Research Article

Sensitivity Analysis of a Three-Species Nonlinear Response Omnivory Model with Predator Stage Structure

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Abstract

Omnivory is defined as feeding on more than one trophic level and is ubiquitous in most natural communities. We investigate a three-species nonlinear response omnivory model incorporating stage structure in the top predator. The model consists of four coupled ordinary differential equations involving fourteen parameters. As estimates from natural systems the parameters are subject to natural intrinsic variability and measurement error. To determine how infinitesimally small changes in the parameters affect the model solution, we derive sensitivity equations and numerically solve for the sensitivities. Our performance measure of the sensitivities shows that the mortality and search rates are the most sensitive parameters with conversion efficiencies at intermediate values. The resource enrichment rates and handling times are the least sensitive.

Keywords: sensitivity analysis, omnivory model, stage structure

1   Introduction

Omnivory is defined as the act of feeding on resources at more than one trophic level [1]. A three-species subset of omnivory involving predation and competition is known as intraguild predation [2]. In this paper, we investigate a model incorporating nonlinear Holling Type II functional and numerical responses as well as stage structure in the top predator. We approximate a natural omnivory system with a deterministic model of differential equations so there is variability in our model inputs. Similarly, the model parameters are limited by measurement error. These errors affect the outcomes or solutions to our model.

We use sensitivity analysis to determine how infinitesimally small changes in model parameter values affect the population densities. There are many variations and applications of sensitivity analysis (see [3, 4, 5, 6] for example). Our method will help us determine which parameter estimates are sufficiently precise for our model to give reliable predictions based upon the dynamics of our model. Also, we will be able to prioritize the parameters to help biologists determine which parameter values should be more closely estimated from empirical data. This in turn should dictate an increase in precision and accuracy with which biologists collect data for specific parameter estimates. Vance et al. [7, 8] used sensitivity analysis to study the parameters of a linear response omnivory model and a nonlinear response omnivory model, respectively.

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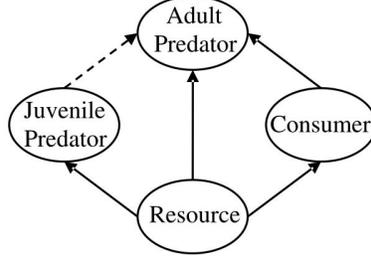[*]Correspondence: `jav6e@uvawise.edu`

Figure 1: Illustration of Three-Species Omnivory with Predator Stage Structure. Solid arrows indicate that one species (base of arrow) is eaten by another species (point). The dashed arrow indicates a growth transition.

2   Stage Structured Omnivory Model

We investigate a model similar to the model given in [9] which consists of a coupled system of ordinary differential equations incorporating nonlinear functional and numerical responses of the basal resource density, R, and intermediate consumer density, C. Also, our model incorporates two stages in the top predator species with the juvenile stage denoted by P_1 and the adult stage denoted by P_2. Our model assumes that the juvenile predator stage feeds on the basal resource and adult predator stage feeds on the basal resource and the intermediate consumer. The intermediate consumer feeds solely on the resource (see Figure 1). The model given in [9] assumes that, in the absence of consumers and predators, the resource population grows according to semichemostat dynamics, whereas we assume the resource population grows logistically to be consistent with previous work conducted by Vance et al. [7, 8].

$$\frac{dP_2}{dt} = \mu_P P_1 - m_P P_2 \tag{1}$$

$$\frac{dP_1}{dt} = \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}P_2 - (\mu_P + m_P)P_1 \tag{2}$$

$$\frac{dC}{dt} = C\left[\frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_C\right] \tag{3}$$

$$\frac{dR}{dt} = R\left[r\left(1 - \frac{R}{K}\right) - \frac{\lambda_{RC}C}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{RP}P_1}{1 + \lambda_{RP}h_{RP}R}\right]$$
$$+ R\left[-\frac{\lambda_{RP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}\right] \tag{4}$$

with initial conditions

$$P_2(0) = c_1 > 0, \qquad P_1(0) = c_2 > 0, \qquad C(0) = c_3 > 0, \qquad \text{and} \qquad R(0) = c_4 > 0.$$

Parameter r is the intrinsic rate of increase of the resource, K is the environmental carrying capacity of the resource, λ_{ij} is the search rate of species j for species i, h_{ij} is the time spent by species j handling species i, and e_{ij} is the efficiency with which species i is converted to new offspring of species j. The natural mortality rate for both of the predator stages is m_P, and m_C is the natural mortality rate for the consumer. μ_P is the rate at which the juvenile predator matures into the adult predator. A summary of the variables and parameters is given in Table 1.

