Team # 441
Problem B

Modeling the upper limit of body size for vertebrates

November 13, 2016

Abstract

As suggested by recent publications on vertebrate's maximal size [1], we have worked on a mathematical model based on resources and energy considerations that can be applied in order to account for the differences in mass between dinosaurs and mammals and that permits to reinforce or discard hypothesis about dinosaur's resources and biological nature. In this paper we analyze the model, apply it with real biological/-paleontological data and use it to give explanations to the maximal body size for land mammals and dinosaurs. Furthermore, other implications of the model are explored in order to give answers to other important questions about dinosaur's nature. In particular, we have found that dinosaurs having similar characteristics to varanids in terms of energy expenditure when extrapolated to larger mass successfully explains observed mass ratios of one order of magnitude between dinosaurs and mammals.

Contents

1   Introduction

1.1   Problem approach

The largest dinosaurs that walked the earth were approximately an order of magnitude (a factor of ten) more massive than the largest land mammals. It has been hypothesized that this may have been due to factors such as, but not limited to, the different levels of oxygen in the atmosphere, the difference in the effort required for giving birth to live young versus laying eggs, differences in metabolic rates, differences in the availability of food sources, or differences in ambient temperature. Develop a model to account for the differences in mass between the largest dinosaurs and the largest land mammals, and evaluate the effectiveness of this model using biological/paleontological data.

As suggested in [2] the constraints limiting body size can be split into two main categories, the constraints imposed by environment, such as resources availability, and the constraints related to the specific species, which include metabolic and structural characteristics. We will focus on finding which is the key or main constraint that imposes the ultimate limit body size.

We think that subtle (or not that subtle but gradual) changes on environmental conditions such as oxygen levels or ambient temperature could be circumvented by the evolution of the species, of both mammals and dinosaurs, thus this factors are not the main responsible for body size limit.

Given that mammals and dinosaurs species have been living during fairly long ages and even coexisted one could say that, at least during some time of their existence, mammals and dinosaurs faced similar environment conditions. Hence, there must be a key among their intrinsic characteristics. Another evidence for this is that most dinosaur species were larger than their mammal equivalent one[1], which also tells us that this key difference should be a general difference between mammals and dinosaurs rather than specific to a single species.

From a physicist point of view, an animal with a given size will exist only if it is viable energetically speaking, that is, if he is able to find enough food to satisfy his energy needs, which of course increase with body size. Therefore the maximum energy available to an animal is what mainly[2] limits his size.

Our approach will be to use models for the dependence of energy expenditure with mass and study their parameters to see if one can achieve a clear distinction between mammals and dinosaurs which allow us to explain the order of magnitude of difference between their maximal masses.

---

[1]Such as the Triceratops (up to 12 tons) against the Rhinoceros (up to h1 ton) or the Ankylosaurus (about 6 tons) against some species of extinct giant armadillos (up to 1 ton)

[2]All other factors may affect the food/energy available thus limiting body size, but indirectly.

2   Model

2.1   Energy expenditure model

The first model we are going to work on is the one proposed by McNab in [1]. On the one hand the field energy expenditure concept is introduced to account for the intrinsic characteristics such as metabolic rate and allometry of the energy vs mass. On the other hand we will have to understand the concept of maximal daily energy expenditure, that accounts for other intrinsic factors as well as the extrinsic ones.

2.1.1   Field energy expenditure

In first place it is supposed that the energetic cost per day [3] of any kind of individual can be approached as a function of its body mass by the following allometric relation:

$$\text{FEE} = a\,\text{M}^b \tag{1}$$

where a is a coefficient that determines the level at which energy is expended (also called mass-independent expenditure), M is its body mass and b is the power of mass (the effect of the allometry). This magnitude is usually referred to as field metabolic rate (FMR) or field energy expenditure, can be measured off real individuals and has units kJ/day.

