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Appendix 1

Applying the IR approach to ratio dependent predator-prey models

Here we show how the IR approach may be applied to an alternative model formulation, the "Ratio dependent" (RD) model, in which the predator's functional and growth responses incorporate predator-dependence, such as might arise through interference between competing predators (Arditi and Ginzburg 1989, Akcakaya et al. 1995). We follow the same procedure as outlined in the main paper, determining the equivalence of the IR and RD approaches to derive an expression for the assimilation efficiency function. Following Getz (1984), a possible RD predator-prey model is:

$$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right) - \frac{I_{MAX}CV}{cC + V} \quad (1)$$

$$\frac{dC}{dt} = \frac{eI_{MAX}CV}{cC + V} - \delta C \quad (2)$$

where c is a constant. Equating the predator's growth response in this model to that of the IR model (Eq. 5 in the main paper) and solving for e gives the following expression for the assimilation efficiency function:

$$e = \frac{k_2\mu_{MAX}(cC + V)}{I_{MAX}(k_2 - V')(k_2 + V - V')} \quad (3)$$

As before it can be seen that assimilation efficiency may vary with prey concentration (V), either increasing or decreasing as prey concentration changes, in a manner similar to that shown in the main paper. In addition, however, assimilation efficiency may also change in response to changes in predator concentration (C). In particular, the manner in which e changes with prey concentration now depends on the density of predators; if $cC > k_2 - V'$ then e decreases with increasing V, if the reverse is true then e increases with V, and if $cC = k_2 - V'$ then e is constant with respect to V. Hence, as predator density crosses a threshold predator concentration given by $C^* = \frac{k_2 - V'}{c}$, the assimilation efficiency function switches from increasing to decreasing (Fig. A1). Furthermore, analysis of this RD approach shows that there may always be combinations of C and V that result in $e > 1$ for a given set of parameter values. Hence, the approach considered here is only strictly applicable over the range of predator and prey densities from which the parameters were estimated.

However, although these predator dependencies are potentially very important from a population dynamic point of view, they do not change the fundamental conclusions of our paper. That is, regardless of what the underlying population dynamic model is, the IR approach enables an expression for the assimilation efficiency function to be derived by comparing the equations for the predator's functional and growth responses, and the shape of this response can be determined by parameterising those responses from experimental data.

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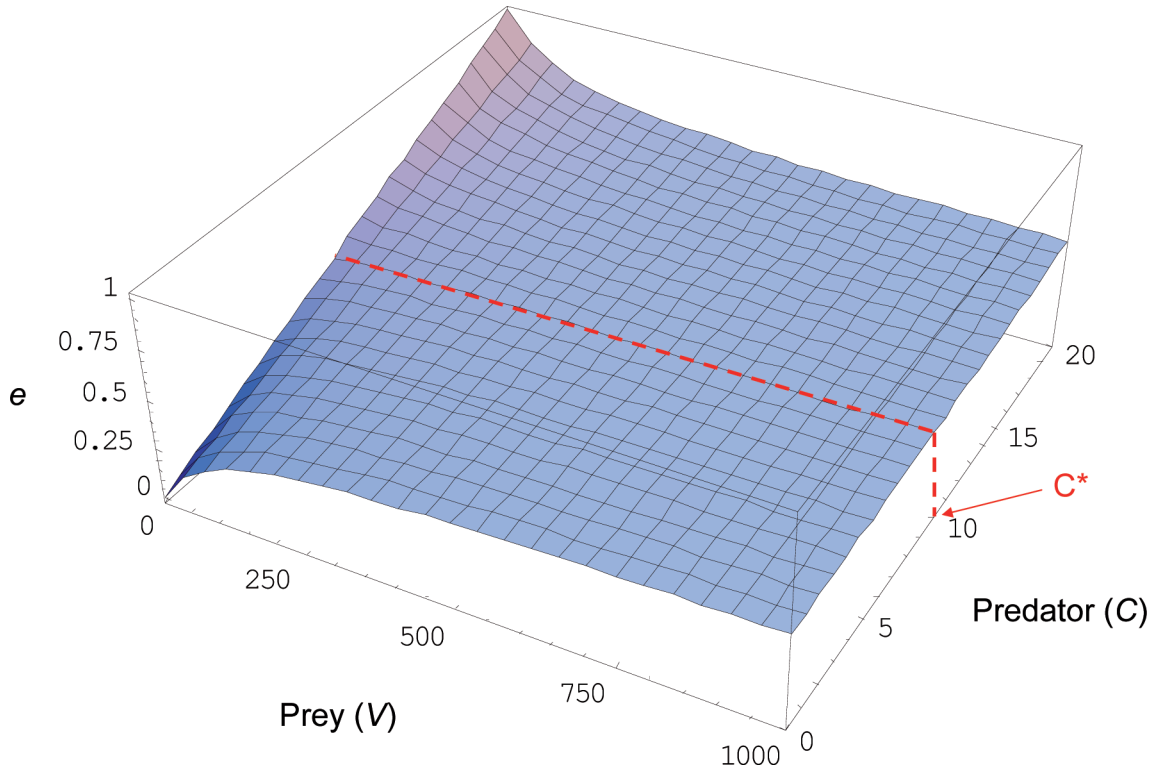

