

Energy Budgets *

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An energy budget is the specification of the uptake of energy from the environment by an organism (feeding and digestion) and of the use of this energy for the various purposes: maintenance, development, growth and reproduction. A static energy budget represents a kind of snapshot of these fluxes for an individual in a given state, while a dynamic energy budget follows the changes of these fluxes during the life cycle of an organism.

I. Why are energy budgets important?

Organisms typically grow during their life cycle, and food uptake and maintenance are coupled to the size of the organism. Ultimate size of organisms (i.e. the ceasing of growth) is controlled by the balance between uptake of energy and drain in the form of maintenance and reproduction. Just after the start of maturation, during the embryo stage, organisms typically don't take up food. Food uptake is initiated at a moment called birth, i.e. the onset of the juvenile stage. Maturation, a form of metabolic learning, ceases at puberty, i.e. the onset of the adult stage, after which energy (metabolite) allocation to reproduction starts. Although not yet very detailed, this natural sequence already structures the underlying processes profoundly. Table 1 summarises stylised empirical patterns in energy budgets.

This short introduction of budgets shows that quite a few processes behind metabolism are tightly interlinked, and can only be studied simultaneously, exploiting the law of conservation of energy. Energy, i.e. the capacity to do work, is, however, only one aspect; mass, where each of the many chemical compounds has its own properties, is another aspect which is at least as important for the understanding of what organisms do and can do in terms of feeding and production of offspring and products (such as faeces). Energy and mass aspects cannot be separated. Mass aspects are substantially more complex to understand since chemical compounds can be transformed (so there are no conservation laws for compounds) and the body can change in chemical composition in response to changes in its nutritional status. We can, however, use conservation laws for chemical elements, (C, H, O and N being the most important ones), and use a variety of homeostasis concepts

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Table 1: Stylised and empirical facts.

Feeding

- Many species (almost all animals and plants) have an embryo stage that does not feed
- During starvation, organisms are able to reproduce, grow and survive for some time
- At abundant food, the feeding rate is at some maximum, independent of food density

Growth

- Many species continue to grow after reproduction has started
- Growth of isomorphic organisms at abundant food is well described by the von Bertalanffy growth curve
- For different constant food levels the inverse von Bertalanffy growth rate increases linearly with ultimate length
- The von Bertalanffy growth rate of different species decreases almost linearly with the maximum body length
- Fetuses increase in weight approximately proportional to cubed time

Reproduction

- Many species (almost all animals and plants) have a juvenile stage that does not reproduce
- Reproduction increases with size intra-specifically, but decreases with size inter-specifically
- A range of constant low food levels exists at which an individual can survive, but not reproduce

Respiration

- Animal eggs and plant seeds initially hardly use dioxygen
- The use of dioxygen increases with decreasing mass in embryos and increases with mass in juveniles and adults
- The use of dioxygen scales approximately with body weight raised to a power close to 0.75
- Animals show a transient increase in metabolic rate after ingesting food (heat increment of feeding)

Stoichiometry

- The chemical composition of organisms depends on the nutritional status (starved vs well-fed)
- The chemical composition of organisms at constant food density becomes constant during growth

Energy

- Dissipating heat is a weighted sum of three mass flows: carbon dioxide, dioxygen and nitrogenous waste

Ageing

- Mean life span typically increases inter-specifically with maximum body length in endotherms, but hardly depends on body length in ectotherms
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to capture what organisms do in terms of mass uptake and use. Mass aspects work out somewhat different for the various taxa. Animals, i.e. organisms that feed on other organisms, acquire the various compounds they need in approximately fixed relative proportions, but bacteria, algae and plants take up nutrients (e.g. nitrate, phosphate, carbon dioxide) and light from the environment almost independently. Yet, the various uptake routes are coupled (in a sloppy way) due to the fact that biomass varies in composition in a limited range only; this gives rather complex stoichiometric constraints on uptake. The ecological literature about stoichiometric constraints on production typically simplifies this and follows chemical elements in particular substrates, cq. nutrients, and considers a constant composition of biomass.

Most use of energy can only be inferred indirectly from observations in ways that involve the comparison of performances between individuals of different size and under different feeding conditions. An example is the allocation of energy (or resources) to growth compared to the fixation of these resources in new tissue. The difference is in the overhead costs of growth, which are notoriously difficult to quantify in static energy budgets. Another example is the allocation of energy to maintenance, i.e. the collection of processes of use of energy that is not directly linked to production of biomass (growth, reproduction). Static energy budgets typically use respiration (the use of dioxygen or the production of carbon dioxide or heat) as a quantifier for maintenance. This must be wrong, however; dynamic energy budgets include, beside maintenance, maturation and overhead costs of assimilation, growth and reproduction in the respiration. Although still popular, we here no longer consider static energy budgets.