The FEE accounts for the total energy that the living being spends in a day because of its intrinsic characteristics. To being with, observe that it just makes sense that a mouse spends less energy in a day than an elephant, because of the difference in their body masses. In addition, in biology is quite common to see that this kind of functions usually follow an allometric law. It can be seen in a number of works that this model describes well real data, but here we try to reproduce McNab's results and verify that the model actually fits with the data. To do this, it is considered the hypothesis that a set of individuals belong to a group with same (or similar) a and b coefficients, then it is verified by simple linear regression with sets of data of the kind $(\log(\text{M}), \log(\text{FEE}))$ that they really have same intrinsic characteristics and that the differences in their energy spending is only due to their difference in mass. The idea behind all this, connecting with what we said in the previous section, is that we would like to gather mammal herbivores in a single group and allow dinosaurs to be in a different one, thus giving a quantitative distinction between these two groups that we aimed to understand.

2.1.2   Maximal daily field expenditure

This model also takes into account the extrinsic characteristics of the studied group making use of the concept of maximal daily field expenditure, K, which sets the upper boundary for the FEE of an individual in the group (the units are again kJ/day) given a particular environment. Understanding this magnitude can be paradoxically easy and tricky at the

---

[3]Actually it should be said the expected value of this magnitude over time, because it may vary across different days but we will treat it as independent of time

same time. It is easy in the sense that one understands immediately that there has to be a limit because the energy you can get from your finite environment in a day is finite (one cannot spend more energy than one can get). It becomes tricky when one stops for a moment to think about which exactly could be this limit for a given species. The maximum is not the naive "the whole energy contained in the environment", it is something more interesting that depends both on the intrinsic characteristics of the individual (i.e. its mobility, facilities to get food from difficult places...) and the extrinsic characteristics or the environment, namely the quantity and quality of the accessible food around, physical boundary conditions, ecological constraints, etc.

In order to understand better the significance of this important parameter let us consider two clarifying examples:

- Consider two identical elephants (so they both have the same a and b), let us put one in an island with a very dense jungle, and the other elephant in lesser dense one. The value of K for this elephant species on the first jungle will be larger than on the second one, allowing the first elephant to grow up to a larger mass than the second.

- Similarly, consider again two identical elephants. Let us put one in an island with a jungle with high quality accessible food (more energetic), and another one in a island with a jungle with less quality accessible resources. It is an exercise similar to the previous example to proof that the one surrounded by higher quality resources will grow bigger than the other, spending more energy eventually.

To mathematically explain those examples consider the simple case where the first jungle consists of identical trees are separated by d. The energy (usable by the elephant) contained on the leaves of each tree is ε. The energy needed to actually eat those leaves can be modeled by

$$\mu = \mu(\mathrm{M}) = \mu_0 + \alpha \mathrm{M}d \tag{2}$$

where μ_0 accounts for the energy needed to eat the leaves once in front of the tree (which for simplicity is supposed to be constant) and where the second term accounts for the energy needed to go from one tree to another which in turn depends on the distance between trees and on the mass of the individual (linearly again for simplicity). If the elephant eats N trees per day his FEE will be $N\mu$. Then his internal energy E change will be

$$\Delta E = N\varepsilon - N\mu = N\left(\varepsilon - \mu\right) \tag{3}$$

where we have assumed that energy is not expended for any other activity than feeding. We will also assume that N is the maximum amount of trees that the elephant can eat in a day, since he does no other activity. If $\Delta E > 0$ the elephant mass will increase, and if $\Delta E < 0$ it will decrease. The mass at equilibrium will be achieved when $\Delta E = 0$, which implies

$$0 = \Delta E = N(\varepsilon - \mu) \implies \mu = \varepsilon \tag{4}$$

which allows us to find the mass at equilibrium (actually the maximum mass)

$$\varepsilon = \mu_0 + \alpha \mathrm{M}d \implies \mathrm{M}_{\mathrm{max}} = \frac{\varepsilon - \mu_0}{\alpha d} \tag{5}$$

Remember, however, that our goal here is to find K, which is the maximal viable value for FEE, that in this case corresponds to

$$K = \text{FEE}_{\max} = N\mu_{\max} = N\varepsilon \tag{6}$$

Now, comparing two jungles with same trees, but different distances between them, the number of trees the elephant can eat per day N will be different. N will be larger in a higher density jungle and therefore K will increase. If the difference is not in the distance but in the nutrients of the trees, what will increase will be ε, also increasing K.

