The Metabolic basis of Ecological and Evolutionary Dynamics

A MulaQuaBio Lecture

January 16, 2025

OUTLINE

- Introduction
- Energy and Metabolic rate
- Importance of Body Size
- Importance of Temperature
- Summary, Questions, and Readings

THE IMPORTANCE OF METABOLISM IN ECOLOGY

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The 'struggle for existence' of living beings is not for the fundamental constituents of food ... but for the possession of the free energy obtained, chiefly by means of the green plant, from the transfer of radiant energy from the hot sun to the cold earth.

– Ludwig Boltzmann 1886, "The Second Law of Thermodynamics"

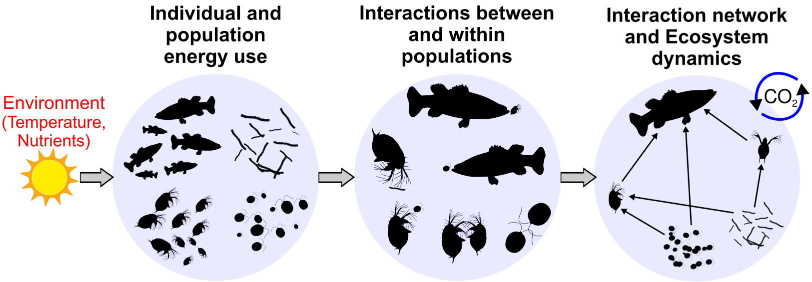
Read Brown et al (2004), "Toward a metabolic theory of ecology"

The importance of metabolism in ecology

- Ecosystems are complex

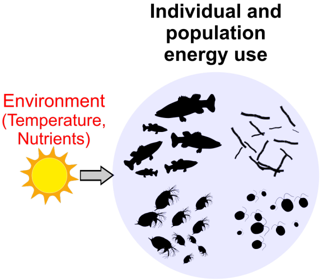
- *A* **metabolic** *(AKA "bottom-up" or "mechanistic") understanding of these complex ecosystems is necessary*

A METABOLIC ECOLOGY ROADMAP



- Individual-level *energy use and metabolic rate* determines:
  - Population growth rate (a measure of the population's fitness)
  - Interaction rates with other individuals (including consumption rates - another lecture)

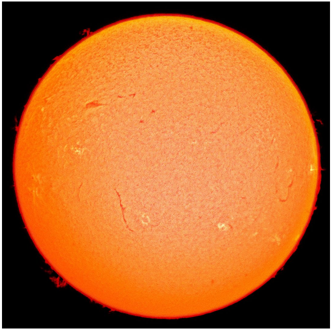
ENERGY AND METABOLIC RATE



- We will focus on the first “stop” on this roadmap in this lecture

Energy and life

- **Energy**: *measurable property of an object that determines its ability to do "work"*
- Life's very "purpose" is to use energy for propagating itself (self-replication)
  - Plants and other *autotrophs* use photons
  - Animals and other *heterotrophs* use energy in chemical bonds
- ATP is the key; watch this: `https://www.youtube.com/watch?v=QImCld9YubE&list=PLFs4vir_WsTyXrrpFstD64Qj95vpy-yo1&index=3`



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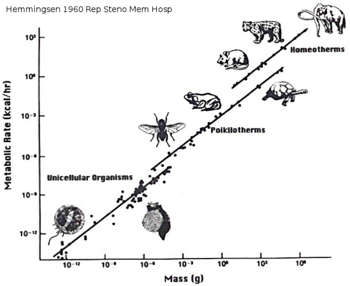
- The Sun is the *ultimate* energy source for *most* of life on Earth

METABOLISM AND METABOLIC RATE

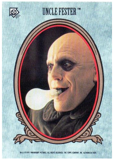
- **Metabolism**: *Set of chemical reactions in a living organism*
- **Metabolic rate**: *Rate of individual's energy use*
  - Usually measured in units of J/s, kcal/s (or /hr or /day), or Watts
- All *living* organisms must be at energy balance:
  - Energy Consumed = Energy Used (for Maintenance + Growth + Movement)
  - Different individuals and organisms invest energy to different degrees in Maintenance vs. Growth vs. Movement
- Metabolic rate at the *cellular level* sets the "pace of life":
  - Individual movement rate (e.g., walking or running velocity)
  - Individual development rate (e.g., from birth to adulthood)
  - Lifespan (duration from birth to death)
  - Maximum population growth rate (r_{max})

