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Author(s): Benjamin T. Martin, Tjalling Jager, Roger M. Nisbet, Thomas G. Preuss, and Volker Grimm

Source: *The American Naturalist*, Vol. 181, No. 4 (April 2013), pp. 506-519

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/669904>

Accessed: 28/03/2013 17:39

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Predicting Population Dynamics from the Properties of Individuals: A Cross-Level Test of Dynamic Energy Budget Theory

Benjamin T. Martin,^{1,*} Tjalling Jager,² Roger M. Nisbet,³ Thomas G. Preuss,⁴ and Volker Grimm^{1,5}

1. Department of Ecological Modelling, Helmholtz Centre for Environmental Research–Umweltforschungszentrum, 04318 Leipzig, Germany; 2. Department of Theoretical Biology, Faculty of Earth and Life Sciences (FALW), Vrije Universiteit (VU), De Boelelaan 1085, NL-1081 HV Amsterdam, The Netherlands; 3. Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106; 4. Institute for Environmental Research, Rheinisch-Westfälische Technische Hochschule (RWTH), Aachen University, Worringerweg 1, 52074 Aachen, Germany; 5. Institute for Biochemistry and Biology, University of Potsdam, Maulbeerallee, 214469 Potsdam, Germany

Submitted April 12, 2012; Accepted December 3, 2012; Electronically published March 8, 2013

Online enhancement: appendixes, supplemental figures, code.

ABSTRACT: Individual-based models (IBMs) are increasingly used to link the dynamics of individuals to higher levels of biological organization. Still, many IBMs are data hungry, species specific, and time-consuming to develop and analyze. Many of these issues would be resolved by using general theories of individual dynamics as the basis for IBMs. While such theories have frequently been examined at the individual level, few cross-level tests exist that also try to predict population dynamics. Here we performed a cross-level test of dynamic energy budget (DEB) theory by parameterizing an individual-based model using individual-level data of the water flea, *Daphnia magna*, and comparing the emerging population dynamics to independent data from population experiments. We found that DEB theory successfully predicted population growth rates and peak densities but failed to capture the decline phase. Further assumptions on food-dependent mortality of juveniles were needed to capture the population dynamics after the initial population peak. The resulting model then predicted, without further calibration, characteristic switches between small- and large-amplitude cycles, which have been observed for *Daphnia*. We conclude that cross-level tests help detect gaps in current individual-level theories and ultimately will lead to theory development and the establishment of a generic basis for individual-based models and ecology.

Keywords: population dynamics, dynamic energy budget theory, bioenergetics, individual-based model.

Introduction

A major objective in ecology is to link processes at different scales through an understanding of how behavior at macro scales emerges from the behavior of individual compo-

nents of the system. This is especially apparent in population ecology, where individual-based modeling (IBM) has been proposed as a tool to cross between scales and unify their associated subdisciplines, for example, physiological and population ecology (Huston et al. 1988; DeAngelis and Mooij 2005; Grimm and Railsback 2005). However, a well-known drawback of IBMs is that they can be complex and data hungry. Consequently, they often are designed for specific species where sufficient data exist. Model designs are then tied to these species and thus lack generality. This makes model development and analyses inefficient because different models are hard to relate to each other, impeding distillation of general insights from IBMs (Grimm 1999; Grimm et al. 1999).

In contrast to this species-specific approach, some theoretical approaches attempt to deduce the diversity among organisms and ecological systems from generic models of individual-level processes, for example, the dynamic energy budget (DEB) theory (Kooijman 1993, 2010) or the ontogenetic growth model (OGM) based on metabolic scaling theory (Hou et al. 2008). These approaches are based on first principles of bioenergetics and thus focus on common and species-independent aspects of organisms and their performance. They apply the same generic model structure for all species and use variation in parameter values to explain differences in life-history patterns among species.

Such standardized generic models hold great potential for advancing the field of individual-based ecology (IBE; Berger et al. 2002). First, they make model development and communication more efficient. This is important for both theoretical and applied models. Instead of designing models from scratch, standard designs can be used that

* Corresponding author; e-mail: benjamin.martin@ufz.de.

Am. Nat. 2013, Vol. 181, pp. 506–519. © 2013 by The University of Chicago. 0003-0147/2013/18104-53782\$15.00. All rights reserved.

DOI: 10.1086/669904

do not need to be justified in detail, because they have been tested and used before. Second, they facilitate comparing models addressing different species and systems. Differences in model behavior can be more easily ascribed to differences in species-specific traits or system-specific controls, whereas without standard submodels they could be ascribed to virtually any detail of the models' structure. Conversely, when the same model structure is used to model different species, we can understand the differences in population level output as a function of differences in individual-level parameters.

Despite the great potential of generic individual-level models as the foundation for IBMs, their ability to accurately capture the dynamics of higher levels of biological organization remains largely untested. Here we focus on performing a cross-level test for one general theory, Kooijman's dynamic energy budget theory (Kooijman 2010; Sousa et al. 2010). DEB is a general theory that describes life-history traits over time over a range of environmental conditions. DEB theory has been used to model individual-level processes for a wide range of animal species, for example, mollusks (Ross and Nisbet 1990; van Haren and Kooijman 1993; Saraiva et al. 2011), zooplankton (Nisbet et al. 2010), and fish (Pecquerie et al. 2009, 2011), and to model population-level processes for microorganisms, for example, bacteria (Kooij and Kooijman 1994; Hanegraaf and Muller 2001) and phytoplankton (Muller 2011). Yet, a primary motivation for the development of DEB theory was to explain population dynamics in terms of individual life-history traits, that is, to obtain unified theory across levels of biological organization (Nisbet et al. 2000). Surprisingly, so far tests of DEB theory that link individual and population process have been sparse and of limited scope (literature reviewed in Nisbet et al. 2010) or have focused on modeling equilibria or population growth rates, for example, de Roos (2008). Here we therefore develop an IBM for a cross-level test of DEB theory. Our cross-level test serves two purposes: to test how well individual-based population models based on DEB theory predict population dynamics and structure and to use possible deviations between model output and data to identify elements of DEB theory that might need to be improved to better capture population-level phenomena.

