Energy balance and the origin of metabolic scaling

Fernando J. Ballesteros\textsuperscript{1,*}, Vicent J. Martinez\textsuperscript{1}, Bartolo Luque\textsuperscript{2}, Lucas Lacasa\textsuperscript{3} and Andrés Moya\textsuperscript{4}
\textsuperscript{1} OAUV, Parque Científico de la Universidad de Valencia, Valencia (Spain).
\textsuperscript{2} Departamento de Matemática Aplicada y Estadística, ETSI Aeronáuticos, Universidad Politécnica de Madrid, Madrid (Spain)
\textsuperscript{3} School of Mathematical Sciences, Queen Mary University of London, Mile End Road, E14NS London (UK)
\textsuperscript{4} Institut Catala`n de Biodiversitat i Biologia Evolutiva, Parque Científico de la Universidad de Valencia, Valencia (Spain).

The origin and shape of metabolic scaling has been a controversial debate since Kleiber found that the basal metabolic rate of animals seemed to vary as a power law of their body mass with exponent 3/4, instead of 2/3, as a surface-to-volume argument would predict. The universality of exponent 3/4 -claimed in terms of the fractal properties of the nutrient network- has recently been challenged according to empirical evidence that observed a wealth of robust exponents deviating from 3/4. More dramatically, recent works show that data may even comply to more complicated non-scaling functions, and suggest that pure scaling might only be an artifact. Here we present a conceptually simple thermodynamic framework, where Kleiber’s law emerges as the trade-off between the energy lost as heat and the energy efficiently used by the organism to maintain its metabolism. This balance tunes the ultimate shape of the law and as such, different effective scalings are recovered as particular cases, thereby reconciling previously inconsistent empirical evidence in mammals, birds, insects and even plants under a unified framework. The model is biologically sound, and also explains additional features such as the relation between energy lost as heat and mass or the role and influence of different climatic environments.

I. INTRODUCTION

The basal metabolic rate $B$ is the minimum energy expended daily by an animal in thermoneutral conditions to keep its metabolism at work. As early as in 1839, Sarrus and Rameaux\cite{1} proposed that metabolic rates might depend on heat dissipation (Fourier’s law) and therefore increase with surface area, something originally checked in dogs by Rubner in 1889\cite{2}. In 1932 Max Kleiber empirically observed\cite{3} that, indeed, a simple and robust allometric scaling between $B$ and the animal mass $M$ could account for most of the metabolic rate variability, $B \sim M^\alpha$. However, he found that $\alpha = 3/4$, instead of $\alpha = 2/3$ that results of heat dissipation according to a simple surface-to-volume argument. Since then, extensive data have been collected, encompassing a fervent debate on the origin and concrete shape of the so called Kleiber’s law. While some of the empirical works seem to comply better to $\alpha = 2/3$\cite{4,5}, a great majority took for granted a 3/4 power law\cite{6,9}, raising it to the level of central paradigm in comparative physiology\cite{10}. This scaling was subsequently elegantly explained by space-filling fractal nutrient distribution network models\cite{11,12,13} (with possible deviations for small masses due to finite size effects), thus apparently closing the debate on its origin. However, additional statistical evidence challenges the validity of $\alpha = 3/4$\cite{14,15,16,17,21,22,23,24} (see also\cite{17} for a recent experimental study of the fractal exponents in human vascular networks). For instance Dodds et al.\cite{18} found that, for masses under 10 kg, a 2/3 exponent gives a better fit, while 3/4 fits better the whole range. In the same vein, Kolokotrones et al.\cite{19}, after fitting the encyclopaedic data set of basal metabolic rates for mammalians compiled by McNab\cite{20}, concluded that the scaling law was not after all a pure power law but had curvature in double logarithmic scale, giving an heuristic explanation as to why different exponents could be fitted depending on the range of masses considered.

