

Predator–prey dynamics and the plasticity of predator body size

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Summary

1. Body size is of fundamental importance to the structure and function of natural systems, yet the factors selecting for certain body sizes are still not well understood. Resource supply levels clearly play a role in setting size, but in current theory, optimality functions for body size are not tied to the population dynamics that govern resource supply, minimizing our ability to understand how body size evolves in response to the ecological context.

2. We integrated the supply-demand (SD) model of body size evolution with a model of predator–prey dynamics to create a dynamic SD model that describes predator body size variation through time. We tested the model with experimental data on body size and abundance dynamics in the *Didinium*–*Paramecium* predator–prey system. We used a new differential equation fitting approach along with independently estimated parameters to determine whether the model could simultaneously capture both abundance and body size dynamics.

3. The dynamics were well described by the model, supporting the notion that body size changes to match bodily demand for resources with the available supply of resources. Surprisingly, despite the 10-fold variation in *Didinium* body size, we found that static model parameters were sufficient to describe the data, suggesting a lack of eco-evolutionary dynamics.

4. A pressing need in ecology is to be able to predict changes in body size under novel scenarios, especially climate warming. The dynamic SD model does this by linking body size to the ecological context in an eco-evolutionary framework. Our approach expands our ability to understand rapid linked changes in traits and abundance.

Key-words: body size evolution, eco-evolutionary dynamics, mutual interference, phenotypic plasticity, predator–prey dynamics, supply-demand model

Introduction

Body size is a fundamental trait linked to many other traits and functions (Peters 1983; Calder 1996). Body size is a strong predictor of ecological interactions because the parameters that govern trophic exchanges between consumers and their resources are functions of size (Yodzis & Innes 1992; Brose 2010; DeLong & Vasseur 2012a). In addition, the size of consumers is tightly linked to the size of resources, causing food webs to be structured by size (Brose *et al.* 2006; Riede *et al.* 2011; Yvon-Durocher *et al.* 2011). It is thus critically important to understand what factors determine body size.

Although some proximate mechanisms for setting size are known (Davidowitz & Nijhout 2004), there is still great difficulty in predicting body size changes under novel

scenarios such as altered food conditions or warmer temperatures. It is still an unsettled question, for example, whether body size is generally set at values that maximize fitness or at values that reflect physiological constraints, independent of the fitness consequences. There are thus unresolved differences among the models that focus on varying levels of proximate and ultimate factors influencing body size (Roff 1986; Panov & McQueen 1998; West, Brown & Enquist 2001). As a result, predicting changes in body size remains quite difficult.

Our inability to predict changes in size from mechanistic theory is a major setback for understanding the effects of climate change on ecological systems. Many species may get smaller across generations as temperatures increase (Daufresne, Lengfellner & Sommer 2009; Forster, Hirst & Atkinson 2012), with potentially important consequences given the role that body size plays in setting ecological interactions (DeLong & Vasseur 2012a; Schneider, Scheu & Brose 2012). Yet many factors in addition to temperature, such as resource levels, may interact in space and

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time to influence body mass patterns (Meiri, Yom-Tov & Geffen 2007; Yom-Tov & Geffen 2011), indicating that a more mechanistic and integrative approach to predicting body size evolution and patterns is needed.

The ecological dynamics that result from trophic interactions also are likely to influence the forces that set size. For example, when the availability of prey changes through time, it can potentially select for different sized predators (Montagnes & Lessard 1999), creating temporal dynamics in body size. These changes in body size may be linked to changes in demographic rates (Ozgul *et al.* 2010), indicating that it is necessary to link body size to demographic parameters in models of population dynamics. Such a link implies that body size dynamics may mediate eco-evolutionary interactions (Yoshida *et al.* 2003), as traits vary through time in response to changing size.

