Metabolism II -- Body Size, Endothermy vs. Ectothermy

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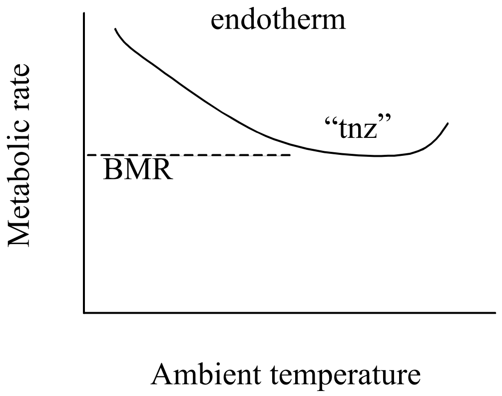
Goals for This Lecture:

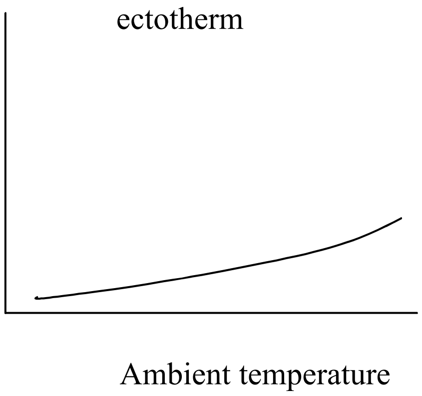
- Understand how size, temperature, and endothermy influence metabolic rate
- Understand *scaling* of "mass-specific" metabolic rates (i.e., per gram or per cell)
- Understand that field metabolic rates are much higher than those in the lab

I. How body size and endothermy/ectothermy influence metabolic rate (SN192-198)

A. A brief digression on terminology
  1. **Endotherm** (birds, mammals) – animals with high metabolic rates and that maintain high body temperature via adjustments in metabolic heat production.
  2. **Ectotherm** (everything else!) – animals with relatively low metabolic rates and whose body temperature depends mainly on external sources of heat

B. Because many factors influence metabolic rate (see Metabolism I), metabolic comparisons must be based on standardized conditions. Which are:
  1. **Basal metabolic rate** (BMR) for *endotherms.* Animal should be fasting, resting, normal sleep period, in thermal neutral zone ("tnz"), non-reproductive, not growing. 2. **Standard metabolic rate** (SMR) for *ectotherms.* Animal should be fasting, resting, non-reproductive. In reporting SMR, the ectotherm's temperature **must** be reported. *Why?*

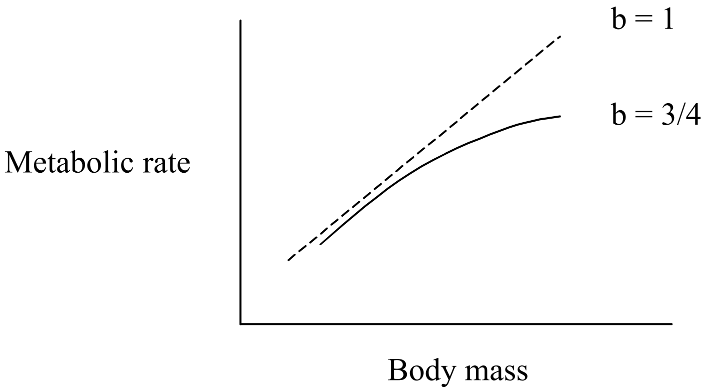




  3. Why does metabolic rate of endotherms increase (± linearly) as ambient temperature decreases below the thermal neutral zone?
  4. Why does metabolic rate of ectotherms increase with body temperature?

C. Body mass (size) is **the** dominant influence on whole-animal metabolism. How does metabolic rate change ("scale) with body size? For example, if species A is *twice as heavy* as species B, is the *metabolic rate of A twice that of B*?
  1. To answer that question, we first measure the metabolic rate of several species of different sized animals (text Table 5.8). Then we fit a "power" or "allometric" function ($\dot{E} = a M^b$, see *and the Allometry "handout"*), which conveniently summarizes all these data.
  2. **If and only** if the exponent b = 1, then the answer is "yes" to the above question: in this case, the relationship will be a straight line, as shown on the figure on the next page.

3. In fact, for most organisms, b is actually close to 0.75 (or ~ ¾). This means that total metabolic rate increases with body size, but **not** in a constant proportion, such that the line isn't straight but is curved. Thus the metabolic rate of species B isn't twice that of A but is something **less** than that.



D. Typical values for vertebrates, where $\dot{E}$ in ml O_2 h^{-1}, M in grams

Taxon	a	b	time (h) for a **1 g animal** to use 10 ml O_2
Endotherms			
passerine bird (42°C)	7.5	.72	1.3
placental mammal(37°C)	3.8	.75	2.6
marsupial (35°C)	2.3	.75	4.3
average =	***4.5***	***.74***	***2.2***
Ectotherms			
lizard (37°C)	.42	.82	23.8
frog (ranid) (25°C)	.29	.75	**?** calculate
fish (25°C)	.20	.70	50
beetles (22-25°C)	.23	.86	**?** calculate
average =	***0.4***	***.78***	***43.5***

(**Exercises:** 1) fill in the "?" values in the table using the allometric values given, 2) calculate the times for a 100-g animal of each taxon to use 10 ml O_2.)

