Ecosystems & Ecophysiology – Lecture 14

Metabolism

Objectives

1. Know the scaling of whole organism metabolic rate with mass$^{0.75}$ in unicells, ectotherms and endotherms.

2. Describe explanations of the scaling of metabolic rate with body size, and their limitations.

3. Understand the difference in level of metabolic rate between endotherms and ectotherms, and some mechanisms of metabolic heat production.

4. Describe the processes of energy production during exercise in animals, and metabolic differences between red and white muscles.

Metabolism

■ Moving on from temperature to look at oxygen; metabolism & respiration. Metabolism is "the use of food to provide energy for work & synthesis"

The most efficient & most commonly used pathways are aerobic, i.e. oxidation with O_2 (Life Processes Lectures 19-21). So rate of O_2 consumption often used interchangeably with metabolic rate (MR), as ml O_2 h^{-1} or similar units

MR can also be expressed in terms of energy, depends to some extent on the molecule being oxidised. For mixed diet 1 ml O_2 consumed ≡ 20 J. Rate of energy use can also be expressed as a power, in Watts. 1 W = 1 J s^{-1}

Usual to compare MR of different organisms using mass-specific values, ml O_2 g^{-1} h^{-1}. Comparisons complicated by the question of scaling

Scaling of metabolism
Table shows scaling of MR in mammals, both whole animal & mass-specific. Elephant much larger than shrew & much greater total MR, but mass-specific rate only 1/100th that of shrew:

	Body mass (g)	ml O_2 h^{-1}	ml O_2 g^{-1} h^{-1}
Shrew	4.8	35	7.4
Mouse	25	41	1.6
Rat	290	250	0.87
Cat	2500	1700	0.68
Sheep	43000	9600	0.22
Horse	650000	71000	0.11
Elephant	3800000	270000	0.070

■ Curve for mass-specific rate. Note logarithmic x axis to give practical scale. Data follow a logarithmic relationship, straightened on a log-log plot

■ Mass-specific oxygen consumption on body mass on log scales shows a straight line of slope –0.25. The equation is:

$$\log \text{l } O_2 \text{ kg}^{-1} \text{ h}^{-1} = \log 0.676 - 0.25 \log \text{kg:} \quad (1)$$

This is equivalent to the allometric form: $\text{l } O_2 \text{ kg}^{-1} \text{ h}^{-1} = 0.676 \text{ kg}^{-0.25}$ (2)
Equation (2) can be changed to show whole animal MR , by multiplying both sides by body mass (i.e. $\text{kg}^{1.0}$)

$$\text{kg}^{-0.25} . \text{kg}^{1.0} = \text{kg}^{(-0.25 + 1.0)} = \text{kg}^{0.75} \quad (3)$$

So for whole animal metabolic rate equation (2) becomes:

$$\text{l } O_2 \text{ h}^{-1} = 0.676 \text{ kg}^{0.75} \quad (4)$$

■ Exponent 0.75 holds for all groups of organisms – unicells, multicellular ectotherms, & endotherms. Within each category MR increases with mass$^{0.75}$. Note (for later) a) 1.0 > slope > 0.67, b) central body mass = 1 mg

■ An exponent of about 0.75 also holds for smaller groupings, e.g.

Passerine birds	$l\ O_2\ h^{-1} = 1.11\ kg^{0.72}$
Non-passerine birds	$l\ O_2\ h^{-1} = 0.68\ kg^{0.72}$
Eutherian mammals	$l\ O_2\ h^{-1} = 0.68\ kg^{0.75}$
Marsupials	$l\ O_2\ h^{-1} = 0.41\ kg^{0.75}$

■ Left histogram shows frequency distribution & fitted normal curve of exponents from many studies of this type, mean = 0.756 (about 0.75)

Right histogram is for intraspecific data, slopes comparing individuals of different body size of a single species. Mean = 0.724 (also about 0.75)

Dashes show fit to group data for comparison. Variation is greater around the intraspecific mean, as size range within a species is smaller so estimate of the slope is more prone to error

■ Reason for the slope of 0.75 is one of the great unsolved problems of physiology, though scaling known for > 100 years

1. Simplest or null hypothesis would be slope = 1.0; scaling of MR per gram tissue independent of the size of the organism from which the tissue comes

Clearly not true (shrew to elephant curve). Larger organisms have lower mass-specific MR, exponent is significantly different from 1.0

2. Rubner proposed the surface area hypothesis in 1883, to explain scaling of MR in mammals

Idea is that most resting metabolism in mammals is for heating. Heat is lost through the surface, so MR would be proportional to the surface area

