

THE SCALING OF METABOLISM¹

Summary: Scaling of metabolism to body size is viewed in light of two models: isometric scaling based on the idea that a unit of mass always has the same metabolism (metabolic rate is proportional to body mass raised to the 1.0 power) and a model where metabolism is scaled isometrically with surface area but allometrically with mass since metabolic rate scales to body mass raised to the 0.67 power. Neither model fits the data that for a wide range of body sizes scales total metabolic rate as the 0.75 power of body mass. Instead, scaling to the 0.75 power of mass is viewed as a solution that optimizes the tendency to maintain a high metabolic rate but within the severe constraint of surface area. The use of scaling as a tool to predict whether or not an animal is "typical" of others of its size and the usefulness of mass-specific measures of metabolism are also both explored.

Be able to derive the mass-specific equation relating metabolism to mass from the total metabolism equation.

I. WHAT SETS METABOLIC RATE – AN INTRODUCTION

A. Many studies have shown that metabolism varies both among individuals within a species (intra-specific variation) and across different species (inter-specific variation). This is true even when we measure many organisms at similar body temperatures, levels of activity, and in similar nutritional states.

1. We are going to ask two main questions:

 HOW do metabolic rates differ among species?

 WHY do these rates differ?

2. We turn to comparative physiology and physiological ecology in order to answer these questions.

B. The first way that we will investigate these questions is to ask: **What is the relationship between the size of an animal and its energy expenditure?**

1. Why is this question important?

a. Animal abundance and diversity: Animals come in all sizes. In certain environments, certain size classes are quite rare.

- Could the rarity of certain sizes in certain environments have anything to do with energy demands (metabolism) of large animals as compared to small ones?
- Is it that certain habitats cannot support large animals, or in other cases, small ones?

b. Application to food production.

- Are some animals more "efficient" than others in converting food into tissue; and if so, is this related to body size?

For instance, certain types of forage cannot be consumed by humans but they can be eaten by animals and converted to meat (e.g., grass, algae). Are some animals better than others to use to exploit these potential resources?

- Surplus foods produced during growing seasons can be converted to biomass of animals and then harvested during a

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season when other food is unavailable (winter, early spring). Are some animals better than others for this and is it related to body size?

2. To standardize our investigation, we need to define specific types of metabolism that will be compared with each other.

a. **STANDARD OR BASAL METABOLIC RATE (SMR or BMR).** The lowest metabolic rate repeatedly observed in an inactive animal at a certain temperature after a period of fasting. This should represent the **MINIMUM AMOUNT OF ENERGY NECESSARY TO MAINTAIN THE ANIMAL.**

1. **Standard metabolism** refers to this type of measurement **when it is done on an ectotherm** (an animal without a significant internal heat source, such as a frog).

2. **Basal metabolism** refers to this specialized type of resting metabolism **when it is measured on an endotherm**, such as a bird or us.

Fasting is an important requirement for BMR and SMR because when food is eaten, the digestive process causes the release of heat. This, and the process of absorption raise the metabolic rate. To remove these factors, the animal is fasted for a time long enough for digestion to be complete. This time varies greatly in different species. Note that this is not the same thing as starvation, which will further decrease metabolic rate.

b. **RESTING:** the metabolic rate of an animal at rest at a particular temperature. The animal is not starved as with standard and basal metabolism.

c. **ROUTINE:** metabolism of an animal taken at temperatures to which it is adapted and has been acclimated. Routine metabolism includes fluctuations due to normal light activity and the animal is not starved prior to measurement.

c. **ACTIVITY:** metabolic rates that are measures of the power or cost of a particular activity, such as running at a certain speed or producing a calling song or flying at a certain velocity.

3. Typically comparisons are made using just one of these conditions – animals' SMR or BMRs are compared with each other or, for example, their maximum rates of activity metabolism are compared.

