Sensitivity Characteristics of Response Surface Models for Estimation of Ecological Parameters in Ratio-Dependent Predator-Prey Systems

Dale B. McDonald
McCoy School of Engineering
Midwestern State University
3410 Taft Blvd
Wichita Falls, TX
USA 76308
940.397.4004

Abstract

*It has been shown that **R**esponse **S**urface **M**odels (**RSMs**) may be used to aid the analyst in the understanding of ecological phenomena. Given a dynamic system model of a predator-prey system, strategic use of analytical and numerical methods may allow for estimation of ecological parameters within mathematical models. This is significant, in particular by noting the manner in which RSMs are constructed. Given scattered (discrete) data, **r**adial **b**asis functions (**RBFs**) and an interpolation parameter denoted by "c" is chosen. What results is a continuous and often differentiable model. This is significant as data collected from field measurements most likely presents in scattered form. The purpose of this treatment is to provide analysts with a pragmatic means by which parameters that are integral components of equations governing predator-prey interactions may be estimated. The fundamental conclusion is that RSM consistency, and insensitivity, to c results in accurate ecological parameter estimation.*

Keywords: Response Surface Modeling, Ratio-Dependent Systems, Ecological Parameters

1. Introduction

While predator-prey interactions are typically described by dynamic system models governed by **o**rdinary **d**ifferential **e**quations (**ODEs**), RSMs that produce continuous and differentiable models are of great utility. A fundamental issue in the study of predator-prey interactions is the inherent difficulty in rectifying the mathematical models with data that is gathered in the field. It is in the spirit of "closing the gap" between theory and practice that it seems natural to use RSMs towards this end. Data collected from the field is by nature discrete while dynamic system models are most likely continuous in time. Therefore, the impetus exists to invoke techniques that are accepting of discrete data to aid in the analysis of predator-prey systems that are by nature continuous. The proposed method for parameter estimation developed is numerical and of course aligns perhaps more closely with the "theoretical" side of parameter estimation in ecological systems. However, given the importance of understanding and sustaining acceptable levels and health of natural resource systems, it is felt that such techniques are necessary to more closely align theory and practice.

In (McDonald, 2013), RSMs created via RBFs were used to estimate ecological parameters. However, this was executed considering a single RBF and interpolation parameter c. Here, that effort is extended so that the analyst may have useful strategies which provide a greater level of assurance that the constructed RSM model(s) (and derivatives) will produce useful, accurate estimates. We will achieve this by demonstrating that function, gradient, and Hessian matrix characteristics of the RSM are insensitive to change in the interpolation parameter when "good" ecological parameter estimates may be gleaned from constructed RSMs.

A useful reference regarding the RBFs and the resulting RSMs so constructed may be found in (McDonald, et al., 2007). This details the manner in which RSMs are created; analytical formulas for gradient vectors and Hessian matrices are also provided. In (McDonald 2013) the special case was considered where a single RSM (cubic) with the interpolation parameter $c = 1.25$ was used to accurately estimate parameters that appeared in the predator biomass time rate of change ODE. This treatment is inspired by (McDonald 2013) but is unique in that it demonstrates use of a control algorithm defined in that effort, coupled with varying c (creating new models with each unique value of c), leads to consistent parameter estimates leveraging several RSMs.

2. Background Information

For the dynamic system model, we consider the ratio-dependent predator-prey system considered in (Kar et al., 2004) which is a variant of a Holling-Tanner model (Sun et al., 2010 and Froda, et al, 2009) given by

$$\dot{x}_1 = rx_1\left(1 - \frac{x_1}{K}\right) - \frac{\beta x_1 x_2}{\alpha + x_1} - qux_1$$

$$\dot{x}_2 = sx_2\left(1 - \frac{x_2}{vx_1}\right)$$

(1)

For comparison, systems with a so-called "prey-dependent" functional responses are often studied; one example where a prey-dependent system was studied in a related fashion to the present treatment is (McDonald 2012). In (1), biomass of the prey is given by x_1 while predator biomass is given by x_2. The carrying capacity for the prey is denoted by K, r is the intrinsic growth rate, β is the maximum harvesting rate, α is the half-saturation level, with q known as the catchability coefficient. The intrinsic growth rate for the predator is denoted by s, and, by inspection, the parameter v represents the ratio of predator to prey biomass at equilibrium (Kar et al., 2004). As in (McDonald, 2013), it is assumed that the harvesting effort u satisfies $0 \leq u \leq u_{max}$. Given the form of (1) it is clear that the prey may be harvested, while the predator is not (predator is protected from harvest).The control algorithm **I**nstantaneous **M**aximization of **N**et **E**conomic **R**evenue (**IMNER**) was developed in (McDonald 2013). The details of the development may be found there, but the fundamental idea was to select a harvesting effort (control variable u) that maximized net economic revenue (Kar et al., 2004) at each instant. It was shown in (McDonald, 2013) that the IMNER algorithm produced sustainable, equilibrium (parameter) values of predator and prey, which provided for the accumulation of revenue important to economic ventures (net economic revenue) and regulatory agencies, typically governmental entities (total discounted net economic revenue). For reference, the net economic revenue is (Kar et al., 2004)

