Parameterising variable assimilation efficiency in predator–prey models

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Our understanding of the dynamics of predator–prey systems has relied heavily on the use of models based on the standard Lotka–Volterra (LV) framework, dating back over 80 years. Although these models have been repeatedly analysed and refined since their initial inception, the way they describe the predator's growth rate has received surprisingly little attention; typically it is simply assumed that the predator's growth rate is linearly related to its ingestion rate according to a constant assimilation efficiency, e. However, for many consumers e is known to decrease at high prey densities. Models that ignore variable assimilation efficiencies overlook potentially important non-linearities, affecting the validity of predictions relating to conservation, invasion biology and pest control. Directly quantifying the relationship between e and prey abundance is, however, difficult. An alternative approach (the independent-response, IR, approach) is to not assume any direct link between the predator’s functional response (the relationship between ingestion rate and prey abundance) and its growth response. This flexibility is invaluable when parameterising models from data; providing the model-fitting process is constrained to ensure that e never exceeds 1, this approach allows considerable insight into whether, and how, e varies with prey density. Here we examine the synergistic value of combining the IR and LV approaches. We illustrate these concepts through analysis of published functional and growth response data and show that, in many cases, e does vary with prey abundance. This paper is the first recognition that these two complementary approaches can be combined into a single framework that allows the relationship between a predator’s functional and growth responses to emerge during the parameterisation process, thereby acting as a compromise between restrictive models that require this relationship to be defined a priori, and completely unrestrained models that allow assimilation efficiencies to exceed 1.

Equations derived from the Lotka–Volterra (LV) predator–prey model have formed the cornerstone of population ecology for over 80 years, and they remain at the forefront of ecological research to this day (reviewed by Turchin 2003). The primary attraction of the original model, and those derived from it, is its simplicity; these models typically comprise a pair of coupled differential equations, describing the changes in abundance (or density, or biomass) of the prey and predator populations, based on four fundamental processes: prey growth, prey depletion through predation, predator growth and predator mortality. Although an oversimplification in themselves, these equations have formed the basis on which our current understanding of trophic interactions, population dynamics, and community structure are founded, and they remain the fundamental basis of many present analyses.

The flexibility and generality of these models have motivated considerable research efforts, both empirical and theoretical, to determine the appropriate forms of the underlying processes, quantify the various parameters and assess the consequences for system dynamics and stability. In particular the relationship between the predator’s per capita predation rate and prey abundance (the functional response) has received considerable attention, both theoretically and empirically. A large number of lab and field studies have quantified predation rates for a variety of taxa, both invertebrate and vertebrate (Murdoch 1969, Hassell et al. 1977, Rindorf 2002, Gilg et al. 2003, 2006). Furthermore, there have been intense discussions in the theoretical literature concerning the form of the functional response and the relative merits of incorporating various prey- and predator-dependencies within it (Watt 1959, Rosenzweig 1971, Royama 1971, Arditi and Ginzburg 1989, Berryman 1992, Gleeson 1994, Abrams and Ginzburg 2000, Jenschke et al. 2002).

However, the relationship between the predator’s per capita rate of increase and prey abundance (the numerical or growth response) has, by comparison, received relatively little attention. Broadly, two approaches have been suggested. By far the most common approach, and that assumed by the standard LV-based models, has been termed the ‘demographic’ numerical response (Bayliss and Choquenot 2002), and assumes a direct coupling between a predator’s functional response (i.e. the rate at which it consumes prey)
and its numerical response. Intuitively, this may seem a logical assumption, as the ability of an individual to reproduce must, ultimately, depend on the resources it consumes. In theory, the relationship between the functional and numerical responses may take a variety of forms. For example, Ginzburg (1998) discussed a general theoretical framework in which the predator's growth response is a decelerating function of the numerical response. However, the overwhelming majority of studies assume that predators assimilate a constant proportion of captured prey biomass. Hence, the predator's growth rate is assumed to be linearly related to their ingestion rate according to a conversion or, in terms of biomass, assimilation efficiency (e), defined as the amount of prey biomass assimilated per predator as a proportion of the biomass removed from the prey population. In this case, e is constrained to lie between 0 and 1 to adhere to the rule of 'biomass conversion' (Ginzburg 1998).