THE IMPORTANCE OF SIZE

- (Resting) metabolic rate (B) increases with body size (M)



The equation[1] of each line is
$$\log_{10}(B) = \log_{10}(B_0) + b\log_{10}(M)$$



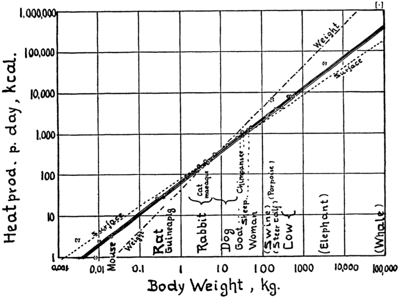
- Your *resting* metabolic rate is ~ 75 W (~ 1500 kcal/day)
- But *right now* hopefully somewhat higher, because otherwise this lecture has already put you to sleep!

- This relationship is actually an allometric "power-law" (AKA a scaling law)[1]: $B = B_0 M^b$

[1] $\log_{10}$ implies the base-10 logarithm, so raising both sides of the equation to the power of 10 gives: $B = B_0 M^b$

WHY RABBITS EAT AND BREED LIKE RABBITS

- Let's look more closely at metabolic scaling in mammals



(Note the units on both axes, *and the whale ([·])!*

- This is from Kleiber's (1947) study (so, AKA "Kleiber's Law")
- The equation[2] of the line is $\log_{10}(B) = 1.83 + 0.74\log_{10}(M)$
  - B = heat produced (measure of metabolic rate)
  - M = weight
- Raising both sides to the power of 10 gives: $B = 67.61M^{0.74}$

- So larger (individual) mammals use more energy

[2] This is *qualitatively* same as the scaling equation in the previous slide, and the anti-log transformation we did there

WHY RABBITS EAT AND BREED LIKE RABBITS

- So larger (individual) mammals use more energy
- But they use less energy *per-cell or unit mass*[3]:
  $\frac{B}{M} = 67.61\frac{M^{0.74}}{M} = 67.61M^{0.74-1} = 67.61M^{-0.26}$
- For example, a mouse weighing approx. 100 g (or 0.1 kg), in order to maintain *metabolic balance*:
  - Needs to consume $67.61 \times 0.1^{0.74} = 12.3$ kcal / day
  - Per unit mass (or per-cell), this is $12.3/0.1 = 123$ kcal / (kg $\times$ day)
- **Thus, larger animals process energy at a slower rate than smaller ones (measured by per-unit mass or per-cell metabolic rate)**

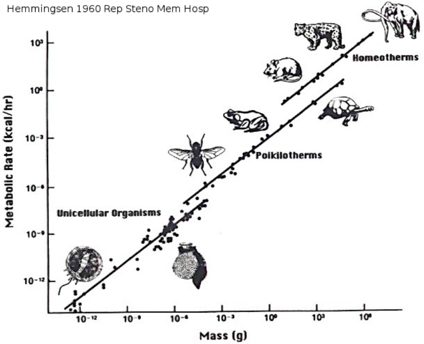
[3] Cell Number = Body Mass, because the average cell's mass does not change with an individual's body size

The importance of size

- The origins of this scaling law for metabolic rate is still being debated
- One is the "Heat dissipation" hypothesis); watch this video `https://www.youtube.com/watch?v=MUWUHf-rzks`.
  - Larger organisms have lower per-cell or per-mass metabolic rate to avoid overheating
- There is also the "WBE (West, Brown, and Enquist) Model":
  - Larger organisms have lower per-cell metabolic rate because they are inherently limited in their their ability to distribute energy and matter to their (trillions of) cells
- The truth is probably a combination of the two hypotheses
- We will *not worry too much* about the origin of scaling laws here, but focus on their *ecological implications instead*

