Fourth Workshop

"Dynamical Systems Applied to Biology and Natural Science"

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Dynamic Energy Budget Theory:
An Axiomatic Theory for Metabolism

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Overview

A proof is that which convinces a
reasonable man; a rigorous proof is that
which convinces an unreasonable man.
- Mark Kac

- The main pillars
  - Occam's epistemological and biological razors
  - Thermodynamics
- The main concepts
  - Homeostasis and metabolic control
- The main implications
  - Indirect calorimetry
  - Intra-specific and inter-specific Kleiber's rules
  - von Bertallanfy growth

Occam's Razor:
Epistemological or Biological?

- (Epistemological) Occam's razor (or Law of Parsimony), attributed to the 14th-century English logician William of Ockham, is the principle that, given two hypotheses consistent with the observed data, the simpler one should be preferred (Esmeir and Markovitch, 2007).
  - "Theories should be made as simple as possible, but not more" Albert Einstein
- In the context of machine learning, the widely accepted interpretation of Occam's razor is that given two consistent hypotheses, the simpler one is likely to have a lower error rate.
  - Empirical evidence both for and against (Esmeir and Markovitch, 2007)
- However, simplicity can be an aim in itself
- Karl Popper argued that simple theories are more falsifiable
- Simplicity in scientific theories?
  - e.g., is Copernicus simpler than Ptolomey? (No, namely before Galileo, *cf.* Arthur Koestler, *The Sleepwalkers*)
- CONJECTURE (Biological Occam's Razor): *Ceteribus paribus*, organisms with simpler control models are evolutionarily favoured

Fundamental Principles of DEB Theory
Occam's Razors

- Pragmatic Application of Occam's Razor
  - Minimum number of state variables
  - Minimum number of parameters
  - Constant functions instead of linear
  - Linear functions instead of non-linear
- Metabolic Control
  - Organisms increased their control over metabolism during evolution [Biological Occam's Razor]
- Cell Universality
  - Cells are metabolically very similar, [Epistemological Occam's Razor] independently of the organism *or* [Biological Occam's Razor] its size

Fundamental Principles of DEB Theory
Occam's Razor (cont.)

- Constant chemical composition and conversion coefficients (Strong Homeostasis)
- At constant food, one state variable and one forcing flow (Weak Homeostasis)
- At variable food, two state variables and one forcing flow (three independent flows)
  - Required by indirect calorimetry

Thermodynamic Constraints

- Laws of thermodynamics
  - 1st Law: Conservation of mass and energy
  - 2nd Law: Entropy increase in adiabatic systems *or* entropy production in all processes
- Thermodynamic constraints must be obeyed, but are not enough to build theories in biological and social systems
- The major divide in Ecology:
  - Ecosystem and physiological ecology, based on energy and mass flows
  - Population and community ecology, based on the behaviour (fitness) of individuals
- An analogous divide in Economics:
  - Ecological economics (clear minority), based on energy and mass flows
  - Neoclassical economics (mainstream), based on the behaviour of humans (utility) and firms (profit)
- Optimisation requires trade-offs, for which thermodynamics is best

