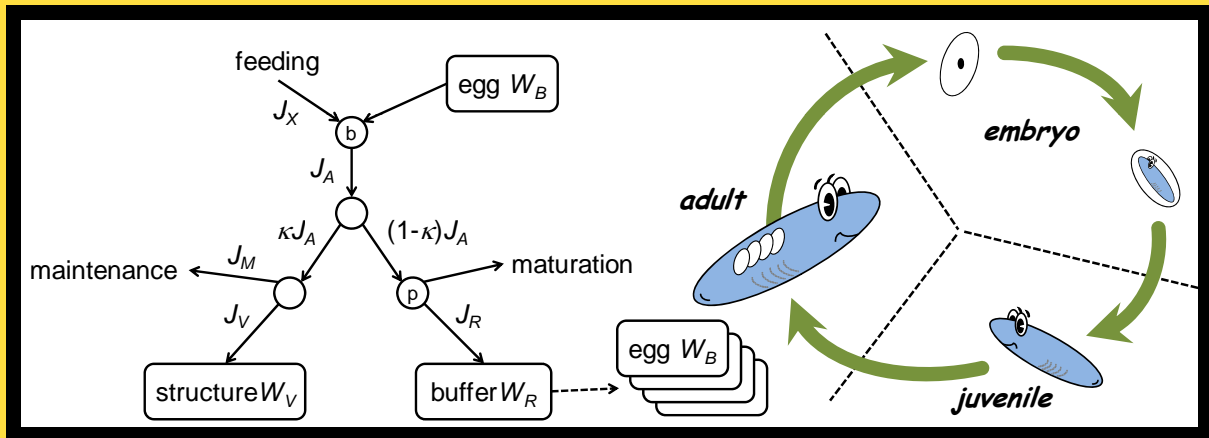


DEBkiss

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.debttox.info/book_debkiss.html. This e-book will (hopefully) be regularly updated and extended with new modules and case studies.

To cite this book, please use the URL given above, but preferably refer to one of the papers in the open literature: e.g., [39] for the general DEBkiss model, and [5] for the basic TKTD extension.

If you spot errors (spelling, grammar, mathematical or conceptual), please notify me by email (see address below).

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Contents

Preface	v
The origin of DEBkiss	v
About this book	v
Support on the web	vi
Disclaimer	vi
1 Introduction	1
2 Theoretical: the core model	3
2.1 Model definition	3
2.2 Derived model results	9
2.3 Extensions	11
2.4 Data requirements	11
2.5 Model summary	12
3 Case study: pond snail	15
3.1 Initial parameter estimates	15
3.2 Fitting growth and reproduction patterns	16
3.3 Predictions for other endpoints	17
4 Maturity and maturity maintenance	21
4.1 Adding maturity maintenance	21
4.2 Maturity in more detail	22
4.3 Comparing individuals with different kappa	25
5 Other extensions	27
5.1 Calculating the respiration flux	27
5.2 Changes in temperature	29
5.3 Deviating growth curves: V1-stage	29
5.4 Deviating growth curves: juvenile food limitation	30
5.5 Deviating growth curves: determinate growth	30
5.6 Dividing organisms: V1-morphs	31
6 Toxicants, uptake and effects	33
6.1 Adding toxicokinetics	33
6.2 Toxicokinetics in eggs	37
6.3 Toxicokinetics in V1-morphs	38
6.4 Toxicant effects	38

6.5	Mixture toxicity	39
6.6	A simple ageing module	40
7	Discussion	43
7.1	Main differences with other energy-budget models	43
7.2	Model applicability	45
	Bibliography	46
A	Derivations	53
A.1	Maximum size and growth rate	53
A.2	Approximate size and age at birth	53
B	Checking the stylised facts	57
B.1	Feeding facts	57
B.2	Growth facts	60
B.3	Stoichiometry facts	64
B.4	Concluding	66

Preface

The origin of DEBkiss

In most of my DEBtox work (starting in 2002), it turned out that the parameter governing the reserve dynamics (g) is almost impossible to obtain from data. Therefore, it was usually fixed to a not-unreasonable value in applications. I never gave this much thought until, in 2011, Ben Martin showed me the problem in detail (as explained in his [69]), and noted that the data suggest a very low reserve density for *Daphnia*.

The discussion with Ben came back to my mind when I was preparing exercises for the 2012 summercourse on TKTD modelling (see <http://www.debttox.info/dynmodtox.html>). The standard DEB animal model [90] is too complicated as a place to start for such a course, and the simplified DEBtox [46] is not transparent enough and lacks the explicit mass balance. I then realised that ‘reserveless’ might well be the way to go: it usually 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 [39]. At this moment, DEBkiss is my main tool for analysing and predicting life-history traits, and so far I have not been disappointed by its ability to capture the life cycle of invertebrates.

