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Sensitivity Analysis of a Three-Species Linear Response Omnivory Model

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Abstract: We investigate a three-species omnivory model with linear functional and numerical responses. Our coupled system of differential equations incorporates the definition of omnivory—feeding on more than one trophic level—using model parameters and state variables. 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. Our analysis allows us to determine which parameters must be estimated with as much accuracy as possible to ensure reasonable population density estimates. We apply theorems on continuous dependence and differentiability with respect to parameters to our model to derive sensitivity equations. Solving the sensitivity equations using an adaptive step numerical integration method and the use of a weighted norm allow for a comparison of sensitivities. We show that small changes in the predator mortality rate cause the greatest change in the model solution. Thus, biologists should take extra care in the field to accurately collect data to determine the predator mortality rate. Also, we determine the least sensitive parameter to be the biological carrying capacity of the basal resource.

Keywords: Omnivory Model, Sensitivity Analysis.

Introduction

Models are developed to approximate natural systems. This fact imposes a limitation on the confidence we place on the model outcomes due to the amount of natural intrinsic variability our model must be subject to. Also, model parameters are limited by measurement error. We use sensitivity analysis to provide an evaluation of the confidence in a three-species linear response omnivory model. This can help biologists know where to concentrate their efforts to decrease mearsurement errors for parameter approximation [7].

Sensitivity analysis involves the use of analytical and computational tools to evaluate how changes in model parameters affect model response variables. There are many variations and applications of sensitivity analysis (see [6], [1] for example). In our case, we investigate how infinitesimally small changes in parameter values affect population densities. This will help us determine which parameter estimates are sufficiently precise for our model to give reliable predictions based upon the dynamics of the model. In turn, we will be able to prioritize the parameters to help biologists determine which parameter values should be more accurately estimated from empirical data.

The unique combination of competition and predation know as omnivory has a relatively recent history of mathematical study [3], [4]. The three-species constellation of omnivory is known as intraguild predation or IGP and involves a top predator feeding on more than one trophic level. The long term survival of species in a linear response omnivory model was studied by Holt et al [3] and Vance [9] using permanence theory.

Omnivory Model

We investigate the model given by Vance [9] which consists of a coupled system of differential equations with the functional and numerial responses being linear functions of the basal resource density, R, and intermediate consumer density, C. Thus our model is governed by Lotka-Volterra dynamics in which a top predator, P, feeds on the basal resource and intermediate consumer and the consumer feeds solely on the resource.

$$\frac{dP}{dt} = P[e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_P]$$
$$\frac{dC}{dt} = C[e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_C]$$
$$\frac{dR}{dt} = R[r(1 - R/K) - \alpha_{RC}C - \alpha_{RP}P]$$

According to our model, the resource population grows according to logistic growth in the absence of consumers and predators. Parameter r represents the intrinsic rate of increase of the resource, and K is the resource carrying capacity in the absence of consumers and predators. The resource declines due to predation by the consumer as well as the predator. The parameters α_{RC} and α_{RP} are the consumption rates of the resource by the consumer and predator respectively. Both the predator and the consumer decline by natural mortality, m_P and m_C, respectively, and the consumer experiences additional mortality (in the form of a consumption rate α_{CP}) due to the predator. The efficiencies with which the predator and consumer convert resources into new offspring are given by e_{RP} (for the predator) and e_{RC} (for the consumer). In addition, the predator converts consumers into new offspring with efficiency e_{CP}.

Sensitivity Analysis

Vance [9] shows that given initial values our model has a unique solution for all non-negative time even though the equations themselves are non-linear. This is important since we must solve the original equations in order to complete the sensitivity analysis.

Our model can be written in the form

$$\frac{dx_1}{dt} = f_1(x_1, x_2, x_3)$$
$$\frac{dx_2}{dt} = f_2(x_1, x_2, x_3)$$
$$\frac{dx_3}{dt} = f_3(x_1, x_2, x_3)$$

where x_j , $j = 1, 2, 3$ represents the species densities for P, C, and R respectively. Also, we denote each parameter by α_i , $i = 1,2, \dots 10$.
The first step in our sensitivity analysis method is to differentiate each equation of our model with respect to each of the model parameters. Then interchanging the order of differentiation, we derive a linear system of equations for the sensitivities,

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

that solves

$$\frac{d}{dt} S_{j,i} = \sum_{k=1}^{3} \left(\frac{\partial \mathrm{f}_\mathrm{j}}{\partial \mathrm{x}_\mathrm{k}} S_{j,i} \right) + \frac{\partial \mathrm{f}_\mathrm{j}}{\partial \alpha_\mathrm{i}}$$

as given by [6].