Figure A1. Relationship between predator and prey density and the assimilation efficiency, as derived from the IR version of the ratio dependent model. The dashed line shows the threshold predator concentration, C*, below which assimilation efficiency increases with prey density, and above which assimilation efficiency decreases with prey density.

Appendix 2

Using data on ingestion, growth and predator cell volume to test the hypothesis of constant efficiency in the IR model

1 Assumptions

We assume that biovolume and biomass are equivalent apart from a multiplicative constant, the mass per unit volume, the same for both predators and prey. We use expressions such as *predator volume* as shorthand for some dimensions such as biovolume per unit habitat size. We also assume that the IR model describes predator-prey interactions when predator and prey abundances are expressed in volumes, not numbers. This seems plausible. For example, we expect a bigger cell to have a higher ingestion rate and a higher total metabolic rate than a smaller cell. It is likely that these relationships will be allometric rather than linear, but we will not explore this added complexity here, and linearity is likely to be a reasonable approximation over a small range of cell volumes.

2 Cell volume

Let C_u be the biovolume of predators per unit habitat size (dimensions *predator volume*) and V_u be the biovolume of prey per unit habitat size (dimensions *prey volume*). We assume the volume of a prey cell is a constant U_v (dimensions volume per prey cell), so that

$$V_u = VU_v \tag{1}$$

where V is the number of prey cells per unit habitat size (dimensions *prey cells*).

We assume that the volume of a predator cell depends on prey abundance, so that

$$C_u = CU_c \tag{2}$$

where C is the number of predator cells per unit habitat size (dimensions *predator cells*). We assume that the volume U_c of a predator cell (dimensions volume per predator cell) is

$$U_c = \left(\frac{U_{max} V U_v}{k_3 + V U_v} + U' \right) \tag{3}$$

where U_{max} is the maximum size a predator cell can attain (dimensions volume[predator cell]$^{-1}$), U' is the predator volume at zero prey density (volume[predator cell]$^{-1}$), and k_3 is a constant (*prey volume*).

3 Ingestion

The rate of prey ingestion I_u, measured in volumes (dimensions *prey volume*time^{-1}) is

$$I_u = \frac{I_{max} C_u V_u}{k + V_u} \tag{4}$$

where I_{max} is maximum ingestion rate (*prey volume*[*predator volume*]$^{-1}$time^{-1}), and k is a constant (dimensions *prey volume*).

Putting together Equations 4, 1 and 2, we get

$$I_u = \frac{I_{max} V U_v}{k + V U_v} C \left(\frac{U_{max} V U_v}{k_3 + V U_v} + U' \right) \tag{5}$$

Dividing Equation 5 by $U_v C$, we get

$$I = \frac{I_{max} V}{k + V U_v} \left(\frac{U_{max} V U_v}{k_3 + V U_v} + U' \right) \tag{6}$$

I has dimensions *prey cells*[*predator cells*]$^{-1}$time^{-1}, and we refer to it as per capita ingestion.