Table 1: Definitions of Variables and Parameters

Parameter	Definition
R	Basal resource density
C	Intermediate consumer density
P_1	Juvenile top predator density
P_2	Adult top predator density
r	Resource intrinsic rate of increase
K	Environmental carrying capacity of the resource
λ_{RC}	Search rate of consumer for resource
λ_{RP}	Search rate of predator for resource
λ_{CP}	Search rate of predator for consumer
h_{RC}	Time spent by consumer handling resource
h_{RP}	Time spent by predator handling resource
h_{CP}	Time spent by predator handling consumer
e_{RC}	Conversion efficiency of resource into consumer
e_{RP}	Conversion efficiency of resource into predator
e_{CP}	Conversion efficiency of consumer into predator
m_C	Natural mortality rate of consumer
m_P	Natural mortality rate for both predator stages
μ_P	Predator maturation rate

3   Sensitivity Analysis

Our model (equations (1), (2), (3), and (4)) can be written in the form

$$\frac{dx_1}{dt} = F_1(x_1, x_2, x_3, x_4) \tag{5}$$

$$\frac{dx_2}{dt} = F_2(x_1, x_2, x_3, x_4) \tag{6}$$

$$\frac{dx_3}{dt} = F_3(x_1, x_2, x_3, x_4) \tag{7}$$

$$\frac{dx_4}{dt} = F_4(x_1, x_2, x_3, x_4) \tag{8}$$

where x_j, $j = 1, 2, 3, 4$ represents the P_2, P_1, C, and R species densities respectively. We represent each parameter by α_i, $i = 1, 2, \ldots, 14$ and define the sensitivity of state variable x_j with respect to parameter α_i as

$$S_{j,i} = \frac{\partial x_j}{\partial \alpha_i} \tag{9}$$

for $j = 1, 2, 3, 4$ and $i = 1, 2, \ldots, 14$.

Available theory given in Rossenwasser [5] allows differentiating each equation in the system above with respect to each of the parameters and interchanging the order of differentiation to derive a linear system of differential equations for the sensitivities

$$\frac{\partial}{\partial t} S_{j,i} = \sum_{k=1}^{4} \left(\frac{\partial F_j}{\partial x_k} S_{j,i} \right) + \frac{\partial F_j}{\partial \alpha_i}. \tag{10}$$

The above equations are called the sensitivity equations and require that

$$\frac{\partial F_j}{\partial x_k}$$

be continuous with respect to independent variable t and state variables x_k for all $j, k = 1, 2, 3, 4$ (see [5]). Differentiation of the initial conditions result in

$$S_{j,i}(0) = 0$$

for each $j = 1, 2, 3, 4$ and $i = 1, 2, \ldots, 14$.

Notice that $\frac{\partial F_j}{\partial x_k}$ does not depend upon the parameter and thus does not change for each parameter. However, $\frac{\partial F_j}{\partial \alpha_i}$ changes for each parameter. We use the term *general sensitivity equations* for the system of linear ordinary differential equations

$$\frac{\partial}{\partial t} S_{j,i} = \sum_{k=1}^{4} \left(\frac{\partial F_j}{\partial x_k} S_{j,i} \right) \tag{11}$$

since the terms $\frac{\partial F_j}{\partial x_k}$ remain the same for each parameter. We use the term *particular part of the sensitivity equations* for the terms

$$\frac{\partial F_j}{\partial \alpha_i} \tag{12}$$

since they change for each parameter. The partial derivatives computed from (12) are given in Table 2 for each of the fourteen model parameters. Notice that each partial derivative is continuous with respect to t, P_2, P_1, C, and R for all positive values.

We define

$$S_{P_2} = S_{1,i} = \frac{\partial P_2}{\partial \alpha_i},$$

$$S_{P_1} = S_{2,i} = \frac{\partial P_1}{\partial \alpha_i},$$

$$S_C = S_{3,i} = \frac{\partial C}{\partial \alpha_i},$$

$$S_R = S_{4,i} = \frac{\partial R}{\partial \alpha_i},$$

consistent with equation (9). For the sake of space, we will suppress the dependence upon the independent variable t in the following equations. The general sensitivity equations for our nonlinear response omnivory model with predator stage structure are

