Lecture 2: Energy Conservation and Allometric scaling (Sept. 10)

Reading Assignment for Lectures 1-2: Phillips, Kondev, Theriot (PKT), Chapter 1
for lectures 3-4: PKT, Chapter 2

Last time I introduced the basal metabolic rate Γ_0. Roughly 100 W for humans (2000 kcal/day).

This must be balanced by a corresponding rate of heat loss. If it is not, you would slowly heat up: "hyperthermia" (a few degrees K is lethal! protein denaturation?). Correspondingly, if heat loss is too large, you slowly cool down (again, a few degrees is lethal).

Energy loss mechanisms:

A. Conduction/convection as a heat loss mechanism.

Assume for the moment that this is entirely via heat conduction through the skin (see below):

$$P_{heat} = \kappa_T \frac{S\Delta T}{d}, \text{ where}$$

κ_T is thermal conductivity:

$$\kappa_T(water) = 0.6\frac{W}{m \cdot K} \text{ (tissue~water)}, \; \kappa_T(air) = 0.025\frac{W}{m \cdot K}$$

S is surface are (exposed skin): S~2 m^2

ΔT = temperature difference: 37 C - T_{room}~10 K

d is thickness of thermal boundary layer: 1 cm?

Thus, estimate:

$$P_{heat} \approx (0.6)\frac{(2)(10)}{0.01} = 1200\,W \text{ (too large by roughly 10x?)}$$

What's wrong with this?

Assumes skin is at surrounding air temp. This would be true if you were immersed in water (there are many deaths from hypothermia in BC's waters!); but, under normal conditions, you are surrounded by an insulating layer of still air (unless it is very windy), e.g., trapped by your clothing. Note that a 1 cm layer of air (as opposed to flesh) reduces heat flow to

$$P_{heat} \approx (0.025)\frac{(2)(10)}{0.01} = 50\,W,$$

which is insufficient to keep you "cool" even if you are not working.

How else can your body use up the metabolic energy?

- Work?
- Radiative heat loss.
- Sweating.
- Additional transpiration.

B. Work as an energy loss mechanism?

Q: Can you "use up" the extra ~1000 kcal by doing work?

A: No.

Calculate gain of PE: (for Tour de France rider going over alpine pass):

How much work can you do with 1000 kcal?

4.2×10^6 J=W, since 1cal = 4.186 J.

e.g., W=mgh=100 kg x (g=9.8 m/s^2) x h, which works out to 4.29 km ~ 14,000 ft.

Comments:

Actually, of course, you work much harder when you are riding over 14,000-foot passes and have even more heat to dissipate. Efficiency η is nowhere near 1.

Upshot: the gain in PE accounts for a relatively small part of the total energy input.

C. Radiative heat loss:

Stephan-Boltmann law:

Any hot surface radiates photons at a rate $P = \varepsilon\sigma T^4$,
where T is the absolute temperature, s is the Stephan-Boltmann constant
$\sigma = 5.67\times10^{-8}\ W/m^2K^4$, and ε~1 the emissivity depends on surface.

Estimate:

Radiative loss: $SP = S\sigma T_{skin}^4 \approx 2\times1\left(5.67\times10^{-8}\right)(300)^4 = 920\ W$

But, this is 10x basal metabolic rate!
Q: What's wrong? Why don't we all freeze?
A: Resolution is that environment radiates back at us:
NET Radiative loss

$$= S\sigma\left(T_{skin}^4 - T_{room}^4\right) \approx S\sigma T_{room}^3(4\Delta T) \approx 2\times\left(5.67\times10^{-8}\right)(300)^3(4\times10) \approx 120\ W$$

(where I simplified by writing $T_{skin} = T_{room} + \Delta T$ with $\Delta T \sim 10\ C$)
OK, now we are in the right ballpark: At the BMR, all the input heat can be taken away by radiative transfer.
But, when you start to exercise, this mechanism is insufficient, which is why you start to sweat and pant.

