

Applying Dynamic Energy Budget (DEB) theory to kangaroo energetics

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How species acquire, use, and allocate energy and other materials is a key question for ecologists who study the interactions between living organisms and their surroundings. For example, understanding how Australia's climatic and nutritional environment affects the growth and reproduction of kangaroos is important for predicting how populations of these species may respond in a changing climate. Indeed, studying common and widespread species like kangaroos can grant insight into the dynamics of the ecosystems in which they live (Gaston 2008, Steffen et al. 2009). However, such interactions within and between organisms and their surrounding environment are often complex and difficult to unravel without a deeper understanding of the driving mechanisms.

Metabolic theories formally quantify how energy is acquired, used, and partitioned in a mechanistic and (ideally) parameter-sparse manner. Such theories describe and quantify the uptake and conversion of energy into biomass, which is a fundamental process occurring at the level of the individual. This process is also constrained by the laws of thermodynamics. Metabolic theories that capture this process may provide a framework for understanding ecological processes at multiples levels, ranging from individuals to populations. Given the need for such information, particularly at the species level, why are such metabolic theories not more widely used?

Surprisingly, two of the main metabolic theories are based on fundamentally different mechanisms and assumptions, and therefore have very different structures and predictions. The theory developed by West, Brown, and Enquist (1997) is based on the mass scaling exponent, which describes whole-organism metabolism. West, Brown, and Enquist (1997) suggest that this mass dependence is a direct consequence of the scaling of both the exchange surfaces of branching hierarchical networks and the resource supply networks (West et al. 1997). They argue that as body size increases, the network is less able to meet the demands of the cells. Numerous models of growth, mortality, survival, population, and community dynamics have been built on this principle and applied to general ecological investigations with successful results. For example, this theory has been applied to predict population growth rates and carrying capacities by first summing across individuals to predict population metabolic rates (Savage et al. 2004). However, it appears that estimated individual metabolic rates are based on empirical relationships.

The second main theory is the Dynamic Energy Budget (DEB) theory of Kooijman (Kooijman 1986, 2010) which has also been shown to be incredibly successful at predicting an organism's uptake and allocation of energy and its resulting life history. This theory has strong support from a large body of literature and can be widely applied for a range of species in a variety of nutritional and climatic environments. Importantly, this theory can also be used to predict metabolic rates, growth, reproduction, mortality,

survival, population and community dynamics, and even metabolic scaling exponents themselves.

Notably, the structure of Dynamic Energy Budget theory is intrinsically different from WBE theory because – as the name suggests – it is about energy budgets that allow for dynamic growth of organisms. An energy budget links the uptake and allocation of energy and other materials to the purposes that this energy is used for, namely: assimilation, maintenance, growth and reproduction. A dynamic energy budget follows the process throughout the animal's lifetime, allowing the organism to grow and change (Kooijman 2010). This directly contrasts with static energy budgets, which offer snapshots of information at a particular age or size. Given that it applies to an organism's entire life span, Kooijman's DEB theory is one of the more parameter-sparse bioenergetic models. Precisely how an organism allocates the energy it assimilates from its food is specified in the structure of the DEB model.

DEB theory is based on a set of certain explicit assumptions which are used to determine how an animal allocates energy for different purposes; these assumptions serve as the foundation for the structure of the "standard" DEB model (Kooijman 1986, 2010). The first main assumption is that an individual's mass is partitioned into structure and reserve. Structure is defined as the components of the cell or individual which require maintenance, while reserves do not require any maintenance. Reserve is built up from the energy that has been assimilated at a certain rate from the food. This reserve is then mobilized at a certain rate, and divided between two distinct purposes. A fixed fraction (κ) of the mobilized energy is allocated to growth (i.e. building structure) and somatic maintenance. The remainder ($\kappa - 1$) is allocated to maturation (or reproduction if sexually mature) and maturity maintenance. Birth happens at a defined threshold of maturity (often linked with a certain size in good conditions) and is defined as the point when the animal begins to assimilate food from the environment (more specifically, when feeding switches from the umbilical cord to the digestive tract). Puberty occurs at a second maturity threshold when the animal has matured enough and switches to allocate energy into reproducing. All maintenance costs are paid first and have priority over growth and maturation (Kooijman 2010). Conceptually, this model is very straightforward and intuitive.