$$\frac{d}{dt}(S_{P_2}) = (-m_P)S_{P_2} + (\mu_P)S_{P_1}$$

$$\frac{d}{dt}(S_{P_1}) = \left(\frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right) S_{P_2} - (\mu_P + m_P)S_{P_1}$$

$$+ \left(\frac{e_{CP}\lambda_{CP}P_2(1 + \lambda_{RP}h_{RP}R) - e_{RP}\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \right) S_C$$

$$+ \left(\frac{e_{RP}\lambda_{RP}P_2(1 + \lambda_{CP}h_{CP}C) - e_{CP}\lambda_{RP}\lambda_{CP}h_{RP}CP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \right) S_R$$

$$\frac{d}{dt}(S_C) = \left(-\frac{\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right) S_{P_2}$$

$$+ \left(\frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2(1 + \lambda_{RP}h_{RP}R)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} - m_C \right) S_C$$

$$+ \left(\frac{e_{RC}\lambda_{RC}C}{(1 + \lambda_{RC}h_{RC}R)^2} + \frac{\lambda_{CP}\lambda_{RP}h_{RP}CP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \right) S_R$$

$$\frac{d}{dt}(S_R) = \left(-\frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}\right)S_{P_2}$$

$$+ \left(-\frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R}\right)S_{P_1}$$

$$+ \left(-\frac{\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} + \frac{\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}\right)S_C$$

$$+ \left(r\left(1 - \frac{2R}{K}\right) - \frac{\lambda_{RC}C}{(1 + \lambda_{RC}h_{RC}R)^2} - \frac{\lambda_{RP}P_1}{(1 + \lambda_{RP}h_{RP}R)^2}\right)S_R$$

$$- \left(\frac{\lambda_{RP}P_2(1 + \lambda_{CP}h_{CP}C)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}\right)S_R$$

with initial conditions

$$S_{P_2}(0) = 0, \ S_{P_1}(0) = 0, \ S_C(0) = 0, \text{ and } S_R(0) = 0.$$

The sensitivity equations are formed by adding the corresponding particular part of the sensitivity equations found in each row and column in Table 2 to the general sensitivity equations given above.

For each parameter that the original system has, we must solve a system of linear sensitivity equations. The number of differential equations in the state system dictates how many differential equations there will be in the linear sensitivity system. For our model, we have fourteen parameters and four variables. Also, although the sensitivity equations are linear, they are forced by the solution to the state equations. Thus, to compute the sensitivities we solve one hundred twelve equations in groups of eight (four model and four sensitivity). To solve the state equations we use the parameter values taken with slight modifications from Mylius et al. [9] and Persson et al. [10] listed in Table 3. This combination of parameter values leads to a stable equilibrium solution for the model with all species present.

We numerically integrate the linear sensitivity equations and the nonlinear state equations using a fourth- and fifth-order adaptive step size algorithm known as ode45 in the computing software Matlab. This is a Runge-Kutta-Fehlberg method that simultaneously obtains two solutions per step in order to monitor the accuracy of the solution and adjust the step size according to user-prescribed tolerances on the error. We use 1×10^{-3} for the relative error and 1×10^{-6} for the absolute error tolerances with initial condition $(1, 1, 2, 3)^T$ for the state equations and initial condition $(0, 0, 0, 0)^T$ for the sensitivity equations.

There are four sensitivities corresponding to the four state variables for each parameter. So we define the weighted euclidean norm

$$||S_i||(t) = \sqrt{w_1(S_{1,i})^2 + w_2(S_{2,i})^2 + w_3(S_{3,i})^2 + w_4(S_{4,i})^2}$$

for each $i = 1, 2, \ldots, 14$ as a performance measure of how small changes in the parameters affect the state variables. Notice that this performance measure is a function of the parameter and time only. For our calculations we let each weight be equal to one so that each of the state variables is weighted equally. Unbalanced weighting could be used if a state variable was considered more important in terms of the performance measure. Also, if the sensitivities are extremely different in magnitude then a weighted norm provides a way to ensure that each sensitivity has approximately the same impact upon the performance measure. In our case, we did not feel that the difference in magnitude of the sensitivities corresponding to a single parameter was significant and thus chose equal weighting.

4 Results

Based upon the numerical values of the performance measures of the sensitivities over time, we define three classes of parameters corresponding to their sensitivities: small, medium,

Table 2: Partial derivatives of the right hand side of original model with respect to the parameters.