E. Key generalizations

1. Exponents ("b") similar among groups, average about **3/4**. **Therefore, in most taxa, metabolic rate increases with mass but not in direct proportion to mass**.
2. <u>Endotherms (of a given size) have **much** higher metabolic rates than do ectotherms of an equivalent size</u> (thus larger "a" by about 10 times on average!). A huge difference.
3. Multicellular ectotherms have higher $\dot{E}$ than do unicellular ectotherms (Fig. 5.11)

4. Variation among endotherms partly due to different $\underline{T_b}$ (or vice versa)--birds are warmer than placentals than marsupials

F. Ecological consequences of scaling: big animals (esp. endotherms) require more food & thus larger home ranges (important implications for design of wildlife preserves).

G. Does metabolism show the same scaling *within* species as *between* species (thus for a "growth series" of individuals of a given species?

1. Studies of intraspecific scaling generally show that the exponent (b) is about 0.67, not 0.75 as in interspecific comparisons.
2. However, human babies scale about b = 1 during first year of life, thereafter b = 0.6. High early metabolism probably related to rapid growth in early life.

II. What accounts for scaling relationships (with size, among taxa)?

A. Fig. 5.1 in your text (originally published by Hemmingsen in 1960) is one of the most famous figures in comparative physiology. It shows that metabolic rate increases with mass$^{\sim 3/4}$ for diverse groups organisms, and it **also** shows that endotherms of a given size have much higher metabolic rates than do ectotherms of equivalent size, and theat "poikilotherms have much higher metabolic rates than unicellular organisms of "the same size." Why these patterns exist has fascinated physiologists for decades. This topic has attracted a variety of explanations over the years, but with little (if any) consensus.

B. In the past few years, some exciting new ideas have been proposed, resulting from a collaboration among physiologists, ecologists, and theoreticians (Los Alamos). In 1997, Geoffrey West and colleagues developed a novel model that is based on fractal networks, and has to do with minimizing the energy lost while transporting materials through the body. (Science 276:122-126, available UW on-line). Their model predicts that metabolic rate should scale with mass to the ¾ power.

C. In late September 2001 (Science 293:2248-2251) , this same group of workers incorporated the effects of *temperature* in their allometric model, as part of the difference in metabolic rates of different taxa relates to differences in temperature, as only the "homeotherms" were measured at 39°C. (and, of course, warmer animals have higher metabolic rates, all else being equal). Statistically correcting for this temperature difference greatly reduced – *but did not eliminate* – the difference in metabolic rates among major taxa. Thus, even after one corrects for differences in size and temperature, unicellular organism still have metabolic rates only 1/20th that of endotherms.

D. Whether West et al. are on the right track remains to be seen, but their model suggests that size and temperature account for most of the known variation in metabolic rates of organisms.

III. Scaling of metabolism *per gram* of animal (SN 192-194)

A. The above analyses deal with whole-animal metabolic rates. But one can also look at metabolic rate per gram of tissue. Why? This approach helps us gain some insight into the relative activity of **tissues** of animals of different sizes.[1] Specifically, how does metabolic rate of a gram of tissue scale with organismal mass?

B. The metabolic rate of a gram of tissue depends strongly on the size of the whole animal. Recall that if one animal is twice as large as another, its metabolic rate is roughly 68% greater,

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[1] Note: Because cell size is independent of animal mass (what is "b" therefore?), the metabolic rate of a gram of tissue is proportional to the metabolic rate of **a cell**. [1 g of elephant has the same number of cells a 1 g of mouse.]

not 100%. A necessary consequence is that 1 g of tissue of the small animal must have a **higher** metabolic rate than 1 g of the large animal tissue. (Figs. 5.9, 5.10)

1. To show this, divide an animal's metabolic rate by its mass. sample values: .75 kJ/ (g day) for mouse, .21 for cat, .11 for human, .05 for cow, .03 for elephant.
2. One gram of elephant has metabolic rate only 4% of that of 1g of mouse! Or 1 g of mouse is producing ~20X (20 times, not %!) heat per unit time as a gram of elephant.
3. A consequence of this pattern – a shrew (smallest mammal) eats nearly its body mass in food per day, whereas a large elephant doesn't (fortunately for zoos and for Africa).
4 Metabolic rate per gram of animal, is called **mass-specific metabolic rate**.

C. The scaling of mass-specific E can be described by a power function. (Simply divide both sides of the whole-animal metabolic equation by M. Thus, for placental mammals, $E/M = 3.8M^{-.25}$ or for lizards $= 0.42M^{-.18}$). [➔ Be able to graph this on arithmetic **and** log-log axes.]

D. This "inverse" relationship **holds** for all organisms. (because all $b < 1$).

IV. How metabolic rates of "free ranging" animals compare with those in the lab?

A. Typical metabolic data are from animals at rest in the lab & necessarily underestimate metabolic rates of animals in nature, which are moving and digesting, at least part of the time. By how much do lab measurements underestimate metabolism of free ranging animals?

B. Dual-isotope technique (**"doubly-labeled" water, a special "handout" will be available**) is now used to estimate metabolic rates (FMR) of **free ranging animals in nature**.

C. Example: Bennett and Nagy (1977) compared lizard, bird, mammal -- all about 12 g in mass. Lizard had low T_b (= body temperature) at night. First, Bennett & Nagy calculated metabolic rate based on lab studies and field T_b profiles, then based on isotope studies.

1. Metabolic requirements in the real world are roughly 3X that in the laboratory!
2. **FMR of a mammal is about 26X that of lizard, bird FMR is 40X that of lizard!**
3. These huge increments (relative to lab differences of only 8X and 14X, respectively) reflect greater activity birds and mammals and to the lowering of T_b by lizard at night.

D. Ecological and physiological (see below) consequences of high metabolic rates of endotherms must be profound. They have high impact on the environment (require lots of food and O_2), and the activity of their physiological systems (respiratory, circulatory, osmoregulatory, digestive) must be very high.

E. Study the appendix on field metabolic rates – you should understand how doubly labeled watr works.