D. Evaporative heat loss: sweating and transpiration:

Evaporation requires energy (why?):
Latent heat of vaporization of water: 2.3 kJ/g ~ 2.3×10^6 J/L (depends on T)
Upshot 1000 kcal ~4.2×10^6 J suffices to evaporate ~2 L of water.
Comments:

This is a significant energy output, especially when panting or sweating
You require several liters of water per day, even at rest.
What you transpire is this PLUS metabolic water generated by processing food.
Water loss is mainly through the lungs for the basal metabolism but, for active work, sweating is an increasingly important contribution.

See problems: Rates of heating up and cooling down.

How does all this change with body mass M?

Allometry, Scaling, and Spherical Cows.

Many biological parameters depend on mass M.
Thus, body volume V is (to an excellent approximation) proportional to M, since $M = \rho V$ and the densities of (almost) all biological organisms is close to that of water, $\rho \approx \rho_{water}$ with,

$\rho_{water} = 1000\ kg/m^3$

so $V = \frac{1}{\rho}M \sim M \sim M^{\alpha}\ (\alpha = 1)$.

Biological parameters that scale with M (at least, approximately) as a power law,

Parameter ~ CM^{α},

are called "allometric" (technically this terminology is only used when $\alpha \neq 1$). In physics, quantities which exhibit power-law dependences of this type are said to "scale (with M) with the power α." I will use these terminologies interchangeably.

Some allometric power laws are no more than geometry. For example, organism linear dimension R and surface area S scale as $M^{1/3}$ and $M^{2/3}$, respectively, for objects of similar shape, since, $R^3 \sim V \sim M$ and $S \sim R^2 \sim \left(M^{1/3}\right)^2$. **2.3**

Comment:
For example,
for cubic objects of side R,

$$V = R^3 = \frac{M}{\rho}, \text{ so } R = \left(\frac{M}{\rho}\right)^{1/3} = \left(\frac{1}{\rho}\right)^{1/3} M^{1/3} \text{ (note dimensions!)}.$$

For spherical objects of radius R,

$$V = \frac{4\pi}{3}R^3 = \frac{M}{\rho}, \text{ so } \boxed{R = \left(\frac{3}{4\pi}\right)^{1/3}\left(\frac{1}{\rho}\right)^{1/3} M^{1/3}.}$$

We write generally $R \approx CM^{1/3}$ with the understanding that the "amplitude" C contains both a dimensional factor (what are the dimensions of C?) and a dimensionless numerical constant which varies from shape to shape but will usually be "of order unity."

Not all allometric relations are geometrical like this.

A. Allometric/scaling behavior of the basal metabolic rate.

The most famous of these relations is

$\boxed{\Gamma_0(M) \approx aM^{3/4},}$ Kleiber's Law, ~1930 ($a \approx 4$; M in kg gives Γ_0 in W)

Called by Ahlborn the "mouse-to-elephant curve" (Ahllborn, Fig. 1.7). This was originally observed by Max Kleiber in the 1930's for warm-blooded (homeotherms) but appears to hold for cold-blooded organisms (poikilotherms) and even single-celled organisms (although with somewhat different amplitudes). See below.

Note: We can get the amplitude $a \approx 4$ by fitting to the human BMR = 100 W for a human adult of mass (say) 3^4 = 81 kg:

$$100 = a(81)^{3/4} = a\left(3^4\right)^{3/4} = a \cdot 3^3$$

Comments:

This is an approximate and empirical relation.
Derive it from log-log fits to data. α is the slope of the best straight-line fit.
You have more confidence if you have more "decades" of data. Six decades for mammals, 18 decades for all organisms (see graphs).
It does not fit all animals; some are off the curve: Outliers?
Scatter means that the exponent is uncertain. $\alpha = 3/4 \pm ?$

Q: Can Kleiber's law be "derived"?
A: Not a trivial result. May not even be "right." But, here's a simple argument:

$$\Gamma_0 = \text{Heat loss rate} = \kappa_T \frac{S\Delta T}{d} \sim M^{2/3}, \qquad \textbf{2.4}$$

supposing that only S is mass dependent and with $S \sim M^{2/3}$ (from above).