II. SCALING

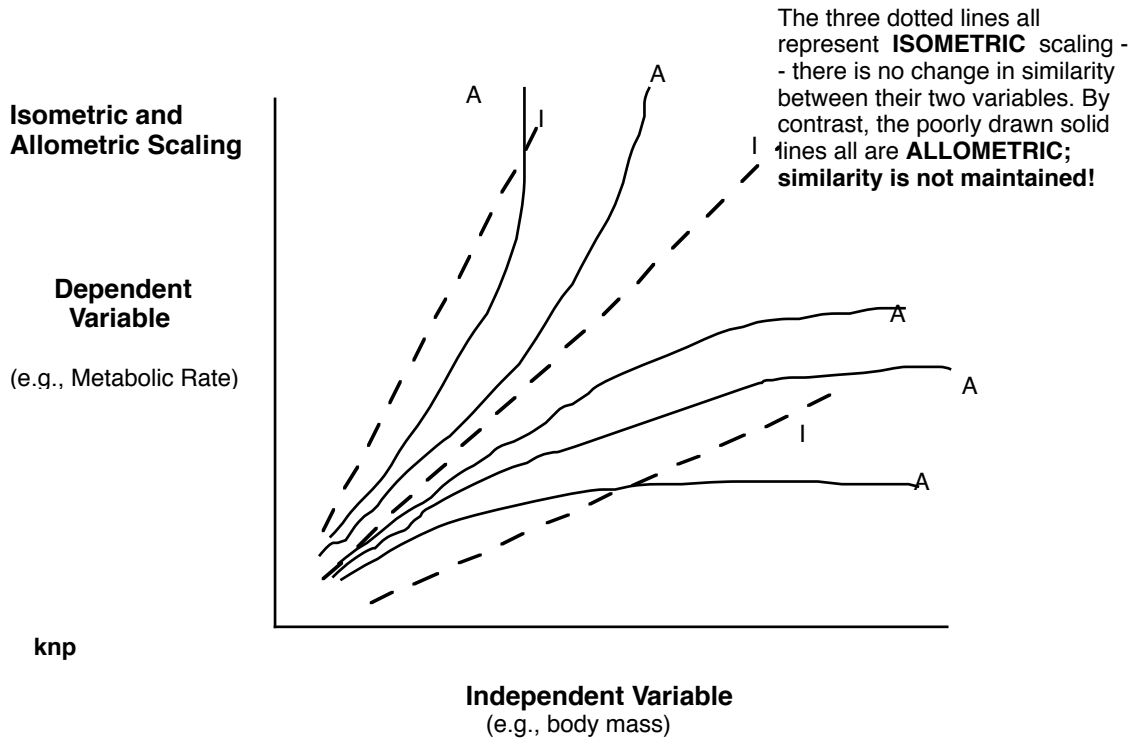
A. The most commonly used tool to compare differences in body size with differences in metabolism is called **SCALING**.

B. Scaling is defined as the **structural and functional consequences of a change in size or in scale among similarly organized organisms.**

C. General types of scaling relationships

a. **ISOMETRIC SCALING**: there is a constant proportional relationship between the variables being scaled (e.g., a constant proportional relationship between metabolic rate and body size). If we plot one of these variables against the other we will obtain a straight line.

b. **ALLOMETRIC SCALING**: there is a change in similarity between the two variables as they change value – one does not have a constant proportional relationship to the other. Thus, the relationship between the two variables is non-linear



c. Here is a general mathematical expression for both allometric and isometric scaling relationships:

$$1. \quad Y = i + aX^b$$

where **i** is the y intercept, **a** is the slope, and **b** is a number that describes the scaling relationship between the variables.

Equation 1 is a more generalized version of the familiar equation

$$Y = b + mX$$

where **b** is the y-intercept, **m** is the slope and **X** is the independent variable. In this case the exponent of **X** is understood to be 1 and the function plots as a straight line.

1. Thus, for any equation **where b (in eq. 1) has a value of 1.0** the plot will be a straight line and the **relationship is isometric**. However, in different cases the rate of change may be different (straight lines with different slopes).

2. On the other hand, notice that if the value of b is different from 1.0, the relationship between Y and X is not constant and we say that the variables are **ALLOMETRICALLY RELATED**.

D. Working with real data.

1. Typically, allometric studies of metabolism on body size involve obtaining measurements of each for a large number of animals of different sizes. The data are then plotted and linear or power functions are fitted to the data using statistical techniques that are termed **regression analyses**.