To bring ecological context to bear on body size evolution, in this paper we link an optimality model for the evolution of body size directly to the ecological dynamics driving resource supply. The supply-demand (SD) model (DeLong 2012) proposes that the optimal body size is that which matches bodily resource demand to the expected environmental supply of resources on a *per capita* basis. The logic is that an organism that is not large enough to use all of the resources that are available will be competitively inferior to an organism that is large enough to do so, while an organism that is so large it cannot meet its nutritional needs will suffer survival or reproductive costs. Thus, the most fit body size is the one that maximizes total resource use given the environmental constraint. The SD model has not been widely tested, but it has successfully predicted the magnitude of body size change in response to temperature for the predatory protist *Actinosphaerium* (DeLong 2012). In this article, we first integrate the SD concept with a classic predator–prey model to produce the dynamic SD model, and we then test the model with new experimental data on the protist *Didinium nasutum* (hereafter *Didinium*) consuming the protist *Paramecium aurelia* (hereafter *Paramecium*).

The model

Our approach begins with the commonly used MacArthur–Rosenzweig (MR) predator–prey model (Rosenzweig & MacArthur 1963):

$$\frac{dR}{dt} = rR \left(1 - \frac{R}{K} \right) - Cf(C, R) \quad \text{eqn 1a}$$

$$\frac{dC}{dt} = eCf(C, R) - dC \quad \text{eqn 1b}$$

The MR model includes logistic growth of the resource R , with intrinsic rate of growth r and carrying capacity K . The consumer C has a type 2 functional response f , that is dependent on the density of both the resource and the consumer (that is, it includes interference competition), as is appropriate for *Didinium* (Salt 1974; Jost & Ellner 2000;

DeLong & Vasseur 2013). Specifically, we used the Hassell–Varley–Holling (HVH) constant interference model (Hassell & Varley 1969; Sutherland 1983; Arditi & Akçakaya 1990; DeLong & Vasseur 2011), $f(C, R) = ((aRC^m)/(1 + ahRC^m))$, where a is the area of capture, h is the handling time and m is ‘mutual’ interference. Other functions were considered, but they did not perform as well as the HVH model (see Appendix S1 in Supporting information). The predators convert prey to new predators with efficiency e and die at rate d , which typically is fixed at a background rate. *Didinium*, however, may show mortality rates that are low at high food density and asymptote at a maximum value at low food density (Minter *et al.* 2011). We therefore also considered the mortality function $d = d_{\max} - ((d_{\max} R)/(R + k_d))$, where d_{\max} is the asymptotic mortality rate and k_d is a half-saturation constant.

We added a third equation to the MR model to describe changes in the predator’s body size across generations:

$$\frac{dM}{dt} = gM(S - D) \quad \text{eqn 2}$$

where M is body size and g is a gradient parameter. Supply is defined as the *per capita* availability of prey, $(S_p R)/C$, where S_p is a scaling parameter determining what proportion of the resource is available per unit time (apparency, *sensu* Gutierrez *et al.* 1994), and predator resource demand D is what could be eaten per unit time given sufficient food, in other words the maximum ingestion rate ($1/h$). Supply and demand both have units of prey per time per predator. The equation causes body size to increase when supply exceeds demand and decrease when demand exceeds supply. Interestingly, the presence of M in the equation suggests greater absolute variance in M as it increases, which has recently been confirmed (Giometto *et al.* 2013). Note that there is no feedback from eqn 2 to eqn 1 unless the parameters in eqn 1 are written as functions of body size (see below).

Equation 2 closely resembles the univariate Breeder’s equation, $R = H^2 S$, where R is the response to selection, H^2 is the broad-sense heritability (due to additive genetic variance, dominance and epistasis) for a single trait in a particular population and S represents the selection differential (Lush 1937). For simplicity, we will assume dominance effects play little role in setting body size. The selection differential represents a fitness difference between the overall population and a subset of the population that passes their genes on to the next generation. To see the relationship between eqn 2 and the Breeder’s equation, we can transform S and D , which are the rates of resource flux per predator, by multiplying the supply and demand fluxes in the parentheses of eqn 2 by the conversion efficiency e and the mass per predator M , giving $(eMS - eMD)$. This differential now represents a fitness difference written in terms of biomass production and has units of mass per time. Factoring out eM and multiplying by the trait transmission efficiency (narrow-sense heritability h^2 plus phenotypic plasticity due to epistatic or environmental effects p^2 ;