Net Economic Revenue $= J^* = u(q(p - \tau)x_1 - C)$ (2)

with total net economic revenue given by

$$\int_0^\infty J^* dt = \int_0^\infty u(q(p - \tau)x_1 - C)dt$$

(3)

Within (2) and (3), q is, as before, the catchability coefficient, C is the cost of fishing per unit effort, and τ is the rate of taxation. More detailed information may be found in (McDonald, 2013), but by instantaneous maximization of net economic revenue, the control law is selected by satisfying

$$max_u[u(q(p - \tau)x_1 - C)]$$

(4)

at each instant. The maximization (4) is equivalent to satisfying first-order necessary conditions for the minimization problem

$$max_u J^* = min_u[-J^*] = min_u[-u(q(p - \tau)x_1 - C)]$$

(5)

It is well known that minimization proceeds by forming the Lagrangian, applied to (5) in this case, and applying first-order necessary conditions (Vincent and Grantham, 1997). This ultimately yielded the IMNER algorithm; the algorithm and the details of the derivation using necessary conditions given by the Lagrangian may be found in (McDonald 2013) stated here it is

$$
\begin{aligned}
u &= u_{min} & if & \quad \sigma > 0 \\
u &= u_{max} & if & \quad \sigma < 0 \\
u &= u_s & if & \quad \sigma = 0
\end{aligned}
$$

(6)

where

$$\sigma = -(q(p - \tau)x_1 - C)$$

(7)

Clearly, σ dictates when harvest is at a minimum level (no harvest), a maximum level (maximum harvesting effort) or at an intermediate level. Of course, the IMNER algorithm is implemented numerically in the following examples. Therefore, we allow the singular control regime (u_s) when $\sigma \leq 0.0001$.

The IMNER algorithm (6) is a version of variable structure control, with σ known as a switching surface because the control varies from minimum to maximum across this surface (Vincent and Grantham 1997). An interesting phenomenon occurs when $\sigma = 0$; the control (harvesting) effort supplied during this time is analogous to singular control. Note that it is this singular control that allows for continual harvest once the predator and prey have reached equilibrium (constant) values (McDonald 2013). For reference, the total discounted net economic revenue, which represents benefits (via taxation) to regulatory agencies is

$$J = \int_0^\infty e^{-\delta t}(pqx_1 - C)u\,dt \tag{8}$$

With the parameter δ known as the instantaneous rate of annual discount (Kar et al. 2004).

3. Consistent Response Surface Models

As in (McDonald 2013) the so-called **p**redator **b**iomass **t**ime **r**ate of **c**hange (**PBTRC**), which is the "right-hand side" of the second of equations (1) will be sampled across a grid of points. That is the right hand side of

$$\dot{x}_2 = sx_2\left(1 - \frac{x_2}{vx_1}\right) \tag{9}$$

$$\dot{x}_2 = F(\mathbf{x})$$

is the PBTRC and is now denoted by $F(\mathbf{x})$. The gradient of (9) is

$$\frac{\partial(\dot{x}_2)}{\partial \mathbf{x}} = \frac{\partial F}{\partial x} = \left[\frac{sx_2^2}{vx_1^2} \quad s - \frac{2sx_2}{vx_1}\right] \tag{10}$$

with the Hessian matrix of $F(\mathbf{x})$ given by

$$\frac{\partial^2(\dot{x}_2)}{\partial \mathbf{x}^2} = \frac{\partial^2 F}{\partial \mathbf{x}^2} = \begin{bmatrix} \frac{-2sx_2^2}{vx_1^3} & \frac{2sx_2}{vx_1^2} \\ \frac{2sx_2}{vx_1^2} & -\frac{2s}{vx_1} \end{bmatrix} \tag{11}$$

Note that while the $F(\mathbf{x})$ is the function to be sampled, we will denote the corresponding RSM, created by evaluating $F(\mathbf{x})$ at sampled data points, by $f(\mathbf{x})$. This is an important distinction that must be clearly made. We are departing from purely, continuous time (ODE) models of predator-prey relationships. Scattered data is what will be gathered from the field. We leverage RSMs to estimate parameters within mathematical models (1, 9). To illustrate this, we must consider both the ecological structure and characteristics