For implementing our IBM, we used the software tool DEB-IBM (Martin et al. 2012), which is a generic IBM-based DEB theory. As a model system, we use laboratory populations of *Daphnia magna*, for which we collected independent data sets on individual performance and population dynamics under different environmental conditions. We first use individual-level data to parameterize a model of individuals that is based on DEB theory. Then we use these DEB individuals to simulate population dynamics and compare them to results from independent

population experiments. Our initial comparison of DEB-IBM model output and data revealed a mismatch between the model and data after the initial peak in population density for all population experiments. Specifically, the model did not capture the decline in population density and the subsequent change in density and size structure following the initial population peak. Our conclusion was that the dynamics of the starvation and recovery mechanisms are poorly understood. We therefore discussed and tested several new alternative size-selective submodels of food-dependent mortality and also formulated and tested a new recovery model. Finally, we compared the model's ability to reproduce additional qualitative patterns, for example, the characteristic occurrence of both small- and large-amplitude cycles under certain resource conditions (McCauley et al. 2008).

Methods

DEB theory is designed to capture the energy budget of a wide range of organisms, environments, and questions. Using DEB theory in a specific context requires setting up specific model equations. Here we introduce the core concepts of DEB theory and then briefly explain our model, which includes the "standard" DEB model (see Sousa et al. 2008 for an in-depth introduction) plus specific submodels of processes that are not fully covered by the standard model. A full, detailed description of our model, following the ODD (overview, design concepts, details) protocol for describing individual-based models (Grimm et al. 2006, 2010), and the implementation of the model in NetLogo (Wilensky 1999) are provided in the supplementary material, available online.

DEB Theory

Conceptually, DEB theory is based on three elements: the rate of energy acquisition of an individual scaling with surface area while maintenance costs scales with volume; the "kappa rule" of diverting a fixed proportion, κ , of assimilated energy to maintenance and growth, with the remainder used for development and reproduction; and the inclusion of "reserve." What makes the theory look more complicated is its unique notation system, which allows the theory to be consistent in notation across applications involving properties with different dimensions, for example, energy, mass, volume, proportions of elemental matter, and more. The user manual of DEB-IBM (Martin et al. 2012) gives a straightforward introduction to the notation and conversion among the various versions and parameterizations of DEB theory. In the following, the three elements of DEB theory and the corresponding model are briefly explained.

First, DEB theory recognizes different components of the biomass of an organism: structural biomass, reserve, and a reproduction buffer in adults. Only structure requires energy for maintenance; reserve does not but is used to fuel other metabolic processes. A key assumption in the “standard” DEB model is that the rate of energy acquisition is proportional to the structural surface area of the organism, which could relate to, for example, the area of filtering appendages or gut surface. Maintenance costs are linked to body volume, which is proportional to structural biomass. These assumptions for assimilation and maintenance provide a mechanistic explanation for the widely used growth model developed by von Bertalanffy (1957).

Second, regarding reproduction, DEB theory assumes that throughout their life cycle, individuals allocate a fraction, κ , of their mobilized energy to somatic maintenance and growth and the remainder to maturation and reproduction (fig. 1). In juveniles, there is therefore a constant flux of energy to “maturation” (increasing the organism’s complexity to enable reproduction), which is switched to the investment in offspring at “puberty.” The kappa rule provides a novel explanation for why organisms do not deviate from von Bertalanffy growth when they begin to reproduce. There are three basic life stages: embryo (feeds on an embryonic reserve, not capable of reproduction), juvenile (feeds exogenously, not capable of reproduction), and adult (feeds exogenously, capable of reproduction). Transitions between these stages are assumed to be marked by fixed maturity thresholds.

Third, DEB theory assumes that assimilated energy first enters a reserve compartment, which serves as a buffer. The rate of energy mobilization depends only on body size and reserve density, that is, the ratio of reserve energy over structural body volume, and is calculated using a homeostasis assumption: at constant food levels, the reserve density should, after some initial equilibration, be constant over the juvenile and adult life stages. The derivation of this argument is the most challenging part of DEB theory (Kooijman 2000, p. 37). DEB theory often uses the term “scaled reserve density,” e , which is the reserve density relative to the maximum reserve density that is obtained if individuals are fed ad lib. Because mobilization of energy depends on the reserve density and not on the instantaneous assimilation rate, it is to some extent buffered from rapid changes in food level. The capacity for buffering depends on a parameter called “energy conductance,” $\dot{\nu}$, which determines the mobilization of the reserve. At the same feeding rate, a larger value of $\dot{\nu}$ will lead to lower maximum reserve density and thus less buffering capacity for changes in food availability.

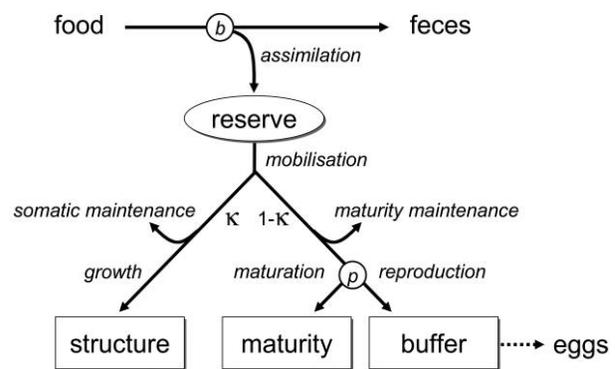


Figure 1: Schematic diagram of the primary DEB state variables (boxes) and fluxes (italics) of the standard DEB model. The circles containing b and p denote maturity switches for birth and puberty, where feeding and allocation to reproduction begin, respectively.

The Model

In the standard DEB model, individuals are primarily characterized by four state variables: structural length, L , which determines actual size, feeding rates, and maintenance costs; scaled reserve, U_E , which serves as an intermediate storage of energy between feeding and mobilization processes; scaled maturity, U_H , a continuous state variable that regulates transitions between the three maturity stages (embryo, juvenile, adult) at fixed maturity levels; and scaled buffer U_R , which is an energy buffer of mature individuals for reproduction; this buffer energy is converted into offspring during reproductive events. Four differential equations specify how these state variables change depending on their current values and environmental conditions, such as food level and temperature. Two additional state variables are needed to characterize the aging process (app. A, available online). We implemented a discretized version of the differential equations using the Euler method. At each time step, individuals forage, then assimilated energy first enters a reserve compartment, from which energy is mobilized to fuel all other processes (see app. A for details). Then, based on the updated DEB state variables, a set of discrete events may occur, such as reproduction or death.

