

Sensitivity analysis of a three-species nonlinear response omnivory model

James A. Vance and Kevin J. Wilson

Abstract—We investigate a three-species omnivory model with non-linear Holling Type II functional and numerical responses. As estimates from natural systems, the model parameters are subject to natural intrinsic variability and measurement error. We use sensitivity analysis to determine how infinitesimal changes in parameters, corresponding to variability and error, affect the population densities. We show that the handling times are less sensitive with the search and mortality rates being the most sensitive.

Keywords—Omnivory, Intraguild Predation, Sensitivity Analysis, Holling Type II Response.

I. INTRODUCTION

Omnivory is defined as the act of feeding on resources at different trophic levels [1]. In particular, we investigate a model incorporating intraguild predation which is a three-species subset of omnivory. The model has nonlinear Holling Type II functional and numerical responses. We approximate a natural omnivory system with a deterministic model of differential equations so there is a certain amount of natural intrinsic variability that our model inputs are subject to. Also, our thirteen model parameters are limited by measurement error. These errors affect the outcomes or solutions to our model.

We use sensitivity analysis to determine how small changes in model parameter values affect the population densities. There are many variations and applications of sensitivity analysis (see [2], [3] for example). Our method involves the use of analytical tools to evaluate how infinitesimal changes in parameters affect the state variables. This 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. Reference [4] used sensitivity analysis to study the parameters of a linear response omnivory model.

J.A. Vance is an Associate Professor of Mathematics at The University of Virginia's College at Wise, Wise, VA 24299 USA (phone: 276-376-4615; e-mail: jav6e@uvawise.edu).

K. J. Wilson was an undergraduate student at the University of Virginia's College at Wise.

II. OMNIVORY MODEL

We investigate the model given by [5] which consists of a coupled system of differential equations with the functional and numerical responses being nonlinear functions of the basal resource density, R , and intermediate consumer density, C . Thus our model is governed by dynamics in which a top predator, P , feeds on the basal resource and intermediate consumer and the consumer feeds solely on the resource (see Fig. 1).

$$\frac{dP}{dt} = P \left[\frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_P \right] \quad (1)$$

$$\frac{dC}{dt} = C \left[\frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_C \right] \quad (2)$$

$$\frac{dR}{dt} = R \left[r \left(1 - \frac{R}{K} \right) - \frac{\lambda_{RC}C}{1 + \lambda_{RC}h_{RC}R} \right] - R \left[\frac{\lambda_{RP}P}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right] \quad (3)$$

with initial conditions $P(0) = c_1 > 0$, $C(0) = c_2 > 0$, and $R(0) = c_3 > 0$.

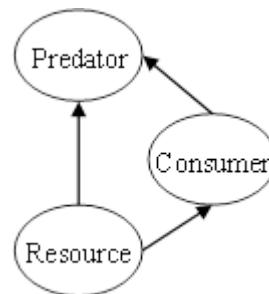


Fig. 1 illustration of three-species omnivory. Arrows indicate that one species (base of arrow) is eaten by another (point).

Parameter λ_{ij} is the search rate of species j for species i , e_{ij} is the efficiency with which species i is converted to new offspring of species j , and h_{ij} is the time spent by species j handling species i . K is the resource carrying capacity and r is the intrinsic rate of increase of the resource. The natural mortality rates of the predator and consumer are m_P and m_C , respectively.

III. SENSITIVITY ANALYSIS

To use available theory from Rossenwasser [3], we write our system of coupled differential equations in the form

$$\frac{dx_1}{dt} = F_1(x_1, x_2, x_3) \tag{4}$$

$$\frac{dx_2}{dt} = F_2(x_1, x_2, x_3) \tag{5}$$

$$\frac{dx_3}{dt} = F_3(x_1, x_2, x_3) \tag{6}$$

where $x_j, j=1,2,3$ represents the P, C, and R species densities respectively. We represent each parameter by $\alpha_i, i=1,2,\dots,13$.

We define the sensitivity of state variable x_j with respect to parameter α_i as

$$S_{ji} = \frac{\partial x_j}{\partial \alpha_i} \tag{7}$$

for $j=1,2,3$ and $i=1,2,\dots,13$.