However, a major problem with this approach is that it ignores various mechanisms by which the proportion of prey biomass that is assimilated may change with prey density, such as 'surplus' (or 'wasteful') killing, where prey are killed but not immediately (or, indeed, ever) consumed (Kruuk 1972, Turchin 2003, Lounibos et al. 2008); 'sloppy feeding' such that consumed prey are assimilated at a lower rate (Moller 2005); and increased faeces production as prey ingestion increases (Gaudy 1974, Valiela 1995). These are clearly well documented phenomena. However, unlike the substantial efforts that have been directed towards the impact of food quality (e.g. stoichiometry, digestibility) on assimilation, they are poorly characterised with regards to changing food quantity (i.e. prey density). Importantly, if it is accepted that e varies with prey density, then the functional form of this relationship must be defined a priori. This, then, raises issues regarding the form of this function and how to parameterise it from empirical data, both of which are non-trivial tasks.

An alternative approach (which we term the 'independent response', IR, approach) is to make no explicit assumption regarding the relationship between the functional response and the predator's growth response, and to derive each one independently. One of the earliest attempts to do this was proposed by Leslie (1948), who described a logistic growth response for the predator that depended on prey availability but not explicitly on prey consumption (Tanner 1975, Berryman 1992). These models are historically important in the development of predator–prey theory. However, they are unsatisfactory because there will always be combinations of predator and prey densities that break the rule of biomass conversion (Ginzburg 1998), allowing predators to produce more biomass than they consume. The IR models we consider allow assimilation efficiency to vary with prey density, but are not based directly on these earlier models. However, by relaxing the relationship between the functional and numerical responses, they allow a greater degree of flexibility, enabling the form of the assimilation efficiency response to be driven by empirical data, rather than being constrained by a priori assumptions about the shape or constancy of the predator's assimilation efficiency function. In particular, our approach defines a family of relationships between the growth and numerical responses, which may be either increasing or decreasing, depending on parameter values. We emphasise that this approach is intended as a means of improving the parameterisation of population dynamic models and so should be considered in an empirical setting (where the model fitting can be constrained to keep e = 1), rather than as a generic population model in its own right (where it is mathematically possible for e > 1). As we describe below, if during the model fitting process, e exceeds 1 then this acts as a warning that the underlying model is inappropriate for that predator–prey system, and further modifications to the underlying model are needed.

Here we explore the synergistic value of combining the IR approach with the classic approach to determine how predator assimilation efficiency varies with prey concentration. We then illustrate the utility of this advance by applying it to existing functional and numerical response data from the literature. Note that at this stage we do not consider issues relating to food quality, due to the relatively large amount of attention devoted to that subject. However, we recognise that food quality and food quantity are likely to be closely related and in many cases the two may be directly linked, making it impossible to separate their effects (Flynn and Davidson 1993, Mitra and Flynn 2006). Developing a framework that incorporates both factors could prove a highly productive avenue of research, and we return to this issue later. Overall, we emphasise the advantages of using independently derived functional and numerical responses and make recommendations for applying this approach to better parameterise population models.

The LV and IR modelling approaches

The LV-based approach to modelling predator–prey dynamics will be familiar to many readers. However, for completeness and to define terms, we begin with an overview of its structure. In its most general form the LV model, and those that have followed it, describing the dynamics of prey ('victims', V) and predator ('consumers', C) populations can be written as:

\[
\frac{dV}{dt} = \text{(prey population growth rate in absence of predators)} - C \text{ (functional response)} \\
\frac{dC}{dt} = C \left[ \text{(numerical response)} - \text{(predator per capita death rate in absence of prey)} \right] 
\]

where, as described above, the numerical response is typically assumed to simply equal the functional response multiplied by a constant assimilation rate, e. Note that we define the numerical response strictly in terms of the reproductive rate of the predator, whereas we define the combination of the numerical response and predator death rate as the predator's growth response (the necessity for this distinction becomes apparent below). Finally, note that we assume the state variables V and C represent population biomasses (or biovolumes), rather than abundances (Berryman 1999).