General DEB theory makes no assumptions about how the reproduction buffer is converted into offspring, because too many different strategies exist. We here assumed that *Daphnia* reproduce in clutches, where energy allocated to embryos is accumulated over one molt period (assumed to have a fixed value throughout the life cycle). The embryos develop during the next molt and hatch at the end of that molting period. We augmented the standard DEB model with a submodel describing response to starvation. Within DEB theory, there are several proposed ways to

Table 1: Parameters of the DEB model for *Daphnia magna* and confidence intervals determined via profile likelihoods

Symbol	Description	Dimension	Value	95% confidence interval
DEB parameters:				
κ	Fraction of mobilized energy to soma678	.657–.700
κ_R	Fraction of reproduction energy fixed in eggs95	Fixed value
k_M	Somatic maintenance rate coefficient	t^{-1}	.3314	.327–.336
k_j	Maturity maintenance rate coefficient	t^{-1}	.1921	.150–.236
U_H^b	Scaled maturity at birth	tL^2	.1108	.0989–.123
U_H^p	Scaled maturity at puberty	tL^2	2.555	2.36–2.844
\dot{v}	Energy conductance	Lt^{-1}	18.1	17.89–18.3
g	Energy investment ratio	...	10	Fixed value
Aging parameters:				
\ddot{h}_a	Weibull aging acceleration	t^{-2}	3.04E–6	1.70E–6 to 4.60E–6
s_c	Gompertz stress coefficient019	.00911–.0273
Prey dynamics parameters:				
$\{J_{XAm}\}$	Surface-area-specific maximum ingestion rate	No. $L^{-2}t^{-1}$	3.80E+05	3.7E+5–4.0E+5
K	Half-saturation coefficient	No. L^{-3}	1,585	1,571–1,600
<i>Daphnia</i> specific parameter values:				
Molt time	Time between reproductive events	t	2.8	...
V_{crit}	Proportion of structural mass below which <i>Daphnia</i> experience starvation mortality4	...
M	Reserve-dependent mortality coefficient	t^{-1}	Varied	...

Note: Units: time (t) = days, structural length of animals (L) = millimeters, abundance of prey = No., and length of the environment (l) = centimeters. A dot over a symbol indicates a rate parameter (two dots represent t^{-2}). Braces around a symbol indicate the parameter is per unit surface area (see Kooijman 2010 or Martin et al. 2012 for the full explanation of notation).

include mortality via starvation (Kooijman 2010), which occurs when the energy mobilized from the reserve and allocated to the soma is not sufficient to pay somatic maintenance costs. A possible starvation submodel assumes that animals can redirect energy from the $(1 - \kappa)$ portion normally allocated to maturation (embryos and juveniles) or reproduction (adults; Kooijman 2010). Our analysis of this set of starvation submodels revealed starvation times far too short (<1 day at 20°C), and they were thus ruled out. This point was previously noted for *Daphnia pulex* (McCauley et al. 1990).

We selected an alternative starvation submodel for our simulations, which assumes that when there is not enough energy to pay somatic maintenance costs, individuals can “burn” structure to pay these costs (“shrinking”). *Daphnia* can survive extended periods of starvation, where their body mass can fall to 30%–50% of their previous maximum body mass (Perrin et al. 1990; Bradley et al. 1991; Cleuvers et al. 1997; Vanoverbeke 2008). We selected a mortality submodel similar to those of Vanoverbeke (2008) and Rinke and Vijverberg (2005), where death occurs when organisms’ mass falls below some threshold of its previous maximum mass. We selected a critical threshold (V_{crit}) of 40% of maximum weight achieved so far, after which in-

dividuals experience a high per capita death rate of 0.35 day⁻¹ (Rohrlack et al. 1999; Rinke and Vijverberg 2005).

Parameterization

The scaled DEB model used by DEB-IBM has eight parameters, with two additional parameters needed for the aging submodel and two parameters for the feeding submodel (table 1). The processes in DEB theory are abstractions; therefore, most of the parameter values cannot be measured directly. Rather, parameters influence various fluxes, which determine observable output like body size over time, reproduction, or survival (Kooijman 2010; Nisbet et al. 2012). Thus, DEB model parameters for a species can be obtained by fitting the model to observed life-history traits over time (Lika et al. 2011). We used a data set for *Daphnia magna* comprising individual growth and reproduction data at four food levels (Sokull-Kluettgen 1998; details of parameterization given in app. B, available online).

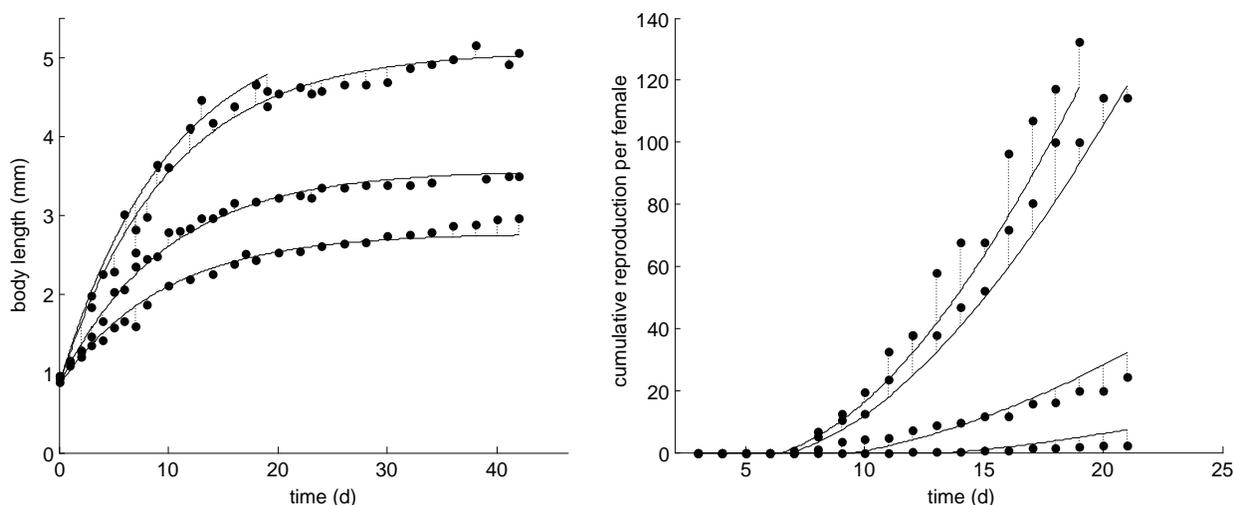


Figure 2: Data for growth (A) and reproduction (B) at four food levels (100,000, 25,000, 5,000, and 1,000 cells mL^{-1}) and the DEB model fit. The experiment was conducted in a flow-through system in 500 mL ADAM medium at a flow-through rate of 360 mL h^{-1} .

