and fluid velocity v_c. It is worth mentioning that the length l_c and the radius r_c of capillaries *are not necessarily invariants*, although, from our third assumption, we need some dynamical scaling-invariant quantities, like the blood flow speed velocity v_0 in the aorta or in the capillaries. The exponents related to these quantities can be obtained from the nutrient fluid conservation in the transportation network. Fluid conservation implies that

$$\dot{Q} = \pi R_a^2 v_a = N_c \pi r_c^2 v_c \ , \qquad (3)$$

where $\dot{Q}$ is the volume rate flow. It is clear that $\dot{Q} \propto B$ is a natural assumption. Since v_a is invariant, the aorta radius scaling is given by $R_a \propto B^{1/2}$ and the aorta length scaling is described by $L_a \propto v_a \tau$. These last relationships imply that the exponents a_R and a_L defined by $R_a \propto M^{a_R}$ and $L_a \propto M^{a_L}$ are $a_R = (2+x)/(6+2x)$ and $a_L = 1/(3+x)$. The transition from the largest length scale (aorta) to the cell length

scale occurs in the arterioles and capillaries. v_c must be scaling-invariant and, since the blood cells have the same size, we can make the extra assumption that r_c is also scaling-invariant. Therefore the density of capillaries N_c/M behaves as $N_c/M \propto B/M$. The capillary length can be invariant or mass dependent. Since the typical cell transport length is not scaling-invariant, the capillary length should also depend on M, namely $l_c \propto v_c \tau_c \propto v_c \tau$.

VI.   THE MMR OF MAMMALS AND BIRDS

The circulatory networks of endothermic animals make a transition from resting to maximum activity in such way that (i) the heart increases its rate and output, (ii) the arterial blood volume increases due to constriction of the veins and (iii) the total flow and muscular flow increase, with all muscular capillaries activated. These facts suggest that we have a "forced movement" during the characteristic time τ, implying that the typical constant velocity can be written as $v = a_0 \tau$ (a_0 is a scaling-invariant acceleration). Therefore the aerobic sustained MMR is limited by an inertial movement accelerated during time τ and the ballistic movement of BMR is now given by $L = v\tau = a_0 \tau^2$.

In the upper limit of the MMR of animals, the MMR-1 scenario, all lengths are related to the inertial accelerated movement ($L_i = a_i \tau^2$, $i = 1, 2, 3$). Since $V_3 \propto L^3$ and $L \propto \tau^2$, we obtain from Eqs. (1) and (2) the metabolic relations:

$$L \propto M^{\frac{2}{7}} \ ,$$
$$\tau \propto M^{\frac{1}{7}} \ ,$$
$$B \propto M^{\frac{6}{7}} \ .$$

These results agree with the ones obtained trough a generalization of West, Brown and Enquist [6] ideas to the MMR [13].

In the BMR description, we had i) a length (L_1) related to diffusion of O_2 and small molecules, ii) a length (L_2) associated to the anomalous diffusion of vesicles and very near to a convection movement and iii) a length (L_3) related the large scale transport of blood by convection. The MMR-1 scenario consider that L_3 is the only relevant length and that L_1 and L_2 evolved to match it. Although this description explains better the empirical data and is more consistent with the maximal restrictions of MMR conditions, we must consider other cases. We call the MMR-2 scenario, when at least the lengths related to ballistic movement (L_3 and L_2) changes to $L_3 = a_3 \tau^2$ and $L_2 = a_2 \tau^2$, respectively. $L_1 = D_1 \tau^{1/2}$ remains the same. Using Eqs. (1) and (2) we obtain that

$$L_3 \propto L_2 \propto M^{\frac{4}{11}} \ ,$$
$$L_1 \propto M^{\frac{1}{11}} \ ,$$
$$\tau \propto M^{\frac{2}{11}} \ ,$$
$$B \propto M^{\frac{9}{11}} \ .$$

When only the length related to the large scale transports changes ($L_3 = a_3 \tau^2$, $L_2 = v_2 \tau$, $L_1 = D_1 \tau^{1/2}$), we have the

MMR-3 scenario. A similar procedure furnishes the following results:

$$L_3 \propto M^{\frac{4}{9}} \; ,$$
$$L_2 \propto M^{\frac{2}{9}} \; ,$$
$$L_1 \propto M^{\frac{1}{9}} \; ,$$
$$\tau \propto M^{\frac{2}{9}} \; ,$$
$$B \propto M^{\frac{7}{9}} \; .$$

