From Allometry to Dimensionally Homogenous ‘Laws’: Reformulation of the Metabolic Rate Relation.

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ABSTRACT

Meaningful laws of nature must be independent of the units employed to measure the variables. The principle of similitude (Rayleigh 1915) or dimensional homogeneity, states that only commensurable quantities (ones having the same dimension) may be compared, therefore, meaningful laws of nature must be homogeneous equations in their various units of measurement, a result which was formalized in the Π theorem (Vaschy 1892; Buckingham 1914). However, most relations in allometry do not satisfy this basic requirement, including the ‘3/4 Law’ (Kleiber 1932) that relates the basal metabolic rate and body mass, which it is sometimes claimed to be the most fundamental biological rate (Brown et al. 2004) and the closest to a law in life sciences (West & Brown 2004). Using the Π theorem, here we show that it is possible to construct a unique homogeneous equation for the metabolic rates, in agreement with data in the literature. We find that the variations in the dependence of the metabolic rates on body mass are secondary, coming from variations in the allometric dependence of the heart frequencies. This includes not only different classes of animals (mammals, birds, invertebrates) but also different exercise conditions (basal and maximal). Our results demonstrate that most of the differences found in the allometric exponents (White et al. 2007) are due to compare incommensurable quantities and that our dimensionally homogenous formula, unify these differences into a single formulation. We discuss the ecological implications of this new formulation in the context of the Malthusian’s, Fenchel’s and Calder’s relations.

1. Introduction

The invariance of nature under scaling of units of measurement has been a powerful tool for the discovery of new phenomena, used for centuries (Fourier 1822) in physics and related
areas (Macagno 1971). Being called dimensional analysis or principle of similitude (Rayleigh 1915), this methodology have been also applied to the solution of complex problems, ranging from the atmosphere behavior under a nuclear explosion (Taylor 1950) to airfoil prototypes (Bolster et al. 2011) and the formation of stars in galaxies (Escala 2015; Utreras et al. 2016).

The scaling invariance is desirable in any branch of science, not only restricted to physics, however, in many areas the fundamental relations have not yet been formulated in a form independent of the scaling of units. In the case of life sciences, particularly relevant are the allometric scaling laws, which relates a physiological variable with body size, which in almost all cases is measured by it mass. Fulfilling the similitude principle implies that these relations can always be rearranged in term of dimensionless parameters/groups, or expressed in graphical terms, that both axis in the relation must have the same dimensions. However, allometric scalings almost never fulfill this property, which is also called dimensional homogeneity. Another way of formulating this issue, is as a phenomena that can be described with homogenous equations only with the aid of as many dimensional constants as there are variables (Bridgman 1937).

This issue is illustrated in the influential book ‘Scaling’ by Schmidt-Nielsen (1984), that shows dozens of relations between physiological variables in species and body mass, being the most notable one the Kleiber’s Law between basal metabolic rate (energy consumption per unit time) and body mass. None of the nontrivial relations satisfies the similitude principle, including the famous Kleiber’s Law, with one notable exception: the allometric relation between swimming speed of fishes and tail-beat frequency (Bainbridge 1958). When fish’s swimming speed is properly normalized dividing it by their body length, thus having frequency units as the tail-beats, the data among different fishes lies into a single curve in the same fashion as, for example, von Kármán (1957) unified different experiment of turbulent flows in pipes using only dimensional analysis.

The self-similarity displayed in Brainbridge’s allometric relation is appealing since it is the same displayed in physics and will be the main topic of this work. However, it is important to note first that there is another partial approach to guarantee similitude: fractal geometry. The possibility of having fractional dimensions allows to satisfy similitude with the use of an extra parameter, the Haussdorf or fractal dimension D. If the fractal dimension is properly chosen, is still possible to close the dimensionality of the relation for power laws with even irrational exponents.

In terms of dimensional analysis, fractal curves can be identified as incomplete similarities, because they only satisfies the properties of local homogeneity and local self-similarity (Barenblatt 2003). Fractals belongs to the group of self-similar solutions of the second kind, which are only valid in a restricted domain. On the other hand, the more general self-similar
solutions of the first kind, or complete similarities, can sometimes be obtained using the tools of dimensional analysis.