Simulation Experiments

Simulations were designed to mimic the experimental settings described in Preuss et al. (2009). Population dynamics were driven by “semi-batch” feeding conditions, that is, a normal portion of food was added each day Monday–Thursday to a 900-mL beaker containing a *Daphnia* population, and three times the normal food level was added on Friday. Three times a week the population was counted in three size classes. The experimental data sets consisted of two experiments conducted at a “low” food level (0.5 mg C day^{-1}), starting with either 5 neonates <24 h old (low-N) or 3 adults and 5 neonates (low-NA), and one experiment conducted at “high” food level (1.3 mg C day^{-1}) that began with 3 adults and 5 neonates (high-NA), resulting in three treatments, with 4 replicates each. For each experimental setup, we ran the model for 42 days and 100 replicates and compared the mean, maximum, and minimum of total population abundance and the abundance of three size classes to corresponding experimental observations. For details of the experimental setups in the model, see the ODD model description in appendix A.

Stochasticity enters the simulations in three ways. First, all mortality either due to aging or starvation is probabilistic. Second, individuals vary in parameter values. We followed the method used in Kooijman et al. (1989), where individuals have a lognormally distributed scatter multiplier that affects the maximum surface area specific assimilation rate. This parameter is scaled out of the model, but the two maturity threshold parameters, U_{H}^{b} and U_{H}^{p} (where

superscripts b and p denote birth and puberty); the maximum surface-area-specific ingestion rate, $\{J_{\text{XAm}}\}$; the half-saturation coefficient, K ; and the compound parameter, g , which is the cost of synthesizing one unit of structure over the product of κ and the maximum reserve density, are all affected by the scatter multiplier (Kooijman 1989; Martin et al. 2012; and ODD of this article). Finally, we assume the amount of food added each day varies due to experimental error, with a standard deviation equal to 10% of the desired food concentration.

Results

Individual-Level Parameterization

Parameterization revealed that the parameters g and \dot{v} (table 1) could not be specified individually (app. B; fig. 2). Further analysis revealed that these parameters positively covaried and their ratio was well determined. This indicates that, at least for *Daphnia* in the given settings, one of these parameters is redundant. An increase in \dot{v} and g together indicates an increasing rate of reserve mobilization and simultaneously a decrease in the size of the reserve. As both parameters increase toward infinity, one ultimately ends up with a “reserveless” DEB model.

To determine the population-level effect of using different values for parameters linked to the reserve dynamics, we ran simulations using parameter sets where the value of g was fixed at incrementally higher values and all other parameter values were estimated (app. B). We found that using fixed values of g within the likely range (10 to

infinity) had negligible influence on population level output. Therefore, the results from our analysis would be independent of the value chosen for g , and we used the parameter set with g fixed at 10 for all further simulations. Using the resulting parameter set, the DEB model explained most of the variation in growth ($R^2 = 0.986$) and reproduction ($R^2 = 0.967$; fig. 2).

*Population-Level Results for the “Standard”
DEB-IBM Daphnia Model*

The model closely matched observations during the initial population growth phase, capturing population growth rate, size distribution, and peak population density for all experimental settings (fig. 3 for the low-N setting; low-NA and high-NA shown in fig. S1, available online). However, after the initial population peak, model predictions and data diverged. This mismatch was not resolved by changing the model parameters within their confidence intervals. We quantified the overall fit by dividing each time series into two periods, the population growth phase and the population decline phase. All predictions after the population peak in the simulations were grouped into the decline phase and all before into the growth phase. We then compared overall agreement of the predictions and observations of total density and the three size classes for each of the two periods, for all experimental setups (fig.

4). As a way of comparing goodness of fit, we report “prediction” R^2 values for each period (growth and decline phases), as well as for the data set as a whole (see app. B). Our analysis revealed a much poorer fit between model predictions and observations during the decline phase (table 2).

Alternative Models of Starvation and Recovery

We implemented an additional starvation submodel (*Daphnia* still have a high probability of dying if they fall below a critical proportion of their previous mass), where mortality was inversely linked to reserve density, e , which is a time-weighted average of feeding history (app. A):

$$\text{Pr}(\text{mortality})d^{-1} = M(1 - e),$$

where M is the reserve-dependent mortality coefficient. To check whether starvation was size selective in the experimental systems, we compared three versions of this new submodel by applying it only to juveniles (negative size selection [NegSS]), only to adults (positive size selection [PosSS]), or to all *Daphnia* (neutral size selection [NeutSS]).

Because we also wanted some indication of how well the starvation models, once parameterized, were able to capture the dynamics of population in other experimental settings, we restricted our parameterization data set to one

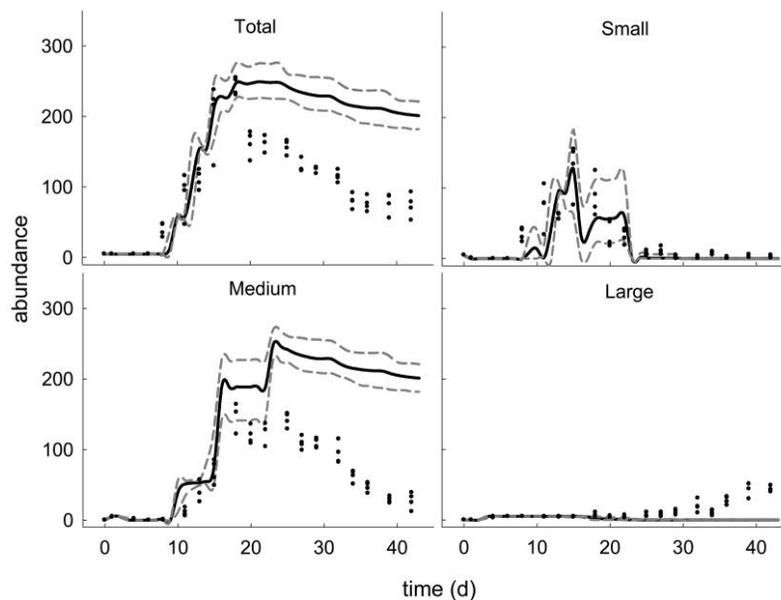


Figure 3: Comparison of data and DEB-IBM predictions at the population level for the low-N experiment. Experiments were initiated with 5 neonates in a 900-mL beaker, and 0.5 mg C was added per day. Simulations with DEB-IBM replicated the experimental conditions. Figures show the mean (thin black line) and maximum and minimum (dashed gray lines) of 50 simulations. Simulations for the low-NA and high-NA experiments are shown in figure S1, available online.

