

Metabolic Theories in Ecology: The Dynamic Energy Budget Theory and the Metabolic Theory of Ecology

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Introduction

Animal metabolism is the processing of material that individual animals take up from the environment. Some fraction of this material is unusable and leaves the body as feces. This fraction is sometimes called the non-metabolic waste and not considered as part of metabolism, because it does not pass the gut wall and therefore not really enters the animals body. The remaining usable fraction of the food uptake is converted into other chemical forms and subsequently used for various life processes such as body maintenance, somatic growth and reproduction. Part of the usable material is thus stored in the body, maybe only temporarily as reproductive output, but a substantial amount of material also leaves the body as metabolic waste, in the form of gas such as carbon dioxide, liquid such as water or urine, or even as solid waste in the form of hairs, feathers, scales and skin. If the focus is on energy, a similar division can be made. The free chemical energy of the food is partly transformed into other forms of chemical energy, while a fraction is used for all kinds of internal work and finally dissipates as heat. Metabolic rate is usually defined as the heat production of an animal. So despite the term, metabolic rate is not sufficient to describe metabolism.

A complete description should also include food intake rate and defecation rate (or at least assimilation rate, which is here defined as the difference between these two rates), somatic growth rate, reproductive rate and the rate at which metabolic waste is produced. The description of these rates can be in terms of power measured as Watt, or in terms of material flows measured for example by C-moles per unit of time.

Ecology is the study of organisms in relation to their environment, and because organisms, as we have seen above, can be considered as processors of material, it is obvious that metabolism and how it is affected by the environment should play a pivotal role in ecology. Influential scholars as Lotka, Elton, Von Bertalanffy, Hutchinson, and Lindeman already long ago emphasized the transfer of material and energy from one component of the ecosystem to another. Despite the important work done by these early scientists, by the end of the previous century the focus in ecology had shifted away from energy and material flows and the subject of metabolism was receiving little attention. But two decades ago, papers by James Brown and colleagues put metabolism again strongly on the research agenda of ecology. Brown was, as many others before him, puzzled by Kleiber's observation that metabolic rate of adult animals of different species is proportional to their mass raised to the 3/4 power. Many scientists tried to find laws that could explain this regularity, but none had convinced the scientific community as a whole. The zoologist Brown and plant biologist Enquist joined forces with the physicist West, and they worked out the idea that whole-organism metabolic rate is limited by the internal delivery of resources to cells. Resources have to be distributed through branching networks, and the fractal-like design of these networks cause the supply rate and therefore the metabolic rate, to scale as a 3/4 power of body volume (West *et al.*, 1997). In later publications they worked out this idea and included other aspects of metabolism, e.g. somatic growth (West *et al.*, 2001; Hou *et al.*, 2008), reproduction (West *et al.*, 2001) and feeding (Hou *et al.*, 2011). The same research group was also interested in the effect of temperature on metabolic rate and claimed that it could be understood from basic cellular processes. Combining the two ideas led to the famous, but much questioned core equation of what has become known as the metabolic theory of ecology (MTE). The equation relates the metabolic rate B measured in Watt, to body mass m measured in kg and temperature T measured in K, and is given by

$$B = B_0 m^{3/4} e^{-E_a/(kT)} \quad (1)$$

where the parameter B_0 in $\text{W kg}^{-3/4}$ is a normalization parameter, E_a in eV is supposed to be the "average activation energy of metabolism" which should be about 0.6 eV, and k is the Boltzmann constant which equals $8.617 \times 10^{-5} \text{ eV K}^{-1}$. Of course, very similar equations were already in use for a long time, but the claim for novelty was that a mechanistic explanation was offered.

More than a decade earlier the Dutch theoretical biologist Kooijman laid the basis of what has become known as the dynamic energy budget (DEB) theory in two papers, which were hardly recognized in those days (Kooijman, 1986a,b). Kooijman, like Brown, was interested in general patterns in biology, not only Kleiber's law but also the observation that the growth of most heterotrophic organisms, in size differing between a yeast cell and an elephant, follows Von Bertalanffy's equation quite accurately. Many more patterns had his interest, and a complete list will follow below. But Kooijman proceeded in a different way than Brown and colleagues. He realized that metabolic rate is related to many fundamental life processes, such as somatic maintenance, growth and reproduction, which each have their overhead costs, and feeding. In his view a description of these fundamental processes should form the core of a metabolic theory, and metabolic rate will follow automatically from the overall energy balance. He further made the assumption that most of these fundamental processes are simply dependent on either surface area or body volume. He also realized that many of the patterns that he was interested in could not be explained by using a one-compartment model animal. At least two compartments are needed, and they were labeled structural body and reserve, where the main

difference is that structure has maintenance costs, but reserve has not. DEB theory claims that it provides the simplest model that is able to explain all the patterns Kooijman had in mind. Simpler alternatives just do not exist. These early 1986 papers already explained a whole series of empirical scaling relationships, and many more predictions would follow during the development of the theory which led to several monographs (Kooijman, 2010).