4 Growth

Let μ_u be the growth rate of the predator population (dimensions [*predator volume*]time^{-1}):

$$\mu_u = \frac{C_u \mu_{max} (V_u - V')}{k_2 + V_u - V'} \tag{7}$$

where μ_{max} is maximum growth rate (time^{-1}), V' is a threshold prey density (*prey volume*) and k_2 is a constant (*prey volume*). Dividing Equation 7 by C_u and substituting $V U_v$ for V_u (Equation 1) gives the specific growth rate μ (time^{-1}):

$$\mu = \frac{\mu_{max} (V U_v - V')}{k_2 + V U_v - V'} \tag{8}$$

5 Estimation

Given measurements of predator cell volume, per capita ingestion, and specific growth rate at a range of prey densities, we can estimate the parameters $\boldsymbol{\theta} = [I_{max}, \mu_{max}, k, V', U_{max}, U', k_3, k_2]$ using Equations 3, 6 and 8 and a maximum likelihood method, if we know the volume U_v of a prey cell. We assume

that measurements of growth, ingestion and volume are independent (plausible if they are determined in separate experiments) and that measurements at different prey densities are independent (plausible if they are made on different cells). We assume that the error for each variable is Gaussian and does not depend on prey density (these assumptions can be checked, as we describe later). We do not need the prey densities used for each set of measurements to be identical.

In summary, we calculate the joint log likelihood for all the data, given the assumptions above, and use numerical methods to find the parameter estimates that maximize the log likelihood. We then check the assumptions of Gaussian errors with constant variance for each set of measurements by examining the residuals. We implemented our methods in R version 2.4.0 Patched (R Development Core Team, 2006).

5.1 Log likelihood

Let the ith out of n_x growth measurements $\mathbf{x} = [x_1 \dots n_x]$ be

$$x_i = \mu_i(\boldsymbol{\theta}) + \epsilon_{xi}$$

where, from Equation 8, the expected growth rate at prey density V_{xi} is

$$\mu_i(\boldsymbol{\theta}) = \frac{\mu_{max}(V_{xi}U_v - V')}{k_2 + V_{xi}U_v - V'}$$

and the error is $\epsilon_{xi} \sim \mathcal{N}(0, \sigma_x^2)$, meaning that ϵ_{xi} has a Gaussian distribution with mean 0 and variance σ_x^2.

Similarly, let the ith out of n_y ingestion measurements, $\mathbf{y} = [y_1 \dots n_y]$, be

$$y_i = I_i(\boldsymbol{\theta}) + \epsilon_{yi}$$

where, from Equation 6, the expected ingestion rate at prey density V_{yi} is

$$I_i(\boldsymbol{\theta}) = \frac{I_{max}V_{yi}}{k + V_{yi}U_v}\left(\frac{U_{max}V_{yi}U_v}{k_3 + V_{yi}U_v} + U'\right)$$

and the error is $\epsilon_{yi} \sim \mathcal{N}(0, \sigma_y^2)$.

Also, let the ith out of n_z predator volume measurements $\mathbf{z} = [z_1 \dots n_z]$ be

$$z_i = U_{ci}(\boldsymbol{\theta}) + \epsilon_{zi}$$

where, from Equation 3, the expected predator volume at prey density V_{zi} is

$$U_{ci} = \left(\frac{U_{max}V_{zi}U_v}{k_3 + V_{zi}U_v} + U'\right)$$

and the error is $\epsilon_{zi} \sim \mathcal{N}(0, \sigma_z^2)$.

At an estimate $\hat{\boldsymbol{\theta}}$ of $\boldsymbol{\theta}$, the expected values of x_i, y_i and z_i are $\hat{x}_i = \mu_i(\hat{\boldsymbol{\theta}})$, $\hat{y}_i = I_i(\hat{\boldsymbol{\theta}})$ and $\hat{z}_i = U_{ci}(\hat{\boldsymbol{\theta}})$ respectively. Let $\hat{\boldsymbol{\sigma}}^{\mathbf{2}} = [\hat{\sigma}_x^2, \hat{\sigma}_y^2, \hat{\sigma}_z^2]$ be the estimated error

variances. The log likelihood $l_{xi} = l(\hat{\boldsymbol{\theta}}, \hat{\boldsymbol{\sigma}}^{\mathbf{2}}; x_i)$ for a single growth observation x_i is the log of the Gaussian probability density with expected value $\hat{x}_i$ and variance $\hat{\sigma}_y^2$:

$$l_{xi} = -\frac{1}{2}(\log 2\pi + \log \hat{\sigma}_x^2) - \frac{1}{2\hat{\sigma}_x^2}(x_i - \hat{x}_i)^2$$