As a specific example, we take the Rosenzweig–MacArthur (RM) model, which is typically assumed to be the sim-
The simplest LV-based predator–prey model that incorporates key features of biological realism: density-dependent prey reproduction and a type 2 functional response (all parameters and their dimensions are defined in Table 1):

$$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right) - \frac{I_{\text{MAX}}CV}{k + V} \tag{2}$$

$$\frac{dC}{dt} = e\frac{I_{\text{MAX}}CV}{k + V} - \delta C \tag{3}$$

where $r$ is the prey specific growth rate, $K$ is the carrying capacity of the prey population, $I_{\text{MAX}}$ is the predator maximum ingestion rate, $k$ is the half-saturation constant, $\delta$ is a predator specific death rate, and $e$ is the (constant) assimilation efficiency. Note that, although we use the RM model as our baseline, what follows may be generalised to a wide range of formulations. For example, in Supplementary material Appendix 1 we show how the following approaches could be applied to ‘ratio dependent’ models that incorporate predator dependence in the functional response (Arditi and Ginzburg 1989, Akcakaya et al. 1995). In this case, the predator growth response is, by necessity, also predator-dependent. However, we also show that for this ratio-dependent model and IR formulation there will always be some combinations of prey and predator densities for which efficiency will be greater than 1. Thus, a modified approach may be needed to provide a general IR model that obeys the rule of biomass conservation across all feasible predator and prey densities.

The alternative, IR, approach that we adopt is one that appears to have its roots in protozoan population dynamics (Taylor 1978), presumably because unicellular organisms make good models for rapid determination of general population dynamics (Gause 1935, 1936). We focus on this formulation since, as will be illustrated below, it has a mechanistic basis that corresponds to the LV-type models. However, the specific details of this function are not fundamental to our argument, and the broad concepts should be applicable to any similar approach where the predator’s functional and growth responses are independently derived, providing the growth response equation gives a sufficiently accurate description of the data. The IR equivalent of the RM model (Eq. 2, 3) is:

$$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right) - \frac{I_{\text{MAX}}CV}{k + V} \tag{4}$$

$$\frac{dC}{dt} = -\frac{C\mu_{\text{MAX}}(V - V')}{k_2 + V - V'} \tag{5}$$

where $r$, $K$, $I_{\text{MAX}}$, and $k$ are as before, $\mu_{\text{MAX}}$ is the maximum growth rate of the predator, $V'$ is the prey concentration where predator growth rate is zero (often referred to as the threshold concentration), and $k_2$ is a constant (where $k_2 - V'$ is the half-saturation constant of the growth response of the predator). Once again, all parameters and their dimensions are defined in Table 1. Note that Eq. 4, describing prey population dynamics is the same as before (Eq. 2). The argument for the predator growth response given in Eq. 5 is that it should follow a similar form to the functional response, but the curve will be shifted, as a portion of the ingested prey is required for maintenance (i.e., $V'$). Energetically, this non-zero intercept represents the food requirement that sustains zero growth, similar to the nutrient balance model of Droop (1983).

Given recent debate about the viability of adopting an IR approach to predator–prey models (Ginzburg 1998, Berryman 1999, Bayliss and Choquenot 2002, Ramos-Jiliberto 2005), and the increasing popularity of using formulations like Eq. 5 to describe empirical data (references in Table 2, Montagnes et al. 1996, 2008, Jakobsen and Hansen 1997, Montagnes and Lessard 1999, Jakobsen et al. 2001, Weisse 2004, Kimmance et al. 2006), we see it as timely to assess the similarities between the LV-based and IR approaches, determine the appropriateness of the IR approach, and provide suggestions on how the latter may be used to inform the former.