Fractals models of the allometric relations became popular in recent years, most notably since West et al (1997), that conjectured a universal ‘1/4 power law’ mass scaling for physiological variables and used fractal geometry to explain it from first principles. This gave considerable attention to fractal models for the allometric relations, however, also debate on the validity of such ‘1/4 power law’ universality (see Hulbert 2014 for a critical review). For example, analysis of 127 interspecific allometric exponents discarded an universal metabolic relation (White et al. 2007). Due to this intense debate, we will start analyzing possible fractals models, to then move towards complete similarity solutions using dimensional analysis tools (Π theorem).

This letter is organized as follows. We start with using dimensional analysis to study possible fractal models for the metabolic rates in §2. Section 3 continues with the search for a dimensionally homogenous metabolic rate equation and compare it against data taken from the literature. Finally in §4, we discuss the results and perspectives of this work.

2. Dimensional Analysis of Fractal Models

The Vaschy-Buckingham Π theorem defines the rules to be fulfilled by any meaningful relation aimed to be law of nature and it is a formalization of Rayleigh’s similitude principle. The theorem states that if there is a meaningful equation involving a certain number, n, of variables, and k is the number of relevant dimensions, then the original expression is equivalent to an equation involving a set of p = n−k dimensionless parameters constructed from the original variables. Mathematically speaking, if we have the following equation:

\[ F(A_1, A_2, \ldots, A_n) = 0, \quad (1) \]

where the Ai are the n variables that are expressed in terms of k independent units, Eq 1 can be written as

\[ f(\Pi_1, \Pi_2, \ldots, \Pi_{n-k}) = 0, \quad (2) \]

where the \( \Pi_i \) are dimensionless parameters constructed from the \( A_i \) by \( p = n - k \) dimensionless equations of the form \( \Pi_i = A_1^{m_1} A_2^{m_2} \cdots A_n^{m_n} \). We will use this theorem to design an equation for metabolic rates that fulfill the similitude principle.

We will follow the more general approach of Barenblatt & Monin (1983) to study a possible the fractal-like nature of biological systems, since it do not depend on a particular mechanistic model like the one in West et al. (1997) or assumes that the basal metabolic
rate ($\dot{V}\text{O}_2$) is directly proportional to the effective fractal surface of the body, as in West et al. (1999). We can construct a model by assuming that the metabolic rate, which is commonly measured in milliliters of O$_2$ per minute and has dimensions $[\dot{V}\text{O}_2] = [\text{M}O_2]/[\text{T}]$, only depends on an absorbing capacity $\beta_D$ with dimensions $[\dot{V}\text{O}_2][\text{L}]^{-D}$, the body mass $W$ with dimensions $[\text{M}]$ and the density $\rho$ with dimensions $[\text{M}[\text{L}]^{-3}$.

Because this model has $n=4$ variables ($\dot{V}\text{O}_2$, $\beta_D$, $W$ & $\rho$) and $k=4$ independent units ($[\text{M}O_2]$, $[\text{M}]$, $[\text{L}]$, $[\text{T}]$), the $\Pi$ theorem tells that no dimensionless parameters can be constructed, since $n-k=0$. Nevertheless, it is still possible to construct the following dimensionless quantity (Barenblatt & Monin 1983):

$$\Pi_1 = \frac{\dot{V}\text{O}_2}{\beta_D(W/\rho)^{D/3}},$$

which illustrates implications of the incomplete similarity fulfilled by fractals functions, in this case allowing to construct a dimensionless $\Pi$ by introducing the extra parameter, the Hausdorff or fractional dimension $D$, regardless of the $\Pi$ theorem rules.