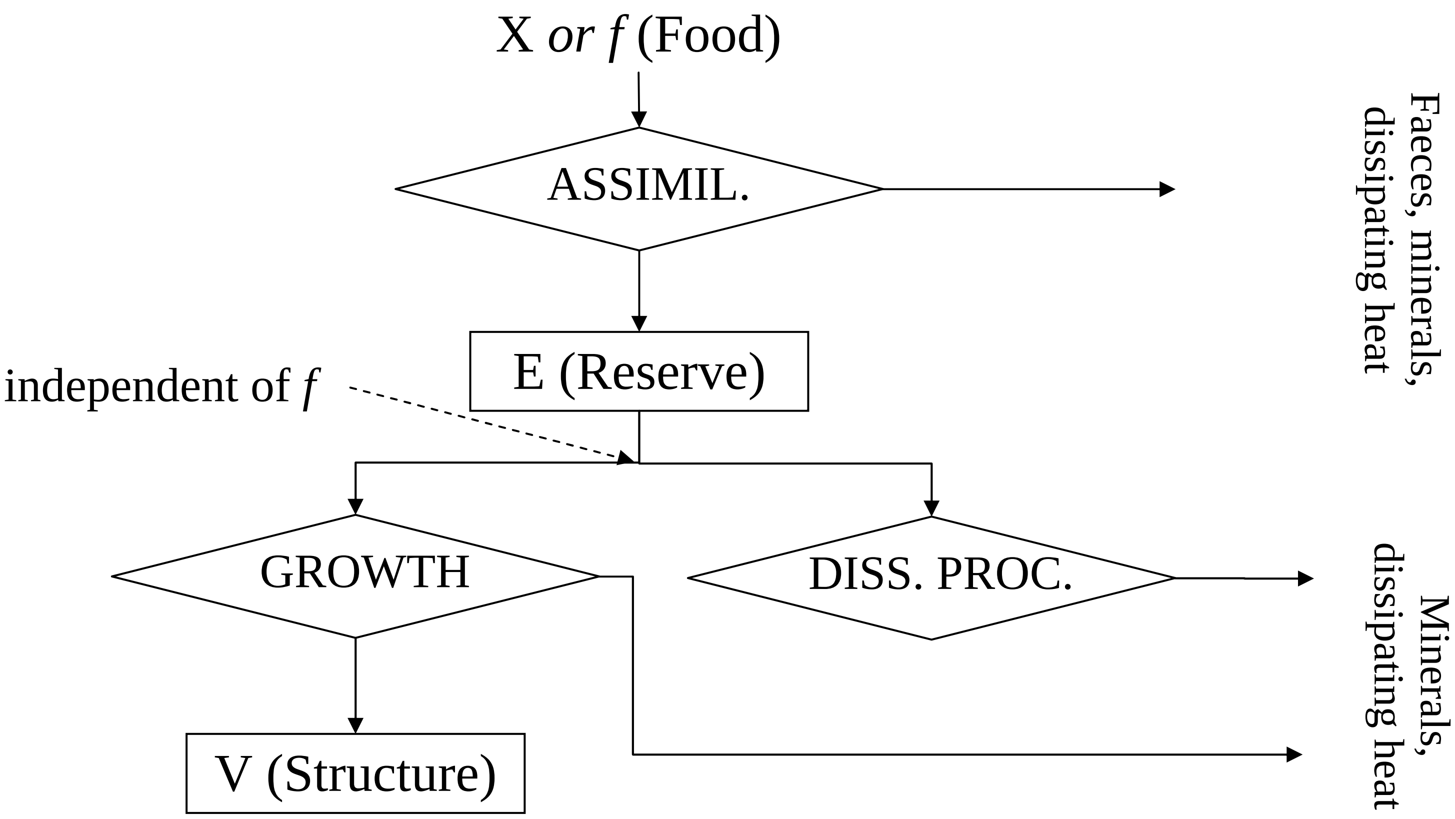
Fundamental Principles of DEB Theory
Thermodynamics

- First Law of Thermodynamics:
  Mass and energy are conserved

- Second Law of Thermodynamics:
  Energy and mass conversion leads to dissipation (entropy production)
  - [Biological and Epistemological Occam's Razor; Strong Homeostasis]
    Entropy production is (mass)volume-specific in maintenance,
    (mass)energy-specific in transformations

- Non-Equilibrium Thermodynamics:
  Mass and energy flows per unit surface depend only on intensive properties
  - e.g., surface-dependent feeding and heating

Topology of the Standard DEB Model



- Specific Biological Assumptions
  - Negligible maintenance needs for reserve (E)

Lika, D., S.A.L.M. Kooijman (2011). The comparative topology of energy allocation in budget models. *J Sea Res* 66:381-91.

