A Gentle Introduction to

Dynamic Energy Budget Theory

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27th of March 2001

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1- Introduction: the founder of DEB theory

Have you ever wandered through a forest and wondered about the amazing diversity of life? It is what biologists do for a living. But there is not just one way to look at life. For one thing you could study the way organisms manage their energy. This is what Dynamic Energy Budget (DEB) theory does. This essay tells you all about the usefulness of this theory, and its basic structure. But before we go into this, let us look at the person that drew up the theory: Bas Kooijman, professor of theoretical biology at the Vrije Universiteit Amsterdam. This may help us to develop an insight into the world of energetics. If your interest is limited to the theory alone, please proceed to chapter 2.

The diversity of life is indeed well known to professor Kooijman. His active interest has made him compile an extensive archive of animal photography taken from books and magazines. But his interest is not limited to animals alone. His eyes sparkle as he tells me about his trips into the woods and even rainforests to photograph both plants and (with the help of his optical instruments) microorganisms. With his pictures, he would like to compensate for the bias towards human interests that dominate pictures in magazines. He makes the point that any brown plant is a lot less likely to appear in a magazine than a colourful plant. To the camera of professor Kooijman, colour does not matter. I imagine that walking through a forest with him would make you wonder at the diversity of life a lot more often.

While all this makes for a fascinating pastime, in his professional career he focuses on quite the opposite side of biology. Instead of examining the differences between organisms, he tries to find similarities between them. Dynamic Energy Budget (DEB) theory, a theory that Professor Kooijman drew up and has been working on for about 20 years now, looks at the way in which organisms get and use their energy. It tries to establish a mathematical framework in which the energy budgets of organisms as diverse as zebras, beetles and bacteria can be captured.

Before asking how such a thing could be done, perhaps it is nice to know how professor Kooijman got the idea in the first place. Ever since his graduation he has been working on mathematical biology. Very early on he realised that when making a model in biology, you should start by looking at the underlying processes that are going on instead of just describing what you see. This would later become an important starting point of DEB theory. His early work in mathematical biology also gave him a good background in statistics. This was something that was not omnipresent among biologists at that time, but very much in demand.

The knowledge of statistics came in very handy indeed in his job as student-assistant. He was able to set up a question hour in which researchers could come to him for advice on the use of statistics. This made him aware of a lot of research that was going on at that time, something that would also come in very handy for DEB. It was this same knowledge of statistics that got him a job in ecotoxicology, the branch of biology that looks at the effects of poisons on the environment. During this work, he at one time studied the effects of toxins on the reproductive output of water fleas. The industry was not satisfied with the outcome of this investigation, and wanted to know whether the reproductive output of one water flea would really say something about the impacts of the toxin on the environment. This is understandable, since they would have to spend millions to reduce pollution for nothing if they were not! This is when professor Kooijman realised that a more complicated model was needed if he was to understand all the effects that a poison could have.

The first approach to this problem was to step to his friends Hans Metz and Udo Diekmann. Together they looked at how you could examine existing models for individuals so that you can predict what a whole population of such individuals would do. This investigation was completed, but now there were so many models for individuals that it would take way too long to examine them all.

Therefore professor Kooijman opted for an other strategy. He would draw up a model for energetics himself, not just for the fish but for as many life forms as he could include. He would always keep in mind that it should include only the bare necessities, but then ALL the bare necessities. This would be needed to make the model both manageable and meaningful at the same time. This became the starting point of DEB theory. Over twenty years of work by him and his colleagues, DEB theory has grown to include a rich diversity of life. Professor Kooijman still describes DEB as a theory in development, although the basic framework has been laid down. As we will see, DEB has come a long way since its outset.

2- What is DEB theory and what are its goals?

So, DEB theory tells us something about organisms and how they use their energy. This can give us information about several things. For example energy uptake can tell us about the food and nutrient requirements organisms have. Also through looking at how the energy is distributed over the body, we can say something about the growth of the organism and the reproductive activity. This information can be applied in several situations.

We have already had a brief glance at one application: investigations into the amount of a toxic substance that can be tolerated. This can be studied with an energy model because toxins often disturb the way energy is used in an organism. But there are more uses for such a model. Nature preserving organisations often want to know about populations of organisms, and predict their behaviour in the future so that nature reserves can be kept in optimal shape. A population of a certain species is nothing more than a couple of individuals living together. Therefore knowing about the energy needs of an individual will tell you a lot about the needs of a population. Basically, if you study an organism, you will very often want to know how it manages its energy. Energy management is an essential part of organism’s struggle for survival.