The idea of the previous example in the most general case shows that different species with same a and b but with different K have different opportunities to grow. The quantity and quality of the resources in the environment are important factors of K, but notice that all other factors affecting the animals diet would also have an impact, this include animal shape, habits and size.

2.1.3   Interpretation

The moral that can be extracted from this model is that given a restraint in total energy expenditure, that is, a fixed K, the individual with a lower mass-independent expenditure, a, can attain a higher mass, m, because it happens that b is approximately constant between[4] 0.67 and 0.85 over a large range in mass [11]. Therefore, the most efficient species are the ones that can achieve the largest masses.

---

[4]The fact that b is always less than 1 reflects the contrasted fact that the FEE per unit of mass decreases with the mass of the individual.

3   Method and results

To begin with we have tried to verify the model by taking real data from [4], where there is a compilation of field metabolic rates (FMR) of wild terrestrial vertebrates as determined by the doubly labeled water technique. The idea is to see if equation (1) describes well the collected data by looking at the r^2 value of the data fits. This will be compared to McNab's results and the results of Nagy, Girard and Brown in [4] to see if there is consistency.

After having checked the model validity, we intend to apply the model to obtain as much information as possible. With this purpose, we will contemplate several hypothesis concerning dinosaurs and test them by direct application of the model.

3.1   Verification of the model

From data in [4] we can estimate the constants a and b, for 79 species of mammals and 55 of reptiles using the relation given by equation (1). By taking logarithms[5] we have that

$$\log \text{FEE} = \log a + b \log \text{M} \tag{7}$$

which is a relation of the form $Y = A + B\,X$, where $a = 10^A$ and $b = B$.

As can be seen in figure 1, if we plot FEE as a function of the body mass of species in log/log scale, the points clearly follow linear tendency. It motivates us to do linear regressions to estimate the parameters a and b. In table 1 we show the results of these linear regressions with the considered data sets.

Table 1: Estimated values for a and b for reptiles and mammals, number of species used to obtain them, adjusted r^2 coefficient and p-value of the F-test done for each linear regression.

Set of individuals, i	a_i	b_i	n° species	adjusted r^2	p-value
Mammals, m	4.8196	0.7341	79	0.9491	$\sim 10^{-16}$
Reptiles, r	0.1965	0.8879	55	0.9440	$\sim 10^{-16}$

The values for r^2 are relatively high (~ 0.95) and the p-values very low, which supports the validity of equation (1). Therefore we can now consider the following allometric relations for mammals and reptiles with the estimated constants:

$$(\text{FEE})_m = a_m \text{M}^{b_m} \approx 4.82\,\text{M}^{0.73} \tag{8}$$

$$(\text{FEE})_r = a_r \text{M}^{b_r} \approx 0.20\,\text{M}^{0.89} \tag{9}$$

These results are in accordance with the ones obtained in [4].