2. Since scaling studies typically look for broad relationships, wide ranges of sizes are considered.

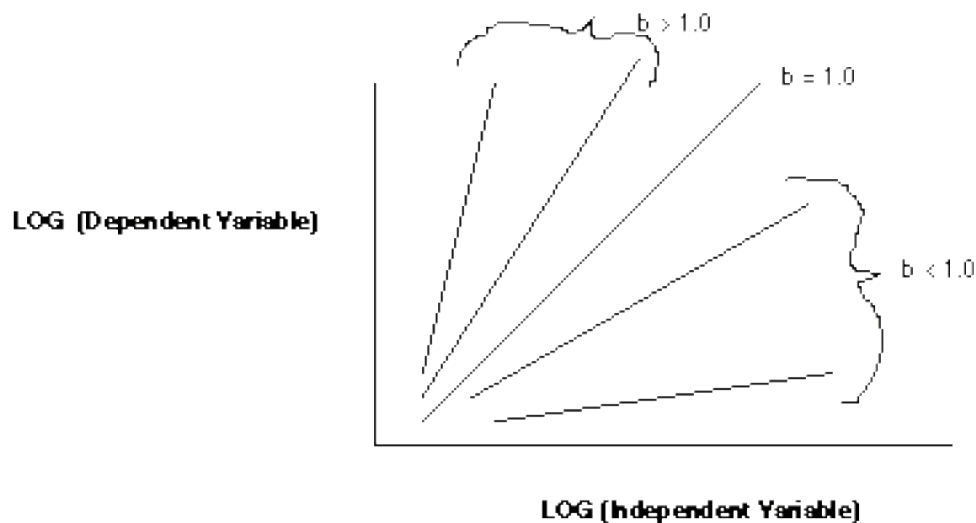
a. Such data are hard to plot on a reasonably sized graph and so the data are commonly compressed by taking the logs (base 10) of the two values that define each point.

b. These transformed data can then be used in regression analysis.

c. An interesting consequence of this is that the regression equation will now be in the following form:

2. $\text{Log } Y = \text{Log } a + b * \text{Log } X$

where **a** is the y-intercept of the double-log plot and **b** is the slope of the line. This slope indicates the scaling relationship.



Notice that allometric relationships for double-logged data are straight lines with slopes significantly greater or less than 1.0; isometric relationships are for straight lines with slopes very close to 1.0.

III. MODELING THE RELATIONSHIP BETWEEN METABOLISM AND BODY SIZE

A. In this section we will consider two **theoretical relationships (models)** of the relationship between metabolic rate and one measure of body size, total body mass.

1. We will first develop and explain these two opposing models
2. Next, we will **test them by seeing if any of them fit the data showing the actual relationship between metabolism and body size** (the data regressions mentioned in the previous section).

Advance warning: You may find the final result of this analysis a bit unsatisfying because neither of these relationships really fits. However, press on because it will help you to gain an increased understanding of the complexity of biological systems and the difficulties involved with modeling.

B. What relationships can we reasonably predict between metabolism and body size?

The models:

1. **THE ISOMETRIC MODEL:** as body size increases, say doubles, the total amount of tissue in the organism doubles. If we assume that adding more tissue should not change the basic metabolic demands, we predict then that as total size measured by mass doubles, so must total metabolism. Thus:

3a. $\text{Metabolism} = a * \text{Mass}^{1.0}$

and

3b. $\text{Log metabolism} = \text{Log } a + 1.0 * \text{Log Mass}$

Notice that the power of our scaling equation for this isometric model is 1.0 in the exponential version of the equation (3a) and the slope is 1.0 in the logged version of the relationship (eq. 3b).

? Assume that for two different groups of animals; $a = 1$ in group Y and $a = 6$ in group Z. If there are animals of mass 1.0 and 2.0 kg in each group, satisfy yourself that regardless of the slope, in either group a doubling of mass results in a doubling of metabolism (that is, isometric scaling).

2. THE ALLOMETRIC MODEL. There are many possible allometric models but let's just develop one that is both biologically reasonable and important in the historical development of scaling in physiology. In this model we will assume that the constraining or determining factor on metabolism is the **surface area available for gas and/or metabolite and/heat exchange.**

a. You may (should) ask yourself, how is the model I just presented is an allometric model? After all it is based on the idea that surface area determines metabolism and it is therefore isometric – i.e.,

4. Metabolism \propto SA or Metabolism = a * SA^{1.0}

b. However, we can re-express this model so that it is in terms of mass instead of surface area. In the process, it will become an allometric model.

c. You are probably asking why we want to do this – why re-express the model in different units?

d. The answer is that in order to compare the two models we want to put the dependent and independent variables into the same units. We cannot easily compare one model that defines points by metabolic rate and mass with an alternative that uses metabolic rate and area!