### Determining the equivalence of approaches

**Characteristics of the predator growth response in a standard LV-based model**

The growth response of the predator for the LV-based approach (Eq. 2, 3) compresses the functional response by
a factor \( e \) and shifts it down the \( y \)-axis, with an intercept of \(-\delta\) (Fig. 1a–b), such that the predator growth response asymptotes at \( \delta_\text{MAX} \). Furthermore, the threshold prey concentration at which the predator growth response is zero (i.e. where it crosses the \( x \)-axis) is given by \( \frac{\delta_\text{MAX}}{e \delta_\text{MAX}} \). Crucially, the LV-based approach explicitly assumes that the functional and predator growth responses have the same shape, with a common half-saturation constant \( k \). Saturating predator growth responses of the form shown in Fig. 1, with negative growth rates at low prey densities and a threshold prey concentration at which net predator growth is zero, are by far the most common reported in the literature, having been observed across a wide range of taxa (Bayliss and Choquenot 2002, Sibly and Hone 2002, Gilg et al. 2003, 2006, Millon and Bretagnolle 2008).

**Characteristics of the predator growth response in the IR model**

The growth response of the predator in the IR model saturates at \( \mu_\text{MAX} \) and has a y-intercept (equivalent to \( \delta \) in the LV model) at \(-\frac{\mu_\text{MAX} V'}{k_2 - V'}\) (Fig. 1c). Furthermore, it crosses the \( x \)-axis at \( V' \) (the threshold prey concentration at which predator growth is zero) which, by comparison with the LV model shows that \( V' = \frac{-\delta k}{e \delta_\text{MAX}} \).

Here, the removal of explicit coupling between the predator's growth and functional responses means that the functional and predator growth responses need not share a common half-saturation constant. As we show below, this can arise if the predator's assimilation rate, \( e \), varies across prey densities. Furthermore, by comparing the parameterised functional and predator growth responses it is possible to infer the functional form of this relationship between \( e \) and prey density.

**Comparing the LV-based and IR approaches**

To compare the LV-based and IR approaches we rewrite the predator's growth response in the IR model in a form similar to that of the LV-based formulation (i.e. Eq. 1). As described above, the per capita death rate of predators in the absence of prey is \( \delta = \frac{\mu_\text{MAX} V'}{k_2 - V'} \). Placing this into the LV-based model (Eq. 3), equating the \( \frac{dC}{dt} \) equations of the two approaches (Eq. 3, 5), and solving for \( e \) shows that the equivalent expression for the assimilation efficiency in the IR model is:

\[
e = \frac{k_2 \mu_\text{MAX}(k + V)}{I_\text{MAX} (k_2 - V')(k_2 + V - V')}
\]

(Hence, the IR model implicitly allows the assimilation efficiency \( e \) to vary with prey density \( V \)). Specifically, from Eq. 6, it can be seen that if \( k < k_2 - V' \), then assimilation efficiency increases with prey density (Fig. 2), possibly as

![Figure 1](image-url)  
*Figure 1. Schematic diagrams showing how (a) the predator’s functional response, (b) predator’s per capita growth rate in the Lotka–Volterra model and (c) predator’s per capita growth rate in the independent response model change with prey density or biomass. The dashed lines show the asymptotes and the dotted lines show the half-saturation values of the responses, expressed in terms of the parameters of the models (Table 1).*

![Figure 2](image-url)  
*Figure 2. Schematic diagram of how the relationship between the half-saturation constants of the functional response and the predator’s growth response \( (k \text{ and } k_2 - V' \text{ respectively}) \) reveals the relationship between the predator’s assimilation efficiency \( (e) \) and prey density in the independent response model.*
energy lost through prey capture decreases with increased prey availability. In this case, to obey the rule of biomass conversion (Ginzburg 1998), we require $e \leq 1$ which, by allowing $V \to \infty$ in Eq. 6 shows that:

$$e_{\nu \to \infty} = \frac{\mu_{\max} k_2}{I_{\max} (k_2 - V)} \leq 1$$

However, if $k > k_2 - V'$, then assimilation efficiency decreases with prey density as would be seen, for example, if the predators indulge in surplus killing. In this case, the maximum value of $e$ occurs when $V \to 0$, in which case we require:

$$e_{\nu \to 0} = \left[ \frac{\mu_{\max} k_2}{I_{\max} (k_2 - V')} \right] \times \left[ \frac{k}{(k_2 - V')} \right] \leq 1$$

to obey the rule of biomass conversion. Finally, if $k = k_2 - V'$ then the predator's functional and growth response curves have the same shape (their half-saturation constants are the same), and the expression for $e$ reduces to:

$$e = \frac{\mu_{\max} k_2}{I_{\max} (k_2 - V')}$$

(7)

