False Exclusion: A Case to Embed Predator Performance in Classical Population Models

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Abstract: We argue that predator-prey dynamics, a cornerstone of ecology, can be driven by insufficiently explored aspects of predator performance that are inherently prey dependent: that is, these have been falsely excluded. Classical (Lotka-Volterra–based) models tend to consider only prey-dependent ingestion rate. We highlight three other prey-dependent responses and provide empirically derived functions to describe them. These functions introduce neglected nonlinearities and threshold behaviors into dynamic models, leading to unexpected outcomes: specifically, as prey abundance increases predators (1) become less efficient at using prey; (2) initially allocate resources toward survival and then allocate resources toward reproduction; and (3) are less likely to die. Based on experiments using model zooplankton, we explore the consequences of including these functions in the classical structure and show that they alter qualitative and quantitative dynamics of an empirically informed generic predator-prey model. Through bifurcation analysis, our revised structure predicts (1) predator extinctions, where the classical structure allows persistence; (2) predator survival, where the classical structure drives predators toward extinction; and (3) greater stability through smaller amplitude of cycles, relative to the classical structure. Then, by exploring parameter space, we show how these responses alter predictions of predator-prey stability and competition between predators. In light of our results, we suggest that classical assumptions about predator responses to prey abundance should be reevaluated.

Keywords: animal energetics, conversion efficiency, death rate, growth rate, ingestion rate, predator-prey model.

Introduction

Understanding population dynamics is central to virtually all ecological research, from theoretical explorations of species interactions, such as predator-driven extinctions and competition, to predictions of ecosystem function and stability. As predator-prey (or more generally consumer-resource) interactions are one of the main building blocks of ecological models, it seems appropriate to include realistic aspects of predator and prey biology when they improve predictions; that is, ignoring such aspects when they may have significant consequences constitutes “false exclusion” (sensu Topping et al. 2015). To this end, age/size-structured and dynamic energy budget models have embraced complexity, providing better predictions and understanding of dynamics (e.g., De Roos et al. 2008; Nisbet et al. 2010). However, parametrizing these models can be difficult or impossible, and for multi-trophic models including such complexity is unlikely to be computationally pragmatic. Consequently, performance at the individual level (i.e., per capita responses) is often translated to generalities that are then applied at population and community levels, based on the classic Lotka-Volterra structure (Turchin 2003; Begon et al. 2012). For instance, in classical population models the shape of the functional response may be considered sigmoidal rather than hyperbolic (e.g., Jeschke et al. 2002), predator-prey ratio dependence may be included (Arndt and Ginzburg 2012), and delayed density dependence may be imposed on prey and predator per capita rates (e.g., Turchin 2003; Li et al. 2013). Likewise, functional complexity in how predators allocate energy to maintenance and reproduction has been incorporated into classical model structures, often even at the expense of parsimony (Topping et al. 2015). In this sense, dynamic energy budget theory that focuses on the partitioning of individual resources (Kooijman 2010) has improved more traditional models. Thus, there is a long history of elaborating on the classical structure by including more realistic predator responses, driven by better understanding and appreciation of their biology.

Here we explore aspects of predator biology that have largely been falsely excluded: prey-dependent conversion efficiency, birth rate, and death rate. In doing so, we address previously recognized yet nevertheless unresolved issues associated with
how aspects of per capita performance are currently viewed and applied in classical population models. As a relevant and translational example of predators, we focus on zooplankton (e.g., Carlotti et al. 2000; Tian 2006). By employing these “model animals,” we empirically explore the prey-dependent responses described above and in doing so generalize the classical population model structure to ask what happens if classical assumptions regarding predator performance are relaxed.

A Revision of the Classical Predator-Prey Model

Most classical models of predator-prey dynamics (where the predator is the consumer, C, and the prey is the resource, R) ultimately rely on two linked equations, based on a framework established ~100 years ago by Lotka and Volterra (see Turcิน 2003). In this structure, prey population growth (eq. [1]) is determined by their prey-dependent specific growth rate ($\mu$), and prey loss occurs when they are consumed by the predator. Only the ingestion rate ($I$) is prey dependent; i.e., the functional response, $I = f_i(R)$. Predator population growth (eq. [2]) is then determined by assuming that the gross increase (typically termed “births,” $b$) is a fixed proportion ($e$) of the ingested prey, and loss of predators is by prey-independent deaths ($d_i$):

$$\frac{dR}{dt} = \mu R - f_i(R)C,$$

$$\frac{dC}{dt} = C[e f_i(R) - d].$$

Therefore, in the classical framework, predator per capita growth rate ($r$; eq. [3a]), which ultimately depends on the predator’s birth ($b$) and death ($d$) rates, is obtained indirectly through the predator’s ingestion rate (eq. [3b]). Neither the per capita growth rate nor the birth rate is explicitly parameterized. Rather, $b$ is obtained indirectly, assuming that a proportion of the prey that is ingested contributes to an increase in predator numbers, and a finite proportion of the ingested prey ($r$) is allocated to survival. Implicitly, then, ingestion leads to births, but new individuals are produced only when $I > I_r$; that is, the birth rate ($b$) is greater than the death rate ($d$), and the specific growth rate ($r = b - d$) is positive. Conversely, when $I < I_r$, the growth rate is negative, and the population declines. Note that above (and below) we discuss populations in terms of numbers (i.e., abundance per area or volume). Although some models replace numbers with biomass, we have chosen the former as it tends to facilitate intuitive understanding of population dynamics.

In this widely accepted structure (e.g., as reviewed by Turcìn 2003; Arditi and Ginzburg 2012; Begon et al. 2012), the proportion of ingested prey that contributes to an increase in predators (i.e., the conversion efficiency, $e$) can then be obtained from the ratio of two constants ($e = d_0/I_r$), where $d_0$ is the per capita predator death rate in the absence of prey (eq. [3b]). Hence,

$$\frac{dC}{dt} = b - d_0 = r$$

or

$$\frac{dC}{dt} = e(I - I_r) = \frac{d_0}{I_r} I - \frac{d_0}{I_r} I_r.$$
Figure 1: Examples of how conversion (c) and assimilation efficiencies (i.e., [ingestion − egestion]/ingestion; panels a–e) and death rates (d; panels f–j) vary with prey abundance. Data points are from the literature, and lines (panels b–j) illustrate trends. a, Predictions of conversion efficiency of the ciliate *Didinium* grown on the ciliate *Paramecium* (Li and Montagnes 2015). b, Assimilation efficiency for the copepod *Acartia*. 
tissue- and organ-level processes expressed by animals (Montagnes et al. 2012); consequently, the individual and combined roles of these three responses in classical population models has not been appreciated.