So far, the emphasis has been on individuals because they are the survival machines of life, and the target for evolutionary selection and change. The rules individuals use for the uptake and use of substrates have profound consequences for sub-organismal organisation of metabolism. Many species are unicellular, so the step to sub-cellular organisation is rather direct. Multicellular species have organisation layers between that of the individual and the cell, and allocation to the various tissues and organs has functional aspects.

At supra-organismal level, populations can be considered as groups of interacting individuals of the same species. Apart from these interactions, at least including food competition, transport of individuals and substrates (cq food) through the environment dominates population dynamics. In most situations seasonal forcing has to be considered, where temperature and water (the typical components of climate) affect substrate availability and uptake.

At planetary level, we only have to remember that all dioxygen in the atmosphere is of biological origin, including the ozon protection shield for UV radiation, and that most important greenhouse gas, atmospheric water, and the minor ones, carbon dioxide and methane, are strongly influenced by biota to understand that the global climate results from complex long-term interactions between biota and the physico-chemical environment

Typical human interests (medicine, agri- and aqua-culture, forestry, sewage treatment, biotechnology) also make intensive use of particular aspects of energy budgets. These considerations illustrate that energy budgets are key to biology and its societal applications.

II. Principles of DEB theory

The Dynamic Energy Budget (DEB) theory is a specific theory that explains each of the patterns as listed in Table 1, exploiting the features that all organisms, i.e. micro-organisms, animals and plants, have in common in a rather abstract perspective. DEB theory is a set of explicit coherent and consistent assumptions (axioms or hypotheses if you wish) that, in combination, specifies a set of models. A modular set-up is exploited, where modules for particular ‘details’ are only ‘clicked in’, if the research question requires it. The standard DEB model, in a sense the simplest one in the DEB family, deals with isomorphs, i.e. organisms that don’t change in shape during growth, with one reserve and one structure feeding on one type of food. It is supposed to apply to animals, i.e. organisms that feed on other organisms; micro-algae need several reserves, plants also need two structures (root and shoot).

A. Homeostasis is key to life

DEB theory uses five homeostasis concepts to capture what organisms do.

- 1 Strong homeostasis is the strict constancy of the chemical composition of pools. This implies stoichiometric constraints on the synthesis of generalised compounds, i.e. mixtures of compounds that do not change in composition. By delineating more and more pools, strong homeostasis becomes less restrictive.
- 2 Weak homeostasis is the constancy of the chemical composition of the individual as a whole as long as substrate availability in the environment remains constant, *even when growth continues*. This implies constraints on the dynamics of the pools. Weak homeostasis in fact implies strong homeostasis.
- 3 Structural homeostasis is the constancy of the shape of the individual during growth. This implies that surface area is proportional to volume to the power $\frac{2}{3}$; a condition referred to as isomorphy, or, $V^{\frac{2}{3}}$ -morphy. Isomorphy is assumed in the standard DEB model, but not in DEB models generally.
- 4 Thermal homeostasis is the constancy of the body temperature. Endotherms oxidise compounds for heating; mammals and birds do it ‘perfectly’, tunas and insects much less so. Homeotherms don’t do this, but make use of spatial differences in temperature to reduce variations in body temperature. Ectotherms (by far the majority of the species) have a body temperature (almost) equal to the environmental temperature.
- 5 Acquisition homeostasis is the constancy of the feeding rate, independent of food availability. This is, to some extent, sported by animals near the demand-end of the supply-demand spectrum at which organisms can be ranked. Most organisms are near the supply-end, see Table 2. Demand systems evolved from supply systems, and developed several adaptations for this while preserving many other properties of supply systems.

Table 2: Comparison between supply and demand systems

Supply	Demand
eat what is available	eat what is needed
can handle large range of intake	can handle small range of intake
reserve density varies wildly	reserve density varies little
low peak metabolic rate	high peak metabolic rate
open circulatory system	closed circulatory system
rather passive, simple behaviour	rather active, complex behaviour
sensors less developed	sensors well developed
typically ectothermic	typically endothermic
evolutionary original	evolved from supply systems
has demand components (maintenance)	has supply components (max size depends on food quality)

B. Reserve mobilisation drives metabolism

Six compelling arguments urge us to partition biomass into two compartments: reserve and structure

- 1 to include metabolic memory; think, for instance, of embryos, which develop, grow and maintain themselves without feeding, or of mother baleen whales which feed only for half a year and then travel 25 Mm while giving birth to a big calf in tropical waters, and feed it daily with 600 litre of milk for several months before resuming feeding in (ant)arctic waters.
- 2 to smooth out fluctuations in resource availability to make sure that no essential type of resource is temporarily absent in the multi-recourse situation
- 3 to allow that the chemical composition of the individual depends on the growth rate
- 4 to understand why mass fluxes are linear sums of three basic energy fluxes: assimilation, dissipation and growth (which is basic to indirect calorimetry)
- 5 to explain observed patterns in respiration and in body size scaling relationships
- 6 to understand how the cell decides on the use of a particular (organic) substrate, as building block or as source of energy.