---

[5]To be consistent with the cited literature we use logarithms with base 10.
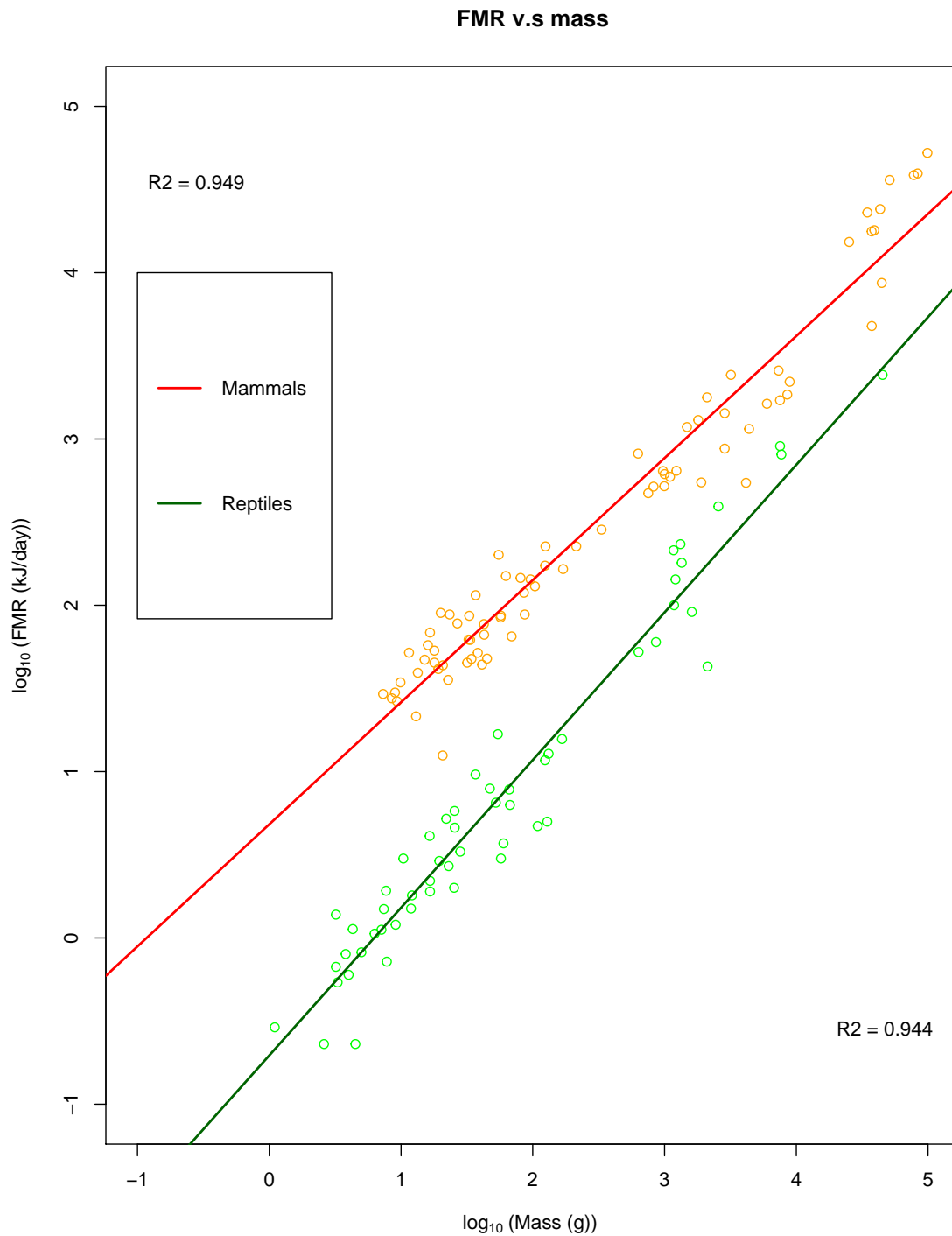
Figure 1: Representation of the field metabolic rates (in kJ/day) as a function of the body mass (in grams) of mammals (red) and reptiles (green) together with the associated linear regression in the log/log scale.

3.2   Applications

In order to be able to compare dinosaurs and mammals we need to set some hypothesis concerning the values of the unknown K values for each of the groups. Concerning the K for mammals, we are going to argue as follows for the rest of our work:

The largest mammal ever observed was one that had approximately achieved the maximal daily field expenditure for mammals, K_m.

As for the counterpart, we will begin setting that the K value of the dinosaurs, K_d, was:

The maximal field expenditure of the mammals cannot be very different from that of the dinosaurs. Thus:

$$K_d \approx K_m$$

The biggest mammal herbivore known to have existed is the Paraceratherium ([6]) which had an estimated weight of around 15 tons and therefore, following the allometric relation (8) would have had a FEE of $8.94 \cdot 10^5$ kJ/d. Since there is no evidence of bigger mammal herbivores it must be that this value is close to K_m. Then we will take

$$K_m \approx 8.94 \cdot 10^5 \, \text{kJ/d} \tag{10}$$

3.2.1   Reptile hypothesis

First let us apply the model and test the widely extended idea that dinosaurs were reptiles. We will set the dinosaur's allometric constants to be that of the reptiles we obtained in table 1 and predict the mass of the heaviest dinosaur:

$$K_d = a_r \left(\text{M}_{\text{max}}^{(d)} \right)^{b_r} \Rightarrow \text{M}_{\text{max}}^{(d)} = \left(\frac{K_d}{a_r} \right)^{1/b_r}$$