Then by differentiating each equation in the system above with respect to each of the parameters and interchanging the order of differentiation, we derive a linear system of differential equations for the sensitivities, called the sensitivity equations

$$\frac{\partial}{\partial t} S_{ji} = \sum_{k=1}^3 \frac{\partial F_j}{\partial x_k} S_{ji} + \frac{\partial F_j}{\partial \alpha_i} \tag{8}$$

as given by [3]. The above mathematical manipulations require that

$$\frac{\partial F_j}{\partial x_k} \tag{9}$$

be continuous with respect to independent variable t and state variables x_k for all $j, k=1,2,3$ (see [3]).

Also, we must differentiate the initial conditions with respect to each parameter and thus

$$S_{ji}(0) = 0 \tag{10}$$

for each $j=1,2,3$ and $i=1,2,\dots,13$. It should be noted that

$$\frac{\partial F_j}{\partial x_k} \text{ remains the same for each parameter and } \frac{\partial F_j}{\partial \alpha_i} \text{ changes}$$

for each parameter.

We use the term *general sensitivity equations* for the system of linear ordinary differential equations

$$\frac{\partial}{\partial t} S_{ji} = \sum_{k=1}^3 \frac{\partial F_j}{\partial x_k} S_{ji} \tag{11}$$

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. Tables 1, 2 and 3 give the partial derivatives computed from (12) for each of the thirteen model parameters.

The general sensitivity equations for our nonlinear response omnivory model are

$$\begin{aligned} \frac{d}{dt}(S_P) = & S_P \left[\frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_P \right] \\ & + S_C \left[\frac{e_{CP}\lambda_{CP}P(1 + \lambda_{RP}h_{RP}R) - e_{RP}\lambda_{RP}\lambda_{CP}h_{CP}RP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \right] \\ & + S_R \left[\frac{e_{RP}\lambda_{RP}P(1 + \lambda_{CP}h_{CP}C) - e_{CP}\lambda_{RP}\lambda_{CP}h_{RP}CP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \right] \end{aligned} \tag{13}$$

$$\begin{aligned} \frac{d}{dt}(S_C) = & S_P \left[\frac{\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right] \\ & + S_C \left[\frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P(1 + \lambda_{RP}h_{RP}R)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} - m_C \right] \\ & + S_R \left[\frac{e_{RP}\lambda_{RP}C}{(1 + \lambda_{RC}h_{RC}R)^2} + \frac{\lambda_{RP}\lambda_{CP}h_{RP}CP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \right] \end{aligned} \tag{14}$$

$$\begin{aligned} \frac{d}{dt}(S_R) = & S_P \left[-\frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right] \\ & + S_C \left[-\frac{\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{RP}\lambda_{CP}h_{CP}RP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \right] \\ & + S_R \left[r \left(1 - \frac{2R}{K} \right) - \frac{\lambda_{RC}C}{(1 + \lambda_{RC}h_{RC}R)^2} \right] \\ & - S_R \left[\frac{\lambda_{RP}P(1 + \lambda_{CP}h_{CP}C)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \right] \end{aligned} \tag{15}$$

where

$$S_P(t) = \frac{\partial}{\partial \alpha_i} P(t) \tag{16}$$

$$S_C(t) = \frac{\partial}{\partial \alpha_i} C(t) \tag{17}$$

$$S_R(t) = \frac{\partial}{\partial \alpha_i} R(t) \quad (18)$$

The sensitivity equations are then formed by adding the particular part of the equations to the general sensitivity equations. For each parameter we must simultaneously solve a system of three linear differential equations for the sensitivities with respect to that parameter. However, the sensitivity equations are forced by the original system of nonlinear equations. Thus, to compute the sensitivities we solve seventy eight equations in groups of six. To solve the original equations we use the parameter values taken from [5] listed in Table 4.

We numerically solve the linear sensitivity equations and the nonlinear model 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 absolute error tolerances with initial condition $(1,1,1)^T$ for the nonlinear model and initial condition $(0,0,0)^T$ for the sensitivity equations. Although numerical integration introduces errors and thus variability into the system, this variability is minimal (1×10^{-3}) and necessary since there are no known analytical methods to solve the nonlinear equations.

Since there are three state variables, there are three sensitivities for each parameter. So we define the weighted norm

$$\|S_i\|(t) = \sqrt{w_1(S_{1,i})^2 + w_2(S_{2,i})^2 + w_3(S_{3,i})^2} \quad (19)$$

for each $i = 1, 2, \dots, 13$ 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 didn't feel that the difference in magnitude of the sensitivities corresponding to a single parameter was significant and thus chose equal weighting.