sensu Frank 1997) gives $(h^2 + p^2) eM (S-D)$. Setting $g = e (h^2 + p^2)$, we arrive at eqn 2. Eqn 2 is thus analogous to the Breeder's equation, with the selection differential equal to the resource differential and g including heritability due to additive genetic variance, epistasis and environmental signals. The parameter g is thus the product of the efficiency of producing new individuals and the transmission efficiency (Frank 1997) of the trait (body size) across generations. Although body size typically is both heritable and phenotypically plastic (Garnett 1981), our experiments involved organisms with extremely low genetic variation (see below), so we expect h^2 to be close to zero.

Equations 1 and 2 represent a simple model integrating the dynamics of abundance and predator body size that can be tested against experimental data. In this study, we tested this model, which we will call the dynamic SD model (eqns 1 and 2), against experimental data on the body size dynamics of *Didinium* through the course of a predator-prey cycle. Our objective was to determine (i) the pattern of body size dynamics in the *Didinium-Paramecium* system, (ii) whether the SD concept can account for those dynamics and (iii) whether it was necessary to account for the body size dependence of predator-prey interaction parameters when describing the dynamics. Our results have important consequences for understanding the evolution of size and its response to environmental change, as well as how eco-evolutionary dynamics unfold.

Materials and methods

We acquired *Didinium* and *Paramecium* from Carolina Biological Supply (Burlington, NC, USA). *Paramecium* was cultured in bottles at room temperature (22 °C) with a mix of bacterial prey but initially inoculated with *Bacillus subtilis*. *Didinium* was maintained in Petri dishes at room temperature with *Paramecium* from the stock cultures as prey. The *Didinium* cultures had extremely low genetic variation, having repeatedly gone through bottlenecks of a few individuals from the supplier and in our laboratory; however, we cannot say with certainty that the populations were pure clones.

We initiated 14 replicate predator-prey microcosms and 10 *Paramecium*-alone control microcosms in 50 mm-diameter plastic Petri dishes. The media was 1:9 spring water/protozoan media (both from Carolina Biological Supply), autoclaved and inocu-

lated with bacteria drawn from the stock cultures and passed through 70 µm cell strainers to remove bacterial flocs and maintain resource conditions for the *Paramecium* (DeLong & Vasseur 2012c). On day zero, a healthy stock of *Paramecium* was mixed and strained, and 5 mL of this stock was added to each of the 24 dishes. On day one, eight *Didinium* cells were washed 3 × in sterile media and added to 14 randomly selected predator dishes. From days 1–9, each culture was sampled by removing 0.2 mL and counting the number of *Didinium* and *Paramecium* cells under a microscope (Leica M165C, Wetzlar, Germany). The microcosms were replenished each day with 0.2 mL strained media inoculated the previous day with the same bacterial stock cultures. Counts were scaled such that entire populations were counted at low densities, while at higher densities, the 0.2 mL subsamples were counted. The samples were retained and pooled for use in foraging experiments (see below) and for measurements of body size. To monitor changes in body size during the course of the experiment, cells of both *Paramecium* and *Didinium* were photographed with a digital camera (Leica DFC420 attached to the counting microscope), and cell lengths and widths were measured using the microscope software. Cell volumes were calculated using the formula for a prolate spheroid. Sample sizes were 19–36 *Didinium* cells per day, 7–60 grazed *Paramecium* cells per day and 14–55 control *Paramecium* cells per day. The abundance and cell size data are available on Dryad (www.datadryad.org).