Under the assumption of independent, identically distributed Gaussian errors, the log likelihood for all the growth data is the sum of the log likelihoods of each of the separate observations

$$l(\hat{\boldsymbol{\theta}}, \hat{\boldsymbol{\sigma}}^{\mathbf{2}}; \mathbf{x}) = \sum_{i=1}^{n_x} l_{xi} = -\frac{n_x}{2}(\log 2\pi + \log \sigma_x^2) - \frac{1}{2\hat{\sigma}_x^2}\sum_{i=1}^{n_x}(x_i - \hat{x}_i)^2 \tag{9}$$

The log likelihoods for the ingestion and predator volume data have similar forms. Because the measurements of each variable are independent, the joint log likelihood $l(\hat{\boldsymbol{\theta}}, \hat{\boldsymbol{\sigma}}^{\mathbf{2}}; \mathbf{x}, \mathbf{y}, \mathbf{z})$ is the sum of the log likelihoods for each set of measurements

$$l(\hat{\boldsymbol{\theta}}, \hat{\boldsymbol{\sigma}}^{\mathbf{2}}; \mathbf{x}, \mathbf{y}, \mathbf{z}) = l(\hat{\boldsymbol{\theta}}, \hat{\boldsymbol{\sigma}}^{\mathbf{2}}; \mathbf{x}) + l(\hat{\boldsymbol{\theta}}, \hat{\boldsymbol{\sigma}}^{\mathbf{2}}; \mathbf{y}) + l(\hat{\boldsymbol{\theta}}, \hat{\boldsymbol{\sigma}}^{\mathbf{2}}; \mathbf{z}) \tag{10}$$

The last term in Equation 9 is a negative sum of squares, weighted by the inverse of the variance. Thus to maximize the joint log likelihood, we need to minimize the weighted sum of squares for each of the three sets of measurements, while simultaneously estimating the variances that provide the weights. The sums of squares are nonlinear functions of $\boldsymbol{\theta}$, so we need to maximize the log likelihood numerically.

5.2 Maximizing the log likelihood

We used numerical methods to find the estimates $\hat{\boldsymbol{\theta}}, \hat{\boldsymbol{\sigma}}^{\mathbf{2}}$ that minimize the joint negative log likelihood (Equation 10). The most effective strategy we found was to choose reasonably good initial parameter estimates by plotting observed and expected growth, grazing and cell volume against prey density for various choices of $\boldsymbol{\theta}$, use a simulated annealing algorithm to find an approximate minimum, and pass the output to a BFGS quasi-Newton algorithm to improve the estimates. These algorithms are the `SANN` and `BFGS` options, respectively, in the `optim` function in R (Venables and Ripley, 2002, p. 436). Different parameters have very different magnitudes, which can lead to numerical problems. We therefore scaled the parameters (using the `parscale` argument in `optim`) by the absolute values of the initial guesses before simulated annealing, and by the absolute values of the simulated annealing estimates before BFGS. We checked that we can recover the the true parameter values of simulated data, and that the estimates from real data converged to similar values from different but reasonably good starting conditions.