Most of these arguments come back in Table 1. The reason for being that detailed is because this complicates the theory and its application quite a bit, so there is a need for a careful cost-benefit analysis in composing the theory. The difference between reserve and structure is in their dynamics; only structure needs maintenance, while reserve is synthesized from substrates taken from the environment and used for metabolic purposes. A substantial part of maintenance relates to the turnover of structure, so compounds in both reserve and structure have a limited life span.

The mobilisation of reserve, within the context of DEB theory, is completely quantified by the requirement of weak homeostasis, but the derivation is rather technical. This

explains why the assumptions for the standard DEB model, see Table 3, seem to ignore reserve dynamics.

C. Development and allocation

Metabolic learning during ontogeny is quantified by the state of maturity, more specifically by the cumulated investment of reserve in maturity; one can think of the installation of (e.g. hormonal) regulation systems. Maturity does not represent mass, energy or entropy; it has the formal status of information. Metabolic switches occur when maturity reaches a threshold, e.g. at cell division, birth, puberty or metamorphosis (in some species). This explains why the age at which these switches occurs varies a lot, and the body length somewhat, with the nutritional conditions. Although body length at stage transitions is typically rather constant, the observation that some taxa, e.g. most bird species, only start reproduction after body weight no longer changes for some time, illustrates that state transitions cannot be linked to length.

Allocation is the set of decision rules for the use of mobilised reserve. The simplest situation, capturing quite a few general aspects of growth and development, is that a fixed fraction κ of mobilised reserve is allocated to somatic maintenance and growth (together called soma), the remaining fraction to maturity maintenance plus maturation or reproduction; both types of maintenance take priority (demand–organisation), rendering growth and maturation (or reproduction) into a supply–organisation. Somatic maintenance comprises the turnover of structure, movement and other forms of behaviour, osmotic work (in freshwater) and heating (in endotherms). Maturity maintenance comprises the maintenance of regulation systems and defence work (e.g. the immune system). The static generalisation of this κ -rule further partitions the allocation to the soma into allocation to body parts (e.g. organs), where each body part receives a fixed fraction of mobilised reserve and maintenance of that part takes priority over growth. The dynamic generalisation releases these fractions and links them to the relative workload of that body part, i.e. its work as fraction of the maximum work a body part of that size can do. This requires a specification of the relationship between organ-size and organ-function.

Generalisations of the κ -rule are basic to the concept heterochrony. They explain, for instance, why relative brain-size decreases during ontogeny of animals in view of heavy duty in the early stages, and why (moderate) use of alcohol leads to large livers in humans. Another application is in understanding how tumour growth depends on the state of the host (i.e. amounts of reserve and structure) and its response to caloric restriction.

D. Surface area–volume relationships

Transport, such as food uptake, in 3-dimensional space (volume), occurs across a 2-dimensional space (surface). Not all of the surface of an individual needs to be involved, it can be a certain fraction (e.g. that of the gut). Since maintenance is linked to (structural) volume, surface area – volume relationships control growth and reproduction.

The simplest situation of no change in shape during growth (structural homeostasis), called isomorphy, approximately holds for most animals. Apart from isomorphs, two special

cases of changing shapes repeatedly pop-up in applications of DEB theory: (i) V0-morphs, where surface area is proportional to structural volume to the power 0, so it remains constant (biofilms, and organisms that increase their structure at the expense of their vacuoles are examples) (ii) V1-morphs, where surface area is proportional to structural volume to the power 1. Growing filaments and sheets are examples.

Many other cases can be seen as static or dynamic mixtures of these three basic types; rods (most bacteria) are static mixtures of V0- and V1-morphs, plants naturally evolve from V1-, via iso-, to V0-morphs during their life cycle and crusts (e.g. lichens or super-individuals such as forests) from V1- to V0-morphs such the their diameter grows linearly in time at constant substrate. Think also of a population of musk-rats, for instance, conceived as a super-individual, that spreads over Europe from individuals released in central Europe. The front of such a population moves at a constant rate for exactly the same reasons why the edge of a forest or a lichen in homogeneous space moves at constant rates: it is the scaling of the surface area for the uptake of resource, relative to the volume that requires maintenance.