From Eq. 3 is straightforward to see that the allometric scaling for the oxygen consumption rate is $\dot{V}\text{O}_2 = AW^{D/3}$, with $A = \Pi_1\beta_D\rho^{-D/3}$. For a fractional dimension $D=2.25$, the usual 3/4 exponent of the Kleiber's Law is recovered. Another interesting quantity to look is the specific metabolic rate, $\dot{V}\text{O}_2/W$, which from Eq. 3 takes the form:

$$\frac{\dot{V}\text{O}_2}{W} = \frac{\Pi_1\beta_DW^{D-1}}{\rho^{D/3}} \propto W^{D-1}.$$  

Since $\dot{V}\text{O}_2/W$ has dimensions of $[\text{M}O_2][\text{T}]^{-1}[\text{M}]^{-1}$, it can be rearranged as equals to $\Pi_1\eta_{O_2}\nu_o$, where $\eta_{O_2}$ is an specific O$_2$ absorption factor, with units $[\text{M}O_2]/[\text{M}]$ and $\nu_o$ that can be identified as a characteristic frequency since it has inverse time units ($[\text{T}]^{-1}$). Assuming an absorption factor $\eta_{O_2}$ independent of $W$, the characteristic frequency scales with body mass as $\nu_o \propto W^{\frac{D}{2}-1}$, which can be directly compared against relevant rates like the respiratory and/or heart frequencies, in which there is considerable data on its scaling with $W$. This gives an independent Hausdorff dimension value needed to fulfill dimensional homogeneity.

For the case of mammals, heart frequencies scales as $W^{-0.25}$ (Brody 1945, Stahl 1967) which for a $\nu_o \propto W^{\frac{D}{2}-1}$, implies a fractional dimension of $D=2.25$, in agreement with the fractional dimension determined from the Kleiber’s Law. A similar result is obtained if we instead use, as characteristic frequency, the respiratory rates of mammals at rest (Calder 1968). In the case of sub groups, for example marsupials mammals have metabolic rates $\propto M^{0.74}$ and heart frequencies $\propto M^{-0.27}$, which gives in both cases a dimension of $D \sim 2.2$. In invertebrates like spiders, the metabolic rates scales as $M^{0.59}$ (Anderson 1970, 1974) and
heart frequencies scales as $M^{-0.41}$ (Carrel & Heathcote 1976), quite different that in mammals but both the metabolic rates and heart frequencies implies the same fractional dimension of $D \approx 1.8$. In birds the scaling is again similar to mammals, proportional to $M^{0.72}$ (Lasiewski & Dawson (1967) and $M^{-0.23}$ (Calder 1968), giving slightly different dimensions of $D = 2.2$ and 2.3 respectively.

We see a general consistency between the fractional dimensions $D$ determined independently from the metabolic rates and heart/respiratory frequencies, regardless of the considerable variations of the $D$ value among groups (especially in the case of invertebrates). It can be argued that such differences, are natural due to the different evolutionary stages among animal groups. Nevertheless, in the case of invertebrates is in addition required to argue in favor of oxygen-absorbing organs that are better approximated by fractal lines ($D < 2$) than by fractal surfaces ($2 \leq D \leq 3$).

Another of the major issues in the exponent of the metabolic rate, is the change of the allometric scaling in the oxygen consumption under aerobic conditions (Weibel 2002), or maximal metabolic rate $\dot{V}_{O_2}^{\text{max}}$. The scaling for $\dot{V}_{O_2}^{\text{max}}$ is approximately proportional to $M^{0.85}$ (with slope variations ranging from 0.83 to 0.88; Savage et. al 2004, Taylor et al 1981, Dlugosz et al 2013, Weibel and Hoppeler 2005 and Bishop 1999) and the heart frequencies under such $\dot{V}_{O_2}^{\text{max}}$ conditions, scales as $M^{-0.15}$ (Weibel and Hoppeler 2004, 2005). Again, both scalings gives the same fractional dimension, which in this case is $D = 2.55$. However, this kind of models based on fractal geometry requires now an aerobic change from $D = 2.25$ to 2.55, in order to explain the change of allometric scaling under aerobic conditions. This assumption of adjustable fractal network is unclear to be fulfilled in nature.

The requirement of adjustable fractal network under aerobic conditions is independent of the particular fractal model studied, unless the model assumes that the metabolic rate is directly proportional to the effective fractal surface of the animal, like in West et. al (1999), in which is not possible to explain the $\propto M^{0.85}$ scaling of the $\dot{V}_{O_2}^{\text{max}}$. In such a case, the maximal possible scaling is $\propto M^{0.75}$, which correspond to volume filling surfaces (West et al. 1999).