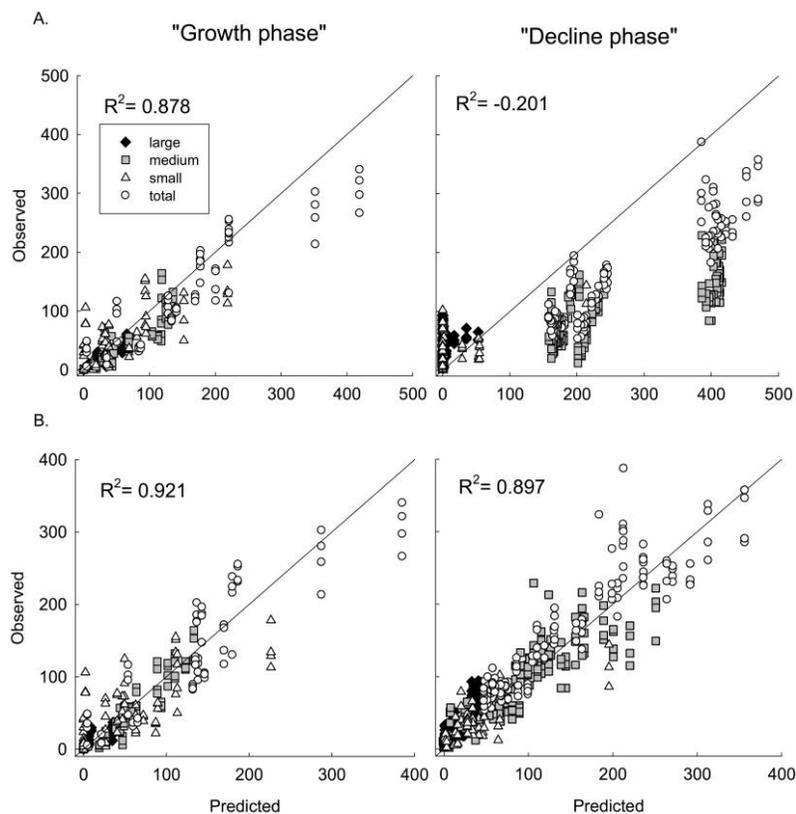


Figure 4: Observed versus predicted values for all three population experiments for total abundance (circles) and three size classes: adult (diamonds), juveniles (squares), and neonates (triangles) for the standard model (A) and the adapted model (NegSS), with the additional juvenile food-dependent mortality submodel (B). The data are divided into two panels: data before the population peak (growth phase) and after (decline phase).

of the population experiments (low-N). We then compared the goodness of fit of the three starvation submodels and to the complete data set (all three population experiment setups; see app. B for details).

Furthermore, standard DEB theory assumes that a *Daphnia* that has shrunk to, for example, 50% of its previous maximum mass behaves physiologically the same as a *Daphnia* with the same state that has not shrunk. This is, however, in disagreement with experimental observations at the individual level, as *Daphnia* recover mass much faster than expected following the standard DEB equations (Perrin et al. 1990; Bradley et al. 1991). One possible explanation is that although *Daphnia* shrink, they maintain their ability to ingest and assimilate energy according to their previous maximum size. This may be due to the fact that *Daphnia* do not shrink in physical length, as they live within a rigid carapace, and thus their feeding appendages keep their previous size even as the mass of the individual shrinks. This can be modeled in DEB by using the maximum achieved value of length in the assimilation formula.

By using this modified recovery model, we found (data not shown) a large improvement in predictions for the timing of individual-level recovery compared to data and predictions from Perrin et al. (1990). Although both models underpredict time to recovery compared to the data, the “fast” recovery model predicts a time to recover (4 days) much closer to the data (between 1 and 3 days) than the “default” recovery (7 days).

Population-Level Results for the Modified DEB-IBM Model

Parameterization of the three starvation submodels on the low-N data set resulted in values of 0.085, 0.39, and 0.090 day^{-1} for M , the mortality constant for the NeutSS, PosSS, and NegSS submodels, respectively. The NeutSS ($R^2 = 0.938$) and NegSS ($R^2 = 0.929$) submodels led to substantially better fits on the parameterization data set (low-N) than the PosSS ($R^2 = 0.638$). On the complete data set (all three population experiments), all three modified

Table 2: R^2 values for the default DEB-IBM and various adapted models

	R^2			$-\ell$
	Growth phase	Decline phase	Total	Total
Standard DEB model	.878	-.2013	.318	199,643
Food-dependent mortality submodels:				
Neutral (all)	.920	.873	.903	28,249
Negative (juveniles only)	.921	.897	.916	24,358
Positive (adults only)	.910	.342	.618	111,757

Note: The R^2 values are shown for before (growth phase) and after (decline phase) the population peak and the entire data set for total abundance, and for each of the three size classes, over 42-day population experiments at three experimental settings. Additionally, the negative log likelihood ($-\ell$) is given for the standard DEB model and the three modified mortality submodels.

starvation submodels better matched the data relative to the standard model, and most of this improvement in model fit relates to increased predictive power during the decline phase (table 2). While the NeuSS and NegSS models fit the parameterization data set nearly equally well (fig. S2, available online), the NegSS model provided the best fit to the complete data set (table 2). This was driven by a better agreement of model and data for the independent data sets, specifically for the high-NA experiment (fig. 5).

The results of the starvation recovery submodel showed an improved fit over the standard recovery model (fig. 6; fig. S3, available online). This result is mainly due to the lack of production of offspring for the standard dynamics compared to the revised model and experimental observations. This lack of production of new offspring then ultimately leads to almost no *Daphnia* in the intermediate size class and results in a population dominated by large *Daphnia*.

Discussion

Having a generic model relating population dynamics to the size, maturity, energy reserves, and current food intake of its constituent organisms would raise individual-based ecology (IBE) to a completely new level. IBE would be then based on firm and increasingly tested theory (Grimm and Railsback 2005). Species would still be expected to show different physiological and behavioral strategies, but with IBMs based on DEB theory or any other kind of generic theory, we would have a much better idea of where and when to use standard approaches and where to look for more specific submodels.

Did our attempt to predict population dynamics from what individuals do indicate that DEB theory is such a generic theory for IBE? The answer is both yes and no. On the one hand, the standard DEB model without ad hoc modifications accurately predicted the population growth rate and peak density of laboratory *Daphnia* populations in different conditions from a model parameter-

ized at the individual level. Our study provides at least one point of evidence suggesting that the DEB model with little modification may be used for many applied purposes requiring an understanding of how population growth rate varies as a function of the environment. For example, in ecotoxicology, population growth rate often is proposed as a composite indicator of toxicity of chemicals, which simultaneously takes into consideration reductions in growth, reproduction, and survival (Forbes and Calow 2002). DEB theory can easily be used to link individual performance under toxicant stress to effects on the population growth rate (see Jager and Klok 2010), and thus this work further supports its use.