We first review past predictions that incorporate the aspects of predator performance described above and offer a revised structure for equation (2). This new framework accounts for prey-dependent allocation of resources through conversion efficiency, leading to changes in starvation, survival, and births. We then present evidence to support the contention that this revised “resource allocation” framework yields new and potentially important insights; that is, using zooplankton, we reveal how the interaction of these responses may produce different and likely more realistic representations of predation. Finally, through empirically informed sensitivity analysis, we explore how predator-prey dynamics and competition between predators might be affected by the revised structure.

Three Issues: Appreciating Prey-Dependent Resource Allocation

First, we support past arguments and observations that “assimilation efficiency” ($e = [1 - E]/I$, where $I$ is ingestion and $E$ is egestion) and, therefore, conversion efficiency ($e$) should decrease with increasing prey availability (fig. 1a–1e). Both physiological and methodological explanations exist for this decrease: (1) with increased prey abundance, the rate of materials transported across the gut wall (i.e., assimilation) may be reduced and gut passage rate may increase (Calow 1977; Straile 1997; Jumars 2000; Mitra and Flynn 2007; Flynn 2009); and (2) measures of ingestion ($I$) often reflect loss from the prey population rather than ingestion per se; that is, prey may be killed but not ingested. This “wasteful” or “surplus” killing can increase with prey abundance (Johnson et al. 1975; Sih 1980; Mckee et al. 1997; Straile 1997; Riechert and Maupin 1998; Lang and Gßdl 2003; Turchin 2003; Appley and Smith 2018; Veselý et al. 2018). Either of these processes, which are exhibited by a wide range of animals, violate the assumption that $e$ is constant (i.e., $d_{0}/I_{i}$; eq. [3b]). Rather, we can predict that $e$ will decrease with increasing prey abundance (e.g., fig. 1b–1e; fig. 2e, short-dashed line), although we note that arguments have been made that $e$ may also increase with prey abundance (e.g., Fenton et al. 2010).

Second, many animals prioritize resources for individual survival (maintenance and somatic growth), and only after these needs are met will they allocate further resources to reproduction (Zera and Harshman 2001; Lika and Kooijman 2003; Speakman 2008; Kooijman 2010). This organism level of energy allocation can be applied to per capita rates used in population models, and equation (2) can then be revised such that below a threshold ingestion rate ($I_{g}$, occurring at prey abundance $R_{b}$; fig. 2b) the production of individuals ($b$) ceases, and energy is allocated only to maintenance; that is, $b$ versus $R$ is a function with a discontinuous first derivative, with $b = 0$ for $I \leq I_{g}$. In contrast to what was implied above (see eq. [3b]), $I_{r}$ (occurring at the prey concentration $R_{r}$; fig. 2d) is not the ingestion rate that allows the predator to just survive (i.e., $b = d$); rather, it combines the ingestion rate needed for survival with that needed to produce new individuals ($I_{b}$). Critically, recognizing and applying the existence of $I_{g}$ (and hence $R_{g}$; fig. 2b) alters the above prediction that $e$ decreases monotonically with prey availability (fig. 1b–1e; fig. 2e, short-dashed line). Rather, as $I \rightarrow I_{g}$, $e \rightarrow 0$. Then as $I$ increases above $I_{g}$, $e$ will increase toward an asymptote or will reach a maximum and subsequently decrease, assuming the above arguments regarding assimilation and wasteful killing apply (fig. 1a; fig. 2e, solid and long-dashed lines). Consequently, we can now predict that $e$ versus $R$ is a unimodal function with a discontinuous first derivative, whereby $e = 0$ for $I \leq I_{g}$ (at prey abundance $= R_{g}$) and—when based on biomass rather than abundance—ranges between 0 and 1 for $I \geq I_{g}$ (fig. 2e, solid and long-dashed lines). For our subsequent analysis (see “Developing a Framework for Implementing Prey-Dependent Resource Allocation”), there are important implications if $R_{g}; R_{b}$ is large (i.e., approaches 1). Here and more generally (e.g., Bayliss and Choquet 2002; Tian 2006; Fenton et al. 2010), studies assume that the numerical response, $f(R)$, is smooth (fig. 2d, short-dashed line), represented by a rectangular hyperbolic function with a non-zero intercept (this is detailed below; see eq. [6], $r$). However, where resources needed to produce new individuals is large compared with those needed to survive (i.e., when $R_{g}; R_{b}$ is large), this is not so: the numerical response will be composed of two apparently saturating curves, forming a complex function (fig. 2d, long-dashed line). Below we argue that when $R_{g}; R_{b}$ is small (e.g., fig. 2b, 2d, 2e, solid lines), the numerical response (fig. 2d) can be approximated by a rectangular hyperbolic function (eq. [6]); see “Developing a
We now explore how the biological realism presented above can be implemented in the current classical structure (eqq. [1], [2]). To do so, we employ the Rosenzweig-MacArthur predator-prey model (eqq. [4], [5]), being a common elaboration that embraces additional reality (Turchin 2003; Arditi and Ginzburg 2012). Here, prey growth is logistic (with carrying capacity, $K$; eq. [4a]), and predator ingestion follows a type II functional response (with a maximum ingestion rate $I_{MAX}$ and a half saturation constant $k$; fig. 2a; eq. [4b]). Predator growth follows the classical framework (eq. [2]), where births are the product of a constant conversion efficiency ($e$) and ingestion rate ($I$), and death rate ($d_0$) is constant (eq. [5a]). This structure can then be modified to better reflect the energy allocation described above by including prey-dependent