Note that the MMR and the heart frequency exponents should be in the intervals $[7/9, 6/7]$ and $[-2/9, -1/7]$, respectively. The predicted values of b and the heart rate exponent f for animals agree with the empirical values (see Tab. II) for animals in exercise-induced MMR conditions. But we must emphasize that the MMR data base is much narrower than it appears. Several references, for example Savage et al. [17] and Bishop [36], represent basically the same data, namely those from the study of Taylor and Weibel [12] with some variation in the data composition. Note also that athletic species have a higher level of MMR than normal (non-athletic) ones [37]. For species with similar body mass, the MMR of athletic species can be 2.5 up to 5 times greater than the normal one. This implies that ρ_4/σ_4 are different for the two groups. The MMR theory just developed must be valid for normal species. Since the MMR exponent for athletic species ($b = 0.94(2)$) is very different from the one ($b = 0.85(2)$) for normal species, it is reasonable to assume that the inertial transport is different for the athletic group. If we assume that $L_3 = c_3 \tau^3$, instead of $L_3 = a\tau^2$, we obtain a large exponent $b = 9/10$, a value near the empirical result.

MMR can also be induced by exposure to low temperature. Oxygen consumption is measured during progressive reduction of the ambient temperature until a decline in this consumption is observed. In these experiments, the animal loses such heat quantity that the usual ways to dissipate it are overwhelm. Then it is possible that the relevant lengths be dominate by heat diffusion ($L_1 \propto L_2 \propto L_3 \propto \tau^{1/2}$). This implies that $b = 3/5$. However, if we consider that the blood transport in the arterial system be also relevant we have that $L_3 = a_0 t_3^2$ and $L_1 \propto L_2 \propto t^{1/2}$. In this case we obtain that $b = 3/4$. It follows that the cold-induced MMR exponent should be in the interval $[0.600, 0.750]$, in a relatively good agreement with empirical values.

VII. OTHER EXPONENTS OF MAXIMUM METABOLISM FOR MAMMALS AND BIRDS

The exponents related to the aorta are easily obtained from Eq. (3). Now the aorta blood velocity is not constant and grows with body mass as $v_a \propto a_0 \tau \propto M^{1/7}$ (MMR-3). In fact this exponent should be in the range $[0.143, 0.22]$. From now on we will discuss the exponents always in MMR-1 scenario which is in better agreement with the empirical data. The exponents related to the aorta radius and length are given by $a_R = 5/14$ and $a_L = 2/7$, respectively. The description of capillary scaling is not so clear. The radius r_c can be assumed invariant since the blood cells do not depend on body mass. There are three possibilities for the blood velocity v_c

and the capillary length l_c: (i) v_c and l_c are invariant, (ii) v_c is invariant and $l_c = v_c \tau_c$ and (iii) $v_c = a_c \tau_c$ and $l_c = a_c \tau_c^2$ with a_c invariant. Since we are assuming that the typical transport length in a cell is not invariant, l_c should not be scaling-invariant. Let us consider the case (ii). Using that r_c and v_c are invariant, we obtain from Eq. (3) that the density of capillaries behaves as $N_c/M \propto M^{-1/7}$. If $\tau_c \propto \tau$ we obtain $l_c \propto M^{1/7}$. On the other hand, if $\tau_c \propto t_2$ and $x = 1/2$ we obtain that $l_c \propto M^{2/7}$.

We discuss now the aorta scaling. As already discussed, it is it is probable that $x = 1/2$. In this case the BMR and MMR theories predict the same exponents a_R and a_L for the aorta radius and length, namely $a_R = 0.357$ and $a_L = 0.286$. These values are in agreement with the empirical values (see Tab.II). The aorta velocity v_a is invariant in the BMR description, in agreement with data (Dawson, 2003) ($v_a \propto M^{0.07}$). On the other hand, in the MMR description v_a must depend on body mass ($v_a \propto M^{1/7}$ (MMR-1)). We do not know any empirical result for v_a in the MMR conditions. So, it could be interesting to experimentally verify this simple prediction for normal species.