In this case, where the functional and growth responses have the same shape, the assimilation efficiency is constant with respect to prey density, as assumed for the standard LV approach. Hence the LV-based model can be seen to be a specific case of the more general IR model. Furthermore, the criterion:

$$k = k_2 - V'$$

(8)

may be used as a means to empirically determine whether assimilation efficiency is constant, based on parameter values estimated from the appropriate experiments; if this criterion is violated, then the functional and predator growth responses are of different shapes, and it cannot be assumed that the predator has a constant assimilation efficiency.

Population dynamic consequences of a variable $e$ in the IR model

Few theoretical papers have explicitly analysed the population dynamic consequences of variable assimilation efficiencies. One example (van de Koppel et al. 1996, Barnes and Sidhu 2005) showed that incorporating a negative exponential relationship between prey (plant) density and predator (herbivore) assimilation efficiency could result in bistability of the system with two stable states, the first involving the predator and prey coexisting and the second with the predator excluded despite the prey being at their carrying capacity. However, the model analysed by van de Koppel et al. (1996) assumed an extreme case, where assimilation efficiencies approached zero at high prey densities, resulting in predator growth rates becoming negative when confronted by highly abundant prey (see their Fig. 3a). This humped predator growth response led to the second stable state, causing predators being excluded at high prey densities. However, such humped growth responses have rarely been observed in empirical studies, with the vast majority being of the saturating form shown in Fig. 1b–c (Bayliss and Choquenot 2002, Sibly and Hone 2002, Gilg et al. 2003, 2006, Millon and Bretagnolle 2008), but see Sibly and Hone (2002, Fig. 4b) for an example of a humped predator growth response.

Here we illustrate the dynamical consequences of the variable assimilation efficiency inherent in the IR model using the graphical method of isocline analysis. The zero net growth isocline (ZNGI) for the prey population is obtained by setting the expression for $dV/dt = 0$ and solving for $C$ which, for both the RM and IR models (Eq. 2 and 4 respectively), gives:

$$C = \frac{r(k + V)(K - V)}{I_{\max} k}$$

resulting in a humped isocline (Fig. 3a). The prey's growth equation in the RM model (determined by setting Eq. 3 equal to zero) shows the prey's isocline is a vertical line (solid line, Fig. 3a), given by:

$$V = \frac{\delta k}{e_{\max} - \delta}$$

As is well established (Rosenzweig and Macarthur 1963), if this isocline lies to the right of the peak in the prey's isocline, the system is stable, with predators and prey coexisting at a stable equilibrium (Fig. 3b–c). However, as the predator's isocline moves to the left of the peak in the prey's isocline, the system becomes increasingly destabilised, resulting in divergent oscillations in predator and prey abundance (Fig. 3d).

Following the same procedure for the IR model shows that the predator's isocline is given simply by $V = V'$ and, if we assume $e$ is constant (i.e. $k = k_2 - V'$), given by Eq. 7, then the predator's isocline overlays that of the LV model and the two models are identical. However, if assimilation efficiency decreases with prey density, such that $k > k_2 - V'$, then the predator's isocline shifts to the right, further stabilising the system (Fig. 3a, 3c). Conversely, an increasing assimilation function ($k < k_2 - V'$) shifts the predator's isocline to the left, potentially pushing it beyond the hump in the prey's isocline, destabilising the system (Fig. 3a, 3d).