Now that we know that it is worthwhile to study energetics, it is important to realise that energetics can be looked at in many ways. Take for example the growth of an organism. If you measure the growth of an organism over time, you get a set of data. Plot these data in a graph, and in most cases you will very easily be able to see a pattern emerging. So you take a pencil, and you draw a line through the data. In this way you can quite easily describe the growth of an organism. Instead of a pencil, you can also take a mathematical formula. If you take a formula such that the graph of the formula fits the points well, you have a mathematical description of the growth of an organism. Is this description useful? Yes, it can be very useful in predicting how that organism may grow in the future. For this reason this approach is used very often in biology. But does it give any understanding of the way in which this organism manages its growth? Not really. For this you need a different approach.

The approach DEB takes is to start by thinking about a mechanism in which an organism could manage its energy. Then you take this mechanism, and see how you can describe it in mathematics. Once you have the mathematics, you look at how it can be applied to the organism that you are studying. Finally, you make predictions based on the model, and then see whether they fit the data that you measured. This is the approach that the DEB model takes. Although it seems rather cumbersome (drawing a line with a pencil takes slightly less time), this approach has great advantages. In the process of modelling many properties of the organism are included. This means that the model will be able to give you information on any properties you include. You have to be careful with this though, because if you include too many properties your model will be so complicated that it is very difficult to grasp, and even more difficult to test by experiments. Therefore the art of modelling is to make a model which includes all the properties you need, but no more than that. As you can imagine, it is quite an intricate task. Now that we know what the goal of DEB is, let’s see how the DEB theory is built up.

3- How does DEB go about its task?

DEB wants to say something about the energy that comes into and goes out of an organism. To say something about this energy flow, it is handy to put very rough limits on how much energy comes in and how much goes out. Looking at the ratio between the surface area and the volume of an organism can set these limits. Why surface area and volume? Well, all the food (energy) that is available to an organism must be taken up. This means that it must be transported into the organism over a certain surface area (in humans, this surface area would be represented by the intestine, the content of which is therefore technically outside our body!). The use of energy takes place in every cell of the body. Cells are not bound to a surface area; the number of cells depends on the volume of the organism.

When an organism gets larger, both its surface area and its volume increase. However, the surface area increases much slower than the volume. Therefore there is a limit to the size an organism can reach, because at a certain point too little energy will be able to come in over the surface to keep all the cells running.

So now we can at least say something about the amount of energy that comes in, based only on the surface area and the volume of an organism. The next step is to find out how this energy is distributed over the different processes that take place in the organism.

What if we had to think of a way in which to model the energy distribution in a system? What starting points can we think of? In modelling, an organism is often assumed to be in steady state. This means that compounds and energy flow through it, but the organism does not change its overall composition. Of course organisms change in the long run, but this change is so much slower than the speed at which energy flows that it hardly has any effect. So we have to model a flow of energy. A flow has to start somewhere, so we have to have input. In an organism, this is quite easy to find: its food. Now the next step. What does it do with its food? First, it has to be digested. This means that some of it will be absorbed into the organism, but some will also be indigestible. This will go out as faeces.

Now it becomes interesting. How does the organism use the digested food? Well, the organism has to grow, it has to reproduce and it has to use some for upkeep. All these things need to be paid for with energy. So we can take the flow of food and distribute it directly over these expenses. This is what many models do. But if this is so, how do animals cope in times of low food availability? Do they die because for example they don't eat during hibernation? They usually live on afterwards don't they? How can we explain that? DEB theory explains this by introducing a step in between the absorption of the food and the actual allocation of it to different processes. The incoming energy is first put into the reserves. The terminology may be a bit misleading here. The reserves are meant to be compounds which can be utilised for energy production at any time, not energy that is stored away and kept inactive until it is really badly needed. This construction makes it possible to explain why organisms are so tolerant of a temporary change in food conditions.

Okay, the energy flows into the reserves. From here it has to be allocated to the different processes that take place. We have already seen a few processes that one could think of to allocate energy to. DEB theory takes the following allocations into account: *dissipating heat*, *structure, maturity, somatic work, maturity work and gametes*. Let's look at them one by one. *Dissipating heat* more or less speaks for itself. Many processes in the organism produce heat, which is dissipated to the environment. The energy allocated to *structure* is spent on increasing and organising the body mass of the organism. So growth comes from this energy allocation. The energy that goes to *maturity* has different destinations in juveniles and adults. In juveniles, it is the energy that is invested in becoming an adult. In adult it is the energy allocated to reproduction. *Somatic work* covers all the cost that an organism makes in keeping itself the way it is. You could think of the costs an organism has in replacing dead cells. *Maturity work* is quite a special allocation. Within the mathematical framework, it was found that this allocation was necessary in order to explain certain reactions of organisms to changing food conditions. Organisms seem to have a so-called “degree of maturation” which indicates how much energy has been invested in maturation already. Energy is needed to maintain this investment, just like energy is needed to maintain the investment in structure.

We now know what components we have in the DEB framework of energy distribution. The next question is: how is energy allocated to each component? You can see this schematically in the figure below, figure 1.