We calculated the population growth rate r of *Paramecium* during the experiment. We drew ~10 individuals from the control populations and incubated them overnight in 0.1 mL of the daily replenishment media in separate replicate Petri dishes. Each day we conducted five to six replicates that were placed alongside open dishes of water in a tray that was covered with plastic wrap to prevent the drops from drying out. The number of *Paramecium* was counted at the beginning (N_1) and the end (N_2) of the incubation, and the growth rate was calculated as $r = (\ln(N_2/N_1))/t$, where t is the number of hours incubated. The growth rates were then converted to per day. The population growth rate of extracted *Paramecium* cells varied from 0.78 to -0.12, generally declining over the course of the experiment. We used the maximum value as a measure of r (Table 1). We estimated the carrying capacity K of the *Paramecium* as the mean of the control culture abundances from days 1–8 (Table 1).

To measure functional response parameters, we incubated 1, 2 or 4 *Didinium* cells under four levels of *Paramecium* density for about two hours (range 1.5–2.5 h), following the general approach in DeLong & Vasseur (2013). In each of 11 experiments, *Didinium* and *Paramecium* were isolated from the pooled samples drawn each day, with one or two dishes sacrificed from the experiment each day to boost availability of individuals. Cells were placed together in a drop in the middle of a 50-mm Petri dish. The volume of the drop used was constant, with different

Table 1. Model parameters with 95% confidence intervals. Observed parameters are from foraging experiments (a , h and m) and control *Paramecium* cultures (r , K). Other parameters were fit, with confidence intervals estimated using profile estimation. The procedure was unable to locate confidence intervals for the parameter C_d

Parameter	Description	Units	Observed	Constrained fit
r	Prey maximum population growth rate	day ⁻¹	0.78 (0.71 to 0.85)	–
K	Prey carrying capacity	R mL ⁻¹	1299 (1195 to 1403)	–
a	Area of capture	mL day ⁻¹ C ⁻¹	9.06 (–29.5 to 47.6)	–
e	Efficiency of conversion	C R ⁻¹	–	0.046 (0.042 to 0.05)
h	Handling time	C time R ⁻¹	0.038 (0.027 to 0.049)	–
d	Predator natural death rate	C day ⁻¹	–	0.90 (0.55 to 1.56)
C_d	Consumer death half-saturation constant	C mL ⁻¹	–	0.0026 (–)
m	Mutual interference	(–)	–1.06 (–2.10 to –0.02)	–
g	Mass change gradient	C R ⁻¹	–	0.015 (0.011 to 0.018)
S_p	Scaling parameter on demand	day ⁻¹	–	0.14 (0.12 to 0.16)

numbers of *Paramecium* pulled in 0.05 mL and *Didinium* pulled in 0.02 mL, for a constant volume of 0.07 mL per dish. The target *Paramecium* densities were ~140, ~290, ~430, ~640 cells mL⁻¹. The drops were covered with the lid of a 30-mm Petri dish to make the cells in the drop easier to see and to minimize evaporation during the course of the experiment. Two or three complete combinations of predator and prey densities (a 'tray') were conducted on days 1–4, after which there were not enough cells to run the trials. The number of *Paramecium* and *Didinium* was counted twice in each drop at the beginning and end of each foraging trial. The means between the beginning and end were used as predator and prey levels and converted to densities given a volume of 0.07 mL. The number of *Paramecium* consumed was taken as the difference between the initial and final mean densities and was expressed as a *per capita* foraging rate given the duration of each trial and the mean number of *Didinium*. We used a non-linear mixed-effects model to estimate the parameters of the HVH models with the `nlmefit` function in Matlab[®]. In the fitting, we used the Roger's predator equation version of the HVH functional response to account for prey depletion during the experiment (Rogers 1972; Bolker 2011; Lang, Rall & Brose 2012). *Paramecium* density and *Didinium* density were predictor variables, foraging rate was the response variable, and tray id was included as a random effect.