Indirect Calorimetry I

- Indirect calorimetry is the empirical observation that dissipating heat is a weighted sum of used dioxygen, produced carbon dioxide and produced ammonia.
- For the standard DEB model, we have the following independent state variables:
  1. Dioxygen (O_2) in the environment
  2. Carbon dioxide (CO_2) in the environment
  3. Ammonia (NH_3) in the environment
  4. Water (H_2O) in the environment
  5. Inorganic internal energy in the environment
  6. Food in the environment
  7. Faeces in the environment
  8. Reserve in the organism
  9. Structure in the organism
  10. Maturity in the organism
  11. Reserve in the reproduction buffer (for adults)

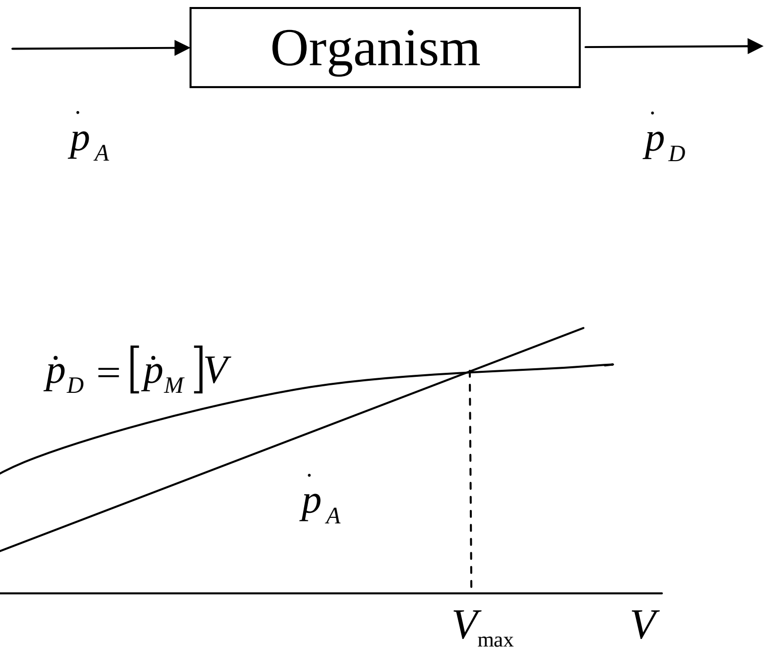
– Note that dissipating heat is a linear combination of the changes in 1, 2, 3, 4 and 5.

Indirect Calorimetry II

- There are conservation laws for:
  1. Carbon
  2. Hydrogen
  3. Nitrogen
  4. Oxygen
  5. Energy
- We assume that reserve in the reproduction buffer has the same composition as reserve and that maturity is massless and energyless
- Due to strong homeostasis, food and faeces are not independent
- So, there are 8 independent thermodynamic state variables and 5 constraints, so 3 degrees of freedom
- Indirect calorimetry is proved

Thermodynamics and Strong Homeostasis Imply Maximum Size

- Non-equilibrium thermodynamics implies surface dependence of uptake processes
- Second law of thermodynamics implies dissipation in all processes
- Strong homeostasis implies that at least a fraction of dissipation is proportional to size