### 3. A Complete Similarity Solution

In the different cases studied we do not found a single (universal) Hausdorff dimension $D$ that explains allometric scaling for all organisms, but we found an excellent agreement in the dimension $D$ determined from two different empirical allometric relations (metabolic rate and frequency). Nevertheless, the fractal model studied in §2 also assumes that the
characteristic frequency \( \nu_0 \) has all the D dependence on the W exponent, therefore in this particular model the variations in the W scaling of the \( \dot{V}_{O_2} \) are secondary, coming directly from its dependence on \( \nu_0 \). Therefore, the agreement between the model and allometric relations, suggests that indeed the W dependence in \( \dot{V}_{O_2} \) and \( \nu_0 \) might not be independent. This motivates us to explore \( \nu_0 \) as an independent physiological variable that controls the metabolic rate \( \dot{V}_{O_2} \).

Taking the characteristic frequency \( \nu_0 \) as a variable in the metabolic rate, we try now a different model with \( n=4 \) independent variables (\( \dot{V}_{O_2} \), \( \eta_{O_2} \), \( W \) & \( \nu_0 \)) and that has now only \( k=3 \) independent units ([M\(_{O_2}\)], [M], [T]), therefore, from the II theorem we know that \( n-k=1 \) dimensionless parameters can be constructed. Is straightforward to see that the quantity \( \epsilon = \dot{V}_{O_2}/W\eta_{O_2}\nu_0 \) is dimensionless, which implies a metabolic rate of the form:

\[
\dot{V}_{O_2} = \epsilon\eta_{O_2}\nu_0 W, \tag{5}
\]

which is a self-similar solution of the first kind or complete similarity.

In order to confirm that the variations of the W scaling in the metabolic rate \( \dot{V}_{O_2} \) comes from its dependence on \( \nu_0 \), the self-similar solution found (Eq. 5) needs to be contrasted against empirical data. For that is required to check if the dimensionally homogenous relation has the correct slope, which must be unity within errors. For that purpose, we collected metabolic rates, masses and characteristic frequencies for different groups (mammals and birds) and aerobic conditions (basal and maximal).

Blue data points in Fig. 1 are the basal metabolic rates \( \dot{V}_{O_2} \) for mammals and the green ones \( \dot{V}_{O_2} \) for birds, taken from Savage et al (2004) and Lasiewski & Dawson (1967) respectively. The respiration rates for both samples were taken from Calder (1968), converted to heart rates \( (f_H) \) by multiplying a factor 4.5 for mammals and 9 for birds (Schmidt-Nielsen 1984). The curves correspond to the least square fit to the data points, being 0.98 the slope of the \( \dot{V}_{O_2} \) for mammals and 1.01 the slope of the \( \dot{V}_{O_2} \) for birds. These slopes are both close to unity as expected to fulfill dimensional homogeneity. The normalization for birds slightly differs from mammals, however, this change in \( \dot{V}_{O_2} \) normalization can be interpreted in our model as evidence in variations in the specific \( O_2 \) absorption factor \( \eta_{O_2} \), since in Fig 1 we assumed \( \eta_{O_2} = 1 \) for both birds and mammals. We decided to choose the heart rate as characteristic frequency \( (\nu_0 = f_H) \) instead of respiration frequency, because otherwise it increases the normalization shift seen in Fig 1, suggesting that the formulation with \( \nu_0 = f_H \) will require less parameters to reach an unique relation.

Another major issue is the change in slope of the metabolic rate when an animal exercises, from \( \dot{V}_{O_2} \) to \( \dot{V}_{O_2}^{max} \), as mentioned earlier in the text. The red points in Fig. 2 display the \( \dot{V}_{O_2} \) in a sample of resting mammals and the yellow ones are the corresponding \( \dot{V}_{O_2}^{max} \) for
the same species under maximal exercise. The sample of mammals was taken from Weibel & Hoppeler (2004), a group that has measured maximal and resting heart frequencies, with the corresponding maximal and basal metabolic rates taken mainly from Weibel, Bacigalupe et al (2004) and complemented with other references (Hinds et al 1993; Weibel 2000; Roef et al. 2002; Savage et al 2004; White et al 2006). The curves correspond to the least square fit to the data points, being 0.94 the slope of the $\dot{V}_{O_2}$ and 1.06 the slope of the $\dot{V}_{O_2}^{\text{max}}$.