V1-morphs have the unique feature that the significance of the levels of the individual and the population completely merge; a population of many small V1-morphs behaves identical to that of a few big V1-morphs with equal total structure and reserve. V1-morphs also have no size-control as an individual (if they would not reset their size by division); they continue to growth exponentially as long as substrate density remains constant. This argument can also be reversed: if we want to understand population characteristics (such as the maximum specific growth rate) in terms of properties of individuals (such as size at division), we cannot consider them as V1-morphs. The population dynamics of V1-morphs is so much simpler than that of other morphs, that it remains attractive to make this simplification for other purposes. This can, for dividing organisms, be defended mathematically as being a good approximation in quite a few situations.

The scaling of surface area to volume dominates the rate of living at all levels of organisation. For instance, the production in lakes is typically nutrient-limited and the acquisition of nutrients is via inflowing water. The amounts of water and nutrients are directly linked to the water catching area of the lake (so a surface), while its effect on (algal) growth is via the concentration of nutrients, which involves the volume of the lake. At the sub-cellular level membranes (surfaces) dominate metabolism, while substrate and product concentrations involve cytoplasm volume.

E. Synthesising Units and chemical transformation rates

Spatial structure, especially within organisms and cells, complicates the application of the concept concentration, which implies homogeneous mixing at the molecular level. DEB theory avoids the use of the concept to quantify metabolism using the dynamics of Synthesising Units (SUs) at several crucial places. SUs can be conceived as generalised enzymes that generally follow the rules of enzyme kinetics, with two far-reaching modifications: (i) their activity depends on arrival rates of substrates, rather than concentrations of substrates and (ii) the dissociation of substrate from the SU-substrate complex is assumed to be small (all bound substrate is transformed to products). If substrates are in a ho-

homogeneous environment, the arrival rate of substrates can be taken proportional to the substrate concentration on the basis of diffusive transport. In the simplest situation, such as in transformation of one substrate into products, SU- and enzyme-dynamics have the same result. Think, for example, of a feeding individual conceived as an SU, that has only two behavioural states: searching for and handling of food; the Holling type II functional response results, and has the same mechanistic background as Monod's model for microbial growth, and Michaelis-Menten's model for enzyme kinetics. The modelling of fluxes has, however, a much bigger flexibility, especially if spatial structure matters, and combines nicely with the concepts of allocation, which basically deals with the partitioning of fluxes. Compounds can be classified as substitutable or complementary, binding to SUs as sequential or parallel; this gives four basic classes from which more complex forms are derived, such as inhibition and co-metabolism. DEB theory uses SU dynamics in the assimilation module, in the mobilisation of reserve and in growth, i.e. the conversion of reserve to structure. SU dynamics is also used if e.g. multiple substitutable reserves are present, such as carbohydrates and proteins for maintenance. It can be shown that active excretion of mobilised reserve that is rejected by SUs for growth in multiple reserve systems is unavoidable, with important ecological consequences (e.g. excretion of toxins by algae in eutrophic waters).

In its simplest form, DEB theory separates metabolic transformations into three macro-chemical reaction equations: (i) assimilation (the conversion of environmental substrate(s) to reserve and products), (ii) dissipation (the conversion of reserve into products) and (iii) growth (the conversion of reserve into structure and products). Substrate, reserve, structure and products are conceived as generalised compounds, the latter are typically released into the environment and include heat. This explains the success of the method of indirect calorimetry, cf Table 1, which quantifies heat as a weighted sum of the fluxes of dioxygen, carbon dioxide and nitrogen waste (e.g. ammonia). Since products serve as substrate for other organisms, these three processes, and their coupling, are of fundamental significance for ecosystem dynamics.

When the log of any metabolic rate is plotted against the inverse absolute temperature, a straight line results in a species-specific tolerance range of temperatures; the slope is called the Arrhenius temperature. This Arrhenius relationship can be understood from fundamental principles under very simple very idealised conditions, remote from the situation in living organisms. DEB theory treats this relationship empirically only. Outside the temperature tolerance range, rates are typically lower than expected on the basis of the Arrhenius relationship. At the high-temperature end, the rates are typically a lot less and the individual dies. At the low-temperature end, the individual typically manages to send itself into a state of torpor. This situation typically occurs during the bleak season, where substrate availability is low. This deviating behaviour can be captured by delineating temperature-dependent transitions of enzymes from an active state and two inactive states (relating low and high temperatures); these transitions again follow the Arrhenius relationship.