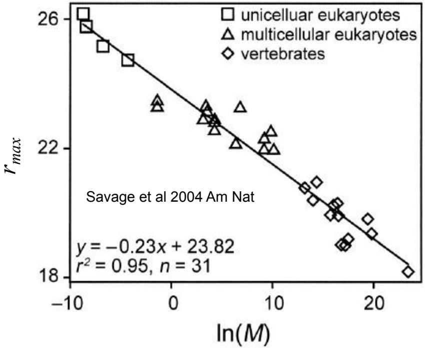
ECOLOGICAL IMPLICATIONS OF METABOLIC SCALING

Because resting metabolic rate,
$B = B_0 M^{0.75}$



Larger plants and animals have lower mass-specific metabolic rate

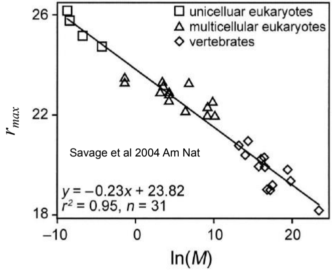
Therefore,
$r_{\max} = r_0 M^{-0.25}$



Population growth rate declines allometrically with body size

IMPLICATIONS OF METABOLIC SCALING

- That is, larger organisms have *relatively* less power to crank out offspring per-unit mass (per-cell)[4]
- That is, $r = r_0 \frac{M^{0.75}}{M} = r_0 M^{0.75-1} = r_0 M^{-0.25}$



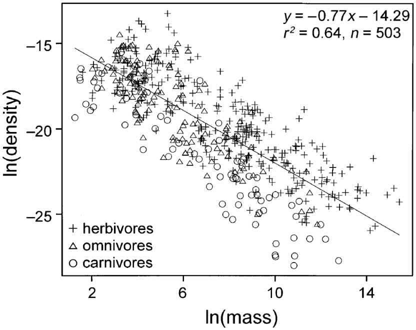
- Therefore, smaller organisms typically show stronger exponential growth

[4] Remember, per-Cell = per-Mass because the average Mass of a cell does not change with body size (Mass) of the whole organism

Implications of metabolic scaling

- So, assuming sufficient energy supply to all species, population density scales *negatively* with body size (*Damuth's law*):

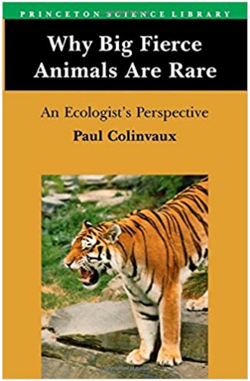
Brown et al., Ecology, 2004



- So big animals and plants are rarer (have smaller population size)

IMPLICATIONS OF METABOLIC SCALING

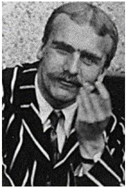
- Carnivores of a given size are rarer than herbivores of the same size because less energy is available higher up in food chains



- This also underlies why *Number and Biomass pyramids* (AKA Ecological pyramids) exist

The importance of size

- Size also affects biomechanics & movement (and therefore species interactions – next lecture)



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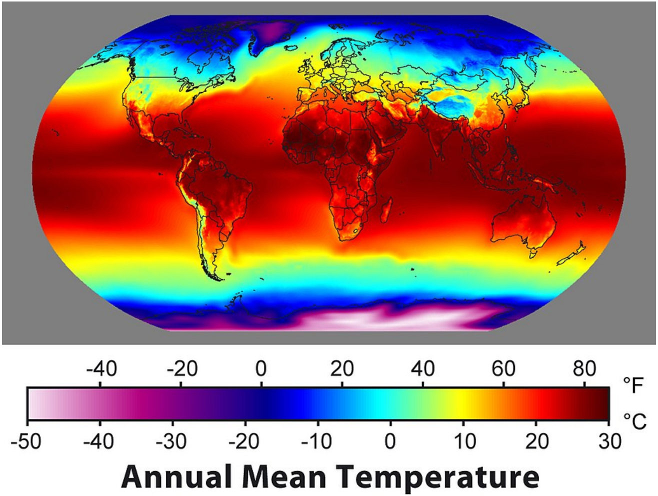
You can drop a mouse down a thousand-yard mine shaft; and, on arriving at the bottom, it gets a slight shock and walks away, provided that the ground is fairly soft. A rat is killed, a man is broken, a horse splashes.