The extra assumption that the capillaries radius is invariant is agreement with the empirical data [3] and with the theoretical-empirical estimations of Dawson [38] ($r_c \propto M^{0.08}$, $l_c \propto M^{0.21}$). In the BMR description, the capillary velocity is also invariant. However, the capillary length l_c should depend on M. If $x = 1/2$ we have that $l_c \propto M^{0.286}$. In the MMR description, we must also have r_c invariant. If we assume that v_c is invariant, we obtain that the capillary density $N_c/M \propto M^{-0.143}$ agrees well with data of muscular capillary density of mammals (see Tab. II). In this case we have that $l_c = v_c \tau_c$, with two possibilities for τ_c: $\tau_c \propto \tau$ or $\tau_c \propto t_2$. Only the second possibility, together with $x = 1/2$ is consistent with v_c invariant. We obtain a result $l_c \propto M^{0.286}$ which agrees with the BMR description and with Dawson estimation.

VIII. THE BMR OF UNICELLULAR ORGANISMS

We present now the BMR of unicellular organisms. The first biological length L_1 is related to the transport of oxygen and small molecules by diffusion, namely $L_1 = D\tau^{1/2}$. The second length is related to large molecules that can be trapped in vesicles by macropinocytoses and pinocytoses and transported in direction of the nucleus. It is described by $L_2 = D_x \tau^{(1/2)+x}$, with $x = 0$ and $x = 1/2$ corresponding to diffusion and ballistic transport, respectively. In order to evaluate the b exponent of unicellular organisms we need to taken in account a third length. A general description of this length is achieved by supposing that $L_3 = D_y t_3^{(1/2)+y}$, with y varying in the interval $[0, 1/2]$ (diffusion movement: $y = 0$, ballistic one $y = 1/2$). To obtain the exponent b we first evaluate V_3 in terms of τ, namely $V_3 \propto DD_x D_y \tau^{(3/2)+x+y}$. Then, we use the relation between mass and τ (see Eq. (1) to find how τ depends on M ($\tau \propto M^{2/(5+2x+2y)}$). Finally, we evaluate each length in terms of M and we use Eq. (2) to obtain how B depends on M. It follows that $B \propto M^{[3+2x+2y/(5+2x+2y)]}$ and $\tau \propto M^{[2/(5+2x+2y)]}$. The case with only diffusion transport ($x = 0$ and $y = 0$) give us $b = 3/5$, a lower bound for the al-

TABLE II: Allometric exponents related to maximum metabolism and other exponents for mammals and birds. Under parenthesis is the error in the last significative of the observed quantities.

Predicted	Observed	Comment	Ref.
Exercise-induced maximum metabolic rate			
0.857 (MMR-1)	0.828(70)	mammals, binning data	[17]
[0.778, 0.857]	0.88(2)	standard animals	[36]
	0.872(29)	mammals	[37]
	0.94(2)	athletic	[37]
	0.85(2)	non-athletic	[37]
	0.882(24)	marsupials	[54]
	0.87(5)	mammals	[19]
Heart rate			
−0.143 (MMR-1)	−0.16(2)	mammals	[35]
[−0.222, −0.143]	−0.15	mammals	[46]
	−0.17(2)	birds, flight	[50]
	−0.146	birds, flight	[49]
	−0.157	birds	[49]
Cold-induced maximum metabolic rate			
[0.600, 0.750]	0.65(5)	mammals	[19]
	0.772(30)	marsupials	[54]
	0.789(40)	theria	[54]
Capillary density			
−0.143 (MMR-1)	−0.14(7)		[2, 55]
Aorta radius			
0.357 (BMR and MMR-1)	0.36	mammals	[2, 47]
[0.333, 0.357] (BMR)	0.335	mammals	[45]
Aorta length			
0.286 (BMR and MMR-1)	0.32	mammals	[2, 45]
[0.286, 0.333] (BMR)	0.31	mammals	[47]

TABLE III: BMR allometric exponent b ($B \sim M^b$) for unicellular organisms. Under parenthesis is the error in the last significative of the observed quantities.

Exponent b		
Predicted	Observed	Ref.
0.714	0.75	[39]
[0.667, 0.714]	0.66(9)	[41]
0.600 (BMR-3)	0.608(5)	[40]

lometric exponent. The upper value for x is $x = 1/2$ (ballistic movement). In this case we have that $b = (2+y)/(3+y)$, implying that the allometric exponent of unicellular organisms is in the interval [0.667, 0.714].

