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An evaluation of two controversial metabolic theories of ecology.

Introduction

There are currently two main metabolic theories receiving attention and contentious debate. One, of course, is the Dynamic Energy Budget theory (hereby referred to as DEB); the other is West, Brown and Enquist's 'Metabolic Theory of Ecology' (hereby referred to as WBE). The contention lies in the fact that while each theory claims to provide a comprehensive explanation, they are based upon very different fundamental principles. Thus, it stands to reason that if one theory is 'correct', the other must be incomplete or inaccurate. The scientific community remains largely divided over the suitability of one theory over the other, and more conclusive research is needed to provide a situation in which the predictions of each theory diverge, and thus both can be directly compared.

In this essay, I will compare and contrast the underlying principles, parameters, equations, and assumptions of the growth models of the DEB and WBE theories, as well as suggest a method by which they can be directly experimentally compared.

Ontogenetic growth provides an ideal place to begin in testing the DEB and WBE theories. In an individual animal, energy and matter are allocated to maintenance, growth and reproduction. Knowledge of this allocation is key to understanding overall metabolism. Maintenance rate and energy supply rate are functions of body size. The energy available for growth is defined as the difference between the maintenance and energy supply rates, and thus models investigating growth are an integral element of metabolic theory, particularly in regard to fundamental energy budget parameters.

In many species we see determinant growth – that is, a period of growth leading up to maturity. This development of an organism from juvenile to adult defines 'ontogenetic growth'. A substantial portion of the energy obtained during this period is allocated to building body mass. The animal then stops growing, and its energy is allocated predominantly to body maintenance and reproduction (Kooijman, 2001). As different energy requirements are needed at different stages of growth and body size, the overall rate of internal processes also changes during ontogenetic growth. As the individual's body size increases, its metabolic rate – relative to its mass - decreases. However, there is much debate regarding the exponent to which metabolic rate scales with size. Academics of the area are generally divided into two groups: those who believe the exponent is mass$^{3/4}$ (supported by the WBE theory), and those who believe it is mass$^{2/3}$ (supported by the DEB theory).

The West, Brown and Enquist theory

Underlying Principles:

In 1997, West, Brown and Enquist produced a now famous paper in which they claimed to explain the ¾ power scaling exponent through biological distribution networks (West et al, 1997). They produced a quantitative model which stated that metabolic rate is limited by the transport of

materials to all parts of an organism through fractally branching, linear networks.
The authors claim that most energy distribution systems incorporate a branching network in which the sizes of the tubes decrease predictably (West et al, 1997). A space-filling fractal (i.e. the same geometry at different scales) structure ensures that all cells are serviced. As animals become larger, the number of cells that need to be serviced increases faster than the number of terminal units of the supply system (e.g. capillaries). Larger organisms take longer to transport materials because the number of terminal units in a network is proportional to body mass$^{3/4}$, and as such so is the rate at which resources are delivered to the cells (Whitfield, 2004).
The theory asserts that scaling laws arise from the interplay between physical and geometric constraints of the supply network, and evolution has increased the efficiency of this network by minimising the energy and time needed to transport materials around the body (Whitfield, 2004).
Under this model, metabolic rate therefore scales with body mass to the ¾ power.

Growth model:

Under both theories, growth ceases when supply rate is equal to maintenance cost.
Under the WBE theory, the assimilation rate of food supplies the total metabolic rate and part of it is stored as tissue biomass. The total metabolic rate is then partitioned between activity costs and resting metabolic rate. The growth model itself only involves resting metabolic rate, with its subcomponents of maintenance metabolic rate and overhead costs of synthesizing new tissue.

In the main paper outlining the WBE growth model, Hou et al argue that all parameters are directly measurable from basic cellular parameters (Hou et al, 2008; West et al, 2001), and therefore this is a first-principles mechanistic model for growth. The assimilated energy available for cellular maintenance and growth is the total energy assimilated by the organism, minus that which is stored in added tissue or used for other costs. Differences in the ultimate size that a species can reach are a result of differences in either size-specific supply rate or size-specific maintenance rate (Van der Meer, 2006).

Assumptions:

In brief, three unifying assumptions are key to the WBE model:
- a fractal-like and space-filling branching pattern is required for the network to supply the entire volume of the organism;
- the final branch of the network is a unit that does not vary in size;
- the energy needed to distribute resources is minimised by the network.

The very few assumptions of the WBE model have been queried, as it may seem infeasible that so few conjectures are adequate for such a complex system as metabolism.