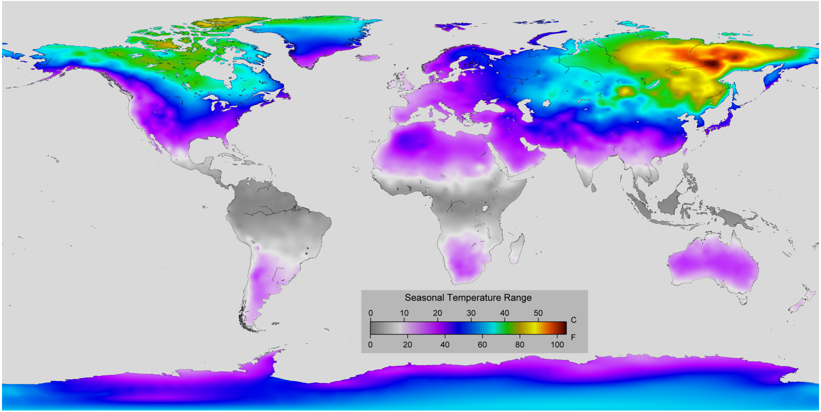
– Haldane 1926, "On being the right size"

- Watch: https://www.youtube.com/watch?v=f7KSfjv4Oq0
- Size is also important in microbes (but in somewhat different ways); Watch: https://www.youtube.com/watch?v=E1KkQrFEl2I

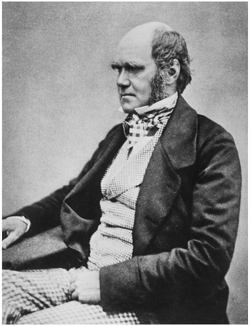
The importance of temperature



The importance of temperature



The importance of temperature



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Climate plays an important part in determining the average numbers of a species, and periodical seasons of extreme cold or drought seem to be the most effective of all checks.

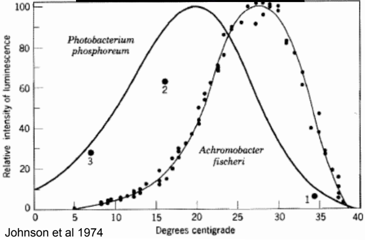
– Darwin 1859, "The origin of species"

THE IMPORTANCE OF TEMPERATURE

- **Recall what Metabolism is**: *Set of chemical reactions in a living organism*
- All chemical reactions are temperature-dependent: reaction rates increase with temperature
  - An increase in temperature raises the average kinetic energy of reactant molecules
- This includes biochemical reactions, and enzyme activity
- The increase in biochemical reaction rate follows the *Boltzmann-Arrhenius equation*
- Therefore, metabolic rates go up (approximately) exponentially with temperature to a point and then decline: this is the "Thermal Performance Curve"

The importance of temperature

- These are a "thermal performance curves" of two bioluminescent bacteria (*A. fischeri* is symbiotic with squids)

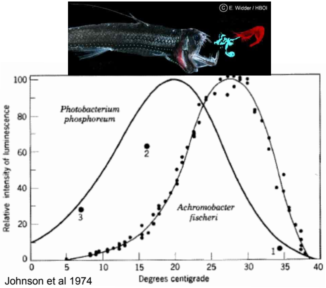


- The increase is due to increase in enzyme (e.g., luciferase) activity (following the Boltzmann-Arrhenius equation)
- The decline is because enzymes stop performing efficiently beyond some *optimal temperature*

- Key biological rates—Respiration, photosynthesis, individual growth, etc.—all also depend upon temperature in a similar way

The importance of temperature

- The mechanistic basis of thermal performance curves (https://youtu.be/6n8fCuDwn74)



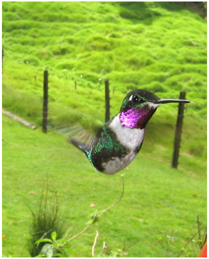
$$B = B_0 \boxed{e^{-\frac{E}{kT}}} f(T, T_{pk}, E_D)$$

T = temperature (K)
k = Boltzmann constant (eV K^{-1})
E = Activation energy (eV)
T_{pk} = Temperature of peak performance
E_D = Deactivation energy (eV)
(J H van't Hoff 1884, S Arrhenius 1889)