Below I discuss and compare the two theories, DEB and MTE, in more detail. A theory in science should be based on assumptions that are in accordance with broadly accepted and more fundamental theories. If measurable quantities are involved in these assumptions, they should be in line with empirical observations. So I will list and discuss where needed the assumptions of the two theories. A theory should further be internally consistent. This will also be discussed. Predictions should be in line with empirical data and finally the theory should not be needlessly complicated. I will comment on the apparent complexity of the two theories. For reasons of convenience I restrict the overview to animals, although both MTE and DEB have something to say about other forms of life.

DEB, Development and Criticisms

The simplest DEB model, which is the standard DEB model, aims to predict a series of empirical patterns observed in living animals. A list of these patterns, which are all related to feeding, assimilation, respiration, growth, development, reproduction and changes in the chemical composition of animals, is provided in Table 1. Subsequently DEB theory provides a set of model assumptions that completely define the mathematical formulation of the standard DEB model. The underlying idea is that this set is as limited and as simple as possible, but the model that follows from it is capable of reproducing the observed patterns. A summary of the model assumptions is provided in Table 2. A graphical representation of the energy fluxes in the standard DEB model is provided in Fig. 1. The model was initially developed by Kooijman (1986a,b), but has been modified in details since then, which basically means that the list of assumptions has been refined, see for example Sousa *et al.* (2008). These assumptions automatically lead to the mathematical description of the model, in terms of a set of coupled differential equations, one for each of the three state variables. State variables and environmental factors are explained in Table 3, and the primary parameters of the model in Table 4. For completeness the differential equation will be given. For reserve density it is

$$\frac{d[E]}{dt} = V^{-1/3}(\{\dot{p}_{Am}\}f - \dot{v}[E]) \quad (2)$$

where f refers to the dimensionless scaled functional response, which is a function of food density X , and can vary between 0 and 1. The scaled functional response relation is basically Holling type II, and is given by $f = X/(X_K + X)$, where X_K is the half-saturation coefficient. This coefficient is directly related to various primary parameters of the DEB model (see Table 4) and to μ_X , which is the chemical potential of the food. It is given by $X_K = \{\dot{p}_{Am}\}/(\mu_X \kappa_X \{\dot{F}_m\})$. The differential equation for structural volume is

$$\frac{dV}{dt} = \frac{(\kappa \dot{v}[E] - \{\dot{p}_T\}) V^{2/3} - [\dot{p}_M]V}{\kappa[E] + [E_G]} \quad (3)$$

which reduces to the well-known Bertalanffy equation when the reserve density is in equilibrium. This happens at constant food density. Finally, the equation for maturity is

$$\frac{dE_H}{dt} = (1 - \kappa)\dot{p}_C - \dot{p}_H E_H \quad (4)$$

for $E_H < E_H^p$. Else, that is when the animals have become mature and $E_H = E_H^p$, maturity does not change anymore and $dE_H/dt = 0$.

Table 1 Empirical patterns on feeding, respiration, growth and reproduction that DEB theory aims to explain

Process	Pattern
Feeding	During starvation, organisms are able to survive for some time, to reproduce and to grow At abundant food feeding rate is at some maximum
Growth	Growth of animals at abundant food is well described by the von Bertalanffy growth curve Many animals do not stop growing after reproduction has started, i.e. they exhibit indeterminate growth Fetuses increase in weight proportional to cubed time The inverse of the von Bertalanffy growth rate of the same species at different food availabilities corrected for a common body temperature decreases linearly with ultimate length The logarithm of the von Bertalanffy growth rate of different species corrected for a common body temperature decreases almost linearly with the logarithm of the species maximum size
Respiration	Freshly laid eggs do not use oxygen in significant amounts The use of oxygen increases with decreasing mass in embryos, but increases with mass in juveniles and adults The use of oxygen scales with body mass raised to a power close to 0.75
Stoichiometry	Well-fed animals have a different body chemical composition than poorly-fed organisms Animals growing with constant food density converge to a constant chemical composition
Reproduction	Reproduction increases with size intra-specifically, but decreases with size inter-specifically

Source: Sousa, T., Domingos, T. and Kooijman, S. A. L. M. (2008). From empirical patterns to theory: A formal metabolic theory of life. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**(1502), 2453–2464.