However, without several more assumptions about homeostasis, the mathematical derivation of the relationships between these different parameters and rates would not be possible. Two of these important assumptions are strong and weak homeostasis. The strong homeostasis assumption states that the compositions of the reserve and of the structure each remain constant (Kooijman 2010). This allows the overall body composition of the animal to be able to change, depending on the percentage of mass that is reserve, and theoretically divides the animal into two separate pools with respective constant compositions and purposes. Following from this, the weak homeostasis assumption states that under constant food conditions, the proportion of reserve to structure will also be constant, assuming the animal has enough food to meet demands (Kooijman 2010). This results in a constant overall composition of the organism. In the standard model, the animal is assumed to be isomorphic and have a consistent shape (and

size-volume relationship) throughout its life. These assumptions allow for the equations of the standard DEB model to be derived by theoretical biologists for general application.

One of the challenges for applying DEB theory is that the equations of the derived DEB models are based on “hidden parameters” that are incredibly difficult or impossible to measure. Even the proportion of structure versus reserve is difficult to measure because individual cells have parts which would be considered structure and parts which would be considered to be reserve. The rates (referred to as powers) of assimilation of food, mobilization of reserves, somatic maintenance, maturity maintenance, growth of structure alone, and allocation to maturity or reproduction are also incredibly tricky to measure. Actual data measured from animals, including whole organism growth rates and reproductive rates at specific climatic and nutritional conditions, are therefore used not to parameterize the model but rather to verify and validate the model’s predictions.

However, measured data may be used to help estimate the hidden parameters in a systematic process. Indeed, because of the structure of the assumptions, there are mathematical constraints for how the hidden parameters co-vary together and can be approximated or solved for using principles of maximum likelihood. Therefore, the hidden parameters of the DEB model can be found, not by measuring them directly, but rather by using this type of approximation procedure based on initial estimates of life history traits.

Importantly, developing an accurate DEB model for a species, like the eastern grey kangaroo, may present certain additional challenges. For example, the standard DEB model does not appear to incorporate lactation costs for the mother. For the eastern grey kangaroo (*Macropus giganteus*), birth occurs when the embryo reaches approximately 0.8 g at 33 days old (Poole 1975), as it reaches a maturity threshold for birth. While permanently in the pouch, the young will have a constant food supply from the mother but will not experience additional thermal costs. The mother, however, will experience increasing costs associated with lactation. At approximately 4 kg, the juvenile starts emerging from the pouch (Poole 1975, Poole et al. 1982). The young will permanently leave the pouch at approximately 6.5 kg at approximately 319 days old (Poole et al. 1982). However, the young will continue suckling, in addition to feeding on grasses, until it is fully weaned at about 8 kg (Poole et al. 1982). It is possible that this will require an extension to the model as implemented by Noonberg et. al. for marine mammals (Noonburg et al. 2010). These species also experience large lactation costs. The authors of this study added lactational costs for the mother based on the demands of the suckling young as well as an additional maturity threshold for weaning. These changes involve modifying and/or extending parts of the standard DEB theory equations. However, such modifications should only be implemented if justified based on phylogeny. For kangaroos, such a modification may or may not be necessary, but this requires further investigation.

In conclusion, DEB theory provides a robust framework for understanding ecological processes at multiples levels. Unfortunately, the “hidden parameters” of DEB theory may present certain challenges and/or deter some researchers from using this model.

This may explain why such theories have not been more widely applied. Unlike the West, Brown, and Enquist model, DEB theory is not based on observed scaling relationships. Rather, based on the assumptions and the structure of the DEB model, DEB theory can be used to derive metabolic scaling relationships. Of course, the exact scaling exponent will most likely depend on the relative proportions of reserve and structure of different individuals. In addition to general patterns, DEB theory can be applied to individual species to predict an organism's growth and reproductive rate in particular nutritional and climatic environments. Such applications are and will be incredibly useful for understanding how individual species – like kangaroos – are currently affected by climate and how they may respond in the future. Although Dynamic Energy Budget (DEB) theory has already been applied to a wide range of species, there is great potential for further application of this model.

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