- But there is more to thermal responses
  - Oxygen limitation
  - Complexity of metabolic network
  - Hormonal regulation
  - Membrane fluidity
- *Read Knapp & Huang 2022 paper*

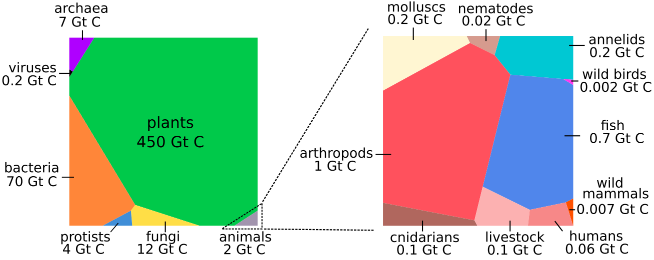
THE ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS OF TEMPERATURE

- *Ectothermic organisms* (more accurately, *poikilotherms*) directly depend on the external temperature to get their "engine running"
- These are the *vast majority* of life on earth: Microbes, Plants, Insects, and many Vertebrates



- *Endothermic organisms* keep their "engine running" by generating their own heat
- These are are *minuscule minority* of life on earth: Basically, Mammals and Birds

The ecological implications of temperature



Bar-On et al, "The Biomass Distribution on Earth" PNAS 2018

- Metabolic rates of the *vast majority* of life depend directly on environmental temperature
- The rest, endotherms, also depend indirectly on temperature (e.g., they eat ectotherms – rabbit eating grass)
- Population growth rates also increase with temperature (to a point - remember the Thermal Performance Curve)

Summary

- Individual metabolism drives individual and population growth rate
- Metabolic rate increases as a power-law with size
  - Thus, size determines population growth rate and population size
- Metabolic rate increases (approximately) exponentially with temperature (to a point)
  - Thus, temperature also determines population growth rate and population size
- *Between metabolic rate and production (r_{max}), lies consumption — what must consumption rate scale like?* (Next lecture)

Readings

1. West, G. B. & Brown, J. H. The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. Journal of Experimental Biology 208, 1575–92 (2005).
2. Brown, J. H., et al. Toward a metabolic theory of ecology. Ecology 85, 1771–1789 (2004).
3. Knapp B. D., & Huang K. C. The Effects of Temperature on Cellular Physiology. Annu Rev Biophys 51, 499–526 (2022).
4. Dell, A. I., Pawar, S. & Savage, V. M. Systematic variation in the temperature dependence of physiological and ecological traits. PNAS 108, 10591–10596 (2011).
5. Arroyo, José Ignacio, Beatriz Díez, Christopher P. Kempes, Geoffrey B. West, & Pablo A. Marquet. ”A general theory for temperature dependence in biology.” Proceedings of the National Academy of Sciences 119, no. 30 (2022): e2119872119.

PRACTICALS

1. Review "Making mathematical statements" section of the MQB's Maths for Biologists Appendix:
   `https://mulquabio.github.io/MQB/notebooks/Appendix-MathsForBiologists/MathsForBiologists.html`
2. Solve problems 1-3 of the Exercise set 1 of "Maths for Biologists" Appendix:
   `https://mulquabio.github.io/MQB/notebooks/Appendix-MathsForBiologists/MathsForBiologists.html`
3. Read and work through to the end of "Some preliminaries" section of Mathematical models in Jupyter Appendix:
   `https://mulquabio.github.io/MQB/notebooks/Appendix-Maths.html`

Discussion Questions

1. Given the way resting metabolic rate scales with body size, what must consumption rate scale like?
2. Why did we focus on *resting* (or "basal") metabolic rate?
3. How much energy would a *resting* rabbit ($\sim$ 1 kg), a human ($\sim$ 70 kg, and an Asian elephant ($\sim$ 4000 kg) need for metabolic balance[5],
   - at the individual level?
   - per unit mass?
4. How does the value you calculated in the previous question compare with the recommended calorie intake for humans? Is it lower or higher? Why?
5. What are the optimal temperatures for the enzyme underlying bioluminescence in the two bacteria in the given example? Why might they have different thermal optima?

[5] Calculate it using Kleiber's law (allometric/scaling equation), as we did for a mouse