Notice that when computing the partial derivatives, the terms $\frac{\partial \mathrm{f}_\mathrm{j}}{\partial \mathrm{x}_\mathrm{k}}$ remain the same for each parameter and the terms $\frac{\partial \mathrm{f}_\mathrm{j}}{\partial \alpha_\mathrm{i}}$ differ for each parameter. Also, for each parameter of the original system, we must solve a system of three linear differential equations each of which is "forced" by the solutions to the original equations [8]. Hence for each parameter we must simultanteously solve the three linear sensitivity equations and the three original non-linear equations. Thus, for our model we end up solving sixty equations in groups of six. To solve the original equations we use the parameter values given in Table 1 provided by Diehl [2].

Table 1: Numerical Approximations for Parameters

Parameter	Approximation
r	0.4
K	2
α_{RC}	0.1
α_{RP}	0.1
α_{CP}	0.05
e_{RC}	0.8
e_{RP}	0.2
e_{CP}	0.5
m_C	0.06
m_P	0.04

We numerically integrate the coupled systems using *Matlab*'s fourth- and fifth-order adaptive step algorithm known as *ode45* to solve the systems. 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 [5]. We use 1×10^{-3} for the relative error tolerance, 1×10^{-3} for the absolute error tolerance, and $(1,1,1)^T$ as the initial conditions.

We use a weighted norm as a performance measure of how small changes in the parameters affect the state variables:

$$\|\boldsymbol{S}_i\|(t) = \left\|(S_{1,i}, S_{2,i}, S_{3,i})^T\right\|(t) = \sqrt{w_1(S_{1,i})^2 + w_2(S_{2,i})^2 + w_3(S_{3,i})^2}$$

The weights may be used to gauge that one species is more important in the measure. However, for our calculations, we weight each species equally. That is, $w_1 = w_2 = w_3 = 1$. Thus we have a performace measure that is a function of the parameter and time only.

Results

We define two classes for the sensitivities based upon the numerical values over time: smaller and larger. The following graphs are plots of the norms of the sensitivies over time. Figure 1 depicts the graph for the smaller norms and Figure 2 depicts the graph for the larger norms.

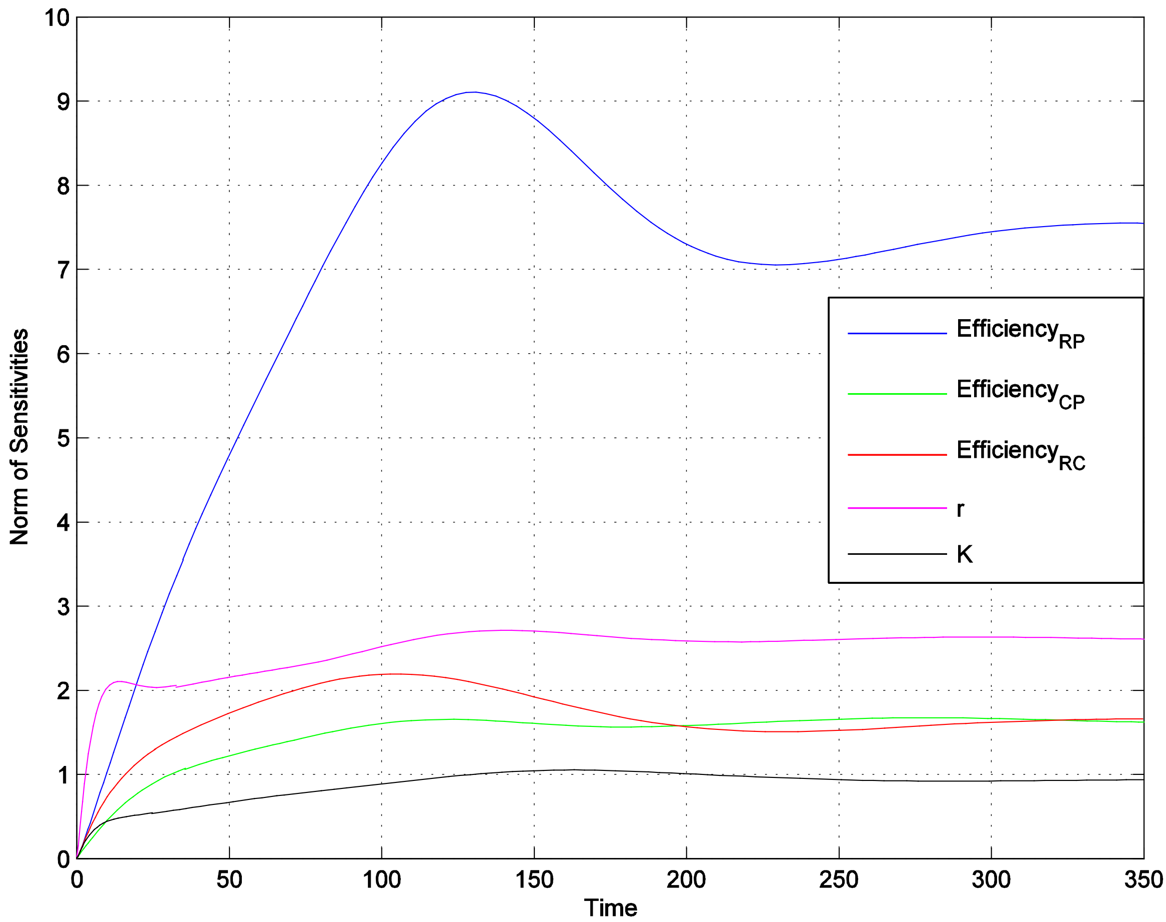

Figure 1: Plot of the norm of (smaller) sensitivities over time.