Parameters:

As stated above, the Hou et al growth model (and indeed all WBE models) dictates that all parameters are directly measurable from fundamental cellular parameters. The theory uses only one state variable (body mass), and three parameters, each per unit of mass:

- Power needed to sustain the organism (a)
- Energy supply rate (m)
- Energetic costs of producing new tissue (g)

However, a number of issues have been raised regarding these parameters. For example, the theory doesn't account for any overhead costs, and its mathematical feasibility has been questioned (van der Meer, 2006; Kozlowski & Konarzewski, 2004). Many people believe that only three parameters are not enough to encompass all of metabolism's complex aspects.

Equation:

Throughout development, the mass of each cell is assumed to be equal, as is the maintenance rate per cell. Therefore it follows that the maintenance rate is proportional to the number of cells, and thus proportional to body mass.
Given the above, the WBE growth equation is as follows (simplified in van der Meer, 2006):

$$\frac{dW}{dt} = \frac{aW^{3/4} - mW}{g}$$

As in the parameters stated above: a = supply rate (per unit of mass)$^{3/4}$; m = maintenance rate (per unit of mass); g = energetic costs of growth (per unit of mass in growth).

Models based on the West, Brown and Enquist theory are being successfully applied in various ecological scenarios (Gillooly & Allen, 2007; Brown et al, 2005). However, debate regarding a number of important aspects of the theory has developed. The universality of the empirically observed scaling has been criticized (Glazier, 2005; White et al, 2003), along with the fundamental principles (Kozlowski & Konarzewski, 2003; Darveau et al, 2002; Chaui-Berlink, 2006), the accuracy of the mathematics (Dodds et al, 2001; Kozlowski & Konarzewski, 2004; Sousa et al, 2009), the breadth of which its applications may be useful (Sousa et al, 2009), and the predictive power of the models (Algar et al, 2007; Terblanche et al, 2007).

The Dynamic Energy Budget theory:

Underlying Principles:

Prior to the West, Brown and Enquist models, a general theory of individual metabolism had already been produced (van der Meer, 2006). This theory, first presented by Bas Kooijman in 1986, is known as the Dynamic Energy Budget model. Whereby the West, Brown and Enquist theory is limited by the internal fractal supply networks that deliver resources to the cells, the Dynamic Energy Budget theory assumes that energetic processes (in particular, food assimilation rate and maintenance rate) are dependent on surface area or body volume (Kooijman, 2001). This results in a metabolic rate scaling exponent of body to the power of between 2/3 to 1, depending on the extent that uptake or maintenance dominates.

From an individual point of view, the organism (i.e. its whole body mass) is described in terms of reserve density and structural body size (Kooijman, 2001). The rate of metabolism is dependent upon a number of factors, including growth, structure and reserve of the organism. 'Structure' refers to the permanent biomass of the organism and thus requires energy for upkeep and maintenance, whereas 'reserve' refers to energy products that are used and replenished and hence no maintenance is needed (Glazier, 2008). Maintenance costs are thus proportional to *structural* body volume. However, as an organism grows, the chemical composition between the structure and reserve pools is altered. Hence, during ontogeny, the rate of change of the *reserve* density must also be added to the structure to obtain the overall weight (Sousa et al, 2008).

The Dynamic Energy Budget theory implies that the volume-specific maintenance rate is independent of ultimate body size; but as the assimilation rate is area-specific, it must be proportional to the ultimate volume. Thus, species whose area-specific assimilation rate is higher tend to grow bigger (van der Meer, 2006).

Growth model:

Under the Dynamic Energy Budget model, energy (and resources) is assimilated proportional to the surface area of the organism (for example, of the gastrointestinal tract or cells) (Sousa et al, 2008). Assimilation is defined as the process of an animal taking up its own food and resources, and thus begins at birth (hatching if the embryo is inside an egg). Food is assimilated and derives energy in the form of metabolites. This energy initially enters a reserve pool (Kooijman, 2001), and the reserve density (the amount of reserves of the structural body, per volume unit) follows first-order dynamics (van der Meer, 2006).