Table 2 The basic assumptions of the standard DEB model

1. An organism is characterized by a structural body, reserves, and maturity. The chemical composition of both structural body and reserves is constant, which is called the assumption of strong homeostasis. Maturity indicates the level of development and represents information, but has no energy or mass capacity
2. Each organism starts its life as an embryo (which does not feed and does not reproduce). When the embryo has reached a certain level of maturity, it changes into a juvenile (which feeds, but does not reproduce). Similarly, a juvenile changes into an adult (which feeds and reproduces) when it has reached the maximum maturity value
3. Ingestion depends upon food density by Holling's disc equation (but recall that embryos do not feed). Both the searching rate and the maximum ingestion rate, the latter similar to the inverse of the handling time, are proportional to the surface area of the organism
4. A fixed fraction of the ingested food is assimilated and enters the reserves
5. Reserve density, which is the amount of reserves per amount of structural body, reaches an equilibrium under constant food conditions. This assumption is called the weak homeostasis assumption. The use of reserves only depends upon the amount of reserves itself and on body volume, which in combination with the weak homeostasis assumption implies that the mobilization of the reserves occurs at a rate proportional to the reserve density
6. A fixed fraction κ of the mobilized reserves goes to somatic maintenance and growth of the structural body, with a priority for maintenance. The rest goes to maturity maintenance and either to maturity (for embryos and juveniles) or to reproduction (for adults)
7. Somatic maintenance rate is basically proportional to structural volume, but in specific cases part of the maintenance costs is proportional to surface area of the organism (e.g. heating rate in endotherms). Maturity maintenance costs are proportional to maturity
8. Energetic costs of growth are proportional to body volume and energetic costs per egg are such that the newborn juvenile has the same energy density as its mother

Source: Kooijman, S. A. L. M. (2010). *Dynamic energy budget theory for metabolic organisation*, 3rd edn. Cambridge: Cambridge University Press.

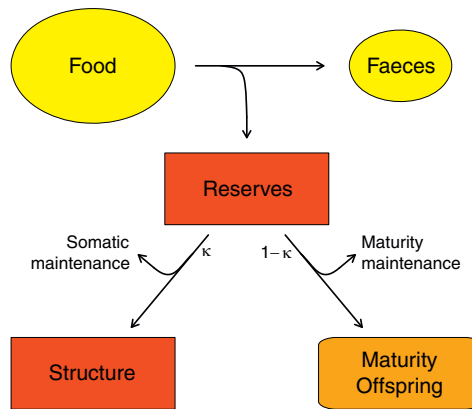

Fig. 1 Conceptual scheme of the main energy fluxes in the standard DEB model.

Table 3 State variables of the standard DEB model and environmental variables

Symbol	Dimension	Interpretation
V	L^3	Structural body volume
$[E]$	eL^{-3}	Reserve density
E_H	e	Maturity
T	T	Temperature
X	$\#l^{-2}$ or $\#l^{-3}$	Food density in the environment

L stands for the dimension length of the structural body, e for energy, $\#$ for mass measured in terms of C-moles, and l for the dimension length of the environment.

For adults the energy flow is channeled to reproduction and the rate of cumulative reproduction is given by

$$\frac{dR}{dt} = \frac{\kappa_R}{E_0} \left((1 - \kappa) \dot{p}_C - \dot{k}_I E_H^p \right) \quad (5)$$

where κ_R is the reproduction efficiency and E_0 the energy content of an egg. The term \dot{p}_C is the rate at which the reserves are mobilized. This rate is given by

$$\dot{p}_C = \frac{[E]}{\kappa[E] + [E_G]} \left((v[E_G] + \{\dot{p}_T\}) V^{2/3} + [\dot{p}_M] V \right) \quad (6)$$

Table 4 Primary parameters of the standard DEB model

Symbol	Dimension	Interpretation	Process
$\{\dot{p}_{Am}\}$	$eL^{-2}t^{-1}$	Surface-area-specific maximum assimilation rate	Assimilation
$\{\dot{F}_m\}$	$l^*L^{-2}t^{-1}$	Surface-area-specific searching rate	Feeding
κ_X	–	Digestion efficiency	Digestion
\dot{V}	Lt^{-1}	Energy conductance	Mobilization
κ	–	Fraction of mobilization rate spent on maintenance plus growth	Allocation
$[\dot{p}_M]$	$eL^{-3}t^{-1}$	Volume-specific maintenance rate	Turnover/activity
$\{\dot{p}_T\}$	$eL^{-2}t^{-1}$	Surface-area-specific maintenance rate	Heating/osmosis
$[E_G]$	eL^{-3}	Volume-specific costs of growth	Growth
k_J	–	Specific maturity maintenance	Regulation/defense
κ_R	–	Reproduction efficiency	Egg formation
E_H^b	e	Maturity at birth	Life history
E_H^p	e	Maturity at puberty	Life history

Source: The "wild card" * stands for two when food density is expressed per area or three when expressed per volume, t stands for time. See further [Table 3](#).