3. THE TRANSFORMATION OF THE SURFACE AREA MODEL

a. To make the transformation we need to know the relationship between mass and surface area.

b. Consider any geometrical shape:

5a. Volume \propto L³ -- or, expressed as an equation:

5b. V = k₁*L³

where **V** = volume and **L** = linear dimension. Notice that the value of **k₁** will differ with different types of shapes; for example, for spheres **a** is 4/3 * Π and for a box it is 1.0, etc.

c. If we take the third root of this equation we can restate eqs. # 5a and b as:

6a. L \propto V^{0.334} -- or as

6b. L = k₁* V^{0.334}

d. We also know that:

$$7. \text{Volume}^{1.0} \propto \text{Mass}^{1.0} \quad \text{or} \quad V^{1.0} = k_2 * M^{1.0}$$

therefore, by substitution of eq. 7 into eq. 6:

$$8a. \quad L \propto M^{0.334} \quad \text{-- or}$$

$$8b. \quad L = k_3 * M^{0.334}$$

d. Now, let us consider surface area (**SA**):

$$9a. \quad SA \propto L^2 \quad \text{-- or}$$

$$9b. \quad SA = k_3 * L^2$$

e. where once again the value of the constant depends on the type of shape we are talking about (for instance 4 * Π for a sphere and 6 for a box). By substitution of eq. 8 into eq. 9:

$$10a. \quad SA \propto (M^{0.334})^2 \quad \text{-- or}$$

$$10b. \quad SA \propto M^{0.67} \quad \text{-- or}$$

$$10c. \quad SA = k_4 * M^{0.67}$$

3. Thus, our relationship between metabolism and mass **for the situation where SA determines (i.e., limits) metabolism** is simply the result of substituting \dot{Q} (metabolic rate) for **SA** (since SA limits \dot{Q} -- see original model and eq. 4) into eq. 10 b and c:

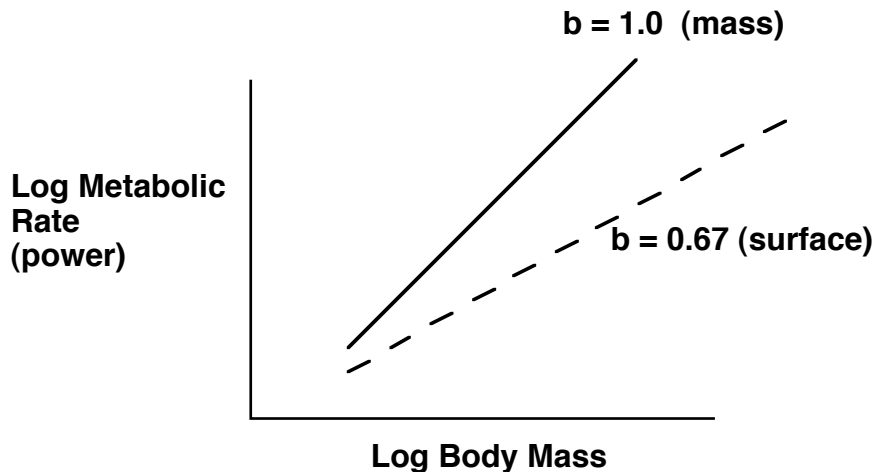
$$11a. \quad \dot{Q} \propto \text{Mass}^{0.67} \quad \text{-- or}$$

$$11b. \quad \dot{Q} = a * (\text{Mass}^{0.67})$$

or in log form:

$$12. \quad \log \dot{Q} = \log a + 0.67 \log \text{Mass}$$

We can now plot our two models on a double-log graph.



C. TEST OF THE MODELS.

1. Recall that we are interested in trends in metabolism that are related to body size. To find these, we must look at a number of different organisms and it is especially important that the species used vary in body size by several orders of magnitude (or more). Otherwise, other differences between similarly sized organisms (for instance, resulting from different growth or reproductive rates or "intrinsic activity level" etc.) might well mask effects related to size.