Parameter	Partial of F_1	Partial of F_2
e_{RP}	0	$\frac{\lambda_{RP}RP_2}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}$
e_{CP}	0	$\frac{\lambda_{CP}CP_2}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}$
e_{RC}	0	0
λ_{RP}	0	$\frac{e_{RP}RP_2(1+\lambda_{CP}h_{CP}C)-e_{CP}\lambda_{CP}h_{RP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
λ_{CP}	0	$\frac{e_{CP}CP_2(1+\lambda_{RP}h_{RP}R)-e_{RP}\lambda_{RP}h_{CP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
λ_{RC}	0	0
h_{RP}	0	$-\frac{\lambda_{RP}RP_2(e_{RP}\lambda_{RP}R+e_{CP}\lambda_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
h_{CP}	0	$-\frac{(\lambda_{CP})CP_2(e_{RP}\lambda_{RP}R+e_{CP}\lambda_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
h_{RC}	0	0
m_P	$-P_2$	$-P_1$
m_C	0	0
μ_P	P_1	$-P_1$
r	0	0
K	0	0

Parameter	Partial of F_3	Partial of F_4
e_{RP}	0	0
e_{CP}	0	0
e_{RC}	$\frac{\lambda_{RC}RC}{1+\lambda_{RC}h_{RC}R}$	0
λ_{RP}	$\frac{\lambda_{CP}h_{RP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$-\frac{RP_1}{(1+\lambda_{RP}h_{RP}R)^2}-\frac{RP_2(1+\lambda_{CP}h_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
λ_{CP}	$-\frac{CP_2(1+\lambda_{RP}h_{RP}R)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$\frac{\lambda_{RP}h_{CP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
λ_{RC}	$\frac{e_{RC}RC}{(1+\lambda_{RC}h_{RC}R)^2}$	$-\frac{RC}{(1+\lambda_{RC}h_{RC}R)^2}$
h_{RP}	$\frac{\lambda_{RP}\lambda_{CP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$\frac{(\lambda_{RP})^2R^2P_1}{(1+\lambda_{RP}h_{RP}R)^2}+\frac{(\lambda_{RP})^2R^2P_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
h_{CP}	$\frac{(\lambda_{CP})^2C^2P_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$\frac{\lambda_{RP}\lambda_{CP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
h_{RC}	$-\frac{e_{RC}(\lambda_{RC})^2R^2C}{(1+\lambda_{RC}h_{RC}R)^2}$	$\frac{(\lambda_{RC})^2R^2C}{(1+\lambda_{RC}h_{RC}R)^2}$
m_P	0	0
m_C	$-C$	0
μ_P	0	0
r	0	$R\left(1-\frac{R}{K}\right)$
K	0	$\frac{rR^2}{K^2}$

Table 3: Parameter values and sensitivity ranking

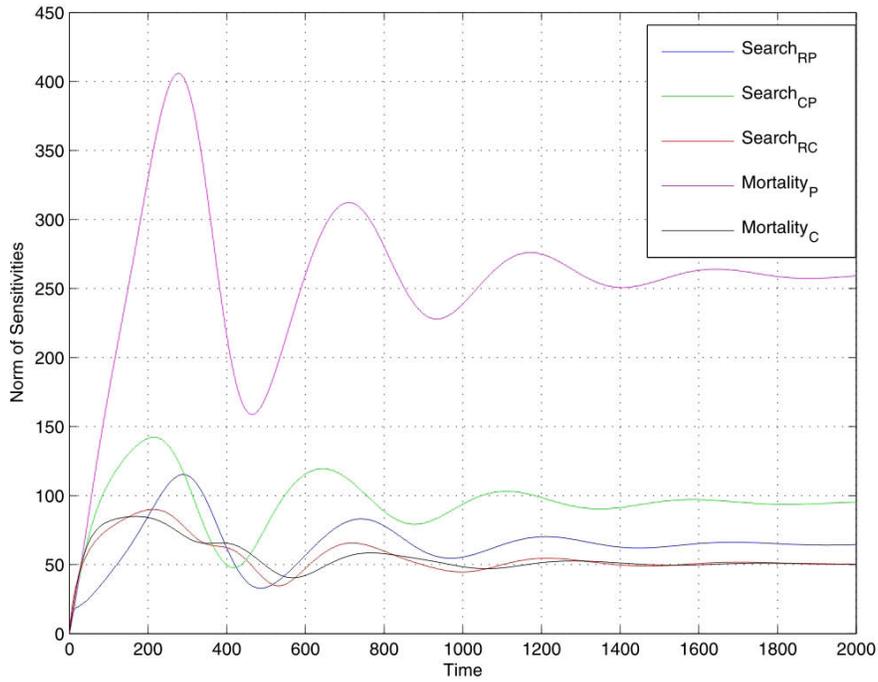| Parameter	Value	Rank	Parameter	Value	Rank
r	0.3	9	K	4	11
λ_{RC}	0.037	4	h_{RC}	3	13
λ_{RP}	0.025	3	h_{RP}	4	12
λ_{CP}	0.025	2	h_{CP}	4	14
e_{RC}	0.6	10	m_C	0.03	5
e_{RP}	0.36	7	m_P	0.0275	1
e_{CP}	0.6	8	μ_P	0.1	6