**Figure 2**: Simulations of predator responses to change in prey abundance: ingestion, $I$ (panel $a$); births, $b$ (panel $b$); deaths, $d$ (panel $c$); specific growth rate, $r$ (panel $d$); and conversion efficiency, $e$ (panel $e$). Equations for response are presented in the panels, with $R = \text{prey abundance (range, 0–75)}$; $I_{MAX} = 20$; $k = 30$; $b_{MAX} = 20$; $k_b = 10$; $R_b = 0$ (short-dashed lines), 2 (solid lines), and 15 (long-dashed lines); $\alpha = 10$; $k_b = 3$; and $d_{MIN} = 1$. $R_b$ is the prey abundance required to provide $I_b$ (i.e., below which births do not occur). $R_c$ is the prey abundance where $b - d = 0$. Note that all values were chosen for illustration purposes and do not represent a specific biological system; therefore, scales are not included in this figure.
conversion efficiency and death functions, \( f(R) \) and \( f_d(R) \), respectively (eq. [5b]):

\[
\frac{dR}{dt} = \mu R \left( 1 - \frac{R}{K} \right) - C f(R), \tag{4a}
\]

\[
f(R) = \frac{I_{\text{MAX}} R}{k + R}, \tag{4b}
\]

\[
\frac{dC}{dt} = C \left( \frac{I_{\text{MAX}} R}{k + R} - d_f \right) = Cr, \tag{5a}
\]

\[
\frac{dC}{dt} = C \left( f(R) \frac{I_{\text{MAX}} R}{k + R} - f_d(R) \right). \tag{5b}
\]

How then might \( f(R) \) and \( f_d(R) \) be obtained, so that we can explore the impact of these prey-dependent responses on predator-prey dynamics? Since the seminal work of Holling (1959), numerous methods have been developed to determine the functional response (eq. [4b]). Likewise, the loss of individuals from a population—and hence \( f(R) \)—may be feasibly estimated in the field or laboratory (e.g., Krebs 1989; Minter et al. 2011; references cited in the fig. 1 legend). However, few methods exist for directly measuring prey-dependent \( e \) (Fenton et al. 2010). As we show that \( e = b/I \), it follows that \( f(R) \) can be calculated as \( f_c(R)/f(R) \). Determining the numerator, the gross increase in individuals \((b)\), which is rarely equivalent to “births” per se, as newborns may die before becoming functionally active, is possible (e.g., long-lived vertebrates) but may be challenging, especially for smaller animals, such as zooplankton. In contrast, it is often relatively simple to measure the prey-dependent specific growth rate (i.e., \( r \), the net change in individuals, providing \( f(R) \), including negative rates at low prey levels (e.g., Fenton et al. 2010). Then, as \( r = b - d \), if \( f(R) \) and \( f_d(R) \) are known, it follows that \( f_c(R) \) can be obtained. Our model animals lend themselves to this approach, and the analysis that we propose relies on predicting \( f_c(R) \) and \( f(R) \), with the recognition that \( R_0 \) is small and the numerical response can be approximated by equation (6) (see “Three Issues: Appreciating Prey-Dependent Resource Allocation”).

Our logic is based on bioenergetics arguments where \( r \) is a function of ingestion (Ginzburg 1998) and thus the numerical response will reflect the functional response (fig. 2a, 2d; Fenton et al. 2010); here growth rate reaches an asymptote \( (r_{\text{MAX}}) \), and the initial curvature of the response is described by \( k_c \) (eq. [6]):

\[
f(R) = \frac{r_{\text{MAX}}(R - R_c)}{k_c + R - R_c}. \tag{6}
\]

The main distinction between the functional response (eq. [4b]) and the numerical response (eq. [6]) is that the latter has a positive \( R \) intercept (i.e., a threshold prey abundance, \( R_c \)) where ingestion \((I_c) \) accounts for maintenance and reproductive costs (fig. 2d). A difference in shape between the numerical and functional responses implies that \( b \) and/or \( d \) are prey dependent (Fenton et al. 2010). Once the numerical response is established, determining the response of \( d \) to prey abundance (i.e., a mortality response; figs. 1f–1j, 2c) provides the relation between \( b \) (and hence \( e \)) and prey abundance (fig. 2e).

For years, work on model organisms such as the water flea Daphnia, rotifers, and protozoa has provided valuable insights into more general predator performance (e.g., as reviewed by Gause 1934; Kooijman 2010). Initial work on protozoa has recognized a need to assess prey-dependent predator responses (Minter et al. 2011; Li and Montagnes 2015) and suggests that including these responses improves model predictability (Li and Montagnes 2015). Here we apply our revised prey-dependent resource allocation structure (eq. [5b]) to several model predators from both marine and freshwater habitats, covering a range of lineages (i.e., two rotifers, two cladocerans, one protozoan), with a view to reveal general trends for zooplankton and argue for their wider adoption. Notably, this is the first time that prey-dependent growth, ingestion, and death rates have been examined concurrently on single predator species. These unique, empirically derived data and the responses that arise from them can then reveal the potential impact of \( f(R) \) and \( f_d(R) \) on predator-prey dynamics.

### Material and Methods

#### Study Organisms, Maintenance, and Experimental Conditions

Four model animals (the rotifers Brachionus calyciflorus and Brachionus plicatilis and the cladocerans Moina macrocopa and Daphnia magna) and the model protozoan Didinium nasutum were grown on prey at a range of concentrations (see fig. 3). Cultures were grown under standard, constant conditions: B. calyciflorus was maintained in purified natural spring water containing the alga Chlorella vulgaris, cultured in Bold’s basal medium (Sigma-Aldrich) at 50 μmol m\(^{-2}\) s\(^{-1}\) (photoperiod, 18L:6D) and 21°C; B. plicatilis was maintained in artificial seawater containing the marine algae Chlorella sp. or Phaeocystis globosa, cultured in 1/2 medium (Sigma-Aldrich); D. magna and M. macrocopa were maintained in purified natural spring water containing the freshwater alga Chlorella sp., cultured in BG-11 medium (Sigma-Aldrich); and D. nasutum was maintained in purified natural spring water containing the ciliate Paramecium caudatum, cultured on the bacterium Aeromonas sobria. Chlorella sp. (marine and freshwater) and P. globosa were grown at 50 μmol m\(^{-2}\) s\(^{-1}\) (photoperiod, 12L:12D) and 25°C. Experiments on B. plicatilis, D. magna, M. macrocopa, and D. nasutum were conducted at 25°C. Predator abundance and P. caudatum abundance were determined by microscopy. Autotrophic prey abundance...
Figure 3: Responses of the model predators (Brachionus calyciflorus, Brachionus plicatilis, Moina macrocopa, Daphnia magna, Didinium nasutum) and the generic predator (used in the model simulations) to change in prey abundance (Chlorella vulgaris, Chlorella sp., Phaeocystis globose, Paramecium caudatum; for details, see table 1). Presented are the functional response (eq. [4b]; row 1), the numerical response (eq. [6]; row 2), the mortality response (eq. [7]; row 3), the birth rate response (row 4), and the conversion efficiency response (row 5). Responses (lines) were fit to data (for the parameters of the responses, see table 1). Solid lines are the fit through the data. Dashed lines are the 95% confidence boundaries for the response. Adjusted $R^2$ values for the fits of curves to data are presented in individual panels. The birth rate and conversion efficiency responses were determined from the functional, numerical, and mortality responses (see "Material and Methods" and table 1). The generic predator responses were generated from parameters presented in table 1. The asterisk indicates that the scale for ingestion (I) rate of D. nasutum (panel xxvi) is in units of prey per hour. Note that the X-axis for all M. macrocopa responses have an origin of $-10^8$ to reveal the trend in panel xx.
was determined by fluorometric methods, standardized by microscopy. For all experiments, prey were harvested in exponential phase, ensuring consistency in their nutritional content. All experiments were conducted at relatively low and constant predator abundances, removing the potential for bias due to predator interference (for further details, see app. sec. A1; the appendix is available online).

