



Trends in Ecology &amp; Evolution

Figure 1. Dynamic Energy Budget Models Output for (A,B) an Arctic Cod Growing at 8.5°C and (C,D) a Desert Tortoise Growing at 23°C Using Parameters from the ‘Add-my-Pet (AmP) Collection’ [11] under the Assumption of Annual Batch Reproduction. Insets (B,D) show associated relative batch reproduction versus relative (post-oviposition) weight from the simulations, with unbroken lines showing fitted hyperallometric curves and dotted lines showing isometric curves. The reproduction allocation parameter, kappa, is constant (at 0.5) but reproductive output is hyperallometric. For the cod, an increasing speed of drawdown on the reproduction buffer (linear function of age) was assumed. Grey dots in (A) are observed cod mass reported by [1], and in (B) are tortoise carapace length [12]. Mass in (A) is partitioned into structural (somatic) mass, stored metabolites (reserve), and reproduction buffer, with drops in mass signifying reproduction events.

### Supplemental Information

Supplemental information associated with this article can be found online at <https://doi.org/10.1016/j.tree.2018.12.006>.

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## Letter

### Should We Care If Models Are Phenomenological or Mechanistic?

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A recent meta-analysis of published data demonstrated that reproductive output increases disproportionately with size in fish [1]. Building on this observation, we hypothesised that growth slows as animals increase in size because of an increasing allocation of energy to reproduction, and we demonstrated that this hypothesis is plausible by fitting a simple model of energy allocation to growth, reproduction, and maintenance to weight-for-age data for a selection of fish species [2]. The fit of our model to growth data was indistinguishable from that of the well-known models of Pütter [3], von Bertalanffy [4,5], and the ontogenetic growth model (OGM) proposed by West and colleagues [6,7]. However, these and other existing models of growth [e.g., dynamic energy budget (DEB) theory] [8,9] fail to predict hyperallometric reproduction, and we therefore suggested that this disconnect between theory and data requires the revision of existing theory [2].

Kearney [10] undertakes such a revision of DEB theory [8,9], and demonstrates that the handling of the reproduction buffer in DEB can be altered to achieve hyperallometric reproduction in two species, which emerges ‘ . . . either due to the way seasonal reproductive output builds up between years in a species with large eggs and small clutch size (the tortoise), or through an increasing drawdown on reproductive buffer with ontogeny (the cod)’ ([10], supplemental information). He then goes on to suggest that physical constraints offer a more parsimonious universal explanation for the similarity in growth curves among species than does the presence of a universally optimal allocation to growth and reproduction that is consistently favoured by natural selection (e.g., [11,12]). He proposes that explanations based on physical constraints should be sought before other explanations, just as others have argued for the primacy of mechanistic over phenomenological models (e.g., [13–15]). Although we applaud any effort to bring theory and data into alignment, we disagree that mechanistic models are always more valuable than phenomenological models.

Modelling approaches in ecology and evolution span a continuum of approaches from phenomenological to mechanistic [14–19]. Phenomenological models use a mathematical function that can be fitted to data to describe underlying biological processes [16,18]. Mechanistic models explicitly track the details of the component parts and processes of a biological system that are hypothesised to give rise to the data [15,16,18]. Mechanistic models therefore have parameters that describe the processes that occur, without reference to data in any one specific case [15]. Phenomenological models can have substantial predictive power, unless a prediction outside of the current known set of parameters is required, in which case mechanistic models should

be superior [20]. Mechanistic models are particularly powerful if sufficient information exists to make *a priori* estimates of parameters and thereby make predictions that are robust to the state of a system.

Most models lie somewhere between the above definitions, incorporating parameters that are estimated by fitting mechanistic functions to empirical data. This latter approach is the one taken by Kearney [10], in which the data for hyperallometric scaling of reproductive output with body mass [1,2] are used to estimate that, in cod, the reproductive drawdown parameter increases with size. Kearney [10] provides no mechanistic justification for the increasing drawdown of the reproduction buffer, and the approach is therefore phenomenological. Similar approaches are taken in the metabolic theory of ecology (MTE) [21], which includes a normalisation constant that is estimated from data. DEB and MTE are both grounded in first principles, but incompletely so; both models include parameters that must be estimated from data [22,23] and are, *sensu strictu*, phenomenological.