In the last decades, a large number of theories of different garment and degrees of formality have been proposed to justify the occurrence of particular scaling forms\cite{21,22}, organized into four major brands (surface area, resource transport, system composition, and resource demand models) by Glazier\cite{22}. For instance, the $\alpha = 3/4$ theories relate to the geometry of nutrient supply networks\cite{11,13} or general geometrical arguments\cite{14} whereas some advocates of the $\alpha = 2/3$ include\cite{4,9}. To name a few other approaches, in the quantum metabolism (QM) model\cite{22} power laws with varying prefactors are found. Similarly, the metabolic level boundaries (MLB) hypothesis\cite{23} predicts a pure power law with a varying exponent which interpolates between $\alpha = 2/3$ and $\alpha = 1$ according to the activity level of the organism (or metabolic intensity). The allometric cascade model\cite{24} on the other hand deals with a linear combination of innumerable allometric components, one for each different tissue, and ends with a complex formula depending on too many free parameters to fit. The three-compartment model\cite{25} deals with a linear combination of three allometric components that model different classes of organs and tissues. The Dynamic Energy Budget\cite{30} comprises a weighted sum of four processes: assimilation, maintenance, growth, and maturation, the first one with exponent 2/3 as Kooijman assumes that surfaces assimilating the incomes (oxygen, food) scale as 2/3 (but West et al.\cite{11} proved that bronchus in lungs scale rather as 3/4). The effect of cell number and size in body mass has also been claimed to be responsible for different allometric
scalings \(37\). Finally, gravity has been also considered as part of the problem \(38\), due to response of body mass to gravity, which scales linearly with mass (see \(10\, 21\, 22\) for reviews).

Not all of the mechanistic explanations for metabolic scaling are necessary exclusive, and quite probably many of these remain valid on appropriately defined limits. Integration of those under a more parsimonious hallmark is, however, certainly needed \(21\). In this work we aim at proposing such a hallmark, with the hope that it might help to reconcile several empirical and statistical results. We show that the heat dissipation phenomenon is, after all, at the origin of Kleiber’s law and its new non-scaling shape. Not all of the organism’s energy income is wasted as heat, and we find that this simple thermodynamic balance allows us to explain in a quantitative way the correct allometric curves for mammals (in different environments), birds, and insects, to account for other biological features such as the relation between energy lost as heat and mass, as well as to extend the analysis to plants.

II. RESULTS

Part of the energy incorporated to the organism from food is used for the synthesis of ATP and proteins, cellular division, etc: it keeps the animal alive. The second law of thermodynamics requires that such process is inefficient, in the sense that a significant part of energy consumption is always dissipated as heat. Let us consider two extreme (unrealistic) situations: in one end, we would have extreme thermodynamic efficiency, where all energy consumed would be efficiently converted into work (hence violating the second law) and the whole body would be a sink of energy with no heat losses. In this situation, the energy consumed needs to be proportional to the total mass -total number of cells-, hence \(B = kM\) for some constant \(k\). At the other extreme of null thermodynamic efficiency, all the energy income should be converted into heat to keep the organism warm, which would work simply as a (dead) heater. As this energy would be subsequently dissipated through the organism surface, thermoregulation would thus put an upper bound for the amount of energy consumption, which according to surface-to-volume arguments, yields an effective “metabolic rate” \(B = k'M^{2/3}\) for some constant \(k'\). Our contention is that living organisms interpolate between these extrema: they are are neither heaters nor optimal energy sinks, but lie somewhere in between, as any thermodynamic system operating away from equilibrium. These hypothesis define an effective model where, if \(f\) is the fraction of the energy income that is used “efficiently” by the cells to keep their metabolism working, then both work generated by metabolism and thermogenesis balances and

\[
B = fkM + (1-f)k'M^{2/3}. \tag{1}
\]

Note that equation (1) is not a pure power law but the linear combination of two, with exponents 1 and 2/3 respectively. It is well known \(21\) that in a double logarithmic plot, this equation yields a curved graph with convex curvature, in good agreement with the findings of Kolokotrones et al.\(16\). For small values of \(M\), this approximates to a power law with exponent 2/3 in accordance with recent results by Dodds et al \(15\), whereas for a large range of masses, this equation approximates to an apparent pure power law with an effective exponent that can range between 2/3 and 1, in good agreement with empirical evidence (entropic considerations prevent the linear asymptotic regime to appear empirically, see however \(18\)). Incidentally, another direct consequence of this model is that bigger animals, that have more difficulty to dissipate heat as their surface/mass ratio is smaller, should have slower metabolisms to cope with smaller \(B/M\) ratios (since \(f\) is independent of \(M\), then \(B/M\) is forced to be smaller in order to generate less heat).