Case studies: comparing the LV and IR approaches to empirical data

The advantage of the IR approach is that it provides an ideal framework in which the functional response and the growth response can be independently determined empirically, without making assumptions regarding their relationship. Clearly, as indicated above, these functions will be linked biologically. Hence, appropriate laboratory experimentation, under controlled conditions, should yield a pair of quantified relationships between prey abundance, and predator ingestion and growth rates from which we can determine the functional form of $e$. We emphasise that we recommend the IR approach for ease of parameterisation from empirical data, and not necessarily for analytical exploration of generic properties; the lack of explicit coupling between the functional and numeri-
and validity of population models. This means that there is an abundance of well-replicated and well-quantified data on protozoan functional and numerical responses in the literature that may be used to explore the concepts presented in this paper. Our emphasis on protozoa is enlightening, and we expect that this work should stimulate similar efforts to be placed on conducting more laborious, but equally enlightening experiments on metazoa.

Estimating protozoan assimilation efficiencies from re-analysis of data from lab studies

Here we explore the utility of the IR approach by analysing published functional and predator growth response data from protozoan microcosm experiments. Based on these data we examined whether (1) the value of $e$ (derived from Eq. 7) is biologically plausible (i.e. $0 \leq e \leq 1$) and (2) the standard assumption of a constant assimilation efficiency (determined by the criterion in Eq. 8) is upheld. To conduct this analysis, predator and prey abundances were converted to biomass (carbon), following standard conversion factors from volumes when carbon estimates were not provided (Table 2). In this analysis, due to lack of appropriate data, we assumed that the predator carbon content was

Figure 3. (a) Predator–prey phase space showing the prey (humped line) and predator (vertical lines) isoclines for the LV and IR models; solid lines = LV model (or IR model, assuming a constant assimilation efficiency; $V' = k_x - k$), dashed line = IR model assuming assimilation efficiency decreases with prey abundance ($V' = (k_x - k) / 1.2$), dotted line = IR model assuming assimilation efficiency increases with prey abundance ($V' = (k_x - k) / 1.2$). The other panels show predator and prey dynamics for (b) the LV model, (c) the IR model with decreasing assimilation efficiency and (d) the IR model with increasing assimilation efficiency. Parameter values are: $r = 5$, $K = 1000$, $p_{\text{MAX}} = 1$, $I_{\text{MAX}} = 10$, $e = 0.6$, $d = 5$, $k = 100$, $k_x = 600$. 
invariant with prey abundance, although this is undoubtedly a simplification.

The analysis (Table 2) suggests that estimates of assimilation efficiencies (ε) for many of the studies are biologically plausible, with ε < 1. However, in all the studies examined, \( k - (k_s - V^*) \gg 0 \), suggesting that the functional and predator growth responses have fundamentally different shapes, and it is unlikely that assimilation efficiency is constant with respect to prey density; from these data we would typically predict that assimilation efficiency decreases as prey density increases.

However, there are at least two, non-mutually exclusive reasons that may generate these outcomes: (1) predator per capita biomass is not invariant with prey abundance; (2) predator mortality rate (δ̄) is not constant with respect to prey biomass. These are briefly discussed below, with specific reference to works on protozoa, but with the recognition that the concepts are directly applicable to metazoans.

Assuming consumer per capita biomass is invariant with victim concentration: there is evidence that per capita consumer biomass (or its proxy, biovolume, assuming a constant volume:biomass ratio) varies with prey abundance. For example, studies on protozoa indicate that individual predator biovolume (\( U_{\text{V}} \)) increases with increasing prey abundance, and this may be modelled by a rectangular hyperbolic response (Montagnes and Lessard 1999), dependent upon the population biomass of prey (\( V_{\text{d}} \)), with a half-saturation constant (\( k_s \)), a maximum volume (\( U_{\text{MAX}} \)) and a minimum volume where there is no food (\( U_{\text{UV}} \):)

\[
U_{\text{e}} = \frac{U_{\text{MAX}} V_{\text{d}}}{k_s + V_{\text{d}}} + U_{\text{UV}} \tag{9}
\]

As we show below, incorporating this empirically determined predator response to prey abundance, alongside the functional and numerical responses, improves the parameter estimation process and lead to more realistic estimates of assimilation efficiency.