Energy utilized from the reserves is given the term *k*, and can be defined as the fraction of mobilized reserve flux (Kooijman, 2010). *k* is broken up and sent to a number of locations. Firstly, a fixed amount (proportional to *k*) is used for maintenance of structure (somatic maintenance) and growth. Growth can be defined as the transformation of reserves into structure (Sousa et al, 2009). If the animal is an endotherm, heating costs are also added onto the distribution of *k*. The remainder of the utilized energy is used for *maturation*, which is the process of building 'complexity' of the organism to attain its full size and structure. Growth will cease when all energy available for the maintenance plus growth portion of *k* is allocated to somatic maintenance (which always has priority over growth). It is generally around this time (though may occur earlier) that the animal hits *puberty*. Puberty can be thought of as a kind of metabolic trigger, whereby the energy originally allocated to maturation is now allocated to reproduction (however part of this energy must still be used for 'maturity maintenance'.

Assumptions:

The DEB theory contains considerably more assumptions than the WBE theory, probably due to the many more parameters it includes. Its basic assumptions are as follows (Kooijman, 2010):
- The amounts of reserve, structure and maturity are the state variables of an individual animal;
- Reserve and structure have constant compositions (termed 'strong homeostasis');
- Maturity represents 'information' regarding the structure of an organism (it does not represent a mass or energy pool);
- Food uptake is initiated (birth) and the reserve allocation to maturity is redirected to reproduction (puberty) if certain thresholds are met ('metabolic switches')
- Food is converted into reserve. This reserve is mobilised at a rate that depends on the state variables (structure and reserve) alone;
- This utilised reserve fuels all other metabolic processes;
- Food is assimilated proportional to body size of the individual animal;
- Food processing time is independent of food density;

- Reserve density does not depend on the amount of structure at constant food density (termed ‘weak homeostasis’);
- Somatic maintenance is proportional to structural volume (but may have additional costs, eg. heating in mammals);
- Maturity maintenance is proportional to the level of maturity;
- The individual animal does not change shape during growth (*isomorpism*). This applies only to the standard DEB growth model, and can be altered if necessary.

The large number of assumptions in the DEB model helps to assure that all bases are covered and a comprehensive and well-fitting model can be constructed and applied with confidence.

Parameters:

Unlike the WBE theory, DEB believes that appropriate parameters for a growth model cannot be restricted to such a small number; nor can they be calculable from basic cellular functions. Rather, DEB theory derives its parameters from fits of growth trajectories. The standard DEB model is characterised by twelve basic parameters, as follows:

- Maximum assimilation rate (surface area specific)
- Searching rate (surface area specific)
- Amount of reserve obtained from food
- Amount of structure obtained from reserve
- Somatic maintenance (surface area specific)
- Somatic maintenance (volume specific)
- Maturity maintenance
- Energy conductance
- Allocation fraction to soma
- Maturation at birth
- Maturation at puberty
- Reproduction efficiency

The large number of parameters used in the DEB model have been criticised, but many scientists also believe that a large amount is necessary to include every aspect and thus provide a robust model that is relatively simplistic without being so bare as to call to question its validity.

Equation:

Though it is based on very different principles, the DEB growth model is mathematically equivalent to the well-known Von Bertalanffy growth curve (van der Meer, 2006; Kooijman, 2010). Von Bertalanffy defined growth as the difference between anabolism and catabolism, but did not apply the energy conservation law to the whole organism (van der Meer, 2006).
A number of derivations relating to the numerous parameters are required in order to construct the standard growth model for DEB. However, we eventually end up with the following equation – similar to Von Bertalanffy, but based on a different biological foundation (from van der Meer, 2006):

$$\frac{dV}{dt} = \frac{kfa - V^{2/3} - mV}{kfR_{max} + g}$$

If the organism is an endotherm, heating costs would also need to be subtracted. In the above equation, a = maximum assimilation rate (per unit of surface area); V = surface area of the organism;

f = scaled functional response (this varied between 0 – 1); R_{max} = maximum reserve density; *k* = proportion of utilized energy that goes to growth + maintenance (+ heating costs for endotherms); *m* = maintenance costs (per unit of volume); *g* = growth.
I will not go into detail over the intricacies of this equation and how it is derived, as that is not the point of this essay. I merely wish to demonstrate the differences in fundamental principles, parameters, and complexity used between the WBE and DEB models. While the DEB model has been criticized for being too complex in the past, there is little doubt that it provides a comprehensive and mathematically sound model, which arguably the WBE model may not.

However, its scaling exponent and some principles of DEB have still been questioned (del Rio, 2008; Chaui-Berlinck, 2007), and while it is arguably not as controversial or questioned as the West, Brown and Enquist theory, it has thus far been unsuccessful in providing a majority-convincing alternative to the competing model.