**Functional, Numerical, Mortality, and Conversion Efficiency Responses**

For all rate measurements, predators were acclimated to defined prey concentrations for ≥48 h prior to the experiment. For autotrophic prey, ingestion rate ($I$, prey predator⁻¹ day⁻¹) was measured by observing the depletion of prey. For ingestion of *P. caudatum* by *D. nasutum*, methods followed those described by Li and Montagnes (2015), where *P. caudatum* were fed fluorescent beads and then *D. nasutum* that had ingested prey could be detected. For all ingestion rates, a defined number of randomly selected predators, chosen to represent the typical population structure and covering the range of developmental stages (to obviate size-related biases), were placed in a container, in the dark, with prey at a defined abundance. For the metazoa, $I$ was determined as the linear decrease in prey abundance over an appropriately short period, depending on the concentration (<2 h); controls containing only prey indicated no prey growth. For the protozoan, $I$ was determined as the increase in predators containing prey over an appropriate period, depending on the concentration (<30 min).

Growth rate measurements were based on widely applied methods (Montagnes 1996). Predator growth rate ($r$, day⁻¹) was determined on initial numbers of 10–80 (for the animals) and 2–30 (for the protozoan). Initial numbers depended on the prey concentration, as at low prey levels the predator numbers decreased (i.e., negative growth rate). Predators were randomly chosen, covering the range of developmental stages (to obviate the need to assess age-specific death rates). Predators were placed in a container filled with prey at a target concentration. After 24 h, predator numbers were determined. For the animals, all individuals were then transferred to a new container with fresh prey, at the target prey concentration. For *Didinium*, where growth was positive, only two individuals were chosen. This process maintained predators at a constant prey level and was repeated for 4–5 days. For the animals, $r$ was then calculated by regressing ln(abundance) against time, over the incubation, while for *Didinium* $r$ was determined each day and the average was calculated.

The death rate was determined by applying methods established for small organisms (Minter et al. 2011); in brief, predators were individually isolated in several containers (~50 isolates per prey concentration), each filled with prey at a single defined concentration; this process was repeated for each prey level. Again, predators were randomly chosen, covering the range of developmental stages (to obviate the need to assess age-specific death rates). Every 24 h for 5–6 days, individual predator survival/death was observed, and each day the original surviving individuals were moved to new containers at the same target prey concentration; that is, if numbers increased due to parthenogenic reproduction (for all animals), only the adult was retained and transferred, and when the protozoan predator increased by clonal growth, one randomly chosen individual was retained. The death rate was then determined by regressing the decrease in ln(abundance) of the original isolates (i.e., containers remaining occupied) against time. The mortality response was represented by equation (7), which embraces features exhibited by the change in death rate with prey abundance and reflects trends observed by us and elsewhere (e.g., fig. 1f–1j; see “Results”):

$$f_d(R) = \frac{\alpha k_i}{k_i + R} + d_{\text{MIN}},$$  \quad (7)$$

where $d_{\text{MIN}}$ is the minimum death rate (day⁻¹) at saturating prey, $\alpha + d_{\text{MIN}} = d_0$, and $k_i$ defines the curvature of the response.

For all experiments, effort was placed on collecting rate measurements across the breadth of prey concentrations, with more measurements at low levels and no replication (Montagnes and Berges 2004). Prey abundances were determined as the average prey level over each incubation; consequently, there are differences in the prey concentrations examined between responses. Functional (eq. [4b]), numerical (eq. [6]), and mortality (eq. [7]) responses were fit to the data using the Marquardt-Levenberg algorithm, which is appropriate for such data (Berges et al. 1994). Standard errors of the estimates and $R^2$ values were obtained as indications of goodness of fit.

Prey-dependent birth rate, $f_b(R)$, and conversion efficiency, $f_c(R)$, responses were obtained from the above-described functional, numerical, and mortality responses. As $b = r + d$, $f_b(R)$ was determined from $f(R)$ and $f_d(R)$, with the caveat that $R_d: R$ is relatively small (see “Three Issues: Appreciating Prey-Dependent Resource Allocation”). Although $e$ may be presented in terms of prey and predator abundance, it is more intuitively understood in terms of biomass, with the latter ranging from 0 (100% inefficient) to 1 (100% efficient). As abundance-based $e = b/I$, the response of biomass-based conversion efficiency to prey abundance was determined by equation (8):

$$f_c(R) = \frac{[f_b(R) M_i + f_d(R) M_k]}{[f_b(R) M_i]},$$  \quad (8)$$

where $M_i$ and $M_k$ are the individual biomass of the predator and prey, respectively (table 1).
Table 1: Abundance-based parameters for predator responses and estimates of predator and prey biomass