We used the program Potterswheel[®] (<http://www.potterswheel.de>), which runs on Matlab[®], to fit the dynamic SD model to the predator–prey data (see Appendix S2 for model file, Supporting information). This program searches parameter space to determine whether a particular ordinary differential equation (ODE) model can fit the experimental data. It can be set up to fit multiple observable variables at the same time, in this case, the population density of both *Paramecium* and *Didinium* and the body size of *Didinium*. The procedure generates a chi-square

statistic and AICc value which can be used to compare models and does not require or assume any particular error distribution in the data. Confidence intervals were produced using profile estimation, which locates the intervals at thresholds in the chi-square statistic with directional changes in the parameter estimates (Raue *et al.* 2009). We first compared fits of the dynamic SD model (eqns 1 and 2) with a constant and a saturating mortality rate, with all parameters estimated by the fit. We then determined whether the model could fit the data even after constraining it with our independent estimates of r , K , a , h and m (Table 1). The purpose of this was to increase our confidence in the results by limiting the parameter space to realistic domains. The fit with all parameters free will be called the 'unconstrained' fit, and the fit with the five independently estimated parameters will be referred to as the 'constrained' fit. Finally, because the parameters that make up consumer-resource models tend to be body size-dependent (DeLong & Vasseur 2012a), we also modified the parameters a , h , e and m by making them allometric functions of *Didinium* size, in the form of $y = b_0 M^b$, where y is the parameter, b_0 is a pre-factor and b is the scaling exponent. This would allow us to determine whether body size-based changes in the parameters were creating a feedback that influenced the abundance or body size dynamics.

Results

The population dynamics of *Didinium* and *Paramecium* followed a typical pattern of increase and decrease (Gause 1934), with complete consumption of the *Paramecium* and subsequent extinction of the *Didinium* at the end of one cycle (approximately 9 days; Fig. 1a,b). The control

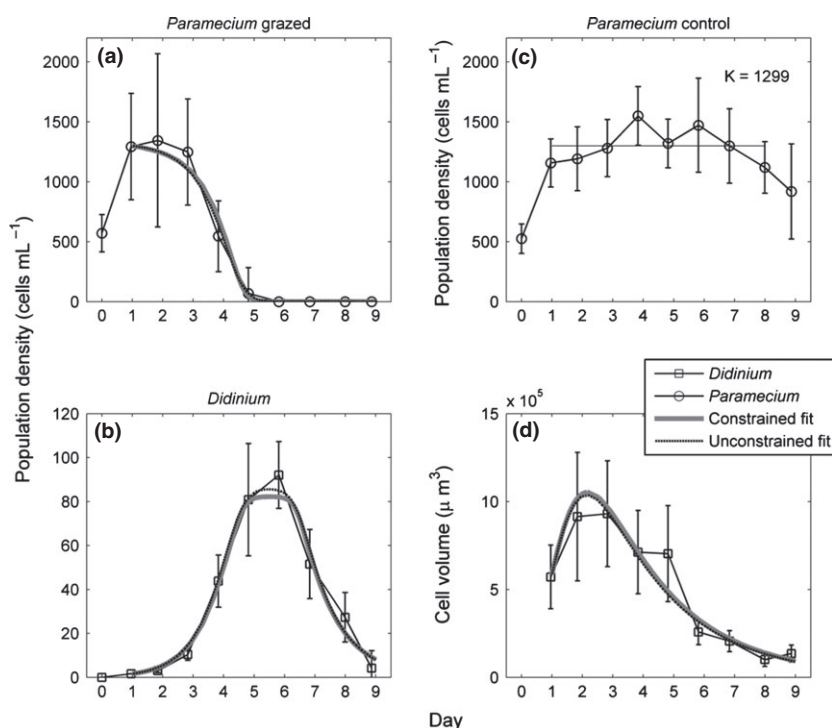


Fig. 1. Time series of abundances and body size. (a) Mean (\pm SE) abundance of the prey *Paramecium* in mixed cultures along with the constrained (grey) and unconstrained (dashed black) fits of the dynamic SD model to the data. (b) Mean (\pm SE) abundance of the predator *Didinium* along with the constrained and unconstrained fits. (c) Mean (\pm SE) abundance of the control *Paramecium* cultures and our estimate of carrying capacity K . (d) Mean (\pm SE) body size of the predator *Didinium* through time along with the fitted model predictions for predator body size.

