## Brian Delius: DEB theory versus MTE 2015/03/27

Studying the flow of energy through ecosystems had provided insights into the mechanisms and modes of ecosystem function and regulation at virtually every scale. However, investigating the flow of energy from the environment through a given organism of a specific species has repeatedly proven to be challenging, particularly over any significant length of time, as organisms of most species are prone to alter the rate at which they take in nutrients from the environment as they grow and mature. When further complicated by the addition of changing environmental variables, models are often either unable to cope with the increasing complexity or they become exceedingly dense and tedious so as to limit their practical value. Arguably, the most popular and widely accepted of the ecological energetic models is commonly referred to as "the metabolic theory of ecology" (MTE). MTE has attempted to overcome the inherent complexity of modeling metabolism by making a few broad assumptions that allow for the elimination of life history variables in the model. The reduction of variables undeniably simplifies these models, but there is some debate as to the magnitude of the cost of such simplifications. In contrast, the Dynamic Energy Budget (DEB) model provides an elegant and integrated means of tracing the flow of energy from a mutable environment through an individual organism by incorporating realistic and experimentally verifiable estimations of species specific life history traits, which effectively balances model complexity and organismal specificity in a way that alternative models fail to do.

In brief, the DEB model takes into an account organism's rates of nutrient ingestion and assimilation, and converts the nutrients to an energy reserve. The DEB model then uses a reserve mobilization rate to divert energy to growth and maturation/reproductive rates. Structural and reproductive maintenance costs are subtracted respectively from each of the two pools of energy mobilized from energy reserves to growth and reproduction; the remainder of the energy diverted to growth and reproduction is then used to calculate the organism's total biomass, energy invested in maturity, and energy allocated to reproduction. Because rates of ingestion, assimilation, mobilization, maturation, reproductive, and growth can all be manipulated, the model is incredibly robust, and is able to be customized to match the life history traits of any organism.

In many ways, the DEB model is in direct philosophical opposition to the MTE model. The MTE model scales body mass and temperature to generate a generalized metabolic rate for a given organism using an extension of Kleiber's law. No species specific physiological or life history traits are incorporated into the model beyond the adjustment of a normalization constant. From a philosophical perspective, the MTE model assumes that every organism of every species, at every point in its lifespan, has a metabolic rate that, after correction for mass and temperature, is essentially identical. Such an assumption greatly reduces the complexity of the mathematical calculations required to model an organism's metabolic rate; however, such simplifications may come at the cost of the model's resolution.

Because the DEB model takes great care to incorporate a wide array of life history traits, it is capable of modeling metabolic differences of an individual organism at different developmental stages, at different points in its reproductive cycle, and under different environmental conditions. When DEB models are

used to explore these sorts of metabolic shifts, model parameters are manipulated with respect to specific physiological processes. In contrast, the MTE model is unable to realistically cope with these sorts of changes except by adjusting the normalization constant or the organism's mass or temperature. Furthermore, when adjusting the normalization constant in the MTE model, no underlying physiological mechanisms are invoked to provide insight into why an organism's metabolic rate is changing. And while empirical data is generally used to appropriately scale adjustments to MTE normalization rates, the actual changes in physiological processes can only be guessed at without the aid of accompanying experiments.

Because of the fundamentally different ways in which the DEB and MTE theories approach modeling metabolism, the two models should be used to answer fundamentally different questions regarding metabolic rates. DEB's careful attention to the modeling of physiological processes make it extremely well suited to study changes in a single organism's metabolic rate as it matures, reproduces, or shifts environmental conditions. Likewise, DEB is also very well suited to make comparisons of metabolic changes across multiple individuals of the same or similar species. However, the relatively complex and mathematically advanced structure of the DEB model that makes it so perfectly well suited to fine scale modeling may be overly precise and effort intensive for studies that want to make broad and general comparisons across a wide range of taxa. Where the DEB theory would require a unique model to be constructed for each taxa, the MTE model could easily be adjusted with empirical calibration of the normalization constants to make comparatively rapid, and less precise, estimations of average metabolic rates of a wide range of taxa.

George E. P. Box famously stated, "... all models are wrong, but some models are useful." The DEB model is undoubtedly a useful and precise tool to assess metabolic change, predict shifts in developmental and reproductive rates in response to varying nutrient availability, and elucidate underlying physiological processes that are responsible for changes in metabolic rate. The much simpler MTE model may be useful to make generalized comparisons of metabolic rates across widely varying taxa, but it ultimately lacks the precision and flexibility offered by the more complex DEB model. Hopefully the DEB model will continue to grow in popularity within the ecological research community so that its precision and flexibility to can be properly exploited to answer essential questions regarding how metabolic rates directly and indirectly regulate and mediate a host of ecological processes.