Since substrate uptake affects substrate availability, and the Arrhenius temperature is species-specific, temperature can have complex effects. Ultimate size (i.e. a state) relates to the ratio of two rates: uptake (food) and drain (maintenance), are affected by temperature;

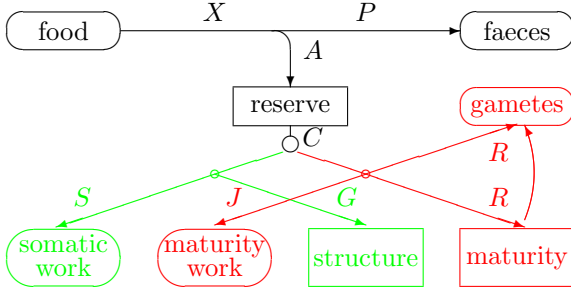


Figure 1: Energy fluxes in the standard DEB model. The rounded boxes indicate sources or sinks. The symbols stand for: X food intake; P defecation; A assimilation; C mobilisation; S somatic maintenance; J maturity maintenance; G growth; R reproduction. The colours illustrate that fluxes G plus S comprise a fixed fraction κ of flux C in the model: the κ -rule for allocation.

food uptake can affect food availability.

If more than one reserve is present, the corresponding assimilation rates might differ in the way they depend on temperature. So these systems are more flexible than the single-reserve systems. Photon capture hardly depends on temperature, for instance, which implies that carbohydrate content becomes temperature dependent. Algae in (ant)arctic waters have much more starch and/or lipids than those in tropical waters, with consequences for those who feed on them.

III. Standard DEB model

The logical links between substrate, reserve, structure and maturity in the standard DEB model are given in Figure 1 and the assumptions in Table 3 quantify all fluxes in this figure uniquely and how they change during the life cycle of the individual. Table 4 gives an overview of its primary parameters (excluding the ageing module). The 14 parameters fully quantify the 7 processes of feeding, digestion, maintenance, growth, maturation, reproduction and ageing during the full life cycle of the individual; so 2 parameters per process, illustrating the simplicity of this model. Efficiency of faecal production κ_X^P (or the equivalent yield of faeces on food y_{PX}) could be added to quantify faeces production and the fluxes of dioxygen and carbon dioxide in association with assimilation. Some parameters scatter widely among species (e.g. E_H^b , E_H^p , \dot{h}_a), others much less (e.g. \dot{v}). The structure of the model could be tested using effect of toxicants. If the (internal) concentration is sufficiently low, a toxicant affects a single parameter, with particular consequences for energetics. Reactions to perturbations provide strong support for the general structure of the model.

The allocation to reproduction is first accumulated in a reproduction buffer; species-specific buffer handling rules convert the content of that buffer into gametes. Some species produce a young as soon as they accumulated enough reserve, others spawn once a year only. These handling rules, together with the feeding rate involve the behavioural repertoire, which is notoriously stochastic. Stochasticity has far-reaching consequences for population dynamics.

The methodology of energy budgets is closely related to that of biophysical ecology. Extensions of the standard DEB model that incorporate more detail on nutritional requirements can make the bridge to the geometric framework of nutrition, allowing a detailed quantification of the niche concept.

Table 3: The assumptions that specify the standard DEB model quantitatively.

- 1 The amounts of reserve, structure and maturity are the primary state variables of the individual; reserve and structure have a constant composition (strong homeostasis) and maturity represents information.
 - 2 Substrate (food) uptake is initiated (birth) and allocation to maturity is redirected to reproduction (puberty) if maturity reaches certain threshold values.
 - 3 Food is converted into reserve and reserve is mobilised at a rate that depends on the state variables only to fuel all other metabolic processes.
 - 4 The embryonic stage initially has a negligibly small amount of structure and maturity (but a substantial amount of reserve). The reserve density at birth equals that of the mother at egg formation (maternal effect). Foetuses develop in the same way as embryos in eggs, but at a rate unrestricted by reserve availability.
 - 5 The feeding rate is proportional to the surface area of the individual and the food-handling time is independent of food density.
 - 6 The reserve density *at constant food density* does not depend on the amount of structure (weak homeostasis).
 - 7 Somatic maintenance is proportional to structural volume, but some components (osmosis in aquatic organisms, heating in endotherms) are proportional to structural surface area.
 - 8 Maturity maintenance is proportional to the level of maturity.
 - 9 A fixed fraction of mobilised reserves is allocated to somatic maintenance plus growth, the rest to maturity maintenance plus maturation or reproduction (the κ -rule).
 - 10 The individual does not change in shape during growth (isomorphism). This assumption applies to the standard DEB model only.
 - 11 Damage-inducing compounds (modified nuclear and mitochondrial dna) are generated at a rate that is proportional to the reserve mobilisation rate; damage-inducing compounds induce themselves at a rate that is proportional to the mobilisation rate. Damage-inducing compounds generate damage compounds ('wrong' proteins) at constant rate, which cumulate in the body. The hazard rate is proportional to the density of damage compounds
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Table 4: The primary parameters of the standard DEB model in a time-length-energy and a time-length-(dry)mass frame and typical values among species at 20 °C with maximum length $L_m = zL_m^{\text{ref}}$ for a dimensionless zoom factor z and $L_m^{\text{ref}} = 1$ cm. The two frames relate to each other via the chemical potential for reserve $\bar{\mu}_E = 550 \text{ kJ mol}^{-1}$ and the volume-specific mass of structure $[M_V] = 4 \text{ mmol cm}^{-3}$. The typical value for the Arrhenius temperature $T_A = 8 \text{ kK}$.