| Predator/prey (biomass)                      | $I_{\text{MAX}}$ ($R \text{ min}^{-1}$) | $k$ ($R \text{ mL}^{-1}$) | $r_{\text{MAX}}$ (day$^{-1}$) | $k_2$ ($R \text{ mL}^{-1}$) | $R_b$ ($R \text{ mL}^{-1}$) | $R_g$ ($R \text{ mL}^{-1}$) | $d_{\text{sen}}$ (mL $R^{-1}$ day$^{-1}$) | $\alpha$ | $k_b$ ($R \text{ mL}^{-1}$) |
|---------------------------------------------|----------------------------------------|---------------------------|-------------------------------|---------------------------|--------------------------|--------------------------|------------------------------------------|---------|---------------------------|
| Brachionus calyciflorus (150 ng)$^a$        | 78.8                                   | 337,600                   | .521                          | 237,700                   | 136,500                  | 112,000                  | .061                                      | .371    | 1,050                     |
| Chlorella vulgaris (5 pg)$^b$                | (6.7)                                  | (108,000)                 | (.14)                         | (65,400)                  | (29,600)                 | (.012)                   | (.031)                                    | (534)   |                           |
| Brachionus plicatilis (130 ng)               | 288                                    | 1,410,000                 | .928                          | 1,298,000                 | 647,700                  | 45,500                   | 0                                         | .857    | 680,800                   |
| Chlorella sp. (marine; 9.6 pg)               | (19)                                   | (155,800)                 | (.067)                        | (299,200)                 | (115,600)                | (.076)                   | (.010)                                    | (258,500)|                           |
| Brachionus plicatilis (130 ng)               | 223                                    | 1,654,000                 | .424                          | 763,300                   | 460,200                  | 1,000                    | .0006                                     | .645    | 399,700                   |
| Phaeocystis globosa (12 pg)                  | (16.0)                                 | (323,000)                 | (.120)                        | (423,300)                 | (223,400)                | (.070)                   | (.110)                                    | (275,600)|                           |
| Moina macrocopa (3,360 ng)                   | 173,250                                | 750,600                   | .968                          | 95,970                    | 24,000                   | 9,200                    | .0529                                     | .358    | 4,960                     |
| Chlorella sp. (freshwater; 2 pg)             | (800)                                  | (115,000)                 | (.043)                        | (24,700)                  | (5,400)                  | (.0186)                  | (.0412)                                   | (3,780) |                           |
| Daphnia magna (9,304.6 pg)                   | 3,390                                  | 194,600                   | .390                          | 119,200                   | 62,700                   | 17,000                   | 0                                         | .324    | 52,400                    |
| Chlorella sp. (freshwater; 2 pg)             | (230)                                  | (37,900)                  | (.06)                         | (35,200)                  | (14,300)                 | (.034)                   | (.034)                                    | (13,300) |                           |
| Didinium nasutum (3.0 $\times$ 10$^5$ μm$^3$)$^c$ | .0123                                  | 91.09                     | 2.079                         | 36.62                     | 9.690                    | 2.4                       | 0                                         | .588    | 18.71                     |
| Paramecium caudatum (3.2 $\times$ 10$^5$ μm$^3$)$^c$ | (.00165)                              | (25.65)                   | (.232)                        | (9.256)                   | (1.550)                  | (.0547)                   | (.0547)                                   | (4.84)  |                           |
| Generic predator (10,000 ng)                 | 70                                     | 2,000,000                 | .7                            | 800,000                   | 600,000                  | 150,000                  | .1                                        | 2       | 100,000                   |

Note: Parameter values are presented with their respective standard errors (directly below) for the functional (eq. [4b]), numerical (eq. [6]), and mortality (eq. [7]) responses. Estimates of $R_b$ were obtained from (fig 3). Parameters for the generic predator were used in model simulations (see "Material and Methods"). Biomass was determined as carbon content (Elementar Analysensysteme) unless otherwise stated.

$^a$ Biomass obtained from Pauli (1989).

$^b$ Biomass obtained from Rocha and Duncan (1985).

$^c$ Biovolumes were determined from ~50 randomly chosen cells, and biovolume was assumed to be a good estimate of biomass.
**Model Exploration**

Analysis of population dynamics involved numerical simulations, as determining analytical solutions was not possible due to the discontinuities in responses; that is, following equations (4a) and (5a) or (4a) and (5b) (as outlined below), under any one set of conditions (e.g., a defined carrying capacity), a numerical simulation was run until steady-state population dynamics arose (i.e., equilibria or constant cycles), and then values of variables (e.g., maximum and minimum abundances of cycles) were obtained. To explore how population dynamics responded to changing conditions, parameters (e.g., carrying capacity, curvature of the mortality function) were varied through a range of biologically realistic values, informed by our empirically derived data and published data on planktonic systems (e.g., figs. 1, 3; Berges et al. 1994; Montagnes et al. 1996; Båmstedt et al. 2000; Besiktepe and Dam 2002; Kimmance et al. 2006; Fenton et al. 2010; Minter et al. 2011; Montagnes and Fenton 2012; Yang et al. 2013; Li and Montagnes 2015). To reveal trends, numerous simulations were performed across the varied parameter; as the solutions were not analytical, inevitably these trends were rarely perfectly smooth (e.g., lines in fig. 4), but they are indicative and proved to be sufficient for revealing differences.

Model evaluations were based on a generic predator (table 1) and a generic prey ($\mu = 1.0$ day$^{-1}$, $K = 10^5$ mL$^{-1}$), as above both reflecting our observed trends (fig. 3; table 1) and those from the literature. Abundance-based predator-prey dynamics either followed the classical structure (i.e., the Rosenzweig-MacArthur model; eqq. [4a], [5a]) with constant values of $d_0$ and $e$ or they followed our revised resource allocation structure (eqq. [4a], [5b]; table 1). For the latter, $f_d(R)$ followed equation (7), and $f_e(R)$ was obtained from $f_I(R)$, $f(R)$, and $f_d(R)$, as outlined above in “Developing a Framework for Implementing Prey-Dependent Resource Allocation” (see table 1, generic predator, for parameters for $f_I(R)$, $f(R)$, and $f_d(R)$, and see fig. 3 for a visual presentation of these functions). For the classical structure, values for a constant death ($d_0$) and constant conversion efficiency ($e$) were obtained as follows. First, $d_0 = \alpha + d_{MIN}$ (eq. [7], where $\alpha$ and $d_{MIN}$ are presented in table 1). Then, to determine $e$ we followed the logic outlined in “A Revision of the Classical Predator-Prey Model”: (i) $R$ was first obtained from numerical response (generic predator, table 1); (ii) then from the functional response (generic predator, table 1) we obtained $I_t$; and (iii) finally, $e = d_0/I_t$ (eq. [3b]).