Surface area scales with the square of linear dimensions L, (i.e. $S.A. \propto L^2$), while mass scales to the cube ($M \propto L^3$). So surface area scales to mass $^{2/3}$, that is mass $^{0.67}$ and MR should do the same

Older analyses did find an exponent of about 0.67 for mammals, but with more data it has been shown to be significantly higher, about 0.75

Another reason to reject this hypothesis is that the exponent is the same for ectotherms, even unicells, in which metabolic heat loss is not a factor

3. Additive scaling. A mixture of a surface area-specific effect proportional to $mass^{0.67}$, and a mass-specific effect proportional to $mass^{1.0}$

Surface area-specific component is no longer thought to be heat loss, but more fundamental aspects such as areas of cell or mitochondrial membranes

Mass-specific effect is seen as a basic cost of living tissues, independent of size. Therefore not scaling to $mass^{0.75}$ as such, but an average of the two other exponents

Possible, but the physiological processes causing these effects, applicable to all organisms, have not been identified

■ **4.** Structural support hypothesis. Organisms are not isometric, they become relatively thicker with increasing size

E.g. height of trees not linearly related to diameter, but to diameter$^{0.67}$, height increases more slowly than diameter for strength of trunk

Theoretical prediction also of 0.67 exponent between height & diameter, of buckling force. Real trees below this prediction by a constant safety factor

Same result for cylindrical structures in animals, e.g. shape & thickness of bones. When equations worked through, predicts that cross sectional area of muscles should be related to mass $^{0.75}$

Force of muscles is linearly related to their cross sectional area so hypothesis is that maximum muscle power (i.e. force/time) is also related to mass $^{0.75}$, so MR (oxygen supply to muscles) also scales to mass $^{0.75}$

But power is related to volume of muscle, as it depends on shortening velocity & so muscle length as well as cross-sectional area. So hypothesis fails, also only applies to organisms experiencing buckling deformation

■ **5.** Fourth dimension. A surface area effect in three dimensions scales with mass$^{2/3}$. But if there were four dimensions, then a surface area effect would scale to mass$^{3/4}$, i.e. mass$^{0.75}$

What is the fourth dimension? Time is the most likely candidate. The life span of animals is proportional to mass$^{0.25}$, so lifetime mass-specific metabolism of animals then scales to mass$^{0.25}$ x mass$^{-0.25}$, i.e. mass^{0}

So animals have a certain "metabolic lifetime", independent of size – small animals just use this metabolic lifetime up faster – live fast & die young

Interesting idea but rather metaphysical & not really explanatory – does scaling of MR or lifespan come first?

■ **6.** Fractal transport systems (West et al. 1997 – recent references at end). Similar to (5) but the fourth dimension comes from fractal scaling of branching transport networks within organisms

Fractal means self-similar at all levels, fine branches are small versions of large ones, either blood vessels in animals or transport tissues in plants

Advanced maths (physicists), weakness is that organisms are not fractally constructed. Also, is MR determined by transport, or transport by MR?

7. Non-fractal transport systems (Banavar et al. 1999). Similar idea, also from physicists. Scaling is a property of dividing transport networks, but does not depend on fractal geometry

Problem with both 6 & 7 is that for more than half the log scale of body size, transport does not depend on branching tubular systems

Central body size on plot (slide 5) was only 1 mg. Transport in unicells & small ectotherms achieved by diffusion, not flow in tubes

■ Scaling with same exponent of 0.75 can be extended to the subcellular level, energy use by mitochondria & the respiratory complex of cytochromes

From West et al. (2002). Again, transport at these levels based on diffusion, not flow in tubes. If really part of the MR scaling pattern, suggests that this is not due to geometry of transport in tubes

■ Tempting to include anything that seems to fit on these allometric plots. Hochachka & Somero (2002) even fit the entire biosphere, total MR (from CO_2 production) & mass of all organisms on earth

Obvious fallacy here. Biosphere made up of all the separate organisms, mass-specific MR of the biosphere must be average of all the organisms, not much lower as would be required by allometric scaling

8. Chance result – Hochachka & Somero (2002) point out that some scaling must occur, just chance that exponent is 0.75 rather than some other value?