Assuming δ̄ is constant: the LV-based framework (Eq. 2, 3) typically assumes that predator mortality is constant with respect to prey density. There are, however, plausible mechanisms through which predator mortality (δ̄) could depend on prey density. For example, prey density may affect the risk of predator starvation, susceptibility to disease, or the structural stability of the predator, all of which could affect predator mortality. If predator mortality does vary with prey density, the growth response of the predator will vary with prey abundance and will have a different shape from the functional response, even if assimilation efficiency is constant.

**A detailed study of two case studies of the protozoan predator–prey systems**

Here we describe a procedure for detailed analysis of varying assimilation efficiency, using two datasets that include functional, growth, and volume (biomass) responses. The first dataset involves the freshwater ciliate *Urotricha farcta* as the predator feeding on the autotrophic flagellate *Cryptomonas sp.* (Montagnes et al. 2008), and the second involves the marine heterotrophic flagellate *Oxyrrhis marina*
feeding on the autotrophic flagellate *Isochrysis galbana* (Kim-
mance et al. 2006). For our analysis we first converted con-
sumer and victim abundances into biovolume (assuming for
simplicity that biovolume is a constant multiple of biomass).
We then used a maximum likelihood method (Supple-
mental material Appendix 2) to estimate the parameters of Eq.
4, 5 and 9. To test the hypothesis of constant efficiency (e),
we compared models with and without the constraint given
by Eq. 8 using a likelihood ratio test. Furthermore, we tested
whether a completely unconstrained model provides a sig-
nificantly better fit to the data than a ‘feasible efficiency’
model in which the model was constrained to ensure that
e \leq 1; if the unconstrained model was significantly better,
and predicted values for e > 1 for realistic prey abundance
levels, then this would indicate that the model was missing
some key biological mechanism and would require further
modification.

For *Urotricha farcta*, we could not reject the hypoth-
esis that assimilation efficiency is constant (Fig. 4; Table
A1 in Supplementary material Appendix 2), providing
a best estimate for e of around 0.35 (Fig. 4). However,
for *Oxyrrhis marina*, the unconstrained model provided
a significantly better fit to the data than the constrained
model (Fig. 5; Table A1 in Supplementary material
Appendix 2), indicating that assimilation efficiency decreased
with increasing prey abundance for this species (Fig. 5d).
Furthermore, the ‘feasible efficiency’ model was not sig-
nificantly worse than the completely unconstrained model.
Therefore, there is no strong evidence that we require
biologically implausible parameters for a model with vari-
able assimilation efficiency to be better than one with con-
stant assimilation efficiency. The feasible efficiency model
does give an assimilation efficiency of 1 (which is at the
limit of what is thermodynamically possible) in the limit
of zero prey density. However, at any non-zero prey den-
sity, it gives assimilation efficiency less than 1, and assim-
ilation efficiency in the absence of prey does not have an
obvious biological meaning. Finally it should be noted that
the varying efficiency models mostly improved on the
fit of the constant efficiency model at low prey densities,
where we have many observations (Fig. 5a–c), whereas the
three models diverged substantially at high prey densities,
where we have few observations. Possibly, collecting more
data at high prey densities would improve our ability to
discriminate between models. However, Monte Carlo
simulations suggest that good designs for estimating this type
of model have most measurements close to the origin, and
only a few near the asymptote, as in the data analyzed here
(Montagnes and Berges 2004). Clearly, more sampling
effort overall would ultimately improve our ability to
discriminate between models.

**Population dynamics of the parameterised IR and LV approaches**

To illustrate the consequences of adopting the IR approach
to develop a parameterised model we compared the predic-
tions of the constant efficiency model (effectively a standard
LV-type model) with those of the IR model parameterised
under the ‘feasible efficiency’ constraint (i.e. e was allowed to
vary between 0 and 1) for the *Oxyrrhis–Isochrysis* experiment
described above.