On the other hand, the unmodified model did not accurately capture the dynamics after the population peak, where there was little food per *Daphnia*. In contrast to the model predictions, the experimental observations showed a sharp decline in *Daphnia* density. This decrease in density also decreased competition for food, allowing those *Daphnia* that survived to consume more and thus grow at faster rates. For this reason, we saw a discrepancy not only in the population density between model predictions and observations but also in the size distribution.

The discrepancy between model predictions and observations for declining populations turned out to be highly informative. It was our hope that cross-level testing DEB would lead us to identify potential limitations of standard DEB theory and possibly find ways to overcome these limitations. Due to the lack of data on starvation, we had to do this inversely, that is, infer from population-level patterns to the individual-level process of starvation. We contrasted three phenomenological starvation models, which differed in their size selectivity. We found that if we assumed negative size selection, that is, starvation of smaller individuals, agreement between predicted and observed population dynamics and structure was improved. One notable contradiction between predictions and observations for the PosSS model was a lack of neonate production after the initial population growth phase. This

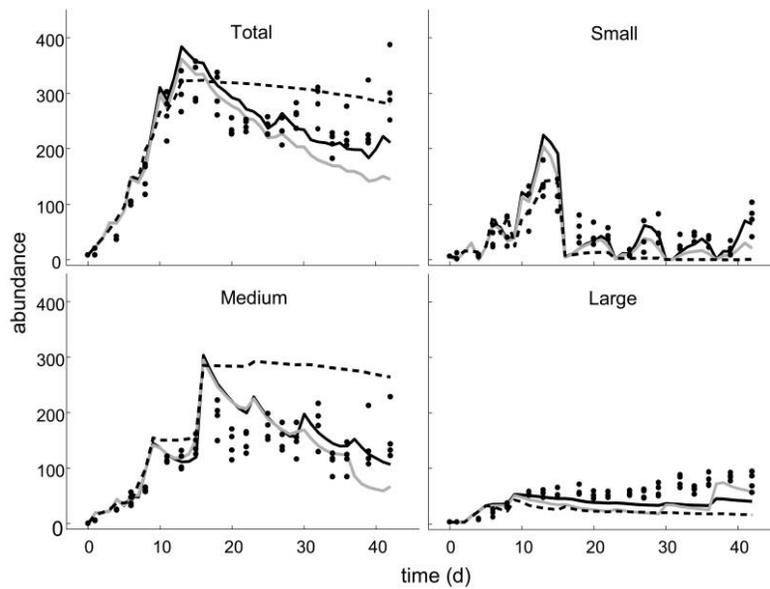


Figure 5: Comparison of the performance of three starvation submodels with data from the high-NA experiment. In each of the three models, a one-parameter food-dependent mortality submodel was applied, but models differed in that it was applied to either only juveniles (solid black line), only adults (dashed black line), or all *Daphnia* (gray line). Simulations for the low-N and low-NA experiments are shown in figure S2, available online.

trend is best observed in the high-food-level experiment (fig. 5). The NeutSS model captured the dynamics and size structure of the population in that it predicted bursts of neonate production; however, compared to the NegSS model, these bursts were too small as there were fewer adults due to the non-size-selective mortality. Consequently, prediction of neonate production in the NegSS model was most appropriate, also leading to the more accurate predictions of the total population abundance (table 1; fig. 4B).

The outcome of our analysis is supported by the previous work on the same population data set using an empirical individual-based population model (Preuss et al. 2009), in which the decline of the population density after the peak was explained as a mixture of starvation and crowding. Crowding causes negative interference (Goser and Ratte 1994) among daphnids, leading to life-strategy shifts and reduced feeding even at the same level of food (Goser and Ratte 1994; Cleuvers et al. 1997). Within this model a crowding submodel was used, calibrated on individual-level data. One of the main factors in this crowding submodel was the increased mortality of juveniles (Preuss et al. 2009), as was also found in this analysis and attributed to starvation.

Increased juvenile food-dependent mortality also was proposed in a different model and experimental system for capturing another aspect of *Daphnia* populations

(McCauley et al. 2008). It has been found in experimental systems (McCauley et al. 1999, 2008) that when *Daphnia* feed on a dynamic prey source, the *Daphnia* population and its algal resource may exhibit either small-amplitude (SA) cycles or large-amplitude (LA) cycles. Replicate populations may exhibit either dynamic pattern and on occasion may alternate between these two multiple attractors. When cycles are observed in the field, the predominant pattern is SA cycles (Murdoch et al. 1998). Besides the magnitude of the fluctuations, the key diagnostic feature of the two cycle types is that in SA cycles, the juvenile development time (time from birth to reproducing adult) is longer than the period of the population cycles, while in the LA cycles, the juvenile development time is shorter than the cycle period (McCauley et al. 2008).

To explore the origin of these dynamics, McCauley et al. (2008) developed a deterministic, two-stage-structured (juveniles and adults) bioenergetic model that includes food-dependent mortality rates estimated separately for adults and juveniles. Their parameterization generated higher food-dependent mortality coefficients for the juvenile stage class than the adults; however, it was not identified as the driver of the bistability. More recently, Ananthasubramaniam et al. (2011) attributed the stabilizing mechanism responsible for generating the small-amplitude cycles to the presence of adults that survived through the population decline phase and were able to reproduce

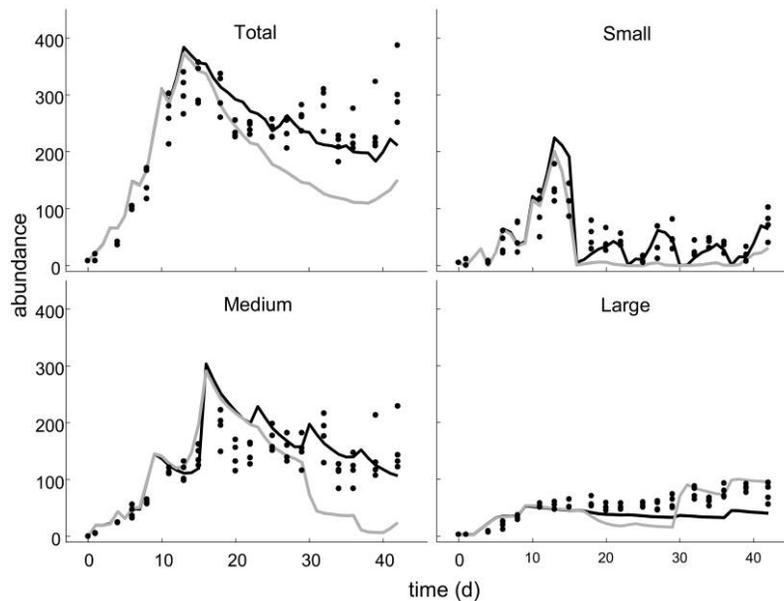


Figure 6: Comparison of alternate starvation-recovery assumptions against the high-NA data set. The gray line shows the scenario where individuals feed at a rate proportional to their current length, while the black line shows the average of 100 model simulations when individuals feed at a rate proportional to their maximum length attained. Simulations for the low-N and low-NA experiments are shown in figure S3, available online.

shortly after the algae population began to recover. This is remarkably similar to the pattern we see in the high-food experiment where the bursts of neonate production observed during the decline phase and the subsequent leveling off of the population decline were predicted only by the NegSS model.