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 [38]. Chris has worked a lot with the ‘Kooijman-Metz’ model from 1984 [58], 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 dismissed the good fits as a fluke, and something specific for the particular data set that we used.

About this book

This book is a reshuffled and extended version of our paper in the Journal of Theoretical Biology [39], and therefore I like to acknowledge the contributions of my co-autors 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 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 want to cite DEBkiss, please refer to the paper in the open literature [39] or to one of the applications. If the equation you use is only in this book, you can refer to this book with the link to the Leanpub webpage: https://leanpub.com/debkiss_book.

If you are new to energy budgets, and want some more background, I strongly advise you to start by reading in my e-book “Making sense of chemical stress”, which can be downloaded from https://leanpub.com/debtox_book. That book provides a math-free conceptual introduction, whereas I here immediately include the math (all pretty basic stuff though).

Support on the web

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

Disclaimer

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, as the quote often attributed to Albert Einstein warns us: “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, 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 [37] or food limitation [96], and to translate the effects on the individual to the population level [70, 38]. The focus in our work is on small invertebrate animals.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 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

¹The models presented might be useful for a broader range of organisms, but there have been very few applications outside the invertebrates so far (and none published).

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.

Dynamic Energy Budget (DEB) theory offers a powerful and formalised framework for building such models [51, 90, 80]. This power, however, comes at a price. Even though the concepts and underlying assumptions are simple, understanding how they lead to the equations of the ‘standard DEB model’ for animals (see [90]) is not. Implementation of the model in software is certainly not straightforward, and the subsequent parameterisation requires an extensive data set. Although efficient procedures and software have been developed to aid the user and to accommodate limited data sets [52, 63], it takes 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, [79]). 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’ [60, 45] and ‘DEBtox’ [46]. 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. 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 [45].

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 direct access to the primary parameters 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 parameterise it on easily-obtained data sets without additional help. Such a model would be suitable for particular applications where simplicity is of key importance, but it may also provide a good teaching tool for theoretical biology in general, and 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.

Chapter 2

Theoretical: the core model

2.1 Model definition

The DEBkiss model is schematically depicted in Figure 2.1, showing the mass fluxes J_* (in dry weight per unit of time). In the possible topologies for energy budget models of [64], it would classify as a $R\kappa_G^{R0}$ model. In the κ models, the fundamental split between investment in the soma and reproduction comes first (on the assimilates obtained from feeding). This contrasts ‘production models’, where maintenance costs are paid before the split (e.g., [66]), and ‘assimilation models’ where the split comes after a storage compartment (e.g., [46, 90]). This topology maintains many of the desirable properties of the standard DEB model [64], especially for small animals, while considerably simplifying the model equations.

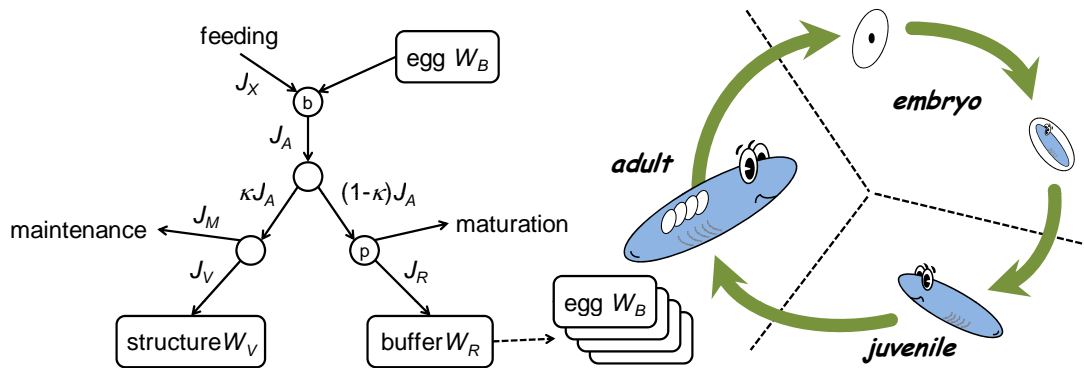


Figure 2.1: Schematic diagram of the energy flows and life cycle of a DEBkiss animal. The parameter symbols are explained in Table 2.1. The nodes b and p denote switches at birth (start of feeding; embryo to juvenile) and puberty (start of reproductive investment; juvenile to adult). The other nodes represent a split of the assimilation fluxes.

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
δ_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	$m_f/(l^2t)$	
K	Half-saturation food density	m_f/l_e^3	
L	Volumetric body length	l	
L_w	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	Physical body weight (total)	m	

Table 2.1: Explanation of symbols, 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 [63].