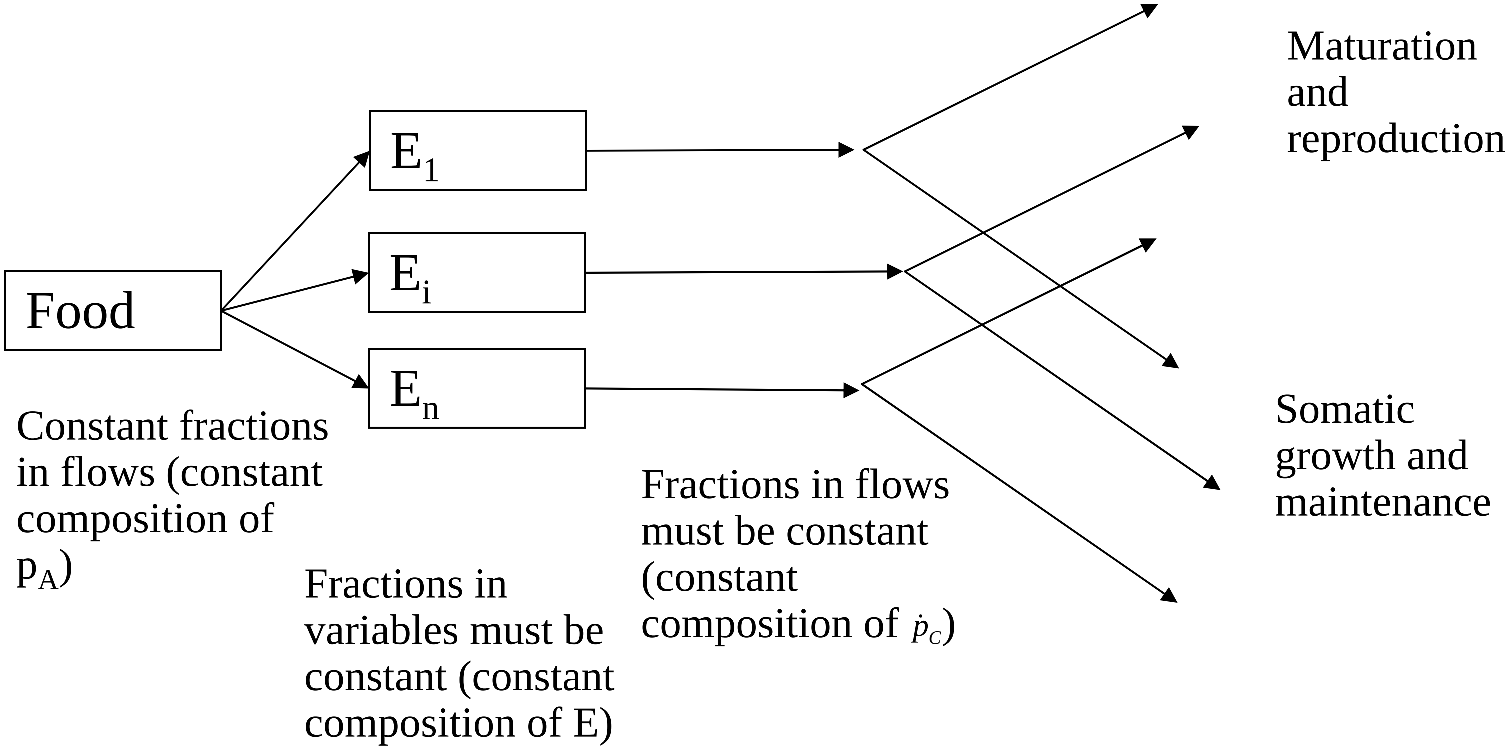


Strict Surface Dependence, Weak Homeostasis and Strong Homeostasis imply von Bertallanfy Growth

- Weak homeostasis means that a single state variable, *V*, describes the organism
- The 2nd Law of Thermodynamics implies the need for maintenance
- Strong homeostasis means that maintenance is proportional to *V*,
- Strict surface dependence (linear non-equilibrium thermodynamics) means that uptake is proportional to $V^{2/3}$

$$
\begin{aligned}
\frac{dE^{tot}}{dt} &= \dot{p}_A - \dot{p}_D = \{\dot{p}_{Am}\} f(X) V^{2/3} - [\dot{p}_M] V \\
E^{tot} &= \alpha V \\
L &= \beta V^{1/3} \\
\frac{dL}{dt} &= \dot{r}_B (L_\infty - L)
\end{aligned}
$$

Strong Homeostasis Implies Partitionability



- Strong homeostasis implies that each category of chemical compounds must represent a constant relative abundance of *E*
- Since mobilisation is independent of assimilation, all categories must be mobilised at the same rate, but note they are only satisfying a fraction of needs of V (partitionability of fluxes):

$$\dot{p}_C(\lambda E, V; \lambda[E_G], \lambda[\dot{p}_M]) = \lambda \dot{p}_C(E, V; [E_G], [\dot{p}_M])$$