Fitting the model in mammals. While \(k, k'\) and \(f\) have biological meaning, as they are independent of \(M\), for now we consider them as constants, and thus by defining \(a := fk\) and \(b := (1-f)k'\), eq. (1) reduces to \(B = aM + bM^{2/3}\), a statistical model that can be fitted to available databases. As can be seen in Fig. 1 and table 1, this model fits exceptionally well the collection of close to 700 mammal basal metabolic

FIG. 1: BMR for mammals. Gray dots: basal metabolic rate data for mammals compiled by McNab \(29\). Red line: fitting of our theory to the data (see table I for statistical tests). Blue line: Kolokotrones et al. statistical model \(16\). Green line: fitting to a pure power law. We also include a logarithmic binning of the data (pink dots) where the curvature is better appreciated (fits have been performed using the raw data).
rates recently compiled by McNab [20]. Statistically, its fitting is as good as the exotic quadratic function
\[ \log B = \beta_0 + \beta_1 \log M + \beta_2 (\log M)^2 \]
proposed by Kolokotrones et al [10] to quantify the curvature underlying metabolic scaling, but has only two free parameters instead of three, and is thermodynamically justified. Interestingly, if the exponents were left as free parameters, the best fit would indeed give 1 and 2/3 within a 0.5% error. Fitting values are \( a = 0.0016(1) \) for the metabolic maintenance term and \( b = k'(1 - f) = 0.079(1) \) for thermogenesis, while a pure power law can be approximated with an effective exponent \( \alpha \approx 0.720(5) \) (see table I). In what follows we focus on the biological variables \( k, k' \) and \( f \); we advance a formula for \( k' \) and accordingly predict an estimation for \( f \), which we show to be on good quantitative agreement with independent empirical evidence.

**Estimating \( k' \) and \( f \).** Note at this point that \( b \) and \( k' \) should be of the same order of magnitude and \( k' > b \) for our model to be consistent: for \( k' > b \) the model would be unrealistically efficient (\( f \approx 1 \)), whereas for \( k' < b \), \( f \) would be negative, which is meaningless. Let us now estimate \( k' \). For a heater of mass \( M \) and density \( \rho \) at constant temperature, heat generated inside its volume \( V \) is balanced with the heat lost through its surface area \( A \). The ‘basal metabolic rate’ of a heater can then be defined as the total heat loss \( Q = qA = k'M^{2/3} \), where \( q \) is the energy loss per time and area units. Now, a simple dimensional analysis yields \( A = [d/\rho^{2/3}]M^{2/3} \), where \( d \) is a dimensionless number depending on the geometry of the body (\( d = 6, 4.83 \) or 7.2 for a cube, a sphere and a tetrahedron respectively). If we only consider convection \( q_C \) and radiation \( q_R \) as sources of heat losses (a fair approximation under the conditions of basal metabolic rate measurement), then \( q = q_C + q_R \), where \( q_C = h_C \Delta T \), \( h_C \) is the convective heat transfer coefficient (for still air \( h_C \) ranges between 3-4 \( W/m^2K \) [23]) and \( \Delta T = T_s - T_e \), the difference between the surface temperature of the mammal (\( T_s \)) and the environment (\( T_e \)). According to Stefan-Boltzmann law, 
\[ q_R = \sigma(T_s^4 - T_e^4) \approx 4\sigma(T_s + T_e)\Delta T \approx h_R\Delta T, \]
where \( \sigma \approx 5.67 \times 10^{-8} Wm^{-2}K^{-4} \) in SI units. Altogether, we end up with a general expression \( k' = d(h_R + h_C)\Delta T \rho^{-2/3} \) where all parameters are indeed empirically observable. As a rough approximation, we can estimate \( k' \) by taking average values for the parameters: \( d \approx 6 \), a water-like density \( \rho \approx 1000kg/m^3 \), and \( h_C \approx 3.5 \). According to Mortola [20] a good average for mammals is \( \Delta T \sim 5^\circ C \). Averaging for \( T_s \) ranging between 15°C and 30°C, and for \( T_e \) being 1 to 10 degrees higher than \( T_e \), \( h_R \) gives values between 5.5 and 6.5, thus we take \( h_R \approx 6 \) as an average. This yields \( k' \approx 3 \) in SI units, for which \( Q(W) = k'M^{2/3} \approx 3M^{2/3}(kg) \). Transforming into appropriate units \( Q(kJ/h) \approx 0.1M^{2/3}(g) \), i.e. \( k' \approx 0.1 \). Note that this estimation depends on several empirical variables that show variability, so this number should be taken with caution (performing a parametric analysis of \( k' \) for a range of plausible values: \( d \in [5, 7], h_C \in [3, 4], T_e \in [280, 300], T_s \in [T_e + 1, T_e + 10] \) we find however \( k' \approx 0.1 \). Note that \( k' > b \) but of similar order of magnitude, as previously required. Since \( b = k'(1 - f) \approx 0.079 \), our simple approximation predicts and estimated \( f \approx 0.21 \), and the efficient energy metabolic consumption per mass unit \( k = a/f \approx 0.0076kJ/hg \). Now, although there are no accurate experimental estimates for \( f \) in the literature, this prediction can be tested against experimental evidence in the following terms. The principal sources of heat in the organism of mammals are the synthesis of ATP through the oxidation of nutrients [27], and the subsequent use of this ATP as energy source for other biological reactions. Animal ATP is generated inside mitochondria via oxidative phosphorylation, or cellular respiration. The oxidation of glucose produces the energy to create ATP from ADP, however, only about 42% [27] of the energy stored in glucose is captured in ATP (the other 58% being converted into heat), thus \( f \leq 0.42 \). ATP is subsequently used to fuel a plethora of biological reactions, and rough estimations [28] quantify that only about 50% of this energy is actually used (ATP hydrolysis is usually higher than the energy necessary to carry subsequent biological reactions), and the rest contributes to heat losses. This gives a (very rough) independent empirical estimation \( f \approx 0.21 \), which remarkably matches our prediction.