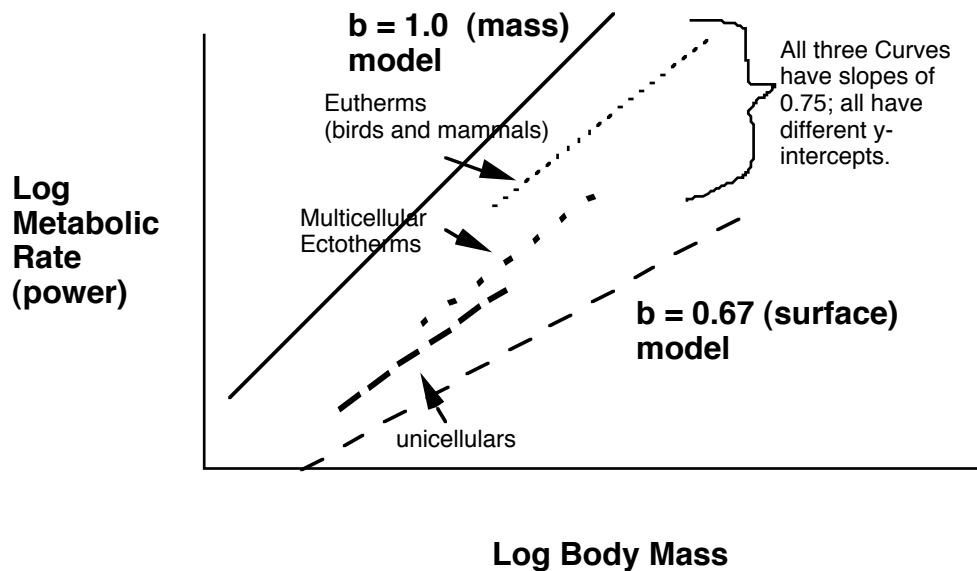
2. The first such attempt was made by Rubner about 100 years ago. He used dogs (the "Chihuahua to St. Bernard" curve – about 2 orders of magnitude). More recently (1930s) Kleiber did it for mammals of different sizes.

3. However, the classic study was done by Hemmingsen in 1960. He collected metabolic rate data for a vast number of different animals and even some plants spanning sizes from bacteria to whales.

? What special problems are involved in measuring the metabolic rates of plants?

When he obtained regressions for log/log plots, his results were somewhat surprising. He obtained three distinctly different lines, each defined by the types of organisms found on the line and the y-intercepts of these lines. The lines were for:

- (i) Unicellular organisms
- (ii) Ectothermic organisms (those whose temperature is mainly determined by external heat sources)
- (iii) Endothermic organisms (those whose temperatures were primarily determined by their own metabolism).



1. The lines are best-fit linear regressions and the R^2 values (measures of the degree to which the data points fit the regression line – 1 is a perfect fit and 0 is no fit at all) for each are between 0.7 and 0.8 (a pretty good fit).

2. Hemmingsen's Conclusions:

a. As predicted, **BIGGER ANIMALS HAVE GREATER METABOLIC RATES AND THEREFORE GREATER ENERGY DEMANDS.**

b. **METABOLIC RATE OVER A WIDE RANGE OF ORGANISMS SEEMS TO SCALE TO THE 0.75 POWER OF BODY MASS.**

c. **THERE ARE 3 DISTINCT LINES THAT DIFFER BASED ON THE VALUE OF THEIR Y-INTERCEPTS.** For example, although it does not look like it, the eutherms' line is roughly 39X more elevated than the ectotherm line.

(a) However, the poikilotherms were taken with body temperatures of 20° C and while most endotherms had body temperatures between 37 and 41° C.

(b) If we correct these lines to the same body temperature (you'll learn how later this week), there is still a **9X difference** with the endotherms having higher rates for a given body size. **THIS IS A VERY IMPORTANT POINT.** The differences are interpreted partially as being due the cost of complexity (energy to maintain a more complex system). This is a hard thing to actually "prove".

d. **Let's consider the 0.75 slopes of all of the lines a bit more:**

i. The **slopes of the lines are all statistically indistinguishable from 0.75**. However, **they are statistically distinguishable from a slope of either 0.67 or 1.0**.

ii. **This sinks both models**

There were attempts to revise the 1.0 model based on the fact that not all parts of the body scale the same way -- as an animal gets bigger, the amounts of bone are proportionately larger than predicted by an isometric model of bone to mass (since a greater cross-sectional area is required for support and this will result in a greater mass).