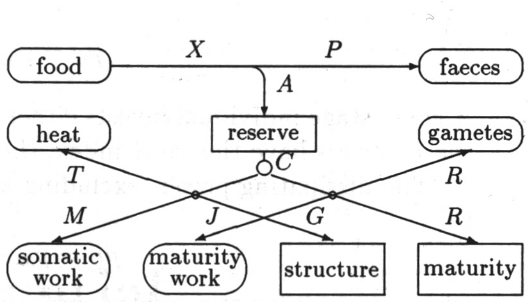

Figure 1: The way energy flows through an organism in the DEB model (taken from source 3)

As you can see in the figure, energy can flow in two directions after the reserves. These directions are indicated by two black dots. Energy flowing to the one dot can go to *structure* or *somatic work* or *heat* and the energy flow to the other dot can go to *maturity work* or *maturity* or *gametes*. There is a special relationship between the two dots. A fixed percentage of all the energy that is used goes to the one dot, while the rest (also a fixed percentage) goes to the other dot. This means that the processes that are grouped under one dot always get the same fraction of the total energy, and therefore only compete for that energy with each other.

We now have a basic overview of the mechanics behind the theory. Is this scheme all we can say about the organism through DEB theory? Not at all. The mechanism we just examined tells about many properties of the organism. But often it takes quite a bit of logical deduction to get all these properties into the open. Examples of such properties are reproductive output, life span and body mass. As the research advances, more and more implications of the energy structure arise.

It is important to realise that this whole construction does indeed lead to practical predictions. For example, if you take a particular organism and measure its mass every so often, DEB will predict what the outcome of the experiments will be. These predictions can be carried out on all sorts of organisms, ranging from bacteria to zebras to even plants. Of course, seeing whether these predictions are realistic gives a good test of the theory. So far, the tests have proven positive.

4- What can we expect from DEB theory in the future?

DEB theory now gives us a solid mathematical basis for examining how energy flows through an organism. Now that the theory is there, we can expect it to be applied to many practical situations. To give you an impression, here are two projects that have been worked on within the DEB context and that are now about to enter society.

Using DEB theory, an investigation has been conducted which looked at sewage cleaning reactors. In these reactors bacteria are often used to clean the water. However, this usually results in an overproduction of bacteria. Removing this overproduction is very expensive and is not very friendly on the environment. Using DEB a new way of designing the reactors has been developed to reduce the excess production. Right now technical projects are examining the designs.

A special branch of DEB theory has been developed to look at the effect of toxins. It has been made into the software package “DEBtox” that can analyse results of the standard experiments that are carried out routinely. In this way it provides a way to look at these data with a well thought out model as background. The OECD (Organisation for Economic Co-operation and Development) the organisation that (among other things) determines how data about toxins should be used in governmental decision making, is considering adding DEBtox to its analysis arsenal.

But the theory itself is not quite finished yet either. Of course minor adaptations are needed every time it is used in practise. But professor Kooijman is a man with a greater vision. At the moment, different lines of research are going on. One of these focuses on the physiology of communities: the relationship between the organisation of matter in the community and its function. Another line of research looks at endosymbiosis. This is a theory that describes the origin of eukaryotic cells. It says that an eukaryotic cell and a bacterium can come to co-operate so closely that the bacterial cell will in the end be able to be absorbed by the eukaryotic cell, and live on inside it.

Professor Kooijman hopes that these two lines of research can come together through applying DEB rules to both these systems, and seeing how they differ in behaviour. The endosymbiosis research is especially interesting, because of its implications. The question is whether one of two organisms, which can both be described by DEB, can live inside the other in such a way that DEB can describe the whole (new) organism. If this were possible, we would have a great tool for studying the energetics within cells, because cells are largely made up out of endosymbionts.

If it is shown to be possible to find a relation between DEB theory applied on cells and DEB theory applied on communities, we have another exciting prospect. It would give us a theory that could say meaningful things about systems as small as cell organelles to things as large as the system earth. Now there is something to dream about at night!

5- Acknowledgements

I would like to thank Professor Kooijman for his assistance in introducing me to DEB theory and for allowing me to interview him on the background of the theory. Without his help this essay had never been written!

6- Bibliography

Source 1: The web site of DEB theory contains a lot of introductory information on DEB as well as information on the latest projects that are being carried out. It can be found at: http://www.bio.vu.nl/thb/deb/ .

Source 2: If you wish to know more about the concepts behind DEB theory, read "Quantitative aspects of metabolic organisation: a conceptual introduction" by Prof. S.A.L.M. Kooijman, June 2000.

Source 3: If you are ready for DEB theory in its full glory, it can be found in "Dynamic Energy and Mass Budgets in Biological Systems" by Prof. S.A.L.M. Kooijman, Cambridge University Press, 1993, second edition 2000.