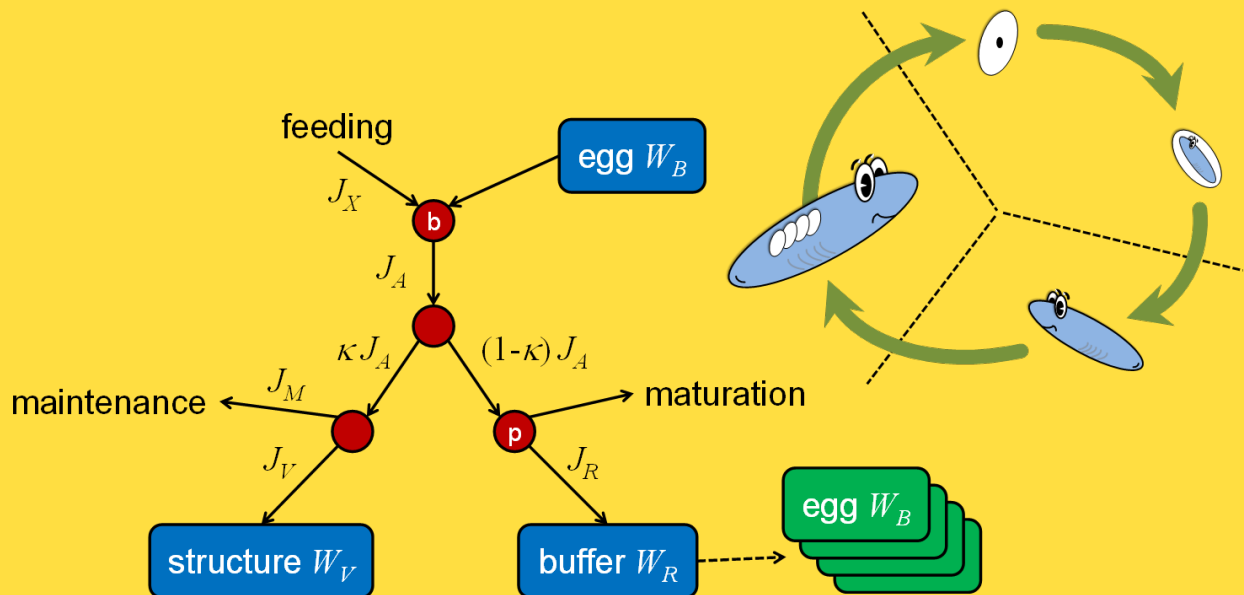


DEBkiss

A SIMPLE FRAMEWORK FOR
ANIMAL ENERGY BUDGETS



Tjalling JAGER

DEBkiss

A simple framework for animal energy budgets

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This e-book is published with Leanpub, and can be downloaded from https://leanpub.com/debkiss_book. The book can be obtained totally free of charge. However, please consider paying for it: that gives me the opportunity to continue working on this book, and on other ones. A version log can be found on http://www.debtox.info/book_debkiss.html. This e-book will (hopefully) be regularly updated and extended with new modules and case studies.

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Alternatively, refer to one of the papers in the open literature: e.g., [65] for the general DEBkiss model, and [49] for the TKTD module and the simplified ‘DEBtox’ model.

If you spot errors (spelling, grammar, mathematical or conceptual), please notify me by email (see address below). Furthermore, I love to receive feedback on this book, whether it has been readable and useful to you, and whether you are missing a topic. So feel free to drop me a line!

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Preface

The origin of DEBkiss

In 2002, I started working on the classical DEBtox model [87, 76]. I soon found out that the parameter governing the reserve dynamics (g) is almost impossible to obtain from data. Therefore, it was routinely fixed to a not-unreasonable value in practical applications. I never gave this much thought until, in 2011, Ben Martin showed me the problem in detail (as explained in his [106]), and noted that the data suggest a very low reserve density for the water flea *Daphnia magna*. The discussion with Ben came back to my mind when I was preparing exercises for the 2012 summercourse on TKTD modelling (see <http://www.debtox.info/dynmodtox.html>). The standard DEB animal model [138] is, for my taste, too complicated as a place to start for such a course, and the classical DEBtox formulation [87, 76] is not transparent enough and lacks the explicit mass balance (and is thus not the best choice, didactically). I then realised that ‘reserveless’ might well be the way to go: it often describes the data well and it is *much* easier to derive, interpret and apply. Together with a non-scaled explicit mass balance, this became DEBkiss [65]. At this moment, DEBkiss is my main tool for analysing and predicting (stress effects on) life-history traits, and so far I have not been disappointed by its ability to capture the life cycle of invertebrate animals (and even for vertebrates, in some cases).