- Metabolic control implies that mobilisation power is independent of *f*

Weak Homeostasis, Partitionability and Metabolic Control Imply Reserve Dynamics I

- Reserve dynamics: $$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$$
- Structure dynamics $$\frac{dV}{dt} = \frac{\kappa[\dot{p}_C]V - [\dot{p}_M]V}{[E_G]}$$
- Assimilation power $$[\dot{p}_A] = \{\dot{p}_{Am}\}V^{-1/3} f$$
- Reserve density dynamics: $$\frac{d[E]}{dt} = \frac{1}{V}\frac{dE}{dt} \underbrace{- \frac{[E]}{V}\frac{dV}{dt}}_{\text{dilution by growth}}$$
- Reserve density dynamics, after replacing structure and reserve dynamics $$\frac{d[E]}{dt} = [\dot{p}_A] - [\dot{p}_C] - [E]\frac{\kappa[\dot{p}_C] - [\dot{p}_M]}{[E_G]}$$
- At constant food, **weak homeostasis** implies that reserve dynamics is indep. of size $$\frac{d[E]}{dt} = [\dot{p}_A] - \dot{H}([E],[E_G],[\dot{p}_M])V^{-1/3}$$
- Subtracting the two equations for the reserve density dynamics $$0 = [\dot{p}_A] - [\dot{p}_C] - [E]\frac{\kappa[\dot{p}_C] - [\dot{p}_M]}{[E_G]}$$

Weak Homeostasis and Partitionability Imply Reserve Dynamics II

- The catabolic power is then

$$[\dot{p}_C] = \frac{V^{-1/3}\dot{H}([E],[E_G],[\dot{p}_M]) + [E][\dot{p}_M]/[E_G]}{1+\kappa[E]/[E_G]}$$

- Imposing **partitionability** of the catabolic power

$$[\dot{H}] = \dot{v}[E]$$

- The reserve dynamics is then

$$\frac{d[E]}{dt} = V^{-1/3}(\{\dot{p}_{Am}\}f - \dot{v}[E])$$

- The steady state (function of food) reserve density is

$$[E]^* = \frac{\{\dot{p}_{Am}\}f}{\dot{v}}$$

- The maximum reserve density is obtained for maximum food, *f*=1 (saturation assumption), so:

$$[E]_m = \frac{\{\dot{p}_{Am}\}}{\dot{v}}$$

Structure Dynamics and Scaling Relations

- The structure dynamics is

$$\frac{dL}{dt} = \frac{1}{3}\frac{\kappa\dot{v}[E]-[\dot{p}_M]L}{[E_G]+\kappa[E]} =$$