Both parameterised models predict the *Oxyrrhis–Isochry-
sis* system should undergo sustained high-amplitude fluc-
tuations, but the LV-based model predicts fluctuations of
longer period, and slightly greater amplitude than the
feasible efficiency IR model (Fig. 6). This increased frequency
Discussion

Although the classical predator–prey models have repeatedly undergone modifications to their basic structure, these have typically focussed on prey growth rate and the functional response of the predator. In contrast, the relationship between ingestion rate (via the functional response) and predator growth rate has received surprisingly little attention. One reason for this is that ecologists recognised very early that predator growth rates should be tightly linked to ingestion rate and assimilation efficiency; this then determined the proportion of ingested energy that was converted into predator biomass. As a result, a very narrow range of modelling approaches has been developed, constrained by this energy conservation law (Turchin 2003), and this may have resulted in blind-spots in previous analyses.

Here we have compared this standard approach to a more flexible one that allows the assimilation efficiency to vary with prey abundance. We recommend this approach because: firstly it provides more accurate parameter estimates; secondly it provides insight into how assimilation efficiency varies with prey density, which can be very difficult to measure directly; and thirdly it reveals areas where model refinement is needed (e.g. when estimated assimilation efficiencies exceed 1).

Previous authors have highlighted the need to consider non-linear assimilation efficiency functions (van de Koppel et al. 1996, Ginzburg 1998). One possibility is to impose a pre-defined non-linear relationship on the model. However, while this is reasonable if there is empirical evidence for that relationship, forcing such a function into a model when the true assimilation efficiency relationship is not known is far from satisfactory. The approach we present has sufficient generality to allow the shape of this function to emerge from the data, drawn from a family of relationships specified by the IR model. It is possible that, while assimilation efficiency may vary with prey density, it does not do so in exactly the way proposed here. A less restrictive approach would be to use non-parametric methods to estimate the relationship between assimilation efficiency and prey density (Jost and Arditi 2000). However, the IR approach we present, appropriately constrained to ensure $e < 1$, provides a specific example of the general principles described in Ginzburg (1998) and forms a useful compromise between the extreme generality of that conceptual framework and the extreme specificity of having to define a single assimilation efficiency function a priori.
Clearly, there are a number of modifications that can be made to our basic approach. One important point is that, at present, it ignores issues of prey quality. Mitra and Flynn (2007, Flynn 2009) developed detailed mechanistic models exploring the inter-relationships between prey quality and quantity, predator gut transit time, satiation rates and assimilation efficiency. These models showed that gut transit times and assimilation efficiencies are likely to change in response to changes in both food quality and quantity, with potentially important implications for trophic dynamics. Furthermore, there may be a tradeoff between prey quality and quantity, such that there may be low concentrations of high quality prey (for example during the exponential phase of growth) or high concentrations of low quality prey (for example during the stationary phase of growth). Under these conditions it may be very difficult to separate the effects of quality and quantity, without conducting carefully designed experiments. By ignoring prey quality, and concentrating on food quality, our approach is simpler than that of Mitra and Flynn (2007, Flynn 2009), requiring estimation of fewer parameters. Furthermore, the emergent assimilation efficiency function in our approach will implicitly account for any changes in food quality that the predators experienced during the experiments, although it will not provide insight into how such changes affect assimilation efficiency or predator growth. It would be very interesting, therefore, to ultimately couple our approach with that of Mitra and Flynn (2007) to explicitly investigate the utility of incorporating prey quality into our more general predator–prey framework.

A further, useful, modification to the IR approach would be to measure empirically predator mortality rate \( \delta \) over a range of prey densities, assessing whether it too is a function of prey concentration. As mentioned previously, if predator mortality varies with prey density, then this may alter the shape of the derived assimilation efficiency function. Once parameterised, this predator mortality response could be used with the functional, numerical and volume responses to provide a more accurate estimate of assimilation efficiency. One next step, therefore, will be to design and perform experiments that provide simultaneously-collected data on growth, grazing, and mortality responses to prey concentration. Such an approach, and the parameter estimates derived from it, would allow the development of models that are more accurate, and more flexible, than traditional LV-based approaches.

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**References**


Supplementary material (available online as Appendix O17875 at <www.oikos.ekol.lu.se/appendix>). Appendix 1 and 2.