Metabolic rates

■ Seen slopes, but also differences in the intercepts for different types of organism, i.e. the heights of the lines. Among animals the main difference is between ectotherms & endotherms

Histograms of intercepts for multicellular ectotherms (at 20^{o}C) & mammals. Note that scale for ectotherms (0-20 J h^{-1}) is 1/20th that for mammals (0-400)

■ Distributions skewed, need log-transformation for analysis. Fitted normal curves show ectotherms well below endotherms, & mammals slightly below birds (as in allometric equations above, slide 6)

Mean value for mammals about 45 x that of ectotherms, but partly due to difference in T_b. After taking this into account (increasing ectotherm value by assuming a Q_{10}), mammal value still 10 x higher than ectotherms

■ Higher rate in endotherms is due to production of metabolic heat for thermoregulation. Value of intercept depends on T_b regulated

Monotremes have lower T_b & lower MR to save energy. Still regulate T_b effectively, just at a lower level than eutherians:

Group	a (J h^{-1})	b	T_b (^oC)
Passerine birds	132	0.73	41
Eutherians	64	0.76	38
Marsupials	48	0.75	35
Monotremes	19	0.75	31

■ Metabolic heating is achieved by exploiting pre-existing metabolic pathways. Whatever the organism or food source being used, about 2/3 to ¾ of the energy of chemical bonds is lost as heat anyway

Most advanced heat production mechanism is in brown adipose tissue BAT (Lecture 11), where ATP production uncoupled from electron transport chain

So ATP not produced. Other metabolic heat producing mechanisms do produce ATP & have to use it up in some way

Simplest way to use up ATP is to increase skeletal muscle activity – shivering. Immediate response to low T_a. ATP used by muscle contractions

Long-term mechanism in mammals is thyroid-stimulated non-shivering thermogenesis. ATP used to pump ions across cell membranes

All animal cells have high internal K^+ and low internal Na^+ concentrations & a resting potential (but only excitable cells can form action potentials)

Normally some leakage of Na^+ & K^+ across the cell membrane, gradients maintained by Na^+/K^+ ATPase, pumps Na^+ outside & K^+ inside

In thermogenesis the leakage of Na^+ & K^+ across the cell membrane increases. Na^+/K^+ pump must therefore work harder, uses up the ATP

Metabolism during exercise

■ The other factor determining metabolic rate is activity level. Have been considering resting metabolic rates so far

Oxygen consumption of animals increases when they are active, by about 10 x in both ectotherms and endotherms – proportional increase the same

Initial intense activity is by anaerobic pathways, even in aerobic animals such as humans. Only longer term activity is by aerobic pathways

■ Three sources of ATP during exercise in vertebrates:

1. Hydrolysis of phosphagens – high intensity but very short term. High energy bond of creatine phosphate used to regenerate ATP. Sufficient to replenish ATP about 6 x. Does not use O_2

2. Anaerobic glycolysis – intermediate intensity & limited duration. Pyruvate fermented to lactate, allows regeneration of NAD^+ (Life Processes Lecture 20). Does not use O_2

3. Oxidation of carbohydrate or fat – lower intensity but long term. Uses large energy reserves efficiently. Requires O_2

Energy stores in human muscle cells (μmol high energy phosphate bond equivalents g^{-1} dry mass):

ATP	Creatine P	Glycogen	Fat
10	60	14,000	24,000

■ Different types of muscle cells adapted for different reactions, in separate blocks in fish. Red muscles (tuna thermoregulation) have high myoglobin (for oxygen transport), aerobic. Used for sustained swimming

White muscles have high capacity for anaerobic glycolysis, bursts of high intensity swimming. Larger use of glycogen & production of lactate:

Δ metabolites (μmol g^{-1}) after burst activity	White	Red
Creatine phosphate	–13	–2
Glycogen (as glucose units)	–23	–2
Lactate	+71	+6

■ Muscle types differ in enzyme levels. White > red for glycolytic enzymes (anaerobic), red > white for krebs cycle (aerobic). Catalytic activity (μmol min^{-1} g^{-1}) for white & red muscles of skipjack tuna *Euthynnus*:

		White	Red
Glycolysis	Pyruvate kinase	1300	190
	Lactate dehydrogenase	5500	510
Krebs cycle	Citrate synthase	2.1	21
	Glutamate transaminase	43	100

■ Recent references for scaling (not in textbooks yet):

Banavar, J.R., Maritan, A. & Rinaldo, A. (1999). Nature **399**: 130-131
West, G.B., Brown, J.H. & Enquist, B.J. (1997). Science **276**: 122-126
West, G.B., Woodruff, W.H. & Brown, J.H. (2002). P.N.A.S. **99**: 2473-2478
(also at www.pnas.org/cgi/doi/10.1073/pnas.012579799)