

40 YEARS OF DEVELOPMENT AND APPLICATION OF DYNAMIC ENERGY BUDGET THEORY

S. A. L. M. Kooijman* and B. W. Kooi

VU University Amsterdam

bas.kooijman@vu.nl (*corresponding author),
bob.kooi@vu.nl

I started to develop Dynamic Energy Budget (DEB) theory [7] in 1979, with the aim to apply it in physiologically-structured population models for any species of organism on earth (micro-organisms, plants, animals) and evaluate effects of toxicants at the population level, modelled as dynamic changes in (particular toxicant-specific) parameter values. The research program radiated substantially over time to ensure coherence with physiology, ecology and evolution [6, 11], involving many co-workers. Metabolic transformations and behaviour are taken into account by Synthesizing Units [5], that exploit the principle of time conservation within the class of Markov processes, while a food-dependent aging module [12, 13] specifies the bottom-line exit dynamics. Attention has been given to a wide range of topics, such as surface area-volume relationships, cytoplasm-mitochondria interactions, organ size and function dynamics, including tumour development, isotope dynamics, mixotrophy, parasitism and symbiosis. A large number of popular seemingly-unrelated empirical models turn out to be special cases of DEB theory, or very good numerical approximations, such a Kleiber's "law" (1932), stating that respiration is proportional to body weight to the power of (about) $3/4$, and Lavoisier's indirect calorimetry (1780), stating that heat production equals a weighted sum of dioxygen consumption and carbon dioxide and nitrogen-waste production. This is remarkable, since DEB theory makes no direct assumption about respiration, but still specifies it (and water dynamics) by closing the balances for chemical elements. Being firmly based on mass and energy conservation and other thermodynamic principles [20], I discuss arguments to expect that DEB theory will have no alternatives with a similar level of generality and simplicity [14]. Simplicity is required for testing generality, due to practical limitations on data availability, and even the present level of simplicity motivated the development of advanced parameter estimation methods [18, 17]. At the same, such a theory must be detailed enough to respect biodiversity for links to evolution; a fine balance indeed. Meanwhile some 850 publications [3] have been written about the theory and its applications by a rapidly expanding community of research workers from all over the world. The Add-my-Pet collection [2] of data, parameters and implied properties has been set up to test the generality of the theory for animals. This collection now has over 2000 species from all larger animal phyla; model predictions for some $3e4$ data sets have a mean relative error of 0.07, supporting the generality of the theory. Apart from a priori predictable patterns in the co-variation of parameter values on plain physical grounds [4], patterns have been identified that relate to ecological and evolutionary adaptations, such as metabolic acceleration [9], 'waste-to-hurry' [8], supply-demand [15] and altricial-precocial spectra [1]. We also found explanations for some remarkable findings, such as why the allocation fraction of mobilised reserve to soma follows a beta-distribution among animal species, with perplexing accuracy [16]. The mean value of this parameter of all species is larger than 0.9, while a value around 0.45 maximizes reproductive output [10]. My expectation is that DEB theory will eventually affect the way we think about ecology and evolution, in satisfying harmony with an army of early workers in this field [19].

References

- [1] Augustine, S. and Lika, K. and Kooijman, S. A. L. M. (2011). *Altricial-precocial spectra in animal kingdom*. Journal of Sea Research, 143, 27–34.
- [2] Anonymous. (2019). *Add-my-Pet* https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/.
- [3] Anonymous. (2019). *Zotero* https://www.zotero.org/groups/500643/deb_library/.
- [4] Kooijman, S. A. L. M. (1986). *Energy budgets can explain body size relations*. Journal of Theoretical Biology, 121, 269–282.
- [5] Kooijman, S. A. L. M. (1998). *The Synthesizing Unit as model for the stoichiometric fusion and branching of metabolic fluxes*. Biophysical Chemistry, 73, 179–188.
- [6] Kooijman, S. A. L. M. (2004). *On the coevolution of life and its environment*. In: Schneider, S.H., Miller, J. P., Crist, E. and Boston, P. J. (eds) *Scientists Debate Gaia; the next century*. Cambridge, Mass: MIT Press.
- [7] Kooijman, S. A. L. M. (2010). *Dynamic Energy Budget Theory for Metabolic Organisation*. 3rd edition. Cambridge: Cambridge University Press.
- [8] Kooijman, S. A. L. M. (2013). *Waste to hurry: Dynamic Energy Budgets explain the need of wasting to fully exploit blooming resources*. Oikos, 122, 348–357.
- [9] Kooijman, S. A. L. M. (2014). *Metabolic acceleration in animal ontogeny: An evolutionary perspective*. Journal of Sea Research, 94, 128–137.
- [10] Kooijman, S. A. L. M. and Lika, K. (2014). *Resource allocation to reproduction in animals*. Biological Reviews, 89, 849–859.
- [11] Kooijman, S. A. L. M. and Troost, T. A. (2007). *Quantitative steps in the evolution of metabolic organisation as specified by the Dynamic Energy Budget theory*. Biological Reviews, 82, 1–30.
- [12] Leeuwen, I. M. M. and Kelpin, F. D. L. and Kooijman, S. A. L. M. (2002). *A mathematical model that accounts for the effects of caloric restriction on body weight and longevity*. Biogerontology, 3, 373–381.
- [13] Leeuwen, I. M. M. and Vera, J. and Wolkenhauer, O. (2010). *Dynamic Energy Budget approaches for modelling organismal ageing*. Philosophical Transactions of the Royal Society B, 365, 3443–3454.
- [14] Lika, K. and Kooijman, S. A. L. M. (2011). *The comparative topology of energy allocation in budget models*. Journal of Sea Research, 66, 381–391.
- [15] Lika, K. and Augustine, S. and Pecquerie, L. and Kooijman, S. A. L. M. (2011). *The bijection from data to parameter space with the standard DEB model quantifies the supply-demand spectrum*. Journal of Theoretical Biology, 354, 35–47.
- [16] Lika, K. and Augustine, S. and Kooijman, S. A. L. M. (2011). *Body size as emergent property of metabolism*. Journal of Sea Research, 143, 8–17.
- [17] Lika, K. and Augustine, S. and Kooijman, S. A. L. M. (2011). *The use of augmented loss functions for estimating Dynamic Energy Budget parameters*. Ecological modelling, in preparation.
- [18] Marques, G. M. and Lika, K. and Augustine, S. and Pecquerie, L. and Kooijman, S. A. L. M. (2019). *Fitting Multiple Models to Multiple Data Sets*. Journal of Sea Research, 143, 48–56.
- [19] Sousa, T. and Domingos, T. and Poggiale, J. C. and Kooijman, S. A. L. M. (2006). *The thermodynamics of organisms in the context of DEB theory*. Philosophical Transactions of the Royal Society B, 365, 3433–3428.
- [20] Sousa, T. and Mota, R. and Domingos, T. and Kooijman, S. A. L. M. (2006). *Formalised DEB theory restores coherence in core biology*. Physical Reviews E, 74, 1–15.