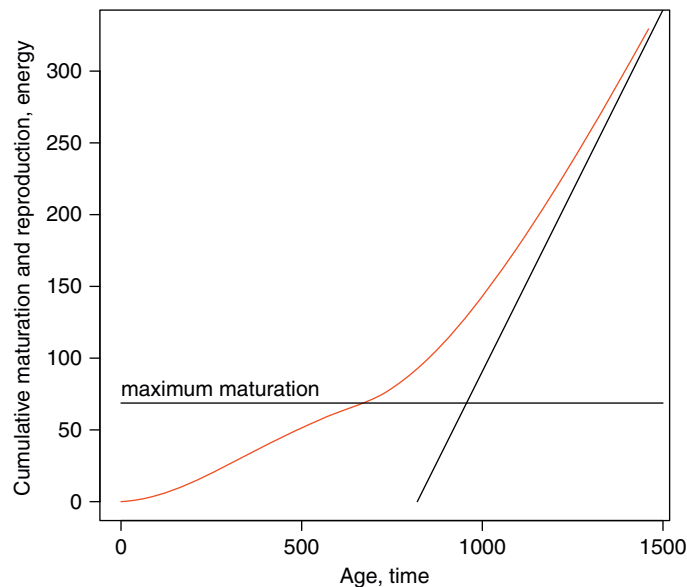


Fig. 2 Cumulative maturation and reproduction as a function of age. Scaled functional response f is 1. When the total investment in maturation has reached its maximum, reproduction starts and the cumulative reproduction steadily approaches a diagonal asymptote.

Combining Eqs. 6 and 5 will give an explicit expression for the reproduction rate as a function of size and reserves ([Fig. 2](#)).

DEB theory has been mainly criticized for its perceived complexity ([Brown et al., 2004](#); [Zuo et al., 2009](#); [Marquet et al., 2014](#)). [Brown et al. \(2004\)](#) state that DEB models are complex, using many variables and functions. They argue that how much complexity in a model is desirable is partly a matter of the purpose for which the model is used, and that there is room for a complementary and even more general approach than DEB, something that MTE offers. [Zuo et al. \(2009\)](#) consider DEB as a very detailed model and they (erroneously) state that the model requires the measurement of 17 variables and 18 parameters. [Marquet et al. \(2014\)](#) even call DEB theory an inefficient theory as it contains too many species specific parameters, which hinders the generation of general predictions.

MTE, Development and Criticisms

The development of the MTE started with a rather technical paper by [West et al. \(1997\)](#), using principles of fluid dynamics to show that optimal transport networks yield a supply rate to the cells that scales with the $3/4$ power of body mass. The network design, which could for example represent the cardiovascular network of a mammal, was based on certain specific assumptions, such as that the capillaries have to reach all cells. Optimal was defined as having minimal energy loss through dissipation and wave reflections. The approach was applauded by many, but also heavily criticized, both by what I for the sake of simplicity will call

biologists and physicists. The biologists questioned the relevance of the assumed network for animal life. A first problem is that closed branching networks are rarely found in animals. Apart for vertebrates and a few invertebrate groups, such as cephalopods, they do not exist in the animal kingdom. A second problem is that cardiovascular networks are probably designed for peak exercise during short periods, and it seems rather unlikely that the much lower resting metabolic rate that Kleiber was talking about, or even the average or field metabolic rate, has the same proportion to the maximum rate for all animal species. The biologists further thought that the predictions on the type of network that resulted from the optimization procedure were far away from reality. The predicted area preservation of the network implies that the flow rate in the capillaries is as large as that in the aorta. If that would be the case for you and me, we would almost immediately die if we would cut ourselves in one of our fingers. But most criticisms pointed to the fact that there is actually no need at all for predicting a 3/4 relationship, because such universal relation simply does not exist in nature. The physicists merely disagreed on the reliability of some more detailed assumptions on the network itself, e.g. it was originally assumed that the network is infinitely large, and they questioned how critical such assumption is for the outcome. They came to the conclusion that more realistic assumptions on the size of the network would have led to a non-allometric relationship that can be approximated by an allometric one with a scaling coefficient of 0.81. Others had major problems with the optimization procedure that had been used. So [Price et al. \(2012\)](#) had to point out in a recent review that “the community at large has not reached a consensus as to whether the theory is or is not logically consistent.” This community at large is in fact rather small, as most biologists are not well equipped to follow the detailed arguments of the physicists in this part of the debate.