Comments:
2/3 close to 3/4 but consensus is that ¾ is a better fit.
Can work harder and justify ¾. See, e.g., Geoffrey West et al., Science 276, 122-126 (1997).
But, why does the same exponent work for cold-blooded and single cell?

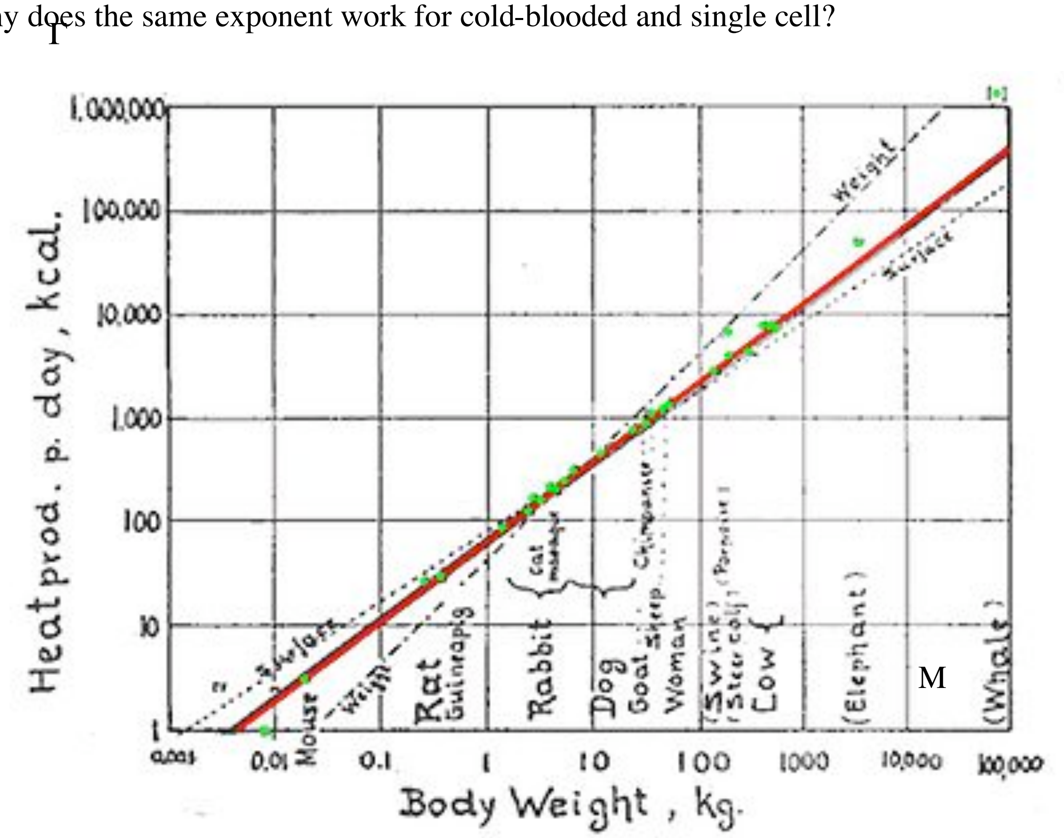
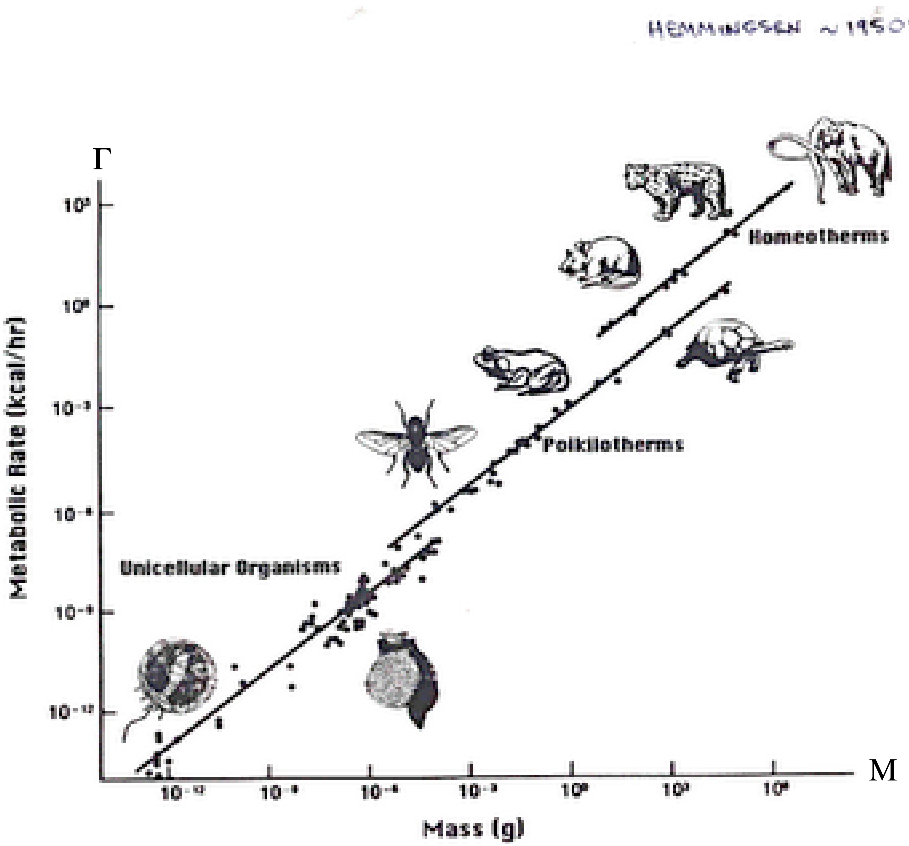