Through these simulations we address three issues associated with how prey-dependent conversion efficiency,
$f_i(R)$, and death rate, $f_o(R)$, may alter model predictions of dynamics. First, to assess differences between responses of the two structures, we performed a bifurcation analysis, to compare the influence of increased prey-carrying capacity ($K$) on predator extinction, predator-prey equilibrium, and the magnitude of limit cycles. In this analysis, four cases were examined: (1) $e$ and $d_i$ were constant (i.e., the classical structure); (2) both $f_i(R)$ and $f_o(R)$ were included (i.e., our revised resource allocation structure); (3) $f_o(R)$ and a constant $e$ were included; and (4) $f_i(R)$ and a constant $d_i$ were included. Second, recognizing distinct differences between predictions of the two structures (see “Results”), we conducted a stability analysis on the resource allocation structure to assess the influence of changing parameters of $f_i(R)$ and $f_o(R)$ over realistic ranges of their responses to prey abundance (based on observations from empirical data): specifically, the curvature of the mortality response was varied by increasing $k_o$ and the shape of the conversion efficiency response was altered by increasing $R_e$, effectively increasing $R_o$ (fig. 5a, 5b). Third, to extend the analysis to evaluate predator competition—a realistic aspect of predator-prey dynamics—and to further assess the effect of prey-dependent $e$ and $d$ when one response remains invariant, we assessed the extent to which differences in $f_i(R)$ and $f_o(R)$ will alter the competitive advantage between two predators ($C_i$ and $C_o$) offered a single prey when one predator exhibits superior levels of $e$ and $d$. Here we applied an additive model of exploitative competition, such that each predator acted independently of the other with interaction only being indirect, via the limiting prey resource. Equations (9) and (10) describe the model, where all parameters are defined above, and the subscripts $i$ represents the superior ($C_i$) and inferior ($C_o$) competing predators. Only death rate, $f_o(R)$, or conversion efficiency, $f_i(R)$, responses of $C_i$ were altered (as described in fig. 5a, 5b):

$$\frac{dR}{dt} = Rµ\left(1 - \frac{R}{K}\right) - C_i \frac{I_{MAX}R}{k + R} - C_o \frac{I_{MAX}R}{k + R} + f_o(R),$$

$$\frac{dC_i}{dt} = C_i \left(f_i(R) \frac{I_{MAX}R}{k + R} - f_o(R)\right).$$

The competition model was initiated with one of each predator per milliliter. To quantify the change in competitive success with respect to altered conversion efficiency and death rate (see fig. 5a, 5b), we determined the time for the inferior predator ($C_o$) to reach an abundance at which it was considered to be functionally extinct ($<$10^{-2} mL^{-1}).

**Results**

**Prey-Dependent Responses**

The predator responses reveal consistent prey-dependent trends across our model taxa (fig. 3, cols. 1–6), following those predicted by our revised theory (compare fig. 2 with fig. 3). Data underlying figure 3 have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.674p6n0; Montagnes et al. 2019). Ingestion and specific growth rates followed typical type II (eqq. [4b], [6]) asymptotic responses (fig. 2a, 2d, fig. 3, rows 1 and 2, respectively; app. sec. 2), with the latter having a positive $R$ intercept (i.e., a growth threshold prey concentration, $R_t$). For all taxa death rates ($d$) followed the predicted trend (fig. 2c; eq. [7]), being maximal when prey were absent and then decreasing toward a minimum with increasing prey abundance (fig. 3, row 3). Prey-dependent birth rate (fig. 3, row 4)—that is, $f_o(R) = f_i(R) + f_o(R)$—followed the predicted (fig. 2b) asymptotic response with a nonzero $R$ intercept ($R_o$), below which $b$ was zero. Values of $R_o$; $R$, were $<$1 (table 1), validating our assumption that equations (5) could be applied to approximate prey-dependent $b$ and $e$ responses (see “Three Issues: Appreciating Prey-Dependent Resource Allocation”). Biomass-based predator conversion efficiency ($e$; fig. 3, row 5; eq. [8]) followed the predicted trend (fig. 2e), rapidly increasing from zero at $R_o$ to a maximum that was relatively consistent across responses (0.1–0.3) and then decreasing as prey abundance increased; the one exception was Brachionus plicatilis fed the poor-quality Phaeocystis globosa, where there was no observable initial increase in $e$ (fig. 3xv). Critically, the predicted nonlinear responses of $b$, $d$, and $e$ would not have been detected if assumptions associated with the classical model structure (eqq. [4a], [5a]) had been applied to assess performance.

**Model Exploration**

The resource allocation framework (eqq. [4a], [5b]) generated distinctly different dynamics to those of the classical framework (eqq. [4a], [5a]) as carrying capacity was increased (fig. 4a–4f). When both prey-dependent $e$ and $d$ were included and compared with the classical model (fig. 4a, 4b), (1) the classical model predicted that the predator persisted when the prey-carrying capacities ($K$) was half that required for persistence by the resource allocation model; (2) for both the predator and the prey, the resource allocation model predictions were more stable than those of the classical model, producing stable equilibrium dynamics over more than twice the range of prey-carrying capacities and, for the predator, an ~20 times lower amplitude of limit cycles when they occurred; and (3) the classical model predicted that cycles drove the predator to extinction (i.e., $<$10^{-2} mL^{-1}) at prey-carrying capacities $>$3.2 $\times$ 10^5 mL^{-1}, whereas for the resource allocation simulations the predator remained extant over the entire range examined. When only prey-dependent $e$ or $d$ were included in simulations, the differences described above also occurred but were not always as pronounced (fig. 4c–4f). These results indicate
Figure 5: Comparisons of varying prey-dependent predator mortality and conversion efficiency responses. 

- **a, b.** Range of variation of the mortality and conversion efficiency responses, based on the generic predator parameters (Table 1) and attributes displayed by experimental animals (Fig. 3). These were then applied to the resource allocation predator-prey model (see "Material and Methods" and eqs. [4a], [5b]).

- **c, d.** Stability boundary analysis for the resource allocation model under different mortality responses (c) and different conversion efficiency responses (d), as described in panels a and b. c, e, f. Days to extinction of the inferior competitor ($C_2$), following the resource allocation model described by equations (9) and (10). Note that the initial numbers of both predators were 1 mL$^{-1}$, with extinction operationally defined as 10$^{-2}$ predators mL$^{-1}$. 
substantive qualitative and quantitative differences between the two frameworks, even when only one of the two functions is included.

The stability analysis indicated that (1) the interaction between prey-dependent death rate (fig. 5a) and carrying capacity ($K$) resulted in altered states of population dynamics (fig. 5c) and (2) no substantive changes in population dynamics occurred with the interaction between the prey dependence of conversion efficiency (fig. 5b) and carrying capacity (fig. 5d).