Testing the two theories

An overwhelming amount of empirical studies have been conducted to test various metabolic theories. Following West, Brown and Enquist's 1997 publication, research testing their theory boomed. Studies using data from mainly birds and mammals (Savage et al, 2006; Duncan et al, 2007; Sieg et al, 2009) became frequent, as well as some involving plants (Coomes, 2006; Muller-Landau, 2006). Many of these studies found support for the body mass$^{3/4}$ exponent (Koehl & Wolcott; Savage et al, 2007); however, comparable amounts posit that body mass$^{2/3}$ is the more suitable exponent (White & Seymour, 2002; Sousa et al, 2008; Kooijman, 2008). Other studies found evidence for neither (de Castro & Gaedke, 2008). Comprehensive reviews that conclude that much more data and different styles of research are needed (van der Meer, 2006; White & Seymour, 2005; Harte, 2004), while other papers suggest that the idea of a general theory is unrealistic and should be rejected (Glazier, 2005; Koehl & Walcott, 2004; Bokma, 2004; O'Hara, 2005; Lockwood, 2008).

At this point in time, there is no consensus as to which theory is the most correct (Aguther & Wheatley, 2004). New studies are emerging continually with results claiming to support or refute any (and occasionally all) (O'Connor et al, 2007; Terblanche et al, 2007) of the theories. The difference between the ⅔ and ¾ scaling exponent results in only a small change in the shape of the predicted growth curves in most situations. Thus it is often difficult to choose which model is the best fit. In most situations, the predictions of the models can be quite similar, and thus it is difficult to tease apart the mechanistic foundations behind them to identify which theory is more accurate (van der Meer,).

In order to do so, further research is required directly comparing the theories (van der Meer, 2006). Surprisingly, very few direct comparisons of the theories within the same experiment have been conducted as of yet. It is difficult to create a situation in which predictions of the different models evidently diverge, but such a study has the potential to shed light on mechanisms underpinning metabolic rate during ontogeny and extrapolate these to higher organisational levels. The Dynamic Energy Budget's ⅔ power scaling law is dependent on the assimilation of nutrients being proportional to surface area to volume ratio (Kooijman, 2008), whilst West, Brown and Enquist's ¾ power scaling law relies on the distribution of nutrients via fractally branching networks (West et al, 1997). Thus, a scenario in which one of these things changes but the other remains constant would provide a circumstance in which the theories' predictions should diverge.

An example of such a scenario could be achieved using an animal that is able to drop (autotomise) and regenerate an appendage. Ontogenetic growth could potentially be simulated by the regrowth of the appendage. For example, many lizard species naturally drop their tails as a form of predator defence. As the tail regenerates it gets larger, and thus body mass increases until it reaches its full size; this is comparable to how ontogenetic growth occurs in juveniles. However, in adults, though the body mass is increasing with tail regrowth, the size of the gut remains the same. Thus, under the DEB theory, which is based upon assimilation of food through the gut surface area to volume ratio, the metabolic rate of the animal (relative to its weight of course) should not change because its gut surface area to volume ratio is not being altered. Conversely, under the WBE theory, which is based on the fractally branching supply network, the metabolic rate should change as the tail grows. This is because the fractally branching network is growing in the tail as well and is thus not constant.

Many scientists believe that a new and improved metabolic theory is required (Robinson, 2004; van der Meer, 2006). Animals with these characteristics may provide a perfect scenario to critically compare the two main metabolic theories of ecology at large today, and are an example of how more thorough comparative experiments can be used to facilitate progress towards a robust metabolic theory of ecology.

I am conducting an experiment involving precisely the above situation in order to test the WBE and DEB theories directly. My model species is the parthenogenetic gecko *Heteronotia Binoei*. By matching animals into genetically identical, weight- and size-matched pairs and removing the tail of one member of each pair, I am able to record the metabolic rate (using flow-through respirometry) and compare the two individuals to each other. Using these clones to contrast against each other will minimize individual variation influencing results. Additionally, I am also measuring the physical tail regrowth at bi-weekly intervals, with the aim of constructing a growth rate curve using my_pet. With a comparable WBE model, I will hopefully gain an insight into the accuracy and application potential of each model, which may have the potential to inform upon a number of important ecological areas.

"Ecology now is like quantum mechanics in the 1930s – we're on the cusp of some major rearrangements and syntheses." – Stephen Hubbell, 2004.

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