**Varying climatic conditions: Polar vs hot desert mammals.** The universality of Kleiber’s law ultimately stems from the universality of cell’s energy
source: the mitochondria, which on average have the same behaviour in all eukaryotes. Consequently, the predicted values for $f$ should be considered a reasonable average value for all mammals. Interestingly enough, mitochondria evidence slight adaptations for animals living in cold and hot environments. For example, for polar mammals, the concentration of thermogenin inside the mitochondria is unusually high (constituting up to 15% of the total protein in the inner mitochondrial membrane). Thermogenin actually uncouples oxidative phosphorylation from ATP synthesis, causing all energy released by the oxidation of glucose to be released as heat, without creating ATP, hence warming up the animal: this and other similar uncoupling proteins are a way to effectively decrease thermodynamic efficiency $f$ in mitochondria. According to our theory, the climatic adaptations in mitochondrial energetic efficiency should cluster polar and desert mammals, have a net effect in the respective values of $f$, and thus in the apparent exponent of a pure power law fitting. In particular, the ratio $b/a = (1 - f)/f$ increases as $f$ decreases, i.e. polar mammals with lower (mitochondrial) thermodynamic efficiency should have larger $b/a$ ratios than hot desert ones, and hence lower effective exponents (closer to 2/3) in a pure power law fit according to eq. 1. We have extracted all polar and hot desert mammals from McNab's dataset, and plotted their basal rates in figure 2 (blue points for polar environments, orange points for hot deserts), along with a fit to the model. Both subsets are clustered, with polar mammals having on average larger metabolic rates than desert ones for a given mass. Both $b/a$ and the effective exponents agree with the predictions of the theory. In fact, the effective slope for polars is $\alpha \approx 0.69$, a value which is closer to 2/3, the expected one for pure heaters (see table 1 for the fitting details). Accordingly, the well-known tendency of polar mammals to be larger than desert ones can be justified in terms of the aforementioned considerations (as polar mammals tend to be more thermodynamically inefficient, they need to be larger to reduce the impact of heat dissipation).