IV. RESULTS

Based upon the numerical values of the performance measures of the sensitivities over time, we define three classes of parameters: small, medium, and large. Fig. 2 depicts the graph of the performance measure of the large sensitivities, Fig. 3 depicts the graph of the performance measure of the medium sensitivities, and Fig. 4 depicts the graph of the

performance measure of the 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}, and the mortality rates, m_i , are denoted by Mortality_i, where i, j are the appropriate P, C, or R as given in (1), (2), and (3). Notice that in all three plots of the performance measures (Figs. 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 4 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 [6].

As shown in Fig. 2 the performance measure or the norm of the sensitivities is the largest for the predator natural mortality rate with a maximum value of approximately 240 and steady state value of around 140. This indicates that small changes in the predator natural mortality rate cause the largest change in the model solution. So variation in the predator mortality rate due to measurement error and/or natural intrinsic variability affects the population densities in a greater way 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 intermediate consumer natural mortality rate and the search rates are quite similar with maximum values ranging from 25 to 110 and steady state values ranging from 40 to 60. However, ranked by steady state performance values, the most sensitive parameters in Fig 2 after the predator mortality rate are the parameters listed in decreasing order $\lambda_{RP}, \lambda_{CP}, m_C, \lambda_{RC}$.

For the intrinsic rate of basal resource increase and the conversion efficiencies all with medium performance measures in Fig 3, the maximum values range from 2 to 12 with steady state ranges of 2 to 7. Ranked by steady state value the next most sensitive parameters are listed in decreasing order $e_{RP}, e_{RC}, e_{CP}, r$.

Fig 4 shows the performance values for basal resource carrying capacity and the handling times. These parameters with smaller sensitivities listed in decreasing order $K, h_{RP}, h_{RC}, h_{CP}$ have maximum values ranging from 0.1 to 1.7 and steady state values ranging from 0.1 to 1.2

V. CONCLUSION

The most sensitive parameter is the predator natural mortality rate. In general, the mortality rates and search rates are the most sensitive with conversion efficiencies and basal resource parameters at intermediate levels. Handling times are less sensitive with the time spent by the predator handling the consumer being the least sensitive.

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. Biologist need not be as accurate in collecting data for the handling times since they affect the species densities the least. This ranking is important since research 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 are to small changes corresponding to natural intrinsic variability and measurement error.

Table 1 partial derivatives of the right hand side of (1) with respect to the model parameters.

Parameter	Partial Derivatives of F_1
r	0
K	0
λ_{RC}	0
λ_{RP}	$\frac{e_{RP}RP(1 + \lambda_{CP}h_{CP}C) - e_{CP}\lambda_{CP}h_{RP}RCP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}$
λ_{CP}	$\frac{e_{CP}CP(1 + \lambda_{RP}h_{RP}R) - e_{RP}\lambda_{RP}h_{CP}RCP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}$
h_{RC}	0
h_{RP}	$-\frac{\lambda_{RP}RP(e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}$
h_{CP}	$-\frac{\lambda_{CP}CP(e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}$
e_{RC}	0
e_{RP}	$\frac{\lambda_{RP}RP}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}$
e_{CP}	$\frac{\lambda_{CP}CP}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}$
m_C	0
m_P	-P

Table 2 partial derivatives of the right hand side of (2) with respect to the model parameters.

Parameter	Partial Derivatives of F_2
r	0
K	0
λ_{RC}	$\frac{e_{RC}RC}{(1 + \lambda_{RP}h_{RP}R)^2}$
λ_{RP}	$\frac{\lambda_{CP}h_{RP}RCP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}$

λ_{CP}	$-\frac{CP(1 + \lambda_{RP}h_{RP}R)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}$
h_{RC}	$-\frac{e_{RC}(\lambda_{RC})^2 R^2 C}{(1 + \lambda_{RC}h_{RC}R)^2}$
h_{RP}	$\frac{\lambda_{RP}\lambda_{CP}RCP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}$
h_{CP}	$\frac{(\lambda_{CP})^2 C^2 P}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}$
e_{RC}	$\frac{\lambda_{RC}RC}{1 + \lambda_{RC}h_{RC}R}$
e_{RP}	0
e_{CP}	0
m_C	-C
m_P	0

Table 3 partial derivatives of the right hand side of (1) with respect to the model parameters.