To test whether our model captures, without any further calibration or modification, the SA/LA cycle patterns explored by McCauley et al. (2008), we used the NegSS model, but instead of simulating the populations in batched environments, we let them feed on a prey following logistic growth. In agreement with previous models, the populations exhibit exclusively SA cycles when the carrying capacity of prey is low and LA cycles when the carrying capacity of the prey is high. Most interestingly, the model also captures the dynamic at intermediate prey carrying capacities where the population exhibits the multiple attractors (LA and SA cycles) proposed for previous models and observed in the lab populations. Particularly convincing is that, as in experimental observations, the model also captures the key diagnostic feature, that under SA cycles the mean juvenile development time was longer than the cycle period, while the opposite was found for LA cycles (fig. 7). We take this finding as strong evidence that our modified DEB model is a realistic and comprehensive representation of laboratory *Daphnia* populations and is

able to reproduce population-level patterns for a wide range of environmental settings.

Our results highlight the importance of understanding resource-dependent mortality for making accurate cross-level predictions. Surprisingly however, this remains a poorly developed area of research. From our analysis of size-dependent mortality submodels, it is clear that not only the overall starvation tolerance of a species is important but that relative tolerance of small and large individuals in a population greatly influences the dynamics (see also de Roos and Persson 2013). Our initial assumption was that mortality is triggered when mass falls below some threshold of the previous maximum mass, so the size dependence of resource-dependent mortality is determined largely by how two fluxes, assimilation and maintenance, scale with body mass. The two most popular theories for individual growth, DEB and OGM, always infer either neutral starvation tolerance or a greater starvation tolerance in juveniles depending on the food conditions. In the case of absolute starvation (going from high food to no food immediately), both theories predict that time to starvation will be independent of body size. In partial starvation, when there is some food level available but where the assimilation flux is less than the energy needed to satisfy the maintenance flux, smaller individuals have an advantage over larger ones because both theories as-

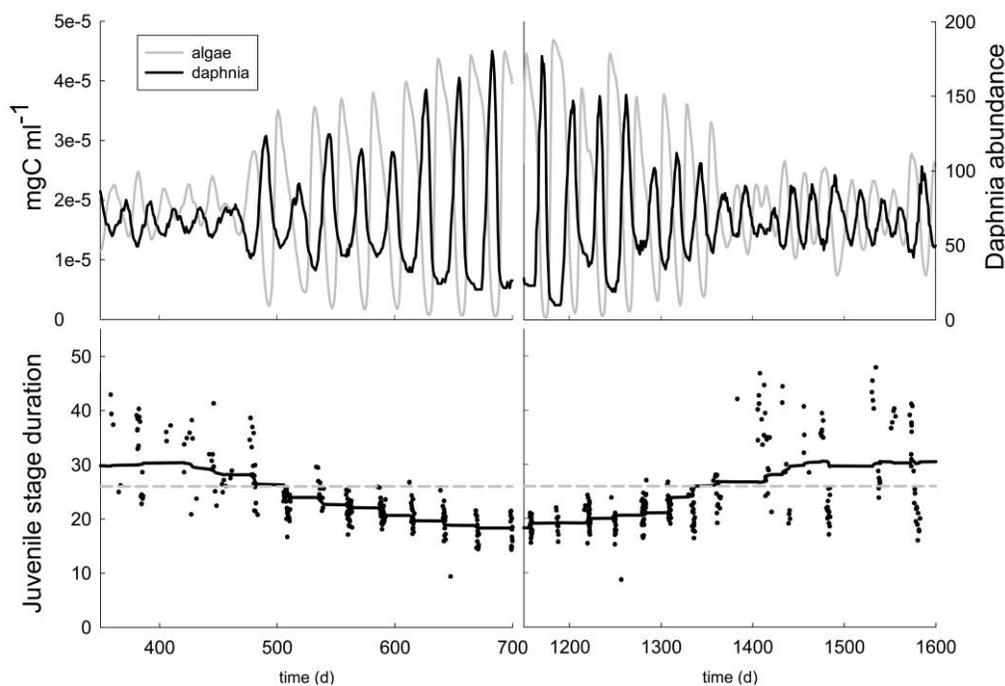


Figure 7: Two characteristic simulations, showing the switches between multiple attractors of large-amplitude and small-amplitude cycles. Simulations were run using the NegSS model where the *Daphnia* feed on a prey source following logistic growth ($r = 1.5$, $K = 5e - 5$ mg C mL⁻¹) in a 30-L system. Simulations were initiated with 5 neonate *Daphnia*.

some decreasing mass-specific assimilation rate with size. Thus, both theories contradict our findings.

While there is relatively little information on the ontogeny of starvation tolerance, the few data that do exist support the indirect conclusions, made from population-level analyses, that starvation tolerance increases with size intraspecifically (McCauley et al. 2008; this study). For two species of *Daphnia*, adults survived longer without food than neonates (Tessier et al. 1983). Additionally, two separate studies on copepods found a clear monotonic pattern of increasing starvation tolerance with size/development for *Calanoides carinatus* (Borchers and Hutchings 1986) and *Pseudocalanus newmani* (Tsuda 1994). If these observed trends turn out to be general, it would suggest both formulations (DEB and OGM) of individual resource dynamics need revisiting. Several hypotheses could explain increasing starvation tolerance with increasing size within a species: (1) V_{crit} could decrease as a function of size; larger individuals can shrink to a lower proportion of their previous maximum mass before they starve. (2) Specific energy storage may increase with size. (3) Mass-specific maintenance costs may decrease with size. (4) Energy utilization to development may be partially inflexible (smaller individuals continue to catabolize energy stores to continue development for some time after food levels decrease). There are not enough data

available to test which if any of these mechanisms may be a valid explanation of the observed trends. What is clear is that due to the importance of the mechanism in determining the types of population dynamics that emerge, no generic theory will be able to capture dynamics at the population level from a generic individual model without accurately capturing the dynamics of how resource-dependent mortality scales with size.