Even if we correct for this sort of thing, the result is a slope of about 0.92; this is still significantly different from the actual measured value.

? WOULD THE EXPONENT RELATING BONE MASS TO BODY MASS

BE $<$ OR $>$ 1? (In other words, do you expect skeletons to increase in mass at the same rate as the general body does?)

? WHAT ABOUT BONE MASS TO BODY LENGTH?

The SA area doesn't really work either, but then why should it?

In accordance with the surface area model, it was believed that metabolism might be determined by **heat loss** (suggested by Rubner from his work with dogs). This is OK for mammals and birds, but most animals (and certainly not unicellulars) do not need to lose large amounts of heat.

Respiratory gases and respiratory surface area were the next justification for the possibility that metabolism should scale to surface area. If you have no specialized organ for exchange of gas, you would be limited by your surface area to the amount of respiratory gas you can exchange. However, animals should be able to come up with any size exchanger they need (but in fact there are some constraints related to body size); that is they **break symmetry**. Adding gills, skin folds and internal lungs are all examples of such broken symmetry.

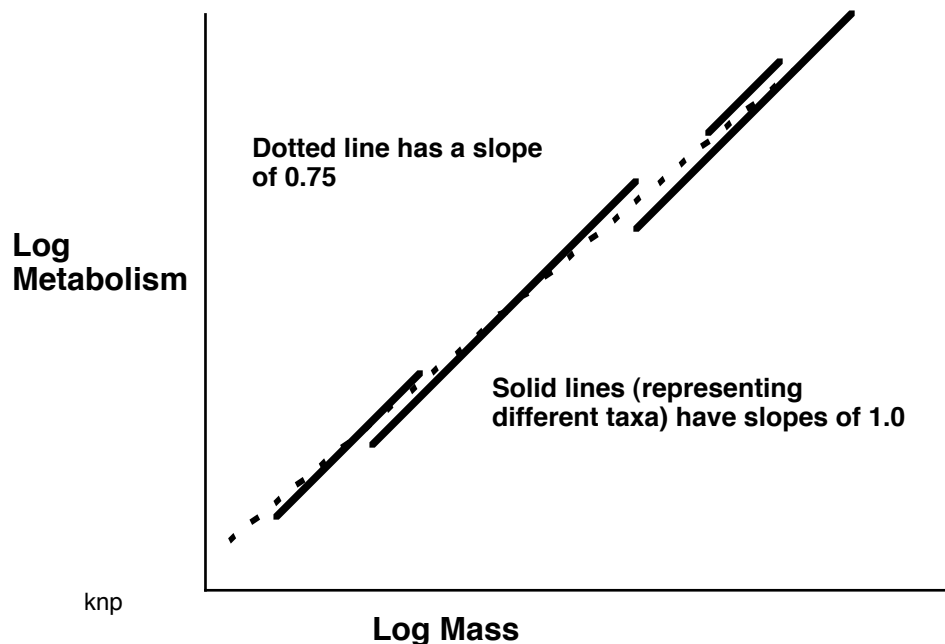
Similar arguments can be made for limits or lack of limits of surface area for excretion or food intake.

3. What kind of explanation can we make for the fact that metabolism seems to scale to the 0.75 power of mass?

a. **Optimal Solution:** This argues that more than one factor is important in setting the relationship between metabolic rate and size. For instance, in its simplest form, the argument would be that both surface area limitations and need to maintain a relatively high

rate of metabolism are both important and so the exponent of 0.75 represents some sort of a compromise, albeit one that seems to indicate that the surface constraints are more important than the need to maintain high metabolic rate. Of course, it could well be that many other factors are also involved.

b. Artifact or indication of inter-group scaling? In many groups, metabolism seems to scale isometrically to mass even though when we look at overall scaling relationships, metabolism still scales allometrically to something near the 0.75. Some have proposed that the 0.75 scaling exponent is nothing more than an artifact:



? Why would having a higher metabolic rate with increased body size be better? Why would maintenance of the highest possible metabolic rate be a good thing? Could it be a bad thing? Think about evolutionary and ecological problems to answer this physiological question.