The development of MTE went on with the paper by [West et al. \(2001\)](#), later followed by [Hou et al. \(2008\)](#). West and co-workers presented the so-called ontogenetic growth model (OGM). The OGM assumed that organism growth rate is proportional to the difference between the supply rate at which resources are delivered to the cells, which was set equivalent to the average resting metabolic rate B , and the maintenance rate B_{maint} , defined as the power needed to sustain the organism in all its activities. The fractal-like design of the network through which the resources are supplied to the cells causes the supply rate to scale as the 3/4 power of body mass, as earlier proposed by [West et al. \(1997\)](#). The maintenance rate was thought to be proportional to body mass $B_{maint} = B_m m$. Hence, the model can be expressed as

$$\frac{dm}{dt} = \frac{B_0 m^{3/4} - B_m m}{E_m} \quad (7)$$

where m is total body mass, t is time, and E_m is the energy required to create a unit of mass of new tissue. Though the OGM was highly influential and widely cited, it was also severely criticized ([Makarieva et al., 2004](#); [Van der Meer, 2006](#)). Criticisms pointed among other things to lack of consistency and incompleteness. The criticism that the OGM lacked consistency referred to the ambiguous definition of metabolic rate. The term was both used for the supply rate of energy and for the maintenance rate. At the same time the difference between these two rates was supposed to be used for the build-up of new body tissue. The proportionality parameter E_m which converts energy into biomass, and which thus converts the difference between the supply and maintenance rate into the rate of biosynthesis, was derived from the empirical combustion energy per unit mass of mammalian tissue, for which a value of 7 kJ/g was used. The use of such parameter is in accordance to the idea that the difference between supply and maintenance is entirely stored into new tissue, but the fact that thus a part of the supply rate is not dissipated causes a problem, as you cannot, almost literally, have your cake and eat it. The problem could only be resolved if not the supply rate, but the maintenance rate would be equated to the resting metabolic rate ([Van der Meer, 2006](#)). Holding on to the notion that the resting metabolic rate equals the supply rate would violate the energy conservation law ([Makarieva et al., 2004](#)). The logic consequence of equating resting metabolic rate to maintenance rate is that the intraspecific scaling power of resting metabolic rate equals 1 ([Van der Meer, 2006](#)). Ironically, this disputes the strong claim that the MTE explains Kleiber's law of a scaling power of 3/4, at least as far as intraspecific comparisons are concerned. The supposed incompleteness of the OGM referred to the fact that the metabolic rate of active animals can be much higher than the resting metabolic rate and to the ignorance of all overhead costs of growth ([Makarieva et al., 2004](#); [Van der Meer, 2006](#)).

A new model by [Hou et al. \(2008\)](#), called the extended ontogenetic growth model (EOGM) and mainly meant to be applied to birds and mammals, aimed to repair these flaws. The EOGM distinguishes between total metabolic rate B_{tot} and resting metabolic rate B_{rest} . The difference between these rates is used for activity. Total metabolic rate is assumed to be proportional to resting metabolic rate, $B_{tot} = f B_{rest}$. Following [West et al. \(1997\)](#) total metabolic rate and thus also resting metabolic rate scale as the 3/4 power of body mass. The new model also takes the overhead costs of growth into account and distinguishes between the energy content stored in newly synthesized biomass and the energy expended in synthesizing this biomass from the constituent materials. The difference between resting metabolic rate and maintenance rate is now entirely used for the overhead costs of growth. This implies that the resting metabolic rate is completely dissipated to heat. The new growth model still looks like the old OGM, but the parameter E_m is now interpreted as the overhead costs of growth. So the problems of violating the energy conservation law or contrasting Kleiber's law were solved. One new problem arose and that is, how are the building materials that need to be stored in newly synthesized biomass transported to the cells? Hou et al. added the rate S at which the energy content of new biomass accumulates, on top of the total metabolic rate B_{tot} in order to arrive at the assimilation rate of food $A = B_{tot} + S$. They further supposed a fixed ratio between the supply of building materials and the overhead costs of growth (both in terms of power): $S = \gamma(B_{rest} - B_{maint})$. This implies that the assimilation rate equals $A = (f + \gamma)B_0 m^{3/4} - \gamma B_m m$. But Hou et al. did not tell how these assimilated products are delivered to the cells and what kind of network is required to do so. The core of MTE is that within organisms the supply rate to the cells is constrained by some specific fractal-like design of branching networks. Consequently, the supply rate scales as the 3/4 power of body mass. Now two options with respect to the design of the network are possible. The

Table 5 Empirical patterns on feeding, respiration, growth and reproduction that MTE theory aims to explain

Process	Pattern
Growth	Growth of animals is well described by a von Bertalanffy type growth curve
Respiration	The use of oxygen scales with body mass raised to a power close to 0.75

Source: West, G. B., Brown, J. H. and Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126; West, G. B., Brown, J. H. and Enquist, B. J. (2001). A general model for ontogenetic growth. *Nature* **413**, 628–631; Hou, C.; Zuo, W.; Moses, M. E., Woodruff, W. H., Brown, J. H. and West, G. B. (2008). Energy uptake and allocation during ontogeny. *Science* **322**(5902), 736–739.