In retrospect, I can now trace the seeds for this development even further back. In 2008/2009, I was preparing a paper with Chris Klok in which we compared three DEB models and how they differ in their predictions for population effects [62]. Chris has worked a lot with the ‘Kooijman-Metz’ model from 1984 [90], which is conceptually very similar to DEBkiss. I had just decided to continue working with the standard DEB model (due to the limitations of DEBtox), so I was not too eager to include such a ‘primitive’ model. However, I was struck by the performance of this simple model without reserve and maturity. At the time, I think I dismissed the good fits as a fluke, and something specific for the particular data set that we used.

About this book

The basis of this book is formed by a reshuffled and extended version of our paper in the Journal of Theoretical Biology [65], and therefore I like to acknowledge the contributions of my co-authors from that paper: Elke Zimmer and Ben Martin. This book combines the paper and its supporting information in a slightly different format, and I will add sub-models or modules to this book as time goes on. I also would like to thank Natnael Hamda and Alpar Barsi who were the first to apply DEBkiss in their PhD projects; I learned a lot from your studies. Finally, I wish to thank Chris Klok for (re-)introducing me to the Kooijman-Metz model.

If you are new to energy budgets, and want some more conceptual background, I strongly advice you to start by reading in my e-book “Making sense of chemical stress”, which can be downloaded from https://leanpub.com/debttox_book. That book provides a highly-readable and math-free introduction into energy-budget modelling (and its application in ecotoxicology), whereas I here immediately dive in and include the math (all pretty basic stuff though). The first three chapters form the backbone of this book: they explain and demonstrate the basic DEBkiss model. The remaining chapters are more technical, and more fragmentary, as they present a large number of potential model extensions with limited background information. I expect people to shop from these sections, if the need arises for their model application, rather than read it all.

At this moment, this book does not contain information about the statistical framework to use for model fitting to data, and error propagation. I might add this in a future version. However, in the meantime, I can refer you to the “Mechanistic modelling essentials” e-book (https://leanpub.com/mechmod_book), the supporting information of [76], and the more recent paper on the parameter-space algorithm [50]. The technical background document for the “Making sense” e-book at <http://www.debttox.info/book.html> is now really outdated, but the information on likelihood functions is still valid.

Support on the web

Matlab packages are available in the BYOM library to play with DEBkiss: <http://www.debttox.info/byom.html>. However, the equations are simple enough to implement into the software of your choice. Several applications of DEBkiss have been (and are being) published, which I will collect at http://www.debttox.info/debkiss_appl.html.

Warnings

I noticed that some of my e-books are offered through other websites, after removal of the title page. Please download this e-book from Leanpub, which is the only place where it is legitimately offered (even for free). That will ensure that you have a complete and correct version, and that you are notified as soon as a new version is available.

This book *will* inevitably contain errors. If you spot one, please let me know so that I can include corrections in updates of this book. I do not accept liability or responsibility for any damage or costs incurred as a result of these errors.

Chapter 1

Introduction

Simple is beautiful, but also practical, as embodied in the engineering principle of KISS (keep it simple, stupid). Complex things tend to break, and when they do, they are difficult to repair. But, the quote often attributed to Albert Einstein warns us not to overdo it: “everything should be made as simple as possible, but not simpler.” Here, we are going to apply the KISS principle to modelling of life-history traits of an animal (in particular: growth, development and reproduction), while heeding Einstein’s caution. How simple can we make a model for such traits of an individual, while still maintaining a degree of realism? This is one stage in a continuous quest for balancing simplicity and realism; a balancing act that will obviously depend on the purpose for which the model will be used. The specific purpose that I have in mind is to apply such a model for individuals to interpret the effects of stressors such as toxicants [61] or food limitation [149], and to translate the effects on the individual to the population level [107, 62]. The focus in this work is on small invertebrate animals, although the models presented might well be useful for a broader range of organisms.¹

At minimum, our model should provide a prediction of reproductive output over the life cycle of an animal, as a function of food availability (which might vary over time). Reproductive output is the most straightforward indicator of individual fitness, and clearly needed for the translation to the population level; in its simplest form we can think of population dynamics as the difference between births and deaths. However, the reproduction rate is not determined by the current food level alone; it also depends on the state of the individual. Body size is an obvious candidate for such a state, as it determines feeding rates (and thereby the available resources for reproduction), and is often an accurate indicator of whether the organism is capable of reproducing. Interpreting the effects of varying food levels and stressors on reproduction therefore requires following (at least) body size as a state variable. Furthermore, because the dynamics of populations often depend on feedbacks between a population and its prey, keeping track of body size (and the associated feeding rates) is an essential aspect in population models.