Discuss ways that general animal designs in terms of Surface/Volume really are similar in different sized organisms. How could they be very different? --try to come up with some examples from your previous courses, for example, invertebrate zoology or chordate.

Critique the optimality explanation of the 0.75 exponent.

IV. Uses of Scaling Relationships

A. Scaling relationships are very useful to biologist since they offer a means to make meaningful comparisons between animals of very different body

size. This is important since we know that many biological factors do depend on size.

B. Mass-specific comparisons. One way to attempt to remove any influence of body size is to divide out the body mass of the organism, that is, express metabolism in mass-specific terms. For example, this allows us to compare the metabolism of 1 gram of silverfish with 1 g of giant squid. Mass-specific metabolism has units of energy/(mass*time).

1. Given that whole organism metabolism scales to the 0.75 power of mass, could we derive a general relationship for mass-specific metabolism?

2. All we need to do is divide our power function by mass:

$$13. \quad \dot{Q} / M = \frac{a(M^b)}{M}$$

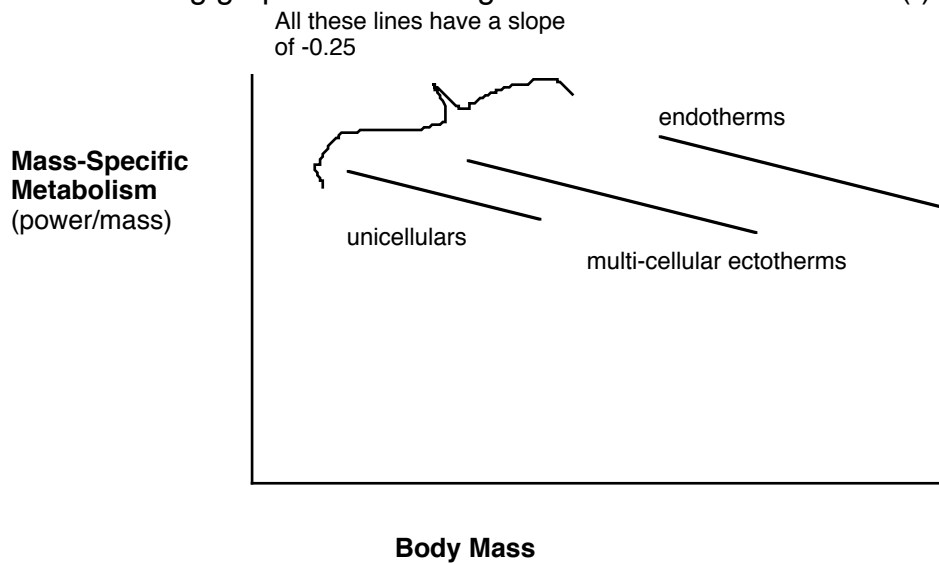
since the exponent for mass is 1.0, and $b = 0.75$, then

$$14. \quad \dot{Q} / M = a * M^{(0.75-1.0)} = a * M^{-0.25}$$

or

$$15. \quad \log (\dot{Q} / M) = \log a - 0.25 * \log M$$

3. The resulting graphs of Hemmingsen's data show 3 lines with (-) slopes.



? What would a plot for isometric scaling look like? For surface area defined scaling?

Are the curves in the order you expect (in terms of y-intercepts)? Explain.

4. If we now compare two different sized animals, for instance a silverfish and a squid, we find that a gram of silver fish has a higher rate of metabolism than a gram of squid!!

5. Remember that **this relationship has little if any ecological significance**: a big animal must eat more than a small one. However, it is interesting because of what it re-iterates about the metabolic differences between cells of small vs. large animals.

Note that it is better to predict the metabolic rate for a "typical animal" from an overall relationship relating metabolism to mass that includes the two species than it would be to simply divide by $M^{0.75}$. The reason for this is use of the regression equations predicts an average, allometrically adjusted metabolism for some general type of animal (e.g., mammals) while dividing by $M^{0.75}$ for each species simply corrects the actual values for mass. Both techniques are, however, far more useful for answering this type of question than is simply looking at total or mass-specific metabolism.