The larger deviation from slope unity can be explained due to the individual slopes in the sample of metabolic rates and frequencies in Fig. 2 in which $\dot{V}_{O_2}$ scales as $W^{0.69}$ and frequency $f_H \propto W^{-0.26}$ that gives an $\dot{V}_{O_2}/f_H$ proportional to $W^{0.95}$. Similarly, the $\dot{V}_{O_2}^{\text{max}}$ scales as $W^{0.90}$ and $f_{H}^{\text{max}} \propto W^{-0.15}$ that gives an $\dot{V}_{O_2}^{\text{max}}/f_{H}^{\text{max}}$ proportional to $W^{1.05}$, instead of proportional to $W^{1.0}$ that is expected from Eq. 5 in both cases, in order to fulfill dimensional homogeneity. These variations from slope unity in the running and resting slopes are therefore due to the lower number statistics, because represent only a subsample of animals that has the three variables measured, in which the metabolic rates allometric exponents differs from the most accepted values ($\dot{V}_{O_2} \propto W^{0.75}$ and $\dot{V}_{O_2}^{\text{max}} \propto W^{0.85}$). On
Fig. 2.— Same as Figure 1, but the yellow points correspond to maximal metabolic rates \( \dot{V}_{O_2}^{\text{max}} \) and the red ones are the corresponding \( \dot{V}_{O_2} \) for the same mammals under basal conditions. The curves correspond to the least square fit to the data points, being 0.94 the slope of the \( \dot{V}_{O_2} \) and 1.06 the slope of the \( \dot{V}_{O_2}^{\text{max}} \).

The shift in normalization seen in Fig. 2 can be interpreted as a change in the \( O_2 \) absorption factor per unit mass, \( \eta_{O_2} \) in Eq. 5, which might be expected due to the shift in the animal’s internal oxygen demands between rest and exercise (Darveau et al. 2002; Weibel & Hoppeler 2005). Under basal conditions, the \( O_2 \) consumption in cellular respiration is mainly determined by the energy demands of basic maintenance processes in the tissues, compared to when an animal exercises that muscle work places a much larger \( O_2 \) demand for energy supply (Weibel 2002). This change in the basic processes and organs that controls the energy demands of animals, should therefore imply a shift in the overall specific \( O_2 \) absorption of them.

Finally, we assume \( \eta_{O_2} = 1 \) for resting animals (blue and green points in Fig. 1, and red ones in Fig. 2) and \( \eta_{O_2} = 5 \) for mammals under exercise (yellow points in Fig. 2), in order to
take into account the differences in the $O_2$ absorption factor discussed before. Fig 3 displays all the data in Fig 1 and Fig 2 with black points, but with the just mentioned two different $O_2$ absorption factor $\eta_{O_2}$. This leads to a single relation with a slope consistent with unity (black dashed line in Fig 3).

![Graph](image)

**Fig. 3.**— Black points are the same data showed in Figure 1 and 2, but we now assume $\eta_{O_2} = 1$ for resting animals and $\eta_{O_2} = 5$ for those under maximal exercise. The red points correspond to flying birds and the cyan ones to penguins under resting and running conditions. Both subsamples shows an overall agreement with the whole relation (black points).

To test the relation found in Fig 3, with the factor of 5 difference in $\eta_{O_2}$ between resting and running conditions, we also plotted data for two additional classes of animals. In cyan, we plot data for penguins under resting and running conditions, taken from Green et al 2005, and for flying birds in red (Berger, Hart & Roy 1970; Aulie 1971; Norberg 1996). Both subsamples, in which we again use $\eta_{O_2} = 1$ for resting samples and $\eta_{O_2} = 5$ for aerobic ones, shows an overall agreement with the whole relation.
4. Discussion and Outlook

We showed that although in different cases the mass scaling in the metabolic rate and frequency can differ from the predicted by the ‘universal 1/4 scaling’, their slopes are consistent with the same Hausdorff dimension D, if it is interpreted in terms of fractal geometry. This motivates us to propose unique homogeneous equation for the metabolic rates, for different classes of animals and for both resting and exercising conditions, in agreement with the empirical data. Therefore, our results demonstrate that most of the differences found in the allometric exponents (White et al. 2007) are due to compare incommensurable quantities, because the variations in the dependence of the metabolic rates on body mass are secondary, coming from variations in the allometric dependence of the heart frequencies on W.