Our model should thus provide us with a good description of at least body size and reproductive output over the entire life cycle (including the embryonic stage) as a function of food availability. It should be based on well-established principles (such as conservation of mass and energy, and consistency with thermodynamics), to ensure

¹Some applications with this model, and closely related ones, have been published for vertebrates in recent years. Especially for fish [66, 28, 105], but also an application to mink [23] and rats [109, 108]. So, the application domain may be larger than I initially thought.

that the model behaviour is physically realistic. Furthermore, the model should include a (possibly crude) representation of biological processes such that we can model stressor effects on these processes. And finally, the core model should be generic and free from species- or stressor-specific argumentation as we do not want to build a new model for each species-stressor combination.

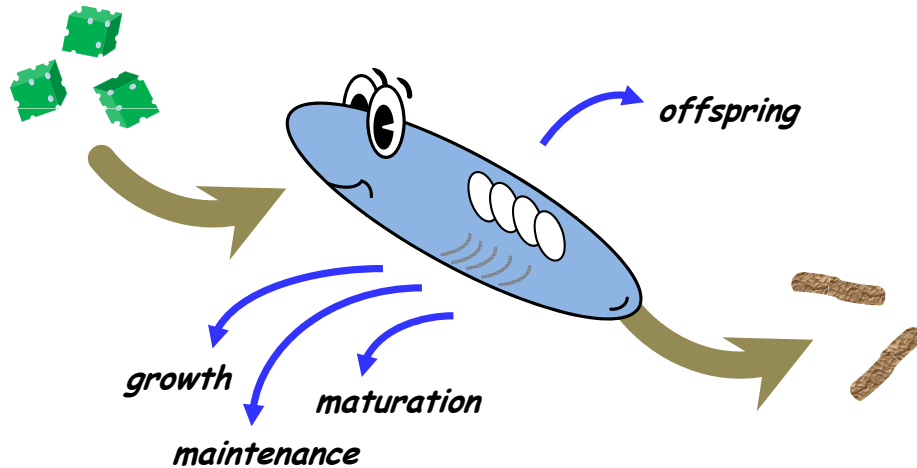


Figure 1.1: The energy budget is key to understanding energy-demanding traits such as growth and reproduction. Such traits are fuelled from the resources obtained by feeding, and thereby constrained by the conservation laws for mass and energy.

The best (and my opinion only) way to understand resource-requiring traits such as growth and reproduction is by focussing on the conservation laws for mass and energy. Growth and offspring production require energy, and compete with other energy-demanding processes such as maintenance of the body. This energy is ultimately obtained from feeding (in animals). Therefore, we need rules for how much food is taken up, and how its resources are allocated over the various energy-demanding traits (Fig. 1.1). Dynamic Energy Budget (DEB) theory is by far the most complete and most ambitious framework in this respect. DEB theory offers a powerful and formalised framework for building such models [81, 138, 122]. This power, however, comes at a price. Even though the concepts and underlying assumptions are mostly simple, understanding how they lead to the equations of the ‘standard DEB model’ for animals (see [138]) is not. Implementation of the model in software is certainly not straightforward, and the subsequent parametrisation requires an extensive data set (and even then it can be difficult to settle on a unique parameter set for a species, see e.g., [125]). Furthermore, the link between state variables and observable properties is rather awkward. Although efficient procedures and software have been developed to aid the user and to accommodate limited data sets [82, 96, 104], it takes some serious study to be able to apply them properly, and even more to verify the code. One would effectively have to rely on the derivations and programming of the developers, which can be an issue for potential users.

The standard model is the simplest complete DEB model, but it is often considered too complex (e.g., as a basis for population modelling, [121]). In many practical fields of application, the interest in dynamic models rapidly declines with the level of complexity. The standard animal model has been simplified, yielding the ‘scaled standard model’

[92, 75] and ‘DEBtox’ [76]. These simplifications, however, have their disadvantages. The use of scaling and compound parameters hampers interpretation of the equations and can lead to difficult-to-spot inconsistencies (e.g., transformation efficiency greater than one) for certain choices of parameter values.² Furthermore, the use of compound parameters hampers the straightforward application of stress due to toxicants, which are assumed to affect metabolic processes and thus primary energy-budget parameters [75].

In short, I believe there is room for a simple and transparent model that fully specifies the life cycle of an (invertebrate) animal, applies an explicit mass balance, and has rather direct access to the primary parameters and state variables that determine the metabolic processes. The model should be simple enough for users to check its consistency, implement into their own software of choice, and to parametrise it on easily-obtained data sets without additional help. Such a model would be suitable for particular applications where simplicity and transparency are of key importance, but it also provides a good teaching tool for theoretical biology in general, and will smooth entry into DEB theory in particular. In this book, I present such a simple model in a formalised manner (starting from an explicit formulation of the simplifying assumptions). I name the model ‘DEBkiss’ to emphasise that the work is highly inspired by DEB theory, but with a strong focus on the KISS principle.