In addition to the size-selective nature of food-dependent starvation risk we also investigated the consequence of assumptions of recovery after a long period of starvation. The standard DEB model does not distinguish between “novel” somatic growth and recovery somatic growth. We tested this assumption against individual-level data (Perrin et al. 1990) and revealed that this assumption grossly underestimated recovery of somatic mass. We thus used an alternate assumption where recovering individuals retain the performance abilities of their previous maximum size. This modified model performed much better at both levels of biological organization tested, although recovery of somatic growth was still underestimated at the individual level. With the new assumption, adult *Daphnia* were able to assimilate food more quickly when food levels began to recover, resulting in neonate production in agreement with observations from the low-NA and, to a greater

extent, high-NA experiments. The poor performance of the default recovery submodel highlights the fact that “novel” and “recovery” somatic growth cannot be treated as equivalent. As most animals can survive periods of starvation by burning existing biomass, this conclusion may not be unique to *Daphnia*.

Our results also bring into question the need to include the state variable “reserve” for the purpose of predicting population dynamics from the characteristics of individuals. We found that the parameters associated with the speed of reserve mobilization and hence the size of the reserve are not easily specified using growth and reproduction data at multiple food levels. Thus, parameterizing the reserve accurately would require some additional data or strong assumptions, for example, relating to the duration of the embryonic period. From our analysis for *Daphnia*, it appears allowing individuals to burn structural body mass to pay maintenance costs is an adequate substitute for reserve to capture how fluctuating food levels affect growth and reproduction output at the individual and population level. However, if reserve is not included, our results suggest mortality should be linked to energy assimilation rather than death occurring only when animals fall below some proportion of their previous mass, as was assumed by McCauley et al. (2008).

In the population experiments, variation in food levels during the day were quite extreme, transitioning from ad lib. feeding conditions during the first few hours after food was added to no food. Yet the reserveless model performed nearly identically to the model with reserve without the resource-dependent mortality submodel at all experimental conditions tested (fig. B2, available online), a finding consistent with previous work using biomass-based models (reviewed by Nisbet et al. 2010). Including the resource-dependent mortality term with the parameters derived when reserve dynamics were fixed to be very fast (g fixed to 100) results in negligible deviations in the population dynamics from those resulting from the parameter set used in this study (g fixed to 10; data not shown). This may be because the “true” maximum reserve density for *Daphnia* is small enough that the time lag between changing food levels and changing mobilization is small. There is some limited evidence of this relating to energy allocated to reproduction; see Tessier et al. (1983) and related discussion by McCauley et al. (1990). The interspecific scaling laws of DEB predict that maximum reserve density will increase with the maximum size of the species, and thus, for larger species the inclusion of reserves may be important.

Whether or not a reserveless model is still actually a DEB model is a matter of semantics. Our concern lies more with identifying the most useful general models as a basis for IBE. One may question, without the reserve

state variable, how the theory differs from other generic models of individual metabolism such as the OGM. Here the biggest advantage of using DEB as opposed to the OGM is not the inclusion of reserve but other distinctive aspects of DEB. For example, OGM does not consider how or from where energy is allocated for reproduction or what mediates life-stage transitions; clearly these are required for capturing population dynamics. With additional assumptions, the OGM might perform similarly to DEB—but this would mean the two descriptions were themselves converging.

How far we can go with generic theory in an IBM context? It may be that the deviations between model predictions and data at the population level are due to species-specific deviations from the DEB model. If species-specific submodels are unavoidable, having a generic model at least reduces the number of structural differences among models of different species and thus increases their comparability. However, it is also possible that generic theory may be able to account for starvation and recovery, but this theory has not been developed. It seems most likely that the answer is some combination of both; there may always be some situations where species-specific models are needed when highly accurate predictions are required; however, it is also likely that with further testing and development we can vastly improve the predictive capabilities of our generic models. What is promising is that the processes that required modification in our study are not species specific; starvation and recovery from starvation are ubiquitous in natural populations. Further experiments at the individual level to guide theory development, especially relating to starvation and recovery, and cross-level experiments to tests theory at the population level are needed. Until these theories are developed, DEB-IBM still serves as a useful starting point that handles the majority of other relevant aspects of individual life history (growth, development, and reproduction).

Acknowledgments

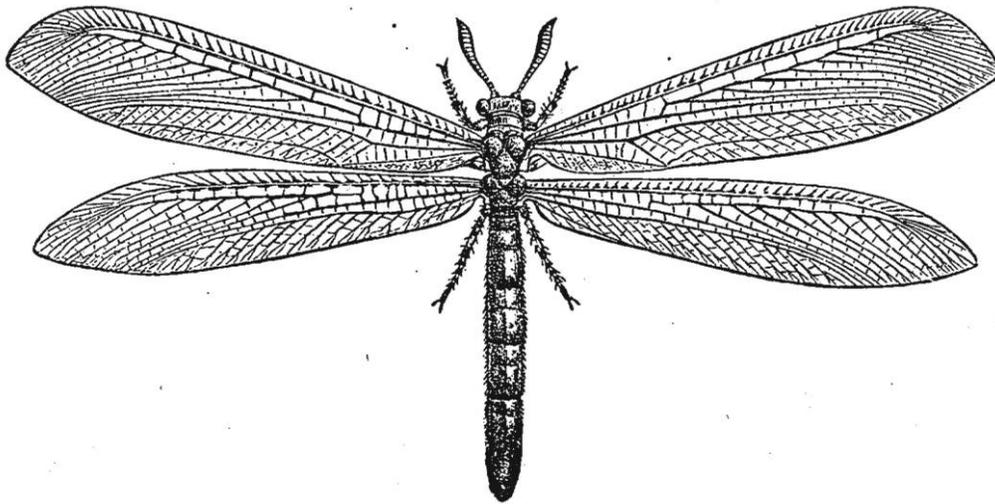
We thank B. Ananthasubramaniam, F. Hartig, L. Stevenson, and E. Zimmer for helpful discussions and two reviewers and the editors for helpful comments. B.T.M., T.J., T.G.P., and V.G. acknowledge support from the European Union under the Seventh Framework Programme (project CREAM, contract PITN-GA-2009-238148). R.M.N. acknowledges support from the National Science Foundation (NSF) under grant EF-0742521 and from the NSF and the US Environmental Protection Agency under Cooperative Agreement EF-0830117.

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Associate Editor: Pejman Rohani
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“On the twenty-ninth of August, while hunting spiders among the rocks on the hill north of Bartholomew’s pond in South Danvers, Mass., I unexpectedly found the pit of an ant-lion (*Myrmeleo immaculatus* De Geer), in a clear space under the shade of a large boulder.” From “The Ant Lion” by J. H. Emerton (*American Naturalist*, 1871, 4:705–708).