The methodology presented in this work could have impact not only on the field of allometry, but also in life sciences in general. For example, the geometry of body cooling (either normal or ‘effective fractal’ surfaces), is part of the debate in theories of metabolic allometry from even before Kleiber’s result. With our new formulation this has no role, narrowing the discussion to the internal respiratory (O₂) transport system. Therefore, we consider that our result illustrates how powerful is to apply the Π theorem in the formulation of empirical biological laws, something that could also help to validate or discard theories in related areas such as ecology.

An open question is why the characteristic frequency changes its W scaling among different classes of living organisms and how this depends on the O₂ transport problem. The reason for this might still have its origin on a ‘fractal like’ transport network, however, the dynamic scaling changes for \( \dot{V}^{\text{max}}_{\text{O}_2} \) should also be partially related to changes in the energy demands (Darveau et al. 2002; Weibel 2002). Since O₂ is a crucial ingredient in the cellular respiration and energy storage via ATP formation, how this is distributed along the body and where ends up being consumed, must play a role in the integrated energy consumption of any organism.

A simple separation of both effects in terms of the complete similarity model presented here, might be to associate the change in the allometric scaling of \( \nu_{\text{O}_2} \) to a change in the transport network itself (which might be fractal as suggested by West et al 1997 and others) and the shift in normalization (\( \eta_{\text{O}_2} \)) to the change of the organs that dominates the energy demand (from those associated to basic maintenance processes to those in muscle work as in Darveau et al. 2002). This might be supported by the fact that cells themselves that have constant metabolic rates under ‘in vitro’ conditions (Gauthier et al. 1990), compared to the basal metabolic rates per cell that scales as \( W^{-0.25} \) under ‘in vivo’ conditions (for a fixed cell mass; West et al. 2002), which can be interpreted as the allometric scaling of \( \nu_{\text{O}_2} \) only be related to the transport system.
An interesting limiting case for the characteristic frequency scaling, are plants that have metabolic rates linearly proportional to W (Reich et al. 2006), which in our model implies a characteristic (respiration) frequency independent of mass. One simple interpretation is since most plants have relatively few living cells that carry out cellular respiration outside of their surface, they do not have the transport requirement and therefore such cells are in a condition more similar to the ‘in vitro’ one (Gauthier et al. 1990), making its characteristic frequency independent of the body mass.

Besides the successes of the relation found, other possible deviations are still documented in the literature. One particularly relevant is related to the temperature dependence, which is more obvious for Ectothermic systems since their body temperatures strongly varies with the environmental one. Gillooly et al. (2001) proposed a temperature corrected normalization for the metabolic rate relation, based in the Arrhenius empirical formula for the temperature dependence of chemical reaction rates.

However, the temperature corrected metabolic relation still has residual variations around of factors 4-5 on the normalization of the metabolic rates between endotherms and ectotherms (Gillooly et al. 2001; Brown et al. 2004). This is approximately the same variation in heart rates reported between endotherms (mammals and birds) and ectotherms (fish, amphibians, reptiles) in Lillywhite et al. (1999), suggesting that Eq 5 with the normalization corrected by an Arrhenius-type exponential dependence on temperature T, to take into account that chemical reactions proceed faster at higher temperatures, might be enough to also account for the metabolic rates of ectotherms.