Now substituting the values of a_r and b_r from table 1 and using $K_d \approx K_m$ we obtain:

$$\text{M}_{\text{max}}^{(d)} \approx 31.51 \, \text{t}$$

Thus, the ratio dinosaurs vs mammals for the heaviest species results:

$$\frac{\text{M}_{\text{max}}^{(d)}}{\text{M}_{\text{max}}^{(m)}} \approx 2.1$$

The result shows that at least one of the hypothesis should be wrong, given that the heaviest dinosaur that has been found (*Seismosaurus halli*) had weighted around 100t (see [2]) and so the expected ratio should be 6.67. Thus, we conclude from this calculations that probably either dinosaurs are not reptiles, or the K_d is not of the same order of K_m (which would mean there was higher resources availability in the dinosaurs ages), or both.

3.2.2 Varanus hypothesis

Given that under the hypothesis $K_d \approx K_m$ we found that dinosaurs could not be reptiles, we are going to fit dinosaurs into a different category. As occurred to McNab, we can see what happens if we put dinosaurs into a subcategory of the reptiles known as Varanus. This suggestion comes from the widely accepted idea that dinosaurs were more active and had higher temperatures than those of other reptiles, and fact that varanids are one of the biggest and most active living lizards, and also have higher body temperatures [5], thus making them more similar to dinosaurs than other reptile species. Notice that we will consider only the six heaviest varanids (with a weight greater than 1.3 kg) as dinosaurs are expected to have relatively large weights.

Now we set the dinosaur's allometric constants to be that of the Varanus we show in table 2 and predict the mass of the heaviest dinosaur as we have done before for all species of reptiles (with available data). Substituting the values of a_v and b_v from table 2 and using $K_d \approx K_m$ we obtain:

$$M_{\text{max}}^{(d)} \approx 158.17\,\text{t}$$

Thus, the ratio dinosaurs vs mammals for the heaviest species is now:

$$\frac{M_{\text{max}}^{(d)}}{M_{\text{max}}^{(m)}} \approx 10.54$$

Observe that this ratio is in the order of 10, as it was expected. It is a bit larger than the supposed 6.67, nevertheless, notice that this tells us that the heaviest dinosaur could had weighted 158 t, while the heaviest *that we have found* weighted around 100t. So we can say that there is still a possibility that there existed heavier dinosaurs and that the hypothesis were right.

Table 2: Estimated values for a and b for varinids, number of species used to obtain them, adjusted r^2 coefficient and p-value of the F-test done for the linear regression. The curve is compared with the mammal one in Figure 2

Set of individuals, i	a_i	b_i	nº individuals	adjusted r^2	p-value
Varanus > 1.3 kg, v	1.3605	0.7095	6	0.9715	$\sim 2 \times 10^{-4}$