Table 6 The basic assumptions of the metabolic theory of ecology, and more specifically of the extended ontogenetic growth model (EOGM)

1. An organism is characterized by its body mass
2. Nine detailed assumptions on the design of the distribution network (not spelled out here, but see assumptions A1–A9 in [Price et al. \(2012\)](#)) result in the prediction that the delivery of oxygen to the cells is proportional to body mass raised to the power 3/4
3. The oxygen delivered to the cells is used for maintenance, overhead costs of growth, and locomotion and other activities
4. Oxygen delivery needed for maintenance is proportional to body mass
5. Oxygen delivery needed for locomotion and other activities is proportional to the oxygen needed for maintenance and overhead costs of growth
6. The material needed as building blocks for new body tissue is proportional to overhead costs of growth. The delivery of this material to the cells is not restricted by the capacity of the distribution network

Source: Interpreted from [West et al. \(1997\)](#) and [Hou et al. \(2008\)](#). See text for further explanation.

network is either designed such that its capacity is just sufficient to transport the matter that is dissipated to heat. This means that the supply rate through the network equals the total metabolic rate $fB_0m^{3/4}$. This option thus implies that the EOGM requires additional and unknown ways of transport to deliver the building materials for biosynthesis to the cells. The other option is that the network is able to transport the building materials as well. It can easily be shown that the network should be designed such that the capacity equals $(f + \gamma)B_0m^{3/4}$. Smaller 3/4 scaling networks cannot transport the assimilated matter when the animals are small. In this case the supply rate is no longer constrained by the network when the animal gets larger. For larger animals the network has a huge overcapacity and it remains unclear by what mechanism the total metabolic rate is constrained. In a personal communication the authors stated that the first option is basically the right one, but that “it is primarily the uptake and delivery of oxygen that has selected for the fractal-like design of the vascular system, the matching design of the respiratory system and the 3/4 power scaling of metabolic rate.” The processing of food is not constrained by the network as food “can be stored in the body and utilized for metabolism on widely varying time scales.” This is an important and essential addition to the original contribution, as it for example suggests that reproduction, which requires very little overhead costs, will hardly be limited by the supply network. Apparently, the transport of food is not hampering the transport of oxygen.

To simplify a comparison with the DEB approach discussed earlier, I also list the type of patterns MTE aims to explain on feeding, respiration, growth and reproduction ([Table 5](#)). [West et al. \(2001\)](#) made a small remark on reproduction, but this was further ignored in the EOGM. Feeding is more recently discussed by [Hou et al. \(2011\)](#), but this paper contains some serious problems, about which a discussion is beyond the scope of the present overview. Hence, a single pattern for respiration and one for growth remain. A list of the underlying assumptions of MTE ([Table 6](#)) also illustrates the more limited scope compared to that of DEB ([Table 2](#)).

Predicting Scaling Relationships

For aerobic animals metabolic rate, which is the rate at which chemical energy is transformed into heat, is usually indirectly measured by the rate of oxygen consumption. DEB theory is clear about the intraspecific scaling relationship of metabolic rate. Maintenance costs are proportional to structural body volume, but there are other processes contributing to the oxygen consumption. For example, only part of the energy that is allocated to growth is fixed in new body tissue, the rest is dissipated as overhead costs. These overhead costs are proportional to the difference between a surface area-related term and a volume-related term. For endotherms, the heating costs, which scale with surface area, also contribute to the total oxygen use. Taking all these other processes into account, DEB theory predicts that the total metabolic rate will scale (if individuals of different size within the same species are compared) with body volume with a power somewhere between 2/3 and 1. The EOGM assumes that the supply rate of oxygen to the cells sets the rate at which chemical energy is transformed into heat. As the supply rate scales with 3/4 power of body mass, so does the metabolic rate. But, only when animals of different size of the same species are compared.

But what about Kleiber's law of the 3/4 power scaling of metabolic rate, which was not based on an intraspecific but on an interspecific comparison? Assuming that such a comparison concerns full-grown adult organisms, implies that growth has ceased. According to MTE all supplied energy is then used for maintenance. This can be seen from setting the growth Eq. 7 equal to zero. It follows that the ultimate size M_∞ equals $(B_0/B_m)^4$. So it seems logical either to assume that the supply parameter B_0 scales with the double square root of ultimate body mass, that is $B_0 = m_\infty^{1/4}$, or to assume that the maintenance parameter scales inversely with

m_∞ , i.e. $B_m = m_\infty^{-1/4}$. MTE makes the second assumption, that is cellular maintenance costs scale interspecifically with a power of $-1/4$. The maintenance costs of a lizard are thus much higher than those of a baby crocodile of the same size. It is this assumption, which comes without any mechanistic biological reasoning, that in fact reveals Kleiber's law. So despite several claims, MTE's main idea of transport of resources to the cells through a fractal-like hierarchy of branching vessels does not suffice to predict Kleiber's law.