Paramecium cultures were stable over this time frame, with a slight drop in abundance at the end of the experiment (Fig. 1c). The body size of *Didinium* increased over days 1–2, peaked and then declined from days 3–9, amounting to 10-fold variation over six to seven generations (generation = $1/r_{\max} = h/e$; Fig. 1d).

Overall, the dynamic SD model was able to capture the dynamics of *Didinium* and *Paramecium* abundance as well as *Didinium* body size (Fig. 1a,b,d). With all parameters free, the model with saturating mortality performed better than the model with a constant mortality (constant mortality: $\chi^2 = 20.3$, $AIC_c = 103.6$; saturating mortality: $\chi^2 = 10.7$, $AIC_c = 94.0$), so we used the saturating mortality model in the constrained fit. When constrained by fixing the parameters r , K , a , h and m at their independently measured values, the model fit the data equally well ($\chi^2 = 11.3$, $AIC_c = 73.7$). Finally, making a , h , e and m allometric functions of *Didinium* size yielded essentially equivalent fits to the data but with higher AIC_c values, indicating no support for dynamically changing parameters (a : $\chi^2 = 10.6$, $AIC_c = 80.1$; h : $\chi^2 = 10.7$, $AIC_c = 74.3$; e : $\chi^2 = 11.2$, $AIC_c = 77.0$; m : $\chi^2 = 11.1$, $AIC_c = 80.6$).

Discussion

Changes in *Didinium* body size through time were observed early in its use as a model predator (Gause 1934; Salt 1974; Hewett 1980), but a clear empirical picture of its variation as well as an explanation for that variation has been lacking. Our data demonstrate that body size dynamics in this species are substantial, with 10-fold variation in body size over only six to seven generations. The dynamic SD model was capable of explaining this pattern with the addition of only two free parameters to a standard predator–prey model. The correspondence of model and data lend support to the SD concept as an explanation for the pattern – that body size changes to match demand to supply – and our use of independently measured parameters to constrain the fit while maintaining good correspondence between model and data strengthens this interpretation. Also, the model captured the abundance patterns well, which indicates that the model provided good approximations of the resource supply to drive the changes in predator body size.

Body size dynamics are not unique to *Didinium*. Other species show changes in body size through a population cycle, including protists, such as *Paraphysomonas imperforata* (Caron *et al.* 1985) and *Strombidium sulcatum* (Fenchel & Jonsson 1988), and the lynx (*Lynx canadensis*) in Alaska (Yom-Tov *et al.* 2007). Thus, body size dynamics may be more integral to predator–prey dynamics than previously realized, but whether the dynamic SD model can adequately describe such dynamics in other systems remains to be seen. Because the underlying structure of the dynamic SD model applies to many predator–prey systems, however, it should be possible to test it against data from many other systems.

Despite the strong dependence of many predator–prey interaction parameters on body size (DeLong & Vasseur 2012b), we were able to get very close correspondence of the model to the data with parameters that did not vary with the body size of *Didinium*. If in reality the trophic interaction was changing as the body size of *Didinium* changed, we might expect the model to be unable to fit the data, but this was not the case. On the face of it, this result suggests the absence of eco-evolutionary dynamics in our system, given that the relevant traits that could be changing are reflected in the model parameters (Yoshida *et al.* 2003). However, we cannot rule out the possibility of eco-evolutionary dynamics for three reasons. First, it is possible that the magnitude of the parameter change with size was simply not large enough to create a mismatch between model and data. Secondly, the fact that our populations had very low genetic diversity might have prevented evolutionary change, even though there was clear evidence of phenotypic plasticity in body size. Finally, we note that many of the interaction parameters are correlated with each other, even after controlling for body size (DeLong & Vasseur 2012a). This means that simultaneous changes in multiple body size-related parameters could create compensatory effects that would mask actual eco-evolutionary dynamics. For example, an increase in the efficiency of conversion e , which would increase the production of new predators, could be accompanied by an increase in handling time h , which would lower consumption rates, at least at higher prey densities. We think a compensatory effect is quite likely, given that there is empirical evidence for such correlations as well as a typically strong dependence of most predator–prey parameters on body size (DeLong & Vasseur 2012a). The implication is that even when eco-evolutionary dynamics occur, they may be masked by other processes (Yoshida *et al.* 2007). Further work tracking parameters in real-time will be required to determine whether predator–prey parameters do indeed vary with variation in the body size of predators.