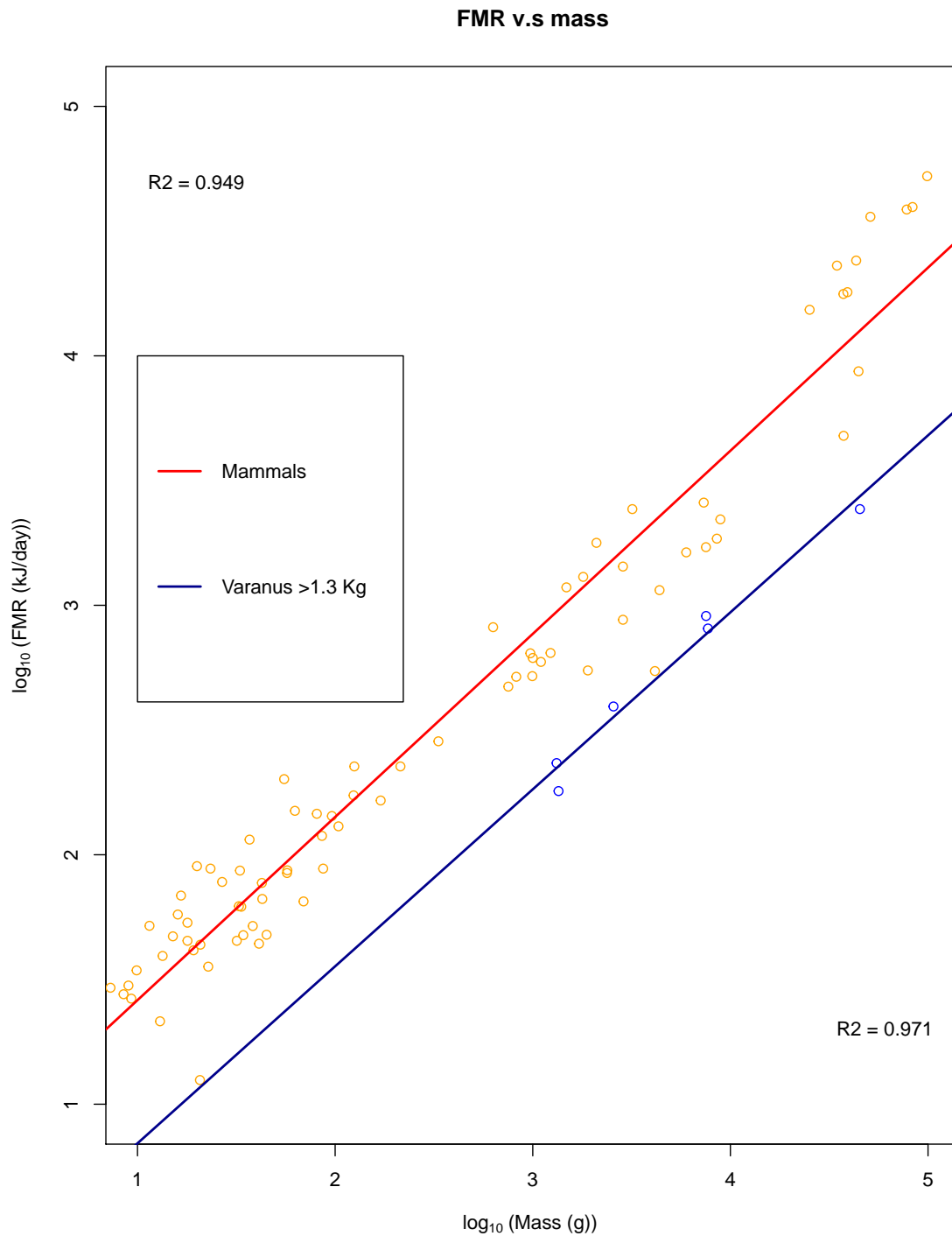$$(\text{FEE})_v = a_v M^{b_v} \approx 1.36\,M^{0.71} \tag{11}$$

Figure 2: Representation of the field metabolic rates (in kJ/day) as a function of the body mass (in grams) of mammals (red) and Varanus lizards (blue) with the associated linear regressions in the log/log scale.

3.2.3   Comparing the goodness of reptile v.s. Varanus hypothesis

Here we consider two of the heaviest and well-known mammals so as to compare them with their physiological/ecological equivalent dinosaurs by using the reptile hypothesis discussed in section 3.2.1 and the Varanus hypothesis discussed in section 3.2.2.

As we did to estimate the value of K_m for the heaviest mammal (see equation (10) and how it was obtained), now we can estimate the K_m corresponding to mammals considered in tables 3 and 4 (the Rhinoceros and the Giraffe), and use it to calculate a prediction mass for the (arguably) ecologically equivalent dinosaur according to each of the hypothesis considered, i.e, we use the relation

$$\mathrm{M}_d = \left(\frac{K_d}{a_i} \right)^{1/b_i}$$

where we take, as in the sections above, $K_d \approx K_m$, and $i = r$ for the reptile hypothesis, $i = v$ for the Varanus hypothesis. In the same way we can compute the mass ratios (M.R), M_d/M_m for both the predicted mass and the mass found in the references.