DEB theory predicts (for convenience restricted here to well-fed ectotherms) a maximum volume that equals $(\kappa\{\dot{p}_{Am}\}/[\dot{p}_M])^3$. Maximum volumetric length (the cubic root of the structural body volume) is thus proportional to the ratio between the maximum area-specific assimilation parameter $\{\dot{p}_{Am}\}$ and the volume specific maintenance parameter $[\dot{p}_M]$. Contrary to MTE, DEB assumes that animals that reach a large ultimate size do not differ in their volume specific maintenance rate from animals that remain small. Animals grow larger because they have higher assimilation capacities. This implies that metabolic rate at ultimate size is proportional to ultimate structural body volume, which seems to contradict Kleiber's law. However, DEB also predicts that species with a large ultimate structural volume have a higher maximum energy density than species that remain small. And because the body mass that is measured in practice is the sum of the structural body mass and the reserve mass, metabolic rate is not proportional to measured body mass. In fact, DEB predicts a non-allometric relationship between metabolic rate and measured body mass, which can be approximated by an allometric relationship with a scaling power very close to $3/4$. For endotherms, heating costs, which are related to surface area, have to be added when animals are outside the thermoneutral zone and the approximate scaling power will then be somewhat lower.

DEB distinguishes between parameters that depend upon the local biochemical environment and those that depend upon physical design. The latter parameters are related to the ultimate size of the organism, the first group of parameters do not depend upon size. The maximum area-specific assimilation parameter is one of the few parameters that belong to the second group. Others are the E_H^b and E_H^p , the maturity at birth and at puberty. A variety of body size scaling relationships follow directly from this parameter classification. One example is the Bertalanffy growth rate, whose relation with ultimate body size can be approximated by a scaling relation with a co-efficient of -1 . One of the first DEB papers already came up with predicted scaling relations for about 20 physiological variables, as diverse as maximum starvation time or minimum incubation time (Kooijman, 1986b).

Complexity

The standard DEB model contains three state variables (Table 3) and 12 primary parameters (Table 4). The extended ontogenetic growth model (EOGM) only considers one state variable and has four parameters. So at first sight DEB seems more complex than MTE. One should, however, realize that DEB is able to make predictions about many more processes than MTE, e.g. embryonic growth in eggs and wombs, hatching, maturation, reproduction, food depression, interspecific scaling etc. MTE has nothing to say about these issues. Of course, this difference comes at a cost. But DEB theory allows a reduction of the standard DEB model under certain restrictions. If food conditions are constant, reserve density is also constant after hatching, and growth can simply be described by a Von Bertalanffy growth equation with only three parameters and one state variable. Note that although the equation is the same, it is based on a different biological rationale than Von Bertalanffy had in mind. He did not apply the energy conservation law to the overall organism, but defined growth as the difference between anabolism (synthesis) and catabolism (breakdown).

Beyond the Organismic Level: Populations and Ecosystems

The standard DEB model provides a detailed description of the flows of energy in and out of the individual organism, including reproduction. It is therefore usable as a building block in either physiologically-structured populations models or agent-based models. Several applications are available, e.g. Martin *et al.* (2013). Ecosystem models have also been (partly) based on DEB theory (Saraiva *et al.*, 2017). MTE is less suited for these goals, as it neither incorporates feeding (but see Hou *et al.*, 2011) nor reproduction. Predictions of MTE at for example the population level are restricted to applying the so-called energy-equivalence rule, which says that every population of animals receives the same amount of energy as food. Linking MTE and this rule predict that population abundance scales with body mass with a scaling coefficient of minus $-1/4$. One should however notice that this prediction entirely relies on the $3/4$ -scaling relationship of metabolic rate, which is not just a result of MTE but also of DEB. In fact, any other explanation of Kleiber's law could have been used. Marquet *et al.* (2014) define an efficient theory as one that generates many predictions. It is a bit ironic that MTE *sensu stricto*, that is the idea of a fractal-like distribution network, has not generated any further hypothesis above the level of the individual. All predictions could have been made as a consequence of Kleiber's law. And several of the few detailed predictions at the level of the individual, such as that of an area-preserving network, are clearly flawed. One therefore could argue that Marquet *et al.* should have categorized the MTE theory as inefficient.