The estimation of parameters from data provides a valuable means of testing mechanistic theories when such parameter estimates can be compared to independent measurements [15]. DEB theory includes the state variables of structure, reserve, maturity, and reproduction buffer [22], and Kearney [10] notes that much confusion in theories of growth relate to the inadequacy of body mass as a state variable. The state variables of DEB are not directly observable [24], however, and therefore their values estimated from model fits cannot be compared to empirically determined values. The fit of Kearney’s [10] revision of DEB to growth data for cod means that hyperallometric reproduction can now be recovered. However, testing the mechanistic basis of this fit directly would require measurement of

changes in the reproduction buffer during ontogeny, which cannot be done: the dissipative process of maturity maintenance cannot be separated from structure maintenance because both are part of standard metabolic rate [25], and state variables cannot be measured, only inferred from fits to data. State variables must therefore be observed indirectly with targeted experiments and evaluated on the basis of conformity with model-derived predictions (e.g., [24] for a discussion of tests to distinguish DEB and OGM). As has been argued by ourselves [2] and others [26,27], the goodness of fit of model predictions to data alone is not a sufficient test of a model. Free parameters derived from fits to data provide too much flexibility, and additional tests are therefore necessary (e.g., [24]).

The power of a model is not dictated by whether it is mechanistic or phenomenological, rather by its capacity to predict biological processes or generate useful testable hypotheses. Phenomenological models such as Kozłowski’s [28] predicted that species subject to elevated mortality rates should evolve to mature and reproduce at a smaller size, and this prediction was borne out by later observations of fishery-induced evolution [29]. The DEB add-my-pet collection includes DEB parameter estimates for hundreds of species of fish (e.g., [22]) but, before Kearney’s adjustment of the reproductive buffer drawdown for cod [10], failed to anticipate widespread hyperallometric scaling of reproductive output observed in fish [1,2]. Instead, standard DEB theory predicted that ‘ . . . an allometric regression of reproduction rate against body weight would result in a scaling parameter between 2/3 and 1, probably close to 1, depending on parameter values’ ([9], p 71). These examples highlight that phenomenological models can have predictive power, and that mechanistic (or apparently mechanistic) models are not automatically sound.

We do not argue for the primacy of phenomenological models over mechanistic ones, or vice versa. We have found mechanistic models to be useful in our own research. We have also made extensive use of quantitative genetic models, which include no information about the allelic states of loci and are therefore phenomenological [17]. Kearney [10] concludes that we have outgrown phenomenological growth models, but that we have not outgrown mechanistic growth models based on a thermodynamically explicit theory of metabolism. Instead of advocating for one modelling strategy over others, we favour a pluralistic viewpoint in which a range of model-based approaches are employed [19], and argue that a model does not have to be grounded in first principles to be valuable. DEB theory is mechanistic but has phenomenological components. DEB failed to anticipate hyperallometric scaling of reproduction. *Post hoc* modifications allow DEB to better reflect reality, but only by making assumptions that have no mechanistic basis and cannot be tested directly.

We agree with Kearney that studies of growth and metabolism conducted in the context of full accounting of energy and mass balances (food in, changes in length and weight, respiration, faeces and eggs out) will be valuable, but we do not agree that an understanding of the processes that yielded these patterns necessarily requires a mechanistic perspective.

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## Science & Society

# Neither Hope nor Fear: Empirical Evidence Should Drive Biodiversity Conservation Strategies

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**In biodiversity conservation, the prevailing consensus is that optimistic messages should be used to inspire people to change their behaviour, but there is scarce empirical evidence that optimistic messages lead to favourable conservation behaviour change.**

## Communicating Conservation

For almost a decade, debate has raged as to whether optimistic or pessimistic messages are better at inspiring the behavioural change needed to halt biodiversity loss. Optimists claim that negative messages can lead to disempowerment, resulting in people failing to take conservation action, while others counter that focusing on good news creates an illusion that there is no biodiversity crisis. Yet there is scarce empirical evidence backing either argument. Indeed, the number of papers advocating for either optimism or pessimism in conservation substantially outweighs the volume of empirical research in this area. We call for the