These results are summarized in tables 3 and 4.

Table 3: Reptile hypothesis results

Mammal	M_m (t)	Dinosaur	M_d (t)	Pred. M_d (t)	Pred. M.R	M.R
Rhinoceros	1-2	Triceratops	6 - 12	3.36 - 6	2.98 - 3.36	6
Giraffe	0.5 - 2	Diplodocus	10 - 15	1.89 - 6	2.98 - 3.79	7.5 - 20

Table 4: Varanus hypothesis results

Mammal	M_m (t)	Dinosaur	M_d (t)	Pred. M_d (t)	Pred. M.R	M.R
Rhinoceros	1 - 2	Triceratops	6 - 12	9.6 - 19.67	9.6 - 9.83	6
Giraffe	0.5 - 2	Diplodocus	10 - 15	4.69 - 19.67	9.37 - 9.83	7.5 - 20

This results confirm what we already saw in previous analysis, which is the fact that the general reptile curve (equation (9)) cannot correctly describe the mass of the dinosaurs. Notice that predicted mass ranges not even overlap the observed mass ranges. The varanid curve (equation (11)) however, gives results a lot more in compliance with observed masses and mass ratios, thus reinforcing the validity of the model.

3.2.4   Possible issues of low metabolic rate

The previous results rely basically on a low energy expenditure on dinosaurs to explain their large mass, however, there are several evidences which show that dinosaurs could not have metabolic rates as low as the ones showed by lizards and other reptiles. This evidences include

- Corporal temperature of dinosaurs was significantly larger that the ambient temperature which suggests that they were not ectotherms ("cold-blooded"). It is speculated that this might be due to their large masses giving them thermal inertia but this might not be enough with such low metabolic rates as the ones of lizards. Actually [3] states that dinosaurs were not endotherms either ("warm-blooded") but instead lay somewhere in between.

- The growth rate is known to be correlated with metabolic rate [3], then, if dinosaurs had such low metabolic rates their growth rate would also have been low. It is supposed that parental care was minimal for dinosaurs then young individuals would be vulnerable to predators until they reach a large enough size. According to [2] *A high BMR thus emerges as a prerequisite for gigantism.*

This suggests that metabolic rates, and therefore mass-independent energy expenditure (the slope a), of dinosaurs has to be higher. In this direction we would like to check if dinosaurs following the varanid FEE curve could fall into the mesotherm category, that is, if their metabolism rate would allow them to maintain a higher temperature than the ambient one.

Thermodynamics tell us that that will be possible if the dinosaur sources of heat provide enough to compensate the heat losses. There are a lot of heat sources and drainers [8] but we think that the most important ones here are on the daily FEE, on the sources side, and convective heat loss in contact with air, on the other one.

Firstly, for the daily FEE, a dinosaur following the varanid curve with mass M would have the FEE that (11) predicts. On the other hand convective heat loss, modeled using Newton's law of cooling, is

$$q = hS\Delta T \tag{12}$$

where h is the heat transfer coefficient, S the surface of the animal in contact with air and ΔT the difference of temperature between the air an the animal skin.

Typical values for this parameters are

$$h = (5{\sim}20) \text{ W/m}^2\text{K} \qquad \Delta T = (1{\sim}10) \text{ K}$$

and the surface, taking the simple but reliable model of an spherical animal yields

$$S = \left(\frac{3}{16\pi^2}\right)^{1/3} V^{2/3} \approx 0.27\text{M}^{2/3} \tag{13}$$

where we have taken the density of the flesh to be approximately 1 kg/m^3. All this leads to values of convective heat loss of

$$q \approx 0.27h\Delta T\mathrm{M}^{2/3} \approx (1.35 \sim 54)\mathrm{M}^{2/3} \tag{14}$$

where the mass M should be in kg.