²The original derivation of Kooijman & Bedaux [87] contained a few errors. Identified and corrected later [17, 76].

Chapter 2

Theoretical: the core model

2.1 Symbols and notation

The symbols for the basic DEBkiss model, with their dimensions, are explained in Table 2.1 (more symbols will be added in subsequent chapters). The first section of the table shows the primary parameters: parameters that are directly linked to a metabolic process, and that do not themselves depend on other parameters. In contrast, the values of secondary or compound parameters (bottom of the table) are fully determined by one or more primary parameters. As an example, maximum volumetric length L_m (the cubic root of maximum body volume) is a secondary parameter, whose value is determined by the primary parameters κ , J_{Am}^a and J_M^v (see Eq. 2.19).

It is always a struggle to come up with a notation that is fully internally consistent, easy to use, and intuitive (e.g., consistent with the expectations of the readers). The main problem is that these goals are mutually exclusive. Thus, the notation used here is a compromise. As much as possible, I tried to follow the DEB convention to use the same leading symbol for parameters with the same dimensions. However, this turned out to be impractical, and led to too many subscripts to distinguish between different parameters. One of the solutions is to work with superscripts in addition to subscripts. This has some drawbacks, mainly that a superscript can be interpreted as ‘to the power’. Fortunately, the superscripts are only used on parameters that are not part of power functions. A minor drawback is that word processors such as Word have trouble with simultaneous sub- and superscripts in text mode.

The superscripts are used to indicate parameters that are volume- or surface-area-specific. As an example, J_M^v is the volume-specific costs for maintenance, and J_{Am}^a is the area-specific assimilation rate at maximum food. Therefore, the dimensions also differ from those of the fluxes J_i (which are in mass per time). Furthermore, superscripts are used when I discuss toxicants in Chapter 5. There, they are used in a different but related manner to indicate that a parameter is scaled or referenced in a certain manner. For example, D^w is used for a scaled damage level, where the damage is referenced to the external concentration in water. Hence, D^w has the dimensions of an external concentration. As another example, k_e^m is the elimination rate for a fully-grown animal; for smaller individuals, this reference value is scaled using the ratio of the actual body size with the maximum body size.

Symbol	Explanation	Dimension	Sugg. value
Primary parameters			
F_m^a	Maximum area-specific searching rate	$l_e^3/(l^2t)$	—
J_{Am}^a	Maximum area-specific assimilation rate	$m_a/(l^2t)$	—
J_M^v	Volume-specific maintenance costs	$m_a/(l^3t)$	—
W_{B0}	Assimilates in a single freshly-laid egg	m_a	—
W_{Vp}	Structural body mass at puberty	m	—
y_{AV}	Yield of assimilates on structure (starvation)	m_a/m	0.8 mg/mg (dwt)
y_{AX}	Yield of assimilates on food	m_a/m_f	0.8 mg/mg (dwt)
y_{BA}	Yield of egg buffer on assimilates	m_a/m_a	0.95 mg/mg (dwt)
y_{VA}	Yield of structure on assimilates (growth)	m/m_a	0.8 mg/mg (dwt)
κ	Fraction of assimilation flux for soma	—	0.8
Conversions			
d_V	Dry-weight density of structure	m/l^3	0.1-0.2 mg/mm ³
$\delta_{\mathcal{M}}$	Shape correction coefficient	—	
Fluxes, states and forcings			
J_A	Mass flux for assimilation	m_a/t	
J_M	Mass flux for maintenance	m_a/t	
J_R	Mass flux to reproduction buffer	m_a/t	
J_V	Mass flux for structure	m/t	
J_X	Mass flux of food	m_f/t	
W_B	Mass of assimilates buffer in egg	m_a	
W_R	Mass of reproduction buffer in adult	m_a	
W_V	Mass of structural body	m	
X	Food density in the environment	m_f/l_e^3	
Other output and secondary parameters			
f	Scaled functional response (0-1)	—	
J_{Xm}^a	Maximum area-specific feeding rate	$m_f/(l^2t)$	
X_K	Half-saturation food density	m_f/l_e^3	
L	Volumetric body length	l	
$L^{\mathcal{M}}$	Physical body length	l	
r_B	Von Bertalanffy growth rate constant	$1/t$	
ΔR	Number of eggs in a clutch	$\#$	
R	Continuous reproduction rate	$\#/t$	
R_m	Maximum continuous reproduction rate	$\#/t$	
t_b	Time between egg laying and birth	t	
W_{Vb}	Structural body mass at birth	m	
W_W	Total body weight	m	

Table 2.1: Explanation of symbols for the basic model, with dimensions given in mass (m for body, m_a for assimilates, and m_f for food), length (l_e for environment, l for organism), numbers ($\#$), time (t). Suggested values for the yields (apart from y_{AV}) based on the typical values in [96].