5.3 Feasible efficiency constraints

The assimilation efficiency (dimensionless) for this model is

$$e = \frac{\mu_{max}(k + VU_v)k_2}{I_{max}(k_2 + VU_v - V')(k_2 - V')} \tag{11}$$

and thermodynamic constraints mean that $0 \leq e \leq 1$. For *Oxyrrhis*, the efficiency from the maximum likelihood estimates in the unconstrained model was greater than 1 at low prey densities. We therefore re-estimated the parameters subject to $e \leq 1$ for all prey densities. Because e is a monotone function of V, we only need to check the efficiencies at $V = 0$ and $V = \infty$. From Equation 11, these are

$$e(0) = \frac{\mu_{max} k_2 k}{I_{max}(k_2 - V')^2}$$
$$e(\infty) = \frac{\mu_{max}}{I_{max}}\left(1 + \frac{V'}{k_2 - V'}\right)$$

where $e(V)$ is the efficiency at prey density V. We then rewrite the optimization problem as

$$\begin{aligned} (\hat{\boldsymbol{\theta}}, \hat{\boldsymbol{\sigma}}^{\mathbf{2}}) &= \arg\min_{(\boldsymbol{\theta}, \boldsymbol{\sigma}^2)} [-l(\boldsymbol{\theta}, \boldsymbol{\sigma}^2; \mathbf{x}, \mathbf{y}, \mathbf{z})] \\ \text{subject to} & \\ e(0) &\leq 1 \\ e(\infty) &\leq 1 \end{aligned} \tag{12}$$

To solve Equation 12, we used a quadratic penalty method (Nocedal and Wright, 1999, p. 501), with slack variables to translate the inequality constraints into equalities (Nocedal and Wright, 1999, p. 519). We gradually increased the weight of the penalty given for violating the constraints, solving the optimization subproblem at each penalty weight by BFGS as in the unconstrained case (with a round of simulated annealing at the first step to find a good starting point). We refer to this model as the feasible efficiency model.

5.4 Standard errors

For the unconstrained and constant efficiency models, the covariance matrix $\boldsymbol{\Sigma}$ for the parameter estimates is approximately $\mathbf{H}^{-1}$, where $\mathbf{H} = \{-\partial^2 l(\boldsymbol{\theta})/\partial\theta_i \partial\theta_j\}$ is the Hessian matrix of second derivatives of the negative log likelihood at the maximum likelihood estimates (Bickel and Doksum, 2001, p. 386). Thus the approximate standard errors are the square roots of the diagonal elements of the inverse of the Hessian. We rescaled V before estimation (in this case, to prey cells nL^{-1}) to avoid numerical problems when inverting the Hessian. For the same reason, we rescaled the parameters as follows to evaluate the covariance matrix. By the chain rule, an element h_{ij} of the Hessian is

$$h_{ij} = -\frac{\partial^2 l(\boldsymbol{\theta})}{\partial(\theta_i r_i)\partial(\theta_j r_j)} r_i r_j$$

Thus, we first evaluate a scaled Hessian $\mathbf{D}$ with elements

$$d_{ij} = -\frac{\partial^2 l(\boldsymbol{\theta})}{\partial(\theta_i r_i)\partial(\theta_j r_j)}$$

where we choose the convenient values $r_i = 1/\theta_i$, so that the denominators of the numerical derivatives are never too small or too large. Then $\boldsymbol{\Sigma} = \mathbf{S}\mathbf{D}^{-1}\mathbf{S}$, where $\mathbf{S}$ is a diagonal matrix with $\boldsymbol{\theta}$ on the diagonal.

For the feasible efficiency model, standard theory does not apply because the parameter estimates are not at an extreme point on the likelihood surface. Instead, we used a nonparametric bootstrap to estimate standard errors. We resampled with replacement from the pairs of measurements of growth, ingestion and predator volume with their associated prey densities, estimated the parameters for each resampled data set, and calculated the sample standard deviation of the resampled parameter estimates (Efron and Tibshirani, 1993, Algorithm 6.1). We discarded a few bootstrap replicates which had obvious optimization problems (very large negative parameter estimates).

5.5 Diagnostics

We used some simple diagnostic methods outlined in Faraway (2005, chapter 4). We plotted residuals against fitted values for each set of data. The absence of strong patterns suggests that the assumption of constant variances was appropriate. We also plotted residuals against quantiles of the Gaussian distribution to check for departures from normality. The only obvious problem was that ingestion residuals were left-skewed for *Oxyrrhis* and right-skewed and long-tailed for *Urotricha*. It is not easy to think of a transformation that would solve all these problems.