Figure 2: Plot of the performance measure for parameters with *large* sensitivities over time.
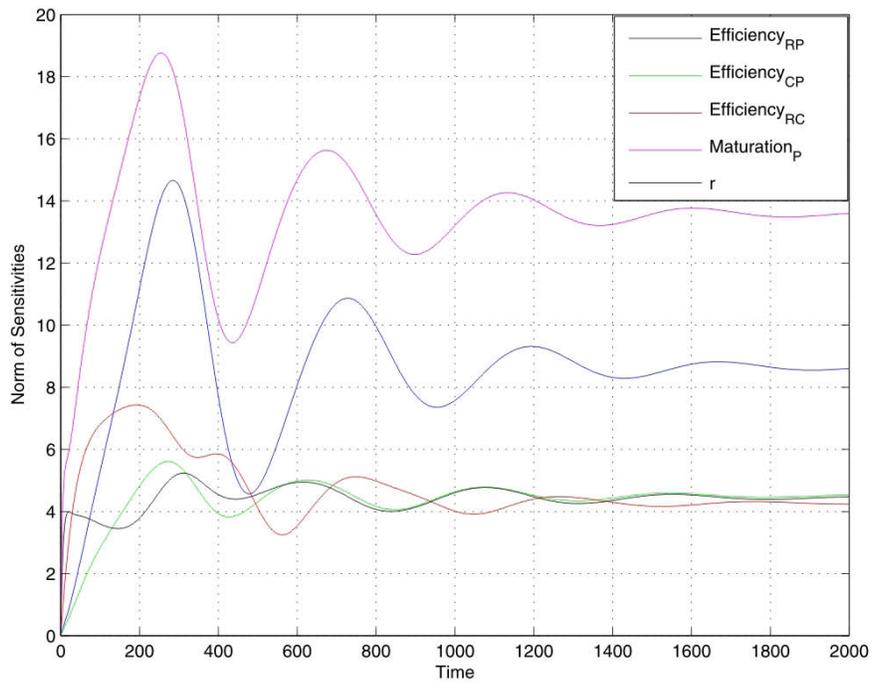

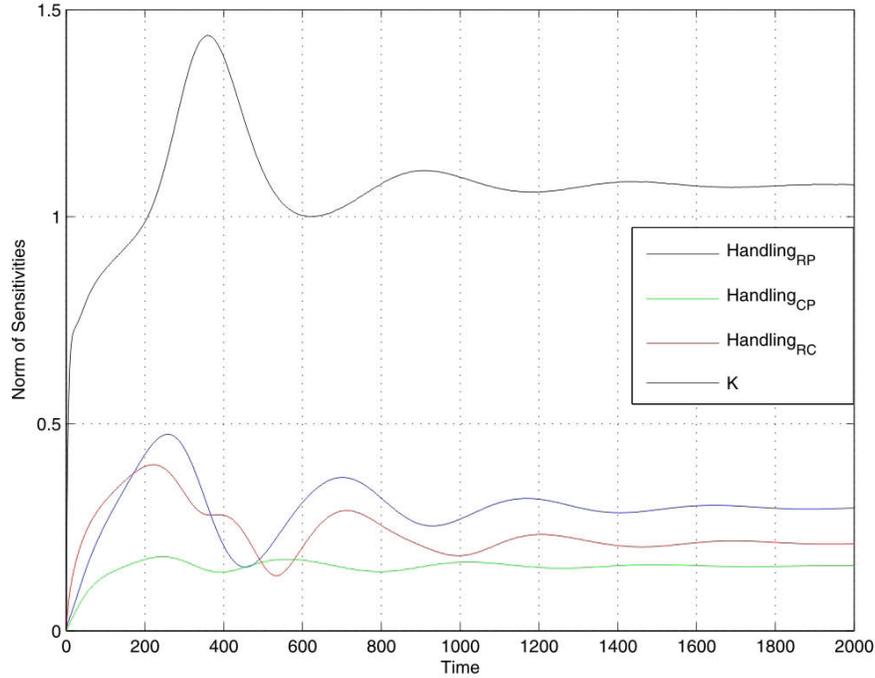Figure 3: Plot of the performance measure for parameters with *medium* sensitivities over time.