Finally, note that while climatic conditions might have an effect on $k'$ (for instance, differences between skin and environment temperatures play a role in the computation of the radiative source $q_r$), the constant related to metabolic maintenance should be considered similar for the whole set of mammals. If this hypothesis is correct, from Fig. 2 it would follow that $f \approx 0.14$ for polar animals and $f \approx 0.4$ for desert ones, while $k' = 0.16$ and 0.109 respectively. These predictions await for experimental confirmation.

In what follows, we extend this analysis to birds, insects and plants. These are smaller databases than the ones used for mammals which however are large enough for accurate statistical analysis. We will show that while in these cases a pure power law model provides reasonably similar statistical results than our proposal, the effective exponent found vary from case to case, thus one would need individual ad hoc theories that could explain the particular effective exponent for each case. On the other hand, all the results indeed comply with a combination of isometric and allometric scalings of the shape of equation 1 with varying pre-factors.

**Extension to birds and insects.** As an extension, we first make use of McNab’s collection of bird’s metabolic rates (more than 500 species) and Chown et al’s insect database (more than 300 species). In the case of birds, we further split the analysis into flying and flightless species, and plot their metabolic rates in both panels of fig. 3. For the case of flying birds (503 species), the apparent power law exponent is $\alpha \approx 0.657$ -deviating from the theoretical prediction 3/4-, but we can see that eq. 1 fits reasonably better the whole range. For flightless species the dataset is much smaller (22 species). Within this category, note that the largest species (emu and ostriches) are known to have abnormally low metabolic rates. In fact, the fitted apparent exponent $\alpha$ varies between 0.74 and 0.8 if these species are removed. In this latter case, no strong differences are found between the pure power law and equation 1 (if no splitting between flying and flightless birds is performed, results are very similar to the flying case, as flightless birds are much less common). Note that flying birds tend to have larger values of $B$ than mammals and comparatively behave closer to the ‘heater’ limit $\alpha = 2/3$. On the other hand, flightless birds cluster towards lower metabolic rates than flying ones, and behave closer to mammals (as a matter of fact, the rates for flightless birds are compatible with the curve found for mammals).

The case of insects is plotted in fig. 4 for which we find yet another different apparent exponent, $\alpha \approx 0.82$. Eq. 1 also gives a good fit to the whole range, although for this case data are highly scattered so it is difficult to compare the accuracy of both models.

Incidentally, note that an analogous formula for $k'$ could be used to estimate $f$ in these cases, provided we had empirical estimates for $T_s$ for these families. It is interesting to see that for insects, we find very small value for $b$, which suggests a small value for $k'$: this can be justified as $\Delta T$ tends to be smaller for poikilotherms.

**Extension to plants.** To round off, we consider the case of plants. In this case, it is neither clear what a basal metabolic rate is, nor if measurements for plants are done in their thermal neutral zone, as many are field studies in forests. Nonetheless, as plants also dissipate energy into heat, being this a limiting factor, then our theory can be extended to this realm. The term associated to heat dissipation must take into account that plants have a branched fractal surface encompassing their volume. As the surface to volume ratio is higher ($S \sim V^{D/3}$ where $2 < D < 3$ is the surface fractal dimension), the risk of overheating is smaller, allowing much bigger sizes than in animals. According to West et al. $S \sim V^{3/4}$, yielding $D \approx 2.25$, and thus our effective model reduces to
\[ B = aM + bM^{3/4}. \]

As the exponents of the isometric and allometric parts are now closer, we expect a much less curved relationship with a higher effective slope ranging between 0.75 and 1. To test these predictions we have used the database of basal metabolic rates compiled by Mori et al. \[51\] that includes about 200 trees and seedlings. They showed measures of metabolic rate against both total mass (including the roots) and above-ground mass. To make the comparison with mammal data homogeneous, we have used metabolic rate against total mass. Figure 5 shows these data, together with a fit to the model. As can be seen in table 1, the fit is excellent. A pure power low model with exponent \( \alpha \approx 0.81 \) (larger than for mammals) is a good fit as well, although our model seems to reproduce slightly better the high mass regime. As in the case of mammals, it is interesting to stress that if the second exponent of the model is left as a variable, the best fitting correctly yields the value \( 3/4 \).