6 Inference

6.1 Is efficiency constant?

If the death rate is constant, the hypothesis of constant efficiency corresponds to the constraint $k_2 = k + V'$, as described in the main text. We can use a likelihood ratio test to evaluate this hypothesis. Let l_c be the log likelihood estimated with the constant efficiency constraint, and l be the log likelihood for the unconstrained model. The unconstrained model will never have a worse log likelihood than the constant efficiency model if the optimization is working correctly, because it has an extra free parameter. However, if the constant efficiency model is the true model, then in the limit of infinite sample size (and approximately for finite sample sizes)

$$2(l - l_c) \sim \chi^2_1$$

where χ^2_1 is a chi-square distribution with one degree of freedom (Garthwaite et al., 2002, p. 87). Thus if the probability of drawing a value at least as large

as $2(l - l_c)$ from a χ^2_1 distribution is small, we should reject the hypothesis of constant efficiency.

For *Oxyrrhis*, we also want to test the null hypothesis of constant efficiency against the alternative hypothesis of feasible but not necessarily constant efficiency. This is a nonstandard case because of the constraint on the feasible efficiency model. We therefore used a parametric bootstrap (Davison and Hinkley, 1997, section 4.2.3) to estimate the distribution of the log likelihood ratio under the hypothesis that the constant efficiency model is correct. Let $\log(LR) = l_f - l_c$ be the observed difference in log likelihoods between the feasible (log likelihood l_f) and constant efficiency (log likelihood l_f) models. We generate R independent simulated samples from the distribution of the data under the constant efficiency model. For each of these, we fit the constant and feasible efficiency models. For the rth bootstrap replicate we obtain the difference in log likelihoods $\log(LR^*_r)$. We then estimate a bootstrap p value,

$$p_{\text{boot}} = \frac{1 + \#\{\log(LR^*_r) \geq \log(LR)\}}{R + 1}$$

(Davison and Hinkley, 1997, Equation 4.13).

6.2 Is efficiency feasible?

We would also like to know whether the unconstrained model is significantly better than the feasible efficiency model. Again, standard theory does not apply, because these two models have the same number of parameters, and differ only in the nonlinear constraints on the feasible efficiency model. We therefore used a parametric bootstrap as above, except that we simulated data under the feasible efficiency model, and fitted both the feasible efficiency and unconstrained models.

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Table A1. Maximum likelihood parameter estimates, log likelihoods and likelihood ratio test results obtained from fitting the unconstrained, feasible efficiency and constant efficiency models (see main text for details) to data on predator growth rate, ingestion rate and volume responses to changes in prey density, using (A) *Urotricha farcta* feeding on *Cryptomonas* sp., and (B) *Oxyrrhis marina* feeding on *Isochrysis galbana*.

A) *Urotricha farcta* feeding on *Cryptomonas* sp.

i) Unconstrained model

Parameter (units)	Estimate (SE)		Log likelihood
I_{MAX} (prey $\mu m^3 mL^{-1}$[predator $\mu m^3 mL^{-1}$]$^{-1}d^{-1}$)	15.7908	(1.5897)	-288.7455
μ_{MAX} (d^{-1})	4.4005	(0.3965)	
k (prey $\mu m^3 mL^{-1}$)	1.9587×10^7	(5.7583×10^6)	
V' (prey $\mu m^3 mL^{-1}$)	6.7210×10^6	(7.7385×10^5)	
k_2 (prey $\mu m^3 mL^{-1}$)	2.9391×10^7	(5.4975×10^6)	
k_3 (prey $\mu m^3 mL^{-1}$)	2.4129×10^7	(7.9518×10^6)	
U_{MAX} (prey μm^3)	3874.728	(426.756)	
U' (prey μm^3)	1079.224	(188.156)	

ii) Constant efficiency model ($k_2 = k + V'$)

Parameter (units)	Estimate (SE)		Log likelihood
I_{MAX} (prey $\mu m^3 mL^{-1}$[predator $\mu m^3 mL^{-1}$]$^{-1}d^{-1}$)	16.2417	(1.1742)	-288.8201
μ_{MAX} (d^{-1})	4.3177	(0.3152)	
k (prey $\mu m^3 mL^{-1}$)	2.1371×10^7	(3.9174×10^6)	
V' (prey $\mu m^3 mL^{-1}$)	6.7319×10^6	(7.5305×10^5)	
k_3 (prey $\mu m^3 mL^{-1}$)	2.3104×10^7	(7.1664×10^6)	
U_{MAX} (prey μm^3)	3813.283	(381.459)	
U' (prey μm^3)	1073.147	(189.690)	