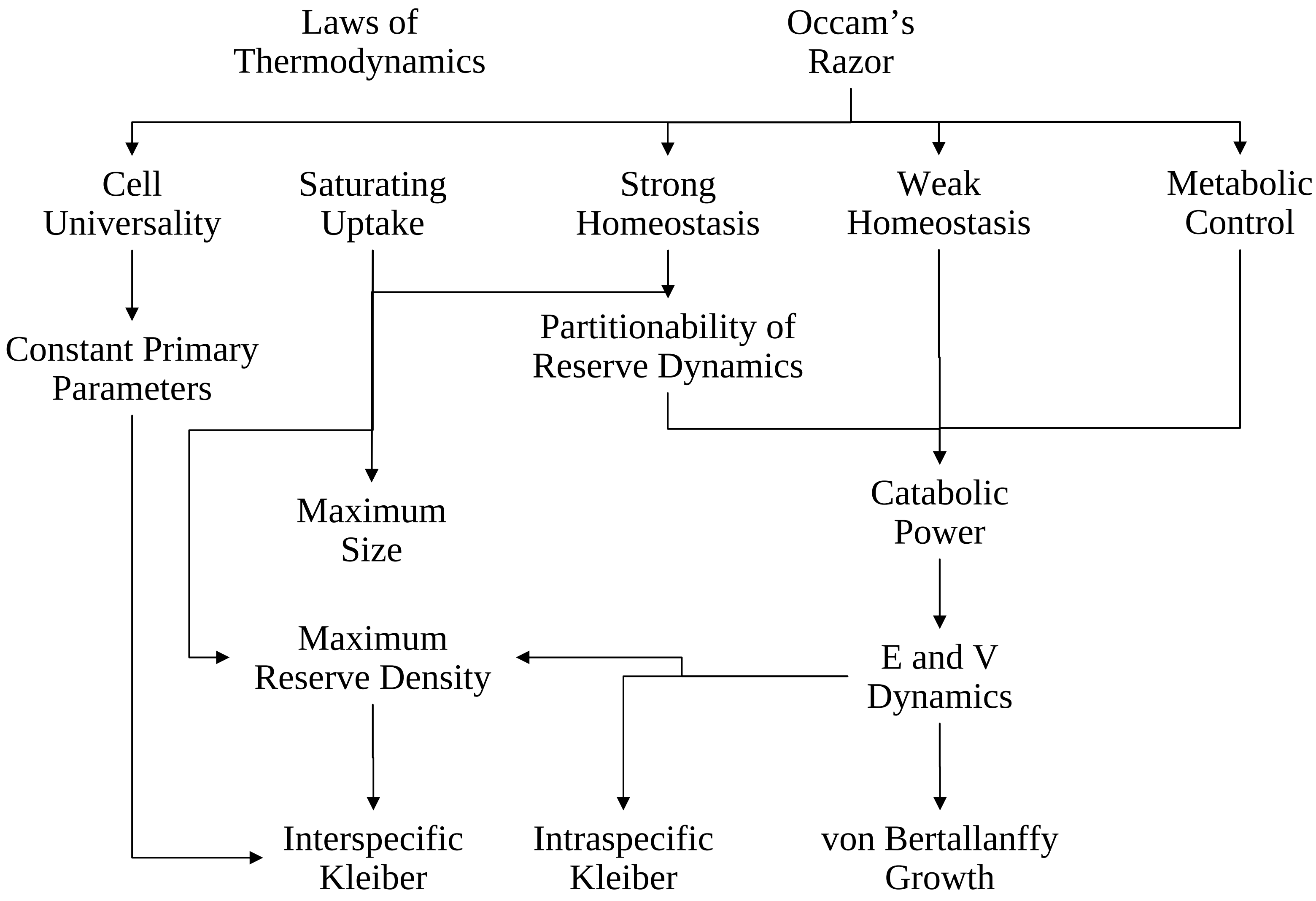
$$= \frac{1}{3}\frac{[\dot{p}_M]}{[E_G]+\kappa[E]}\left(\frac{\kappa\dot{v}[E]}{[\dot{p}_M]} - L\right)$$

- Considering the maximum reserve density, the maximum length is

$$L_m = V_m^{1/3} = \frac{\kappa\{\dot{p}_{Am}\}}{[\dot{p}_M]}$$

- Cell universality implies that volume specific maintenance is constant, so surface specific assimilation is proportional to length
- So, maximum reserve density is, across species, proportional to $V^{1/3}$, which means that it increases with size, hence maintenance needs decrease with size (Kleiber's rule)

Implications of the Fundamental Principles



Sousa, T., T. Domingos, S.A.L.M. Kooijman (2008). From empirical patterns to theory: a formal metabolic theory of life. *Phil. Trans. R. Soc. B* 363: 2453-2464.

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Conclusions

- DEB theory is built on a set of fundamental epistemological, physical and biological principles
- DEB has the characteristics of a robust research program
- One way forward for DEB is its development as a general pertubation theory, coupled with systematic statistical fitting procedures (preferably automatic)

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