Relatively small changes in the differences in conversion efficiency and death rate (fig. 5a, 5b) between two consumers that were competing for the same resource revealed pronounced advantages for the superior competitor. This suggests that subtle differences in both of these prey-dependent parameters will influence outcomes of competition, as illustrated by days to extinction of the inferior predator (fig. 5e, 5f).

Discussion
Here we address false exclusions (sensu Topping 2015) by embedding aspects of predator performance into the classical structure for assessing predator-prey (consumer-resource) population dynamics. We show that prey-dependent performance associated with resource allocation (death rate, birth rate, and conversion efficiency) apply within and between lineages of zooplankton from marine water and freshwater, suggesting common phenomena (figs. 1–3). Specifically, we delineate a conceptual framework (fig. 2) and support it with empirical evidence (fig. 3) to indicate that both the predator’s conversion efficiency ($e$) and death rate ($d$) vary in a predictable manner with prey abundance. When embedded into the classical structure, these $e$ and $d$ responses result in marked changes (figs. 4, 5). Consequently, we support their future consideration in bi-, tri-, and multitrophic models that are currently based on the classical structure (e.g., Carlotti et al. 2000; Lévy 2015; de Ruiter and Gaedke 2017). Furthermore, as zooplankton are model organisms (e.g., Kooijman 2010), our findings will hopefully stimulate a wider audience to consider the revised resource allocation structure (eq. [5b]) when assessing consumer resource dynamics.

Considering the implications of this added complexity seems justified, as we reveal qualitative and quantitative trends that differ from those predicted by the classical framework, trends that could affect predictions associated with trophic stability and ultimately ecosystem functioning. Furthermore, there is evidence, for a protozoan-based system, that embedding prey-dependent per capita growth rate (i.e., indirectly including prey-dependent $d$ and $e$) in the classical structure improves a model’s predictive ability compared with independent, experimentally obtained time series data (Li and Montagnes 2015). Here, although we have not compared our predictions for zooplankton to independently obtained time series data, we do find substantial differences between the two model structures even when only one of the two prey-dependent functions is included (fig. 4). Interestingly, the impact of prey-dependent $d$ alone is greater in altering the bifurcation of the response and less in altering the prebifurcation response, while the impact of prey-dependent $e$ alone is more similar, but not identical, to that of combining prey-dependent $e$ and $d$ (fig. 4). This suggests that interactions between these function should be explored in the future and that including both prey-dependent $e$ and $d$ may be needed to provide realistic predictions. Furthermore, both stability and competition analyses suggest that the impact of these responses on population dynamics may be profound and have wider implications (fig. 5), with the competition analysis building on past arguments regarding resource competition (Tilman 1982). Our empirically informed findings therefore provide strong evidence that (1) where the classical structure is embedded in ecosystem models (specifically aquatic but also more generally) it may be prudent to add the complexity outlined by our resource allocation structure (eq. [5b]) and (2) theoretical studies that explore consumer-resource dynamics and competition outcomes might at least carefully consider the influence of both prey-dependent conversion efficiency and death rates.

Why Have Prey-Dependent $e$ and $d$ Not Been Fully Appreciated?
Arguably, resources are the most important driver of ecosystems. As such, prey-dependent responses have long been integral to predator-prey and larger population models (e.g., logistic growth, the functional response, and occasionally the numerical response; Turchin 2003; Fenton et al. 2010; Arditi and Ginzburg 2012). Likewise, resource-dependent responses are employed to compare the functional biology of consumers (e.g., Tilman 1982) and have been directly or indirectly included in complex population models based on dynamic energy budgets (e.g., Nisbet et al. 2010). However, for the classical structure (eqq. [1], [2]), prey-dependent death rate and conversion efficiency (fig. 2) are rarely directly, or even indirectly, considered. Two recent exceptions are studies by Minter et al. (2011) and Montagnes and Fenton (2012); these indicated that when viewed in isolation prey-dependent death rate and conversion efficiency, respectively, both had substantive influence on predator-prey dynamics relative to outcomes of the classical structure. However, to assess mortality, Minter et al. (2011) studied only one protozoan-based system and relied on published estimates for some parameters, and Montagnes and Fenton (2012) inappropriately used only published values of assimilation efficiency to predict conversion efficiency (values that were twofold larger than those we have
obtained), and their theoretical analysis of responses failed to recognize $R_d$ and hence the decrease in $e$ at low prey abundances.

Here we significantly build on these works. We concurrently measured rates on individual species, with a focus on animals (fig. 3), and based the analysis on an improved theoretical evaluation (fig. 2). In doing so, we indicate that both prey-dependent responses can independently alter predator-prey dynamics and critically that their combined effect produces substantial differences in predator-prey dynamics compared with those produced by the classical structure (fig. 4).

More generally, the influence of prey abundance on predator mortality and uptake efficiencies has been considered. Over three decades ago consumer death rate, especially at low resource levels, was recognized as critical in dictating competitive advantage (Tilman 1982). Likewise, there are indications that the death rate will decrease with increasing prey abundance (fig. 1). It therefore seems perplexing that although Ginzburg (1998) alluded to this very issue, emphasis has not been placed on assessing or implementing prey-dependent mortality, with some notable exceptions (e.g., Tian 2006; Minter et al. 2011) and with a recognition that prey-dependent mortality can be accounted for in the more complex dynamic energy budget models (e.g., Nisbet et al. 2010). Similarly, four decades ago Calow (1977) reviewed the literature on assimilation efficiency ($e = [I - E]/I$, where $I$ is ingestion and $E$ is egestion), some of which was already more than 30 years old, and remarked on its prey dependence. Likewise, Straile (1997) remarked on the prey dependency of gross growth efficiency ($GGE = r/I$). Since then, there have been numerous examples of prey-dependent $e$ and $GGE$ (e.g., fig. 1; Gigüère 1981; Kremer and Reeve 1989; Urabe and Watanabe 1991; Jumars 2000; Kimmanche et al. 2006; Lombard et al. 2009; Kooijman 2010) but little attention to the prey dependency of conversion efficiency ($c$). Both $e$ and $GGE$ may be incorporated into predator-prey models as surrogates of $e$, but they are not $e$, which is central to the classical predator-prey structure (eqq. [2], [3b], [5a]). Furthermore, except for a handful of analyses regarding how prey-dependent “efficiency” might affect predator-prey dynamics and predator growth (Franks et al. 1986; Mitra and Flynn 2007; Flynn 2009; Fenton et al. 2010; Montagnes and Fenton 2012), there has been little exploration of such prey-dependent “energetic efficiencies” on population dynamics using the classical structure.