In terms of dimensional analysis, this can be derived assuming two additional variables T and T_a that controls the metabolic rate, being T_a an activation temperature defined as the activation energy E_a divided by the Boltzmann constant k_B (T_a ≡ E_a/k_B). In such a case, we have now a model with n=6 independent physical variables (V_{O_2}, η_{O_2}, W, T, T_a, ν_o) that has now only k=4 independent units ([M_{O_2}], [M], [T], [Θ]), therefore, n-k=2 dimensionless parameters can be constructed (Π_1 = V_{O_2}/W\eta_{O_2}ν_o, Π_2 = T/T_a). In this case, the Π theorem states that there is an equation f(Π_1, Π_2) = 0 and if the function f is regular and differentiable, we can use the implicit function theorem to advocate the existence of a function Π_1 = ε(Π_2). Unfortunately, the functional dependence of ε on the second dimensionless parameter Π_2 cannot be determined by dimensional analysis, therefore assuming an exponential form inspired in the empirical Arrhenius formula, namely ε(Π_2) = ε_0 e^{-1/Π_2}, we get

\[ \dot{V}_{O_2} = \epsilon_0 \eta_{O_2} \nu_o e^{-T_a/T} W. \]
Eq. 6 can also be used to explain ecological phenomena and make predictions in a similar fashion as Gillooly et al. (2001) uses the temperature corrected relation on the metabolic theory of ecology (Brown et al. 2004). To properly perform this, all the laws relevant to explain an ecological phenomena needs to be formulated in a form independent of the scaling of units (with dimensionally homogenous equations). Once that is achieved, dimensional analysis can also be applied to solve ecological problems in a similar way as engineering does it with physical laws (Bridgman 1937). The lack of well formulated laws in life sciences is probably the ultimate origin of the problems faced by theories such as the metabolic theory of ecology, which produces inaccurate statements (universal 1/4 power scaling; White et al. 2007) and ecological implications (Duncan et al. 2007). Well formulated empirical laws should precede theory, as happened historically in physics and chemistry.

Nevertheless, is still possible to discuss implications of Eq. 6 for ecological relations formulated also as dimensionally homogenous equations. One of such is the population growth, which is an exponential controlled by the ‘Malthusian parameter’ or intrinsic rate of natural increase, \( r_m \), which has inverse time units and therefore should be associated to a frequency. Since its allometric scaling is \( r_m \propto W^{-0.25} \) (Fenchel 1974), is natural to associate it in our model with the characteristic (heart) frequency under basal conditions \( (\nu_0 \propto W^{-0.25}) \). However, less obvious is to find a causal connection between two frequencies that represents very different processes and timescales (internal circulation versus population growth). A possible link is in the total number of heartbeats in a lifetime \( N \), which is approximately constant and equals to a billion for different mammals (Cook et al. 2006), then if the lifetimes scale inversely to the ‘Malthusian parameter’, we have: \( r_m \propto 1/t_{\text{life}} \sim \nu_0/N \propto W^{-0.25} \). This is more natural timescale for controlling the exponential population growth and also has the same allometric scaling of population cycles (Calder 1983).

A constant total number \( N \) of heartbeats in a lifetime for mammals, \( t_{\text{life}} = N/\nu_0 \), can also be used to relate the normalization \( A_{ls}^+ \) in the relation for the total energy consumed in a lifespan (Atanasov 2006), to our normalization \( (\epsilon \eta_O_2 \) in Eq. 5). For \( N \) equals to a billion and converting 1 ltr \( O_2 = 20.1kJ \) (Schmidt-Nielsen 1984), the \( A_{ls}^+ = 7.158 \times 10^5kJ/kg \) determined by Atanasov (2006) implies an \( \epsilon \eta_O_2 = A_{ls}^+/N = 10^{-4.45}mlO_2g^{-1} \), which is about the same number that can be determined independently from Figs 1 & 3.

Finally, for further fine-tuning of the metabolic rate relation, a coherent dataset of measurements is required. Ideally, this needs to be for all the variables measured on the same animals and the original formulation of the metabolic law should stay strictly with measured quantities, for example with metabolic rates in ml \( O_2 \) per min instead of energy-related units (watts or ergs/sec), to avoid assumptions in the conversion factors that produces undesirable extra scatter in the relation. Also, it will be interesting to test its predictions,
for example to look for the temporal validity of Eq. 6 as an animal starts exercising and increases its O\textsubscript{2} consumption. In terms of ecology, an interesting test is to see if population ecology parameters scale as ν\textsubscript{o} instead of universal 1/4, being a good candidate to see changes in allometric scaling of r\textsubscript{m} of big outliers from ‘1/4 scaling’ in the metabolic relation under basal conditions, such as spiders (Anderson 1970, 1974) or other organisms (White et al 2007).

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