Finally from (11) and (14) we get, for a mass of 100 tonnes

$$\mathrm{FEE} = 6.45 \cdot 10^5\mathrm{kJ/day} \qquad q \approx (2908 \sim 116316)\mathrm{W} \tag{15}$$

converting units to easily compare

$$\mathrm{FEE} \approx 7.5\mathrm{kJ/s} \qquad q \approx (3 \sim 116)\mathrm{kJ/s} \tag{16}$$

This results show that the FEE predicted by the varanid curve might be of the same order of magnitude than the convective heat loss, given than the difference in temperature between the dinosaur and the air is small enough and that the heat transfer coefficient h is not too large, which might be accomplished by thicker skin which isolates better corporal temperature. Also, we are not taking into account the heating from solar radiation, which may also be an important factor.

What we want to stress here is that our simple heat model finds no relevant evidence to reject the varanid metabolic rate, as a valid metabolic rate to allow mesothermy on larger individuals. Therefore, it might be possible that the varanid curve actually describes well the dinosaur metabolism.

4   Conclusions

Regarding to the results that we obtained by using the different approaches and the models we have considered we can conclude that

- The main model based on the allometric relation given by equation (1) behaves very well when describing the dependence of the field metabolic rate with the body mass of species that belong to the same class, such as mammals and reptiles, with which we have worked during this paper.

- The reptile hypothesis discussed in section 3.2.1 does not agree with the fact that *the largest dinosaurs that walked the earth were approximately an order of magnitude more massive than the largest land mammals.* On the contrary, the Varanus hypothesis, discussed in section 3.2.2, is more in compliance with this fact, and gives good predictions for equivalent dinosaur masses when compared with the associated mammals ones, as seen in section 3.2.3.

- The fact that dinosaur energy expenditure does not follow the general reptile curve, but rather the Varanus lizards one, reflects a higher metabolic rate for dinosaurs in comparison with other reptiles which might be the explanation for their so debated thermoregulation system, which lies between ecto and endothermy. This effect however is only possible due to their large masses.

5   Further Investigations

In this final section we would like to sum up several ways to go on with the research

- Try to find more accurate values for the K_d by considering approaches different from the one that consisted of approximating $K_d \approx K_m$.

- Evaluate the effectiveness of the models considered using more biological and paleontological data.

- Use the model to test other hypothesis about dinosaurs.

References

[1] Brian K. McNab (2009), *Resources and energetics determined dinosaur maximal size* Proc. Natl Acad. Sci. USA 106, 12 184 – 12 188 (doi: 10.1073/pnas.0904000106)

[2] Sander et al. (2011), *Biology of the sauropod dinosaurs: the evolution of gigantism* Biology Review. 2011 Feb;86(1):117–155 (doi: 10.1111/j.1469-185X.2010.00137.x)

[3] John M. Grady et al. (2014), *Evidence for mesothermy in dinosaurs* Science 13 Jun 2014: Vol. 344, Issue 6189, pp. 1268-1272 (doi: 10.1126/science.1253143)

[4] Nagy KA, Girard IA, Brown TK(1999) *Energetics of free-ranging mammals, reptiles, and birds.* Ann Rev Nutr 19:247–277

[5] McNab BK, Auffenberg W (1976) *The effect of large body size on the temperature regulation of the Komodo dragon, Varanus komodoensis.* Comp Biochem Physiol A 55:345–350.

[6] Paraceratherium, `https://en.wikipedia.org/wiki/Paraceratherium`

[7] Kleiber's law `https://en.wikipedia.org/wiki/Kleiber%27s_law`

[8] Teng Fei et al. (2011) *A body temperature model for lizard as estimated from the thermal environment* Journal of Thermal Biology 37 (2012) 56–64

[9] Dinosaur sizes, `https://en.wikipedia.org/wiki/Dinosaur_size`

[10] Allometry, `https://en.wikipedia.org/wiki/Allometry`

[11] Nagy KA (2005), *Field metabolic rate and body size.* Review. J Exp Biol 208:1621–1625