Fig. 1. Log. metabol. rate/log body weight

(from Wikipedia)



Allometric scaling of metabolic rate for a selection of homeotherms (birds and mammals), poikilotherms (fish, reptiles, amphibians, and invertebrates), and unicellular organisms. The sol-l lines all have a slope of .75. Modified from Hemmingsen, 1960.

I found this on the web: http://justjoep.blogspot.com
The original reference is:
A.M. Hemmingsen, Reports of the Steno Memorial Hospital and Nordisk Insulin Laboratories 9, 6—110 (1960).

B. Other allometric scaling relations: (Table 1.2, Ahlborn, Ch. 1) 2.6

Table 1.2. Allometric parameters for mammals. Most data are data adapted from Vogel [1988], more extensive allometric data are given by Schmidt-Nielsen [1984]

parameter	factor a	exponent α
body surface in m^2	0.11	0.65
brain mass (man) in kg	0.085	0.66
brain mass (non primates) in kg	0.01	0.7
breathing frequency in Hz	0.892	− 0.26
cost of transport (running) in J/m · k	7	− 0.33
cost of transport(swimming) in J/m · kg	0.6	− 0.33
effective lung volume in m^3	$5.67 \cdot 10^{-5}$	1.03
frequence of heartbeat in Hz	4.02	− 0.25
heart mass in kg	$5.8 \cdot 10^{-3}$	0.97
life time in years	11.89	0.20
metabolic rate in W	4.1	0.75
muscle mass in kg	0.45	1.0
skeletal mass (cetaceans) in kg	0.137	1.02
skeletal mass (terrestrial) in kg	0.068	1.08
speed of flying in m/s	15	1/6
speed of walking in m/s	0.5	1/6

we will derive these

Amusing note:

heart rate (beats/sec) ~ $M^{-0.25}$

lifetime (sec/lifetime) ~ $M^{0.20}$

So, heartbeat/lifetime ~ $M^{-0.05} \sim M^{0} \sim$ (almost) independent of mass!