Figure 4: Plot of the performance measure for parameters with *small* sensitivities over time.

and large. Figure 2 depicts the graph of the performance measure of the parameters corresponding to large sensitivities, Figure 3 depicts the graph of the performance measure of the parameters corresponding to medium sensitivities, and Figure 4 depicts the graph of the performance measure of the parameters corresponding to small sensitivities. Notice the changing scale on the vertical axes. In the legends of the graphs, the handling times, h_{ij}, are denoted by Handling$_{ij}$, the conversion efficiencies, e_{ij}, are denoted by Efficiency$_{ij}$, the search rates, λ_{ij}, are denoted by Search$_{ij}$, the mortality rates, m_i, are denoted by Mortality$_i$, and the maturation rate, μ_i, is denoted by Maturation$_i$ where i, j are the appropriate P_2, P_1, C, or R as given in Table 1. Notice that in all three plots of the performance measures (Figures 2, 3, 4) the values of the performance measures vary over time but eventually level to a steady state. This is because the parameter values listed in Table 1 lead to a steady state solution of the original model with all three species present. For analysis on the parameter space that leads to all three species present also known as permanent coexistence for this model see [11].

As shown in Figure 2 the performance measure or the norm of the sensitivities is the largest for the predator mortality rate with a maximum value of approximately 410 and steady state value of around 260. This indicates that small changes in the predator mortality rate cause the largest change in the model solution. So variation in the predator mortality rate due to measurement error or natural intrinsic variability affects the population densities to a greater extent than the other parameters. To give an overall ranking of the parameters we consider the value of the performance measure per parameter at steady state since there are many oscillations in the performance measures over time until steady state is reached.

The performance measures for the consumer mortality rate and the search rates are quite similar with maximum values ranging from 80 to 140 and steady state values ranging from 50 to 95. Ranked by steady state performance values, the most sensitive parameters in Figure 2 after the predator mortality rate listed in decreasing order are λ_{CP}, λ_{RP}, λ_{RC}, and m_C. The maximum values for the parameters in Figure 3 range from 5 to 19 with steady state values ranging from 4 to 13. Ranked by steady state values the medium sensitive parameters listed in decreasing order are μ_P, e_{RP}, e_{CP}, r, and e_{RC}. Figure 4 shows the performance

values for the resource carrying capacity and the handling times. These parameters with smaller sensitivities listed in decreasing order K, λ_{RP}, λ_{RC}, and λ_{CP} have maximum values ranging from 0.2 to 1.4 with steady state values ranging from 0.1 to 1.1.

5   Conclusion

The most sensitive parameter is the predator mortality rate. Vance et al. [7, 8] found the same result for a linear response omnivory model and a nonlinear response omnivory model respectively. In general, the mortality rates and search rates are the most sensitive. Conversion efficiencies, the maturation rate and resource enrichment parameters are at intermediate levels. Handling times are less sensitive with the time spent by the predator handing the consumer being the least sensitive. A ranking has been provided in Table 3 with a ranking of 1 corresponding to the most sensitive parameter and 14 corresponding to the least sensitive parameter.

For parameters with larger sensitivities biologists should take extra care in the field or lab collecting data for that parameter value. Thus biologists should pay closer attention to data collection for the mortality rates. Since the handling times affect the solutions to the state equations the least, biologists need not be as accurate in collecting data to estimate those parameters. This ranking of parameters can contribute significantly to research project efficiency since most projects have limited funding and confined time frames for completion of data collection. It should be noted that biologists have no control over the natural intrinsic variability in the model parameters. Thus to use the model for species density predictions and management decisions requires a concerted effort to reduce the measurement errors that can be controlled. This is another important contribution of our sensitivity analysis.

The ranking of the parameters may be affected by the use of a weighted norm performance measure since it is a global measure. A relative measure could provide additional insight into how sensitive the parameters of our three-species nonlinear response omnivory model with predator state structure are to small changes corresponding to natural intrinsic variability and measurement error. Also, the sensitivities and rankings depend upon the parameter values given in Table 3. Thus, significantly different parameter values could change the rankings.

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