Likelihood ratio test
Unconstrained v. Constant efficiency models:
Likelihood ratio statistic = 0.1491, df = 1, p = 0.699

B) *Oxyrrhis marina* feeding on *Isochrysis galbana*

i) Unconstrained model

Parameter (units)	Estimate (SE)		Log likelihood
I_{MAX} (prey $\mu m^3 mL^{-1}$[predator $\mu m^3 mL^{-1}$]$^{-1}d^{-1}$)	5.3716	(0.5164)	-314.6392
μ_{MAX} (d^{-1})	1.0757	(0.1296)	
k (prey $\mu m^3 mL^{-1}$)	2.3888×10^{6}	(5.6896×10^{5})	
V' (prey $\mu m^3 mL^{-1}$)	4.6218×10^{5}	(4.0709×10^{4})	
k_2 (prey $\mu m^3 mL^{-1}$)	8.0232×10^{5}	(2.5161×10^{5})	
k_3 (prey $\mu m^3 mL^{-1}$)	4.4712×10^{8}	(2.3478×10^{9})	
U_{MAX} (prey μm^3)	4.8492×10^{4}	(2.4888×10^{5})	
U' (prey μm^3)	1633.324	(51.5874)	

ii) Feasible efficiency model ($0 \leq e \leq 1$)

Parameter (units)	Estimate (SE*)		Log likelihood
I_{MAX} (prey $\mu m^3 mL^{-1}$[predator $\mu m^3 mL^{-1}$]$^{-1}d^{-1}$)	5.2495	(0.7045)	-315.7597
μ_{MAX} (d^{-1})	1.2482	(0.1505)	
k (prey $\mu m^3 mL^{-1}$)	2.2045×10^{6}	(6.4687×10^{6})	
V' (prey $\mu m^3 mL^{-1}$)	4.9332×10^{5}	(6.1502×10^{4})	
k_2 (prey $\mu m^3 mL^{-1}$)	1.3275×10^{6}	(3.0683×10^{5})	
k_3 (prey $\mu m^3 mL^{-1}$)	1.0185×10^{10}	(2.0566×10^{11})	
U_{MAX} (prey μm^3)	1.0942×10^{6}	(2.0584×10^{7})	
U' (prey μm^3)	1629.726	(61.8019)	

*standard errors were estimated from 977 nonparametric bootstrap replicates. We ran 1000 replicates, of which we discarded 23 for which there were obvious optimization problems.

iii) Constant efficiency model ($k_2 = k + V'$)

Parameter (units)	Estimate (SE)		Log likelihood
I_{MAX} (prey $\mu m^3 mL^{-1}$[predator $\mu m^3 mL^{-1}$]$^{-1}d^{-1}$)	4.9696	(0.4411)	-318.8895
μ_{MAX} (d^{-1})	1.5387	(0.1593)	
k (prey $\mu m^3 mL^{-1}$)	1.8979×10^{6}	(4.4051×10^{5})	
V' (prey $\mu m^3 mL^{-1}$)	5.1676×10^{5}	(7.6954×10^{4})	
k_3 (prey $\mu m^3 mL^{-1}$)	6.7863×10^{8}	(3.7063×10^{9})	
U_{MAX} (prey μm^3)	7.6879×10^{4}	(4.1360×10^{5})	
U' (prey μm^3)	1618.489	(51.4516)	

Likelihood ratio tests

Unconstrained v. Constant efficiency models:
Likelihood ratio statistic = 8.5004, df = 1, p = 0.004

Feasible v. Constant efficiency models:
Likelihood ratio statistic = 6.2595, p = 0.021 estimated from 999 parametric bootstrap replicates

Unconstrained v. Feasible models:
Likelihood ratio statistic = 2.2410, p = 0.099 estimated from 999 parametric bootstrap replicates