Environmental change appears to be driving shifts in body size for many organisms (Sheridan & Bickford 2011), with potentially profound but mostly unknown consequences. With the dynamic SD model, it may be possible to predict some of these changes, as the parameters that govern the ecological systems can be related to changing environmental conditions such as temperature (Vasseur & McCann 2005). Although the SD model can predict body size changes in response to temperature in laboratory studies (DeLong 2012), it is not clear how changing the ecological context under warming will influence body size changes. Many species appear to be getting smaller as the climate warms (Daufresne, Lengfellner & Sommer 2009; Gardner *et al.* 2011), and understanding those changes will require understanding body size evolution in the context of ecological dynamics, rather than in terms of temperature alone. As productivity may be altered by temperature, there may be interactive effects of temperature and resource levels on the evolution of size, potentially altering species interactions,

food web stability and broad patterns of body size in space and time (Jablonski 1997; Yom-Tov & Geffen 2011; Binzer *et al.* 2012; Shurin *et al.* 2012). Our approach enables experimentalists and theoreticians to explore these effects in an integrated way, allowing body size to evolve in a plausible fashion within an ecological context.

The evolution of body size is of considerable importance to ecology because of the role body size plays in structuring trophic interactions and food webs, as well as the broad links between body size and physiological, ecological and evolutionary rates (Peters 1983; Brown *et al.* 2004; Yvon-Durocher *et al.* 2011; DeLong & Vasseur 2012b). Despite considerable work on the evolution of body size (Roff 1986; Wikelski 2005), we have lacked a coherent theory that links optimization processes involved in setting size with the ecological dynamics that set the context. Our results here suggest that the dynamic SD model takes an important step towards accomplishing this integration. Given the simple nature of the model and its ability to be integrated with population models, we expect the dynamic SD model to help us understand body size evolution in a changing world.

Finally, our study made use of new tools to test ODE models against experimental data. The Potterswheel toolbox provides a powerful way of fitting ODE models to data, estimating the model parameters and discriminating among competing models. This advance is important because it provides a useful way for determining whether widely used ecological models are actually consistent with observable patterns. Frequently, simple versions of predator–prey models form the basis of much of ecological theory, without knowing how well the models fit any particular data set. In addition, model simulations are often based in part on guessed parameters yielding only a qualitative assessment of the model predictions (Boit *et al.* 2012; Schneider, Scheu & Brose 2012). In our case, the ODE fitting procedure revealed that the classic MacArthur–Rosenzweig model was insufficient, as both saturating mortality and mutual interference are both supported by the data. This result would have been very challenging to obtain without ODE fitting methods. Given the abundance of dynamic data available, these new ODE fitting tools could provide a simple way of identifying which forms of predator–prey models are supported enough to be used as the basis for the theoretical work and for simplifying comparisons of model simulations with experimental data.

Acknowledgements

JPD was supported by a Yale University Brown Fellowship and University of Nebraska – Lincoln and TCH was supported by Yale University. DAV acknowledges support of NSF DEB 1050803. We appreciate the helpful comments of B. Rall, M. Pfrender and an anonymous reviewer.

Data accessibility

Data deposited in the Dryad repository: <http://doi:10.5061/dryad.077vm> (DeLong, Hanley & Vasseur 2014).

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Received 23 April 2013; accepted 12 September 2013

Handling Editor: Michael Pfrender

Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1. The choice of a functional response.

Appendix S2. Dynamic supply-demand model file for Potters wheel[©].