C. The regression equations for metabolism on mass are also useful in providing a standard for comparisons of an animal's metabolism with "expected" for its body size.

1. **The regression equations will predict an expected value of metabolism for a given body size and type of organism (unicellular, etc.).** This expected value is based on the average of many similar organisms.

2. We can then compare this with the actual metabolism that we measure for the species and see what "percent of expected" it is.

? Can you see any clinical use for the type of measures just described? (Think in general terms, not just in terms of metabolism).

3. This sort of comparison will be very useful in seeing if a given type of organism is really different from other animals in terms of its metabolism. If differences are noted, then we can try to figure out what their causes are.

? If one finds a relationship between metabolic rate and food type, habitat or taxon (ex.: marsupials vs. placental mammals), does that mean that metabolic rate is set by one of those factors? For instance, does consistently lower rates of metabolism in monotremes and marsupials compared to placentals, even when mass is corrected for, mean that the more ancient monotremes are marsupials

are phylogenetically constrained to have low metabolic rates? If not, what does it mean? Explain.
(What are monotremes?)

APPENDIX: Conversion of Units in Allometric Equations²

Whenever working with power functions, it is vital to know the units that are being used. When converting between measurement systems (such as grams to kilograms), special care must be used if these numbers are raised to a power different than 1.0. The problem will arise in converting the numerical value of the constant in the equation.

Consider the allometric equation:

$$a) \dot{V}_{O_2} = k * M^{0.75}$$

if M is mass in kilograms and \dot{V}_{O_2} is rate of oxygen consumption in liters of O₂ per hour, then what must be the units of k?

$$\text{Ans.: } k = \frac{\text{liters } O_2}{h * kg^{0.75}}$$

Notice that to cancel the units of mass (kg raised to the 0.75 power, the units of k must also be in kg^{0.75}.

Equation (a) has the following numerical form for mammals:

$$(b) \dot{V}_{O_2} \left(\frac{\text{liters } O_2}{h} \right) = 0.676 \left(\frac{\text{liters } O_2}{h * kg^{0.75}} \right) * M^{0.75}$$

Now, let's convert equation (b) to another form that uses mass in g, not kg, to predict metabolism in $\left(\frac{\text{liters } O_2}{h} \right)$. In doing this, we must recognize that our new equation will look just like (b) except that we will be enter g instead of kg for M^{0.75}. Now since a 1 kg animal is also a 1000g animal, both equations better give the same answers. To do so, the value of k will have to be changed by some factor. Simple logic tells us that to predict the same metabolism when using a number for

² See *Animal Physiology* by K. Schmidt-Nielsen for a well-written and more detailed explanation of this conversion.

mass that is larger than before, the value of k will need to decrease. But by how much?

The simple answer would be by 1000X. However, in entering the mass of the animal in grams, we are not entering a mass that is 1000X greater. Instead, we are entering a number that is $1000^{0.75}$ or 177.83 (even though it is the same mass and must predict the same metabolism. We must therefore divide the constant k by this number.

$$\begin{aligned} \text{Thus, } k_2 \left(\frac{\text{liters } O_2}{h * g^{0.75}} \right) &= \frac{k_1}{1000^{0.75}} \\ &= 0.0038 \frac{\text{liters } O_2}{h * g^{0.75}} \end{aligned}$$

Let's see if the two equations give (as they must if they are to be correct!) the same answers:

for a 10 kg animal:

$$\begin{aligned} \text{b) using kg: } \dot{V}_{O_2} \left(\frac{\text{liters } O_2}{h} \right) &= 0.676 \left(\frac{\text{liters } O_2}{h * kg^{0.75}} \right) * kg^{0.75} \\ &= 0.676 * 5.623 \\ &= 3.8 \frac{\text{liters } O_2}{h} \end{aligned}$$

$$\begin{aligned} \text{c) using g } \dot{V}_{O_2} \frac{\text{liters } O_2}{h} &= 0.0038 \left(\frac{\text{liters } O_2}{h * g^{0.75}} \right) * g^{1000} \\ &= 0.0038 * 10,000^{0.75} \\ &= 0.0038 * 1000 \\ &= 3.8 \frac{\text{liters } O_2}{h} \end{aligned}$$

? How would you make a conversion from liters to ml? From hours to minutes?
Be able to inter-convert between each of these systems of measurement.