There are several explanations for the current neglect of $e$ and $d$ prey dependence. First, parsimony of the standard predator structure (eqq. [2], [3b], [5a]), where $e$ and $d_0$ are invariant, makes it appealing, a view reflected by the ecological canon (e.g., Peters 1983; Turchin 2003; Arditi and Ginzburg 2012; Begon et al. 2012). Also, only requiring $d_0$ and $I$, (as outlined above in “A Revision of the Classical Predator-Prey Model,” eq. [3b]) has undoubtedly played a role, as these can be relatively simple to measure; in contrast, obtaining multiple rates, especially at low abundances, is challenging.

Still, for ~100 years ecologists have improved on the current classical framework (as outlined by Turchin 2003; Arditi and Ginzburg 2012), adding complexity where needed. In that tradition, we show that when attention is paid to obtaining and applying measurements of prey-dependent $e$ and $d$ (figs. 2, 3; table 1), marked differences in the predictions of predator-prey dynamics occur (figs. 4, 5). This provides compelling evidence that specifically plankton biologists—and recognizing zooplankton as model organisms all ecologists—should consider parameterizing these predator responses.

Assessing prey-dependent responses also provides insights into organismal performance. For instance, consider assimilation efficiency ($e$): if the energy needed for survival and reproduction ($I_1$; fig. 2) is a large component of the energy ingested ($I$), then conversion efficiency, $e = (I - E - I_1)/I$, will be significantly lower than $e$ at subsaturating prey abundances, as appears to be so (figs. 1, 3). Likewise, at low prey levels, as $R \to R_0$, then $e \to 0$ (fig. 2), but measurements at low prey abundance are rare and require attention, as this is where responses may vary most (figs. 1–3), potentially conferring competitive advantages (fig. 5; Hassell et al. 1977; Tilman 1982). Understanding why responses change at low prey abundances may also provide mechanistic insights, akin to the behavioral shifts reflected by type III functional responses (Hassell et al. 1977; Real 1977; Jeschke et al. 2002; Turchin 2003). For instance, $I_0$ (fig. 2) might represent the energy required to maintain structures for egg production, find and interact with mates, or reach and maintain a critical size before investing energy toward reproduction. Such costs have been considered in the context of understanding dynamic energy budgets (Lika and Kooijman 2003; Kooijman 2010) and evolutionary and behavioral trade-offs between the allocation to somatic growth and reproduction (Reznick et al. 2000; Sarma et al. 2002; Speakman 2008). As a cautionary note, we emphasize that measurements at low prey abundances are subject to high variability due to experimental error and stochasticity associated with measuring few prey. Estimates of $R_d$ by our methods, which rely on predicting growth and death rates at low prey abundances, must then be obtained from multiple treatments at low abundances, as we have done.

How Might We Progress?

Our revised resource allocation structure (eq. [5b]) offers opportunities for exploring trophic stability, ecosystem dynamics, and functional biology. For instance, both abiotic (e.g., temperature) and biotic (prey quality and size) factors
affect energetic efficiencies and death rates (e.g., *Chlorella* sp. vs. *Phaeocystis globosa* as food for *Brachionus plicatilis* in fig. 3; McConnachie and Alexander 2004; Kimmance et al. 2006; Mitra and Flynn 2007; Yang et al. 2013). Likewise, following arguments of Arditi and Ginzburg (2012) it may be that both $c$ and $d$ also depend on predator abundance (Brown et al. 1994; Ohman and Hirche 2001; Forrester and Steele 2004), providing a framework for the further investigation of ratio-dependent responses. Equally possible is that $c$ and $d$ may vary with nutritional history (i.e., past prey abundances in a fluctuating environment), as both the functional response and the numerical response are altered by past prey levels (Li et al. 2013; Li et al. 2018). Finally, if the functional and numerical responses are better predicted by a sigmoidal function (i.e., type III responses) rather than the rectangular hyperbolic functions (i.e., type II responses) that we assumed, shifts in rates at low prey abundances may alter predictions of $e$ at these low abundances. Future efforts might explore these added complications in the context of our revised structure.

There are empirical and computational methods for providing prey-dependent estimates of $c$ and $d$, but the experimental challenges we face depend on the system and the animals. For instance, standard techniques can determine assimilation efficiency ($e$) for large animals by measuring the biomass (or caloric content) of ingested and egested materials (Calow 1977; Southwood 1978; Båmstedt et al. 2000; Henderson 2016), although for some large animals (e.g., in aquatic systems) collecting feces may be impossible and using isotope tracers is a more pragmatic approach (Båmstedt et al. 2000). Likewise, for large animals, methods exist to determine maintenance and reproductive costs (Sarma 2002; Speakman 2008; Henderson 2016). It may then be possible, following the logic laid out in the introduction, to predict prey-dependent conversion efficiency ($c$) for many large animals. In contrast, death rate measurements for larger long-lived animals may be challenging (Krebs 1989), either in nature or under controlled conditions, and often proxies or indices must be relied on (e.g., fig. 1j); new methods to estimate prey-dependent death rate are needed. For small organisms, (e.g., insects, nematodes, zooplankton, meiofauna) with relatively rapid rates, death rate may be assessed by the methods we provide here (fig. 3; Minter et al. 2011), but determining $c$, where egested material is minute, is problematic. Furthermore, determining and separating metabolic costs associated with maintenance and reproduction may be challenging for small animals (Runge and Roff 2000). However, for small animals, directly measuring per capita growth rates is relatively simple, and we have shown here how these may be used to assess $e$. Finally, in the introduction (fig. 2) we highlight that if the ratio of prey needed for producing new individuals is large relative to that for survival (e.g., $R_0: R > 1$), then the numerical response is not smooth (fig. 2d, long-dashed line); for animals that invest substantial energy into reproduction, a more complex analysis may be necessary to assess conversion efficiencies. In summary, applying multiple approaches is undoubtedly the solution to appreciate the magnitude of prey-dependent conversion efficiency and death rate, so that these vital rates may be incorporated into future models across all taxa.

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