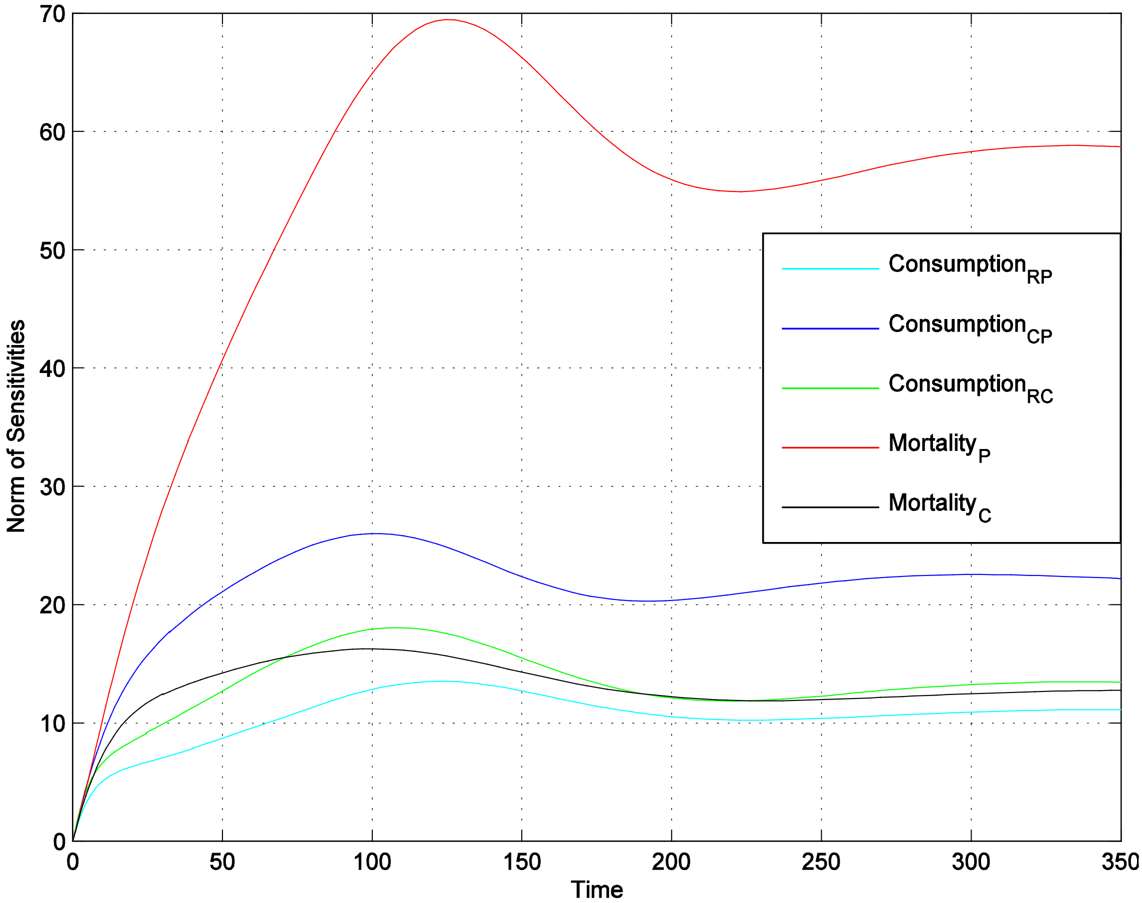

Figure 2: Plot of the norm of (larger) sensitivities over time.

As seen in Figure 2, the largest value for the norm of the sensitivities for any model parameter is less than seventy. In fact, the most sensitive parameter is the predator mortality rate, m_P. The next most sensitive parameters in the larger class are the parameters listed in decreasing order: $a_{CP}, a_{RC}, m_C, a_{RP}$.

For the smaller class, the next most sensitive parameters listed in decreasing order: $e_{RP}, r, e_{RC}, e_{CP}, K$. Thus, the least sensitive parameter is the resource carrying capacity. Also, the consumption rates are more sensitive than the conversion efficiencies.

Conclusion

Since the norm of the sensitivity for the predator mortality rate is the largest, small changes in the predator mortality rate cause the largest change in the model solution. Thus, biologist should take extra care in the field to accurately collect data for the predator mortality rate. Biologist need not be as accurate in collecting data for the resource carrying capacity since it affects the solution the least.

One limiting factor in our sensitivity analysis method is that our performance measure is a global mearsure. A relative measure could add additional insight into model parameters, their sensitivies, and the affect on the model solution.

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