As a final comment, Mori et al. stated in their paper that they found a concave curvature in their data. But this was due to the fact that they were mixing measures from adult individuals with measures from seedlings, which are growing quickly and have an altered metabolism. If we exclude seedlings and consider masses higher than 10 g we find no vestige of concavity (if fact, for masses higher that 0.1 g curvature is imperceptible).

### III. DISCUSSION

In this contribution we have built on Swan’s \[39\] (essential energesis is not enough to keep mammals warm) and the heat dissipation limit (HDL) paradigm \[5\] (which assumes that the capacity to dissipate heat is in fact a limit more restrictive than the energy supply). Our effective model for the body mass dependence of basal metabolic rate (whose qualitative shape was already known to interpolate among several possible effective exponents \[21\]) is justified on simple yet sound thermodynamic arguments which are biologically motivated, and successfully accounts in a simple and quantitative way for a range of biologically relevant features. We have confirmed that the wealth of different apparent exponents found for mammals, birds, insects and plants emerge possibly due to an combination of isometric (\( \sim M \)) and allometric (\( \sim M^{2/3} \)) mechanisms operating underneath. In our proposal, the pre-factors have a clear thermodynamic meaning and can vary according to exogenous con-
FIG. 5: Extension of the model for plant data. Green dots: metabolic rate data for plants compiled by Mori et al. (M > 10g). Green line: fitting of the model. Red line: fitting of a pure power law (see table I for statistical tests).