specific searching rate	$\{\dot{F}_m\}$	$6.51 \text{ cm}^{-2} \text{ d}^{-1}$	$\{\dot{F}_m\}$	$6.51 \text{ cm}^{-2} \text{ d}^{-1}$
assimilation efficiency	κ_X	0.8	y_{EX}	0.8 mol mol^{-1}
max spec. assimilation rate	$\{\dot{p}_{Am}\}$	$22.5 z \text{ J cm}^{-2} \text{ d}^{-1}$	$\{\dot{J}_{EAm}\}$	$0.041 z \text{ mmol cm}^{-2} \text{ d}^{-1}$
energy conductance	\dot{v}	0.02 cm d^{-1}	\dot{v}	0.02 cm d^{-1}
allocation fraction to soma	κ	0.8	κ	0.8
reproduction efficiency	κ_R	0.95	κ_R	0.95
volume-spec. som. maint. cost	$[\dot{p}_M]$	$18 \text{ J cm}^{-3} \text{ d}^{-1}$	$[\dot{J}_{EM}]$	$0.033 \text{ mmol cm}^{-3} \text{ d}^{-1}$
surface-spec. som. maint. cost	$\{\dot{p}_T\}$	$0 \text{ J cm}^{-2} \text{ d}^{-1}$	$\{\dot{J}_{ET}\}$	$0 \text{ mol cm}^{-2} \text{ d}^{-1}$
maturity maint. rate coeff.	\dot{k}_J	0.002 d^{-1}	\dot{k}_J	0.002 d^{-1}
specific cost for structure	$[E_G]$	2800 J cm^{-3}	y_{VE}	0.8 mol mol^{-1}
Weibull ageing acceleration	\ddot{h}_a	$10^{-3} z \text{ d}^{-2}$	\ddot{h}_a	$10^{-3} z \text{ d}^{-2}$
Gompertz stress coefficient	s_G	0	s_G	0
maturity at birth	E_H^b	$275 z^3 \text{ mJ}$	M_H^b	$500 z^3 \text{ nmol}$
maturity at puberty	E_H^p	$166 z^3 \text{ J}$	M_H^p	$0.3 z^3 \text{ mmol}$

A. Co-variation of parameter values and r - K strategies.

DEB theory captures the differences between organisms in parameter values, which are individual-specific to allow for evolutionary change. Parameter values are partly under genetic control. Adaptations concern changes in parameter values as implications of this approach. Think, for example, of geographical size variations as adaptations to food availability at the growing season; the Bergmann-rule states that the maximum body size of species tends to increase from the equator towards to poles. Towards the poles of the Earth, seasonality becomes more important, where the bleak season thins populations, and so reduces competition during the breeding season. Predictable food levels can to some extent be fixed in parameter values within one species in ways that are more clearly demonstrated inter-specifically. The main difference between intra- and inter-specific parameter variations is the amount of variation.

Notice that structure and reserve are state variables, not parameters, and they vary during the life of an individual, even if its parameters remain constant. Although we can compare an old (large) individual of a small bodied species with a young (small) individual of a bigger bodied species, the result can be complex. Even if they have the same size (i.e. length or weight), their metabolism will differ. For simplicity's sake we confine inter-species comparisons to fully-grown individuals.

A powerful property of the standard DEB model is that its structure allows us to predict the covariation of parameter values across species without using any empirical argument or new assumption. This is due to three properties:

- 1 the parameters can be classified into two classes: intensive parameters that only depend on the very local physico-chemical sub-organismal conditions and design pa-

rameters that depend on the size of the individual, see Table 4.

2 simple functions of design parameters (typically ratios) are intensive.

3 maximum length is a function parameters, of which only one is a design parameter.