Parameter	Partial Derivatives of F_3
r	$R\left(1 - \frac{R}{K}\right)$
K	$\frac{rR^2}{K^2}$
λ_{RC}	$-\frac{RC}{(1 + \lambda_{RC}h_{RC}R)^2}$
λ_{RP}	$-\frac{RP(1 + \lambda_{CP}h_{CP}C)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}$
λ_{CP}	$\frac{\lambda_{RP}h_{CP}RCP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}$
h_{RC}	$\frac{(\lambda_{RC})^2 R^2 C}{(1 + \lambda_{RC}h_{RC}R)^2}$
h_{RP}	$\frac{(\lambda_{RP})^2 R^2 P}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}$
h_{CP}	$\frac{\lambda_{RP}\lambda_{CP}RCP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}$
e_{RC}	0
e_{RP}	0
e_{CP}	0
m_C	0
m_P	0

Table 4 parameter values for the nonlinear response omnivory model.

Parameter	Value
r	0.3
K	3
λ_{RC}	0.037
λ_{RP}	0.025
λ_{CP}	0.025

h_{RC}	3
h_{RP}	4
h_{CP}	4
e_{RC}	0.6
e_{RP}	0.36
e_{CP}	0.6
m_C	0.03
m_P	0.0275

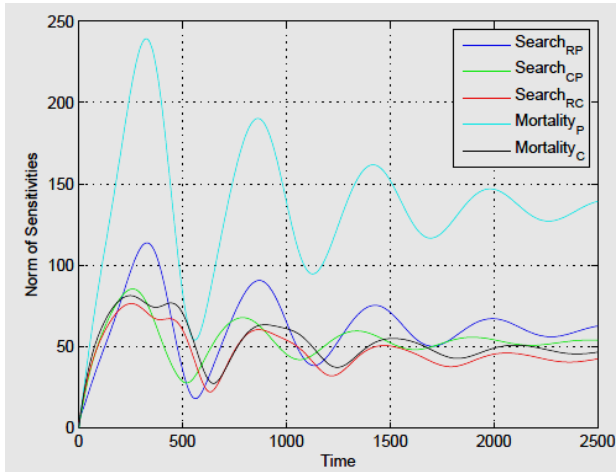


Fig 2. plot of the performance measure for large sensitivities over time.

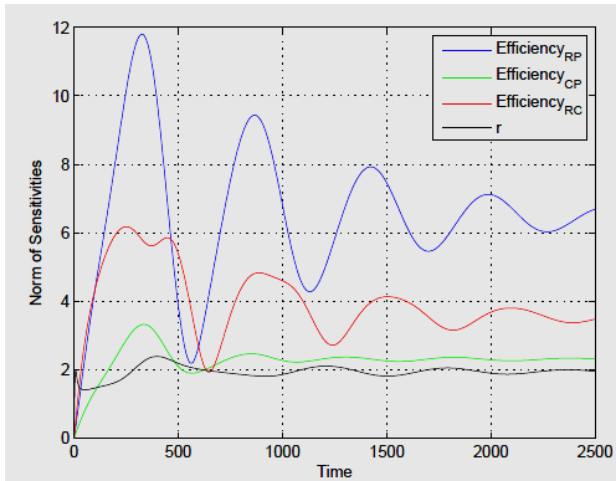


Fig. 3 plot of the performance measure for medium sensitivities over time.

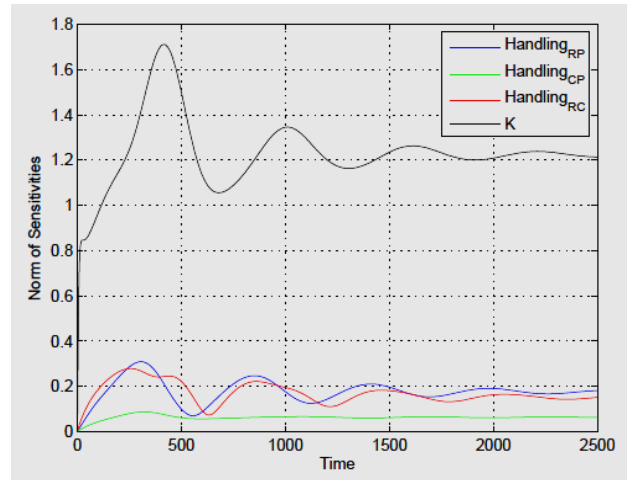


Fig. 4 plot of the performance measure for small sensitivities over time.

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