[1] Sarrus and Rameaux, Rapport sur une memoire adresse a l’Academie royale de Medecine. Commissaire Robiquet et Thillaye, rapporteurs. Bull. Acad. R. Med. (Paris), 3, 1094-1100 (1839).
[2] Rubner, M., Uber den einfluss der korpergrosse auf stoff-fund kraftwechsel. Z. Biol. 19, 536-562 (1883).
[3] Kleiber, M. Body size and metabolism. Hilgardia 6, 315-353 (1932).
[4] Heusner, A. A. Energy metabolism and body size. Is the 0.75 mass exponent of Kleiber’s equation a statistical artifact? Respir. Physiol. 48, 1-12 (1982).
[5] Speakman, J. R. & Krol, E. Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. Journal of Animal Ecology 79, 726-746 (2010).
[6] White, C. R. & Seymour, R. S. Mammalian basal metabolic rate is proportional to body mass2/3. Proc. Natl. Acad. Sci. USA 100, 4046-4049 (2003).
[7] Bartels, H. Metabolic rate of mammals equals the 0.75 power of their body weight. Exp. Biol. Med. 7, 1-11 (1982).
[8] Feldman, H. A. & McMahon, T. A. The 3/4 mass exponent for energy metabolism is not a statistical artifact. Respir. Physiol. 52, 149-163 (1983).
[9] Savage, V. M. et al. The predominance of quarter-power scaling in biology. Funct. Ecol. 18, 257-282 (2004).
[10] White C.R. and Seymour R.S., Allometric scaling of mammalian metabolism, J. Exp. Biol. 208, 1611-1619 (2005).
[11] West, G. B., Brown, J. H.& Enquist, B. J. A general model for the origin of allometric scaling laws in biology. Science 276, 122-126 (1997).
[12] West, G. B., Brown, J. H.& Enquist, B. J. A general model for the structure and allometry of plant vascular systems, Nature 399 (6745):664-667 (1999).
[13] J.R. Banavar, A. Maritan, and A. Rinaldo, Size and form in efficient transportation networks, Nature 399, 130 (1999).
[14] J.R. Banavar, T.J. Cooke, A. Rinaldo and A. Maritan, Form, function and evolution of living organisms, Proc. Natl. Acad. Sci. USA 4, 9 (2013).
[15] Dodds, P. S., Rothman, D. H. & Weitz, J. S. Re-examination of the 3/4 law of metabolism. J. Theor. Biol. 209, 9-27 (2001).
[16] Kolokotrones, T, Savage, V. Deeds, E. J. & Fontana, W. Curvature in metabolic scaling. Nature 464, 753-756 (2010).
[17] Newberry M.G., Ennis D.B., Savage V.M., Testing Foundations of Biological Scaling Theory Using Automated Measurements of Vascular Networks, PLoS Comput. Biol. 11 (8) (2015).
[18] Glazier, D.S. Beyond the "3/4-power law: Variation in the intra and interspecific scaling of metabolic rate in animals. Biol. Rev. 80, 611-662 (2005).
[19] Kozlowski, J. & Konarzewski, M. West, Brown and Enquist’s model of allometric scaling again: the same questions remain. Funct. Ecol. 19 (4) 739-743 (2005).
[20] McNab, B.K. An analysis of the factors that influence the level and scaling of mammalian BMR. Comp. Biochem. Physiol. A 151, 5-28 (2008).
[21] White, C. R. and Kearney, M. R. Determinants of interspecific variation in basal metabolic rate. J Comp Physiol
\begin{table} 
| Data set & model | Parameters fit | \( b/a \) | \( r^2 \) (%) | \( \chi^2/\log\chi^2 \) | AIC |
|----------------|----------------|-------|-------------|----------------|-----|
| **Mammals (all)** | \( B = c M^\alpha \) | \( c = 0.0692(2), \alpha = 0.720(5) \) | 95.2 | \( \chi^2 = 1.07 \) | -473 |
| \( \log B = \beta_0 + \beta_1 \log M + \beta_2 (\log M)^2 \) | \( \beta_0 = -0.95(3), \beta_1 = 0.54(2), \beta_2 = 0.031(4) \) | 96.1 | \( \chi^2 = 1.01 \) | -523 |
| \( B = aM + bM^{2/3} \) | \( a = 0.0016(1), b = 0.079(1) \) | 49 | 97.9 | \( \chi^2 = 1.00 \) | -517 |
| **Polar mammals** | \( B = aM + bM^{2/3} \) | \( a = 0.0084(5), b = 0.14(1) \) | 167 | 98.9 | \( \chi^2 = 0.78 \) | -15 |
| **Desert mammals** | \( B = aM + bM^{2/3} \) | \( a = 0.0023(6), b = 0.066(4) \) | 29 | 97.2 | \( \chi^2 = 0.62 \) | -63 |
| **Plants** | \( B = cM^\alpha \) | \( c = 0.005(8), \alpha = 0.81(1) \) | 95.7 | \( \chi^2 = 1.04 \) | 29 |
| \( B = aM + bM^{2/3} \) | \( a = 0.00023(7), b = 0.0061(7) \) | 27 | 95.8 | \( \chi^2 = 1.04 \) | 27 |
| \( B = aM + bM^\beta \) | \( a = 0.0002(1), b = 0.006(1), \beta = 0.75(7) \) | 30 | 95.8 | \( \chi^2 = 1.04 \) | 29 |
| **Flying Birds** | \( B = cM^\alpha \) | \( c = 0.143, \alpha = 0.657 \) | 88.4 | \( \log \chi^2 = 98.5 \) | -710 |
| \( B = aM + bM^{2/3} \) | \( a = 0.0032, b = 0.13 \) | 40.6 | 90.9 | \( \log \chi^2 = 96.0 \) | -708 |
| **Flightless Birds (all)** | \( B = aM + bM^{2/3} \) | \( a = 0.0038, b = 0.061 \) | 16 | 85.7 | \( \log \chi^2 = 0.69 \) | -25 |
| **Flightless Birds (without outliers)** | \( B = cM^\alpha \) | \( c = 0.04, \alpha = 0.8 \) | 98.6 | \( \log \chi^2 = 0.62 \) | -28 |
| \( B = aM + bM^{2/3} \) | \( a = 0.0036, b = 0.061 \) | 16 | 98.7 | \( \log \chi^2 = 0.66 \) | -29 |
| **Insects** | \( B = cM^\alpha \) | \( c = 0.006, \alpha = 0.817 \) | 60.4 | \( \log \chi^2 = 49.8 \) | 459 |
| \( B = aM + bM^{2/3} \) | \( a = 0.004, b = 0.0021 \) | 0.525 | 58.9 | \( \log \chi^2 = 50.9 \) | 466 |