The covariation of parameter values just concerns a tendency that is based on physico-chemical principles. Species-specific deviations from the mean pattern reflect species-specific adaptations. The better we can characterise this mean pattern, the more we can appreciate the deviations from it and recognise what properties make a particular species special.

Only four parameters in this list of Table 4 depend on size: the surface area-specific assimilation rate, the Weibull ageing acceleration and the maturity levels at birth and puberty. The specific assimilation rate must be proportional to maximum length, because both other parameters that control it, the allocation fraction to soma and the specific somatic maintenance costs, are intensive parameters. The Weibull ageing acceleration is proportional to maximum length, because it is proportional to the specific assimilation rate. Maturity density is intensive, which is most easy to see when the maturity and somatic maintenance coefficients are equal, $k_J = [\dot{p}_M]/[E_G]$, and the maturity density remains constant during growth, so it must be independent of size. Maturity thresholds must, therefore, be proportional to cubed maximum length.

The application of these simple relationships is in writing a physiological quantity of interest, such as body weight, or respiration rate, as a function of the primary parameters. We now know how each of the primary parameters depend on maximum length, so we know how this function depends on maximum length.

Feeding rate increases with squared length intra-specifically, but with cubed length inter-specifically. Reproduction rate increases with size intra-specifically, but decreases with size inter-specifically. Strange enough, respiration rate scales somewhere between a surface and a volume, both intra- and inter-specifically, but for very different reasons. Intra-specifically, when we follow a growing individual at constant food, body weight is proportional to the amount of structure (weak homeostasis), but the allocation to growth declines with size; the overhead costs of growth contribute to respiration. Inter-specifically, when we compare fully grown adults and growth plays no role, respiration is dominated by maintenance. Since reserve density increases with maximum length, and maintenance is only paid for structure, weight-specific maintenance decreases with maximum length. Reserve density increases with maximum length, because it equals the ratio of the specific assimilation rate and energy conductance, while the latter is intensive. The length of the juvenile period tends to increase with body length, as does life span in endotherms, because they typically have a positive Gompertz stress coefficient (around 0.5), see Table 4. Life span in ectotherms, however, hardly depends on body size because for them the Gompertz stress coefficient is small. The consequence is the ectotherms can only evolve big maximum body sizes if they manage to decrease their ageing acceleration rate.

The ecological literature describes r and K strategies, frequently used symbols for the parameters for growth and carrying capacity in the logistic equation. The supposed

differences in properties between r and K strategists mainly follows patterns that DEB theory expects for small, respectively large, bodied species.

IV. Ecosystem structure and function

Ecosystems have a structural (abundance of the various biota) and a functional aspect (nutrient recycling). In a food pyramid at steady state, the top predators mainly suffer from ageing and some accidental losses, so their reproduction rate is low to compensate for these small losses. DEB theory expects low reproduction rates for large-bodied species at low food densities. At the bottom of the pyramid the predation pressure is typically high, rendering losses due to accidents and ageing insignificant, so the reproduction rate must be high to compensate. DEB theory expects high reproduction rates for small-bodied species at high food densities. At the very bottom are nutrients and light as input for the producers that serve as food for the consumers. This gives a natural focus on the processes of nutrient supply and nutrient recycling to fuel the ecosystem; microbial degradation plays a key role. Think, for instance, of a tree. Its leaves last a year only, and without assistance of microorganisms in the soil to release the nutrients locked into the leaf litter, the tree would have a short life time. Leaf litter is a waste product for trees, as are nutrients for the microorganisms; a clear example of syntrophic interactions. Once recognised, such syntrophic interactions can be seen everywhere and represent the dominant form of interaction. DEB theory is specifically designed to deal with such interactions since it specifies product formation quantitatively and SU-dynamics takes care of fluxes in a network.

V. Evolution of the individual as dynamic system

A possible evolutionary scenario of the basic DEB models is presented in figure 2, where the top row refers to the evolution of prokaryotes, from which the eukaryotes (second row) evolved. The increasing control over the chemical composition of the individual's structure during evolution induces stoichiometric constraints on growth. Since the concentrations of the various complementary substrates fluctuates wildly in the local environment, individuals (here prokaryotic cells) need to store substrates in reserves to smooth out these fluctuations. The evolution of strong homeostasis might well have been via weak homeostasis.

When uptake became more efficient by using proteins that require turnover, the need to increase the reserve capacity increased; the continuous need of resources otherwise combines poorly with a temporary absence of substrates. While homeostasis creates the need for reserves, maintenance enhances it.