In Tab.III it is shown the empirical values of b as well the predict values. The value of the exponent obtained by Hemmingsen [39] ($b = 0.75$) is out of our predicted range. However, Prothero [40] observed that Hemmingsen had lumped together two metabolically different groups (prokaryotes and eukaryotes). When he excluded bacteria, flagellates, and marine zygotes from Hemmingsen's data sample, he obtained $b = 0.608 \pm 0.05$ for eukaryotes, a value just above our lower bound (BMR-3). On the other hand, Phillipson [41] studied the BMR scaling of 21 unicellular species and found $b = 0.66 \pm 0.092$.

IX. SUMMARY

We developed a theory for the allometric scaling of metabolism based in four ad-hoc postulates: i) mass density ρ_{d+1} and ii) available energy density σ_{d+1} are scaling-invariant quantities, iii) dominant transport processes, which are characterized by scaling-invariant quantities, drive the metabolic scaling and iv) there is only one relevant characteristic time because the resource rates of these processes are matched in order to have an optimal nutrient delivery. A lower bound for all metabolic exponents, namely $b_{min} = 3/5$, is found when we consider all transport processes as diffusive ones.

The BMR of mammals and birds is obtained when we have A) diffusion, describing the transport of oxygen and small molecules, B) ballistic transport ($L_3 \propto v_0 \tau$), which is related to the blood delivery in large scale and C) anomalous diffusion that represents the vesicular transport inside a cell and between cells of a tissue. Assuming that the last process is very close to the ballistic transport we obtained that $b = 5/7$. This value is in good agreement with the best empirical estimation for BMR (0.69), obtained by White and Seymour (2005) for mammals without ruminants. We believe that these large mammals should be included in some way in the empirical analysis, implying that the real empirical b value for mammals should be around 0.71. The 2/3-law is obtained when the anomalous diffusion process is near normal diffusion. Therefore $b = 2/3$ is a lower bound for BMR of mammals and birds. On the other hand, the 3/4-

law appears as an upper bound for BMR since this value is obtained when all transport processes are ballistic. Therefore the b exponent for mammals and birds is the interval $[2/3, 3/4]$. Interesting, the empirical value for birds is close to the low limit. The predict interval for the exponent related to heart rate (or respiration rate) is $[-1/3, -1/4]$ and the most probable value is $-2/7$. They are in agreement with the empirical values for mammals and birds. However, this exponent was not recently studied in a comprehensive way as was done for the b exponent.

The aerobic sustained MMR is described by an inertial movement accelerated during time τ ($L_3 \propto a_0\tau^2$). The upper limit for the MMR exponent ($b = 6/7$) is obtained when all transport processes are proportional to the accelerated one and the lower limit ($b = 7/9$) occurs when only the length related to the large scale transport (L_3) changes to the accelerated movement. Since during strenuous exercise the transport systems are stressed to their uttermost, we believe that the upper limit describe better the MMR scaling. The predict value for b and for the heart rate exponent are in good agreement with the empirical values. However, the data base is still narrow. The cold-induced MMR is studied by considering that usual heat transport processes are overwhelm and that we have a new metabolic state where only heat diffusion is important. The different empirical exercise induced MMR exponents obtained for athletic species and non-athletic one can be explained qualitatively by assuming that the accelerated movement for athletic species is different ($L_3 \propto c_0\tau^3$, for example).

The exponents related to the aorta and capillaries of mammals are obtained through fluid conservation. Aorta blood velocity is scaling-invariant in BMR conditions but grows with mass in the exercise-induced MMR situation. This exponent, which is predicted to be in the interval $[0.143, 0.22]$, was never measured. The empirical determination of this exponent seems to be easy and interesting. Moreover, it can be an experimental test of the importance of the transportation processes for the metabolic scaling. The exponents characterizing the length and radius of aorta and capillaries in the BMR description have the same values as that of the upper limit of exercise-induced MMR situation.

The predict values agree with the empirical ones. On the other hand, the capillary density must be described by the MMR scenario and the predict value also agrees with the experimental value.

Finally we discussed the BMR of unicellular organisms. In this case we have two diffusion transport processes, which are related to the transport of oxygen and small molecules, and one anomalous diffusion process that describes vesicular transport. An extra reason to use anomalous diffusion as the third transport mechanism is that it allow us to easily change this transport mechanism from pure diffusion to a ballistic motion in the theoretical description. The predicted range $[2/3, 5/7]$ was compared with the few results of the literature.

X. ACKNOWLEDGEMENTS

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