Temperature Effects

Temperature is, apart from food availability, another important environmental variable that affects metabolism. Both DEB and MTE use the Van't Hoff-Arrhenius equation to describe the dependency of physiological rates on temperature. This equation has

its origin in statistical thermodynamics, where the behavior of a system containing a very large number of a single type of molecules is predicted from statistical considerations of the behavior of individual molecules. In its basic form the Van't Hoff–Arrhenius equation looks like

$$\dot{k}(T) = \dot{k}_{\infty} e^{E_a/(kT)} \quad (8)$$

where $\dot{k}(T)$ is a reaction rate that depends upon the absolute temperature T (in Kelvin), \dot{k}_{∞} is a (theoretical) maximum reaction rate, which is the reaction rate when all molecules would react. The term $\exp(E_a/(kT))$ is the Boltzmann factor, which gives the fraction of the molecules that obtain the critical activation energy E_a (in joules per molecule) to react. This fraction increases with increasing temperature. The constant k (not to be confused with the reaction rate \dot{k}) is the Boltzmann constant and equals 1.38×10^{-23} J/K. The Van't Hoff–Arrhenius equation can also be re-written in the form

$$\dot{k}(T) = \dot{k}_1 \exp \left(\frac{T_A}{T_1} - \frac{T_A}{T} \right) \quad (9)$$

where \dot{k}_1 is the reaction rate at a reference temperature T_1 , and T_A the so-called Arrhenius temperature (which equals E_a/k). The Van't Hoff–Arrhenius equation is approximate for bi-molecular reactions in the gas phase, and Kooijman (2010) emphasizes the enormous step from a single reaction between two types of particles in the gas phase to physiological rates where many compounds are involved and gas kinetics do not apply. He therefore regards the application of the Van't Hoff–Arrhenius relation to physiological rates as an approximation only, for which the parameters have to be determined empirically. For this reason, Kooijman prefers the use of an Arrhenius temperature instead of the use of an activation energy, which would give a false impression of mechanistic understanding. Initially, MTE expressed the more candid view that the Van't Hoff–Arrhenius equation must be applied because it links whole-organism metabolism directly to the kinetics of the underlying biochemical reactions (Gillooly *et al.*, 2001). They furthermore stated that for all aerobic species a single parameter value for E_a can be used, because such species have the same biochemistry. This point of view has been criticized by, among many others, e.g. Glazier (2015). Similar to Kooijman, they stress that the Van't Hoff–Arrhenius equation is just a statistical generalization, and they too conclude that at present we still lack a clear understanding of the relationship between temperature and metabolism at the organismal scale. Glazier also pointed to the huge variation in estimates of the Arrhenius parameter. Indeed the claim of mechanistic understanding has never been substantiated.

Within MTE E_a and k are expressed in eV instead of joules and for E_a usually a value of 0.6 or 0.65 eV is used. Dividing by the Boltzmann coefficient gives an Arrhenius temperature of about 7000 or 7500 K, which is not far from the value of 8000 K used as the default value in DEB theory (Kooijman, 2010). But, as mentioned earlier, in DEB theory the Arrhenius parameter is considered as an estimable parameter, and estimates vary in practice mostly between 6000 and 10,000 K, which is, expressed in eV, equivalent to the range 0.52–0.86. Glazier (2015) mentions even an observed range of 0.2–1.2 eV for various metabolic processes.

Summary

Metabolic ecology describes the uptake of energy and matter by individual organisms and the subsequent allocation to various life processes such as body maintenance, somatic growth and reproduction. The ecological role that organisms play is strongly related to their metabolism and understanding the determinants of metabolism is essential to understanding this ecological role. Two alternative and influential theories on metabolic ecology, the dynamic energy budget theory (DEB) and the metabolic theory of ecology (MTE) are described in detail, with a focus on the underlying assumptions and predictive power. Core of the DEB theory concerns the assimilation of food, limited by the surface area of the organism, the transfer into reserves and the allocation of mobilized reserves, also limited by the reserve-structural body interface, to the various life processes. Metabolic rate, i.e. heat production, follows consequentially from making the energy balance. MTE, on the other hand, considers the supply rate of oxygen, limited by a branching fractal network, as setting the pace of life. Fuel will automatically be available. The theories are further compared in terms of complexity and internal consistency. At first sight, DEB seems to be the more complex theory, but if the scope and predictive power are also considered, it appears that DEB cannot be considered as more complex than MTE. The limited scope of MTE, exemplified for example by the ignorance of reproduction and the possibility of variable food intake rate, the lack of internal consistency and the low predictive power, makes it the least efficient theory of the two.

Further Reading

A contrasting view is expressed by Glazier (2015), who believes that in both DEB theory and MTE the importance of informational control, as mediated by various genetic, cellular, and neuro-endocrine regulatory systems, is underestimated (but see Kooijman, 2010, pp. 15–16).

Recently, several papers suggested ways to test the DEB and MTE theories against each other (Kearney and White, 2012; Maino *et al.*, 2014). Kearney and White (2012) came up with a list of 10 possible tests for which DEB predictions and MTE predictions differed. One example is a test on limb regeneration, in for example lizards. DEB predicts a regeneration rate up to threefold faster than ontogenetic growth rate, whereas these rates should be equal according to MTE. Maino *et al.* (2014) point to the relationship between inter- and intraspecific scaling of biological rates (see also discussion above) that should point to tests that could lead to a further refinement of the current metabolic theories.

See also: General Ecology: Ecophysiology

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