Reserves could originally be built up by delaying the processing of internalised substrates, but the need to increase reserve capacity came with the need to temporarily store them in a form that does not create osmotic problems, for otherwise they start to interfere with metabolism. To ensure continuity of the fuelling of maintenance, the payment of maintenance cost internalised from fluctuating external substrates to much more constant mobilised reserve.

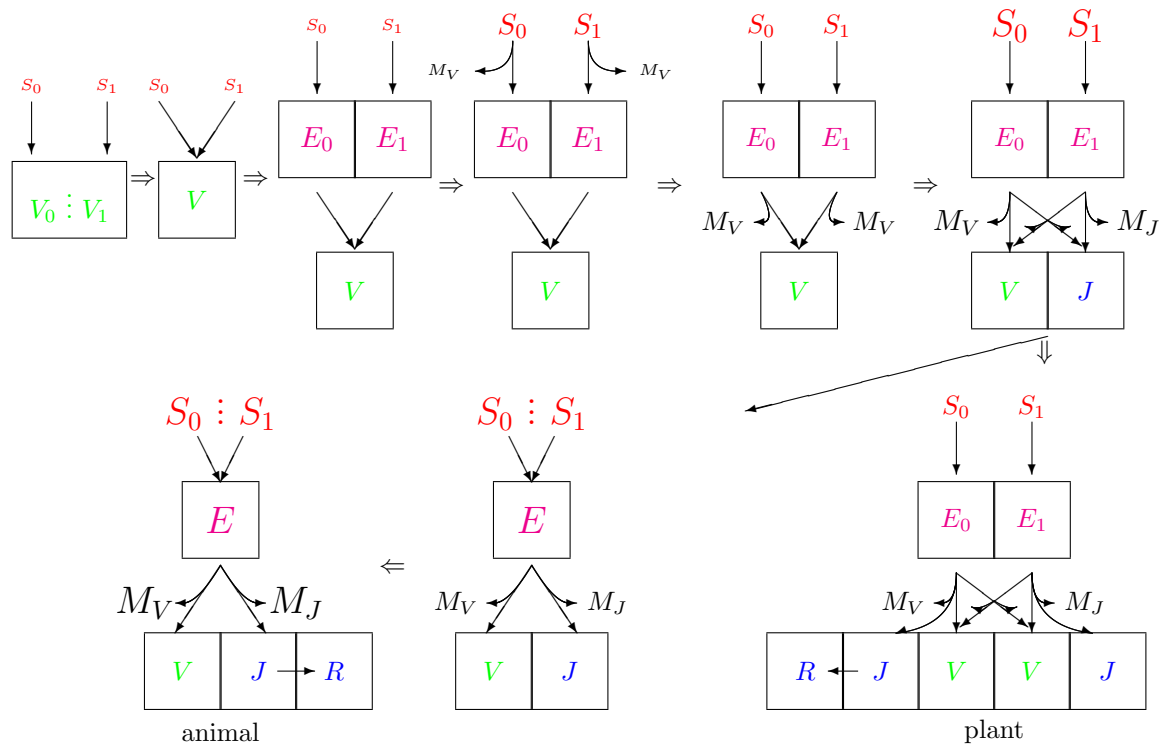


Figure 2: Steps in the evolution of the organisation of metabolism of organisms. Symbols: S substrate, E reserve, V structure, J maturity, R reproduction, M_V somatic maintenance, M_J maturity maintenance. Only two of several possible types of E are shown. Font size reflects relative importance. Stacked dots mean loose coupling. The top row shows the development of a prokaryotic system, which bifurcated in a plant and an animal line of development.

Size control, i.e. the resetting of cell size by division and the control of surface area-volume ratios, boosted population growth, but came with the need to install a maturity program. These steps were already taken before the eukaryotes evolved.

After the invention of phagocytosis by eukaryotes, feeding on other living creatures became popular in one line of development, which coupled the uptake of the various complementary substrates and induced a covariation of reserve densities. This encouraged the animal line of development, where homeostatic needs finally reduced the number of independent reserves to one, and the juvenile stage evolved an embryo and adult stage simultaneously with the invention of reproduction. The pattern came with the evolution of mobility, sensors and a neuronal system to allow for fast information exchange between otherwise rather isolated cells.

Another line of development did not start to feed on living creatures and kept their reserves independent, but evolved an increased capacity to cope with changes in the local environment: the plant line of development. They partitioned their structure in a root and a shoot and invented the use of products (wood) to adapt their shape during growth. They became masters of the art of torpor to escape bleak periods, and evolved a much more open (but slow) mass communication between cells. They invented the embryo/adult

stages independently.

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Information about the DEB research program and its results can be found at <http://www.bio.vu.nl/thb/deb/>.