**TABLE I: Fitting results and goodness of fit.** Fitting functions considered for the different datasets, parameter fits with errors, ratio \( b/a \) (when applicable), and goodness of fit parameters \( r^2 \) (Pearson version, the closer to 100 the better), reduced chi-square \( \chi^2 \) \([a]\) and logarithmic standard \( \chi^2 \) (both the smaller the better), and Akaike Information Criterion \( \text{AIC} \) \([b]\) (both the smaller the better). Nonlinear Regression used through Marquardt algorithm. \( \chi^2 \) is the reduced version (the standard in particle physics and astronomy): residuals are normalised by the standard deviation of the data and the statistic is then normalised over \( n-p \), where \( n \) is the total number of data and \( p \) the number of parameters to fit (good models and fits get values close to 1, and the golden rule is the smaller the better). \( \log \chi^2 \) on the other hand measures the standard \( \chi^2 \) statistic applied to logarithmically regularized data (the smaller the better). In the case of mammals, eq.1 is statistically superior than a pure power law. In the rest of the cases, both models fit equally well the data. However note that for the pure power law model one systematically finds different exponents in each case, whereas in eq.1 the exponents are fixed and only prefactors vary.

\begin{thebibliography}{99}
[22] D.S. Glazier, Metabolic scaling in complex living systems, *Systems* 2, 4 (2014).
[23] McNab, B.K. Ecological factors affect the level and scaling of avian BMR, *Comp. Biochem. Physiol. A* 152: 22-45 (2009).
[24] Chown, S.L., Marais E., Terblanche J.S., Klok C.J., Lighton J.R.B., and Blackburn, T.M. Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. *Func. Ecol.* 21: 282-290 (2007).
[25] Blaxter, K. M. Energy metabolism in animals and man. Cambridge University Press; Cambridge, MA (1989).
[26] Mortola, J. P. Thermographic analysis of body surface temperature of mammals. *Zoological Science* 30, 2: 118-124 (2013).
[27] Rhoades, R. A. & Bell, D. F. Medical Physiology. Lipincott Williams & Wilkins, Baltimore, Maryland, USA, 4th edition (2013).
[28] Barnasi, M. Human Nutrition: A Health Perspective. Hodder Arnold, London, UK, 2nd edition (2003).
[29] Lodish, H. F. et al. Molecular Cell Biology. W. H. Freeman, New York, USA (2000).
[30] Whither P.C., Energy, Water, and Solute Balance of the Ostrich Struthio camelus. *Physiological Zoology* 56, 4 (1983). Maloney S. K. Maloney and Dawson T.J. Sexual Dimorphism in Basal Metabolism and Body Temperature of a Large Bird, the Emu. *The Condor* 95, 4 (1993).
[31] Mori S. et al. Mixed-power scaling of whole-plant respiration from seedlings to giant trees. *Proc. Natl Acad. Sci. USA* 107, 1447-1451 (2010).
[32] Agutter, P. S. & Wheatley, D. N. Metabolic scaling: consensus or controversy? *Theoretical Biology and Medical Modelling* 1, 13(2004).
[33] Glazier, D. S. A unifying explanation for diverse metabolic scaling in animals and plants. *Biol Rev* 85, 111-138 (2010).
[34] Darveau, C.-A. et al. Allometric cascade as a unifying principle of body mass effects on metabolism. *Nature* 417, 166-170 (2002).
[35] Painter, P. R. Data from necropsy studies and in vitro tissue studies lead to a model for allometric scaling of basal metabolic rate. *Theor. Biol. Med. Model.* 2, 39 (2005).
[36] Kooijman, S.A.L.M. Dynamic Energy Budget theory for metabolic organisation. Cambridge University Press, Cambridge, UK (2010).
[37] Kozlowski, J., Konarzewski, M, Gawelczyk, A.T. Cell size
as a link between noncoding DNA and metabolic rate scaling. *Proc. Natl. Acad. Sci. USA* 100, 24 (2003).

[38] Economos, A. C. Gravity, metabolic rate and body size of mammals. Physiologist (Suppl 22):S71 (1979).

[39] Swan, H. Thermoregulation and bioenergetics: patterns for vertebrate survival. American Elsevier, New York, USA (1974).

[40] Bevington, P. R. & Robinson, D. K. Data reduction and error analysis for the physical sciences. Mc Graw Hill, New York, USA, 3rd edition (2003).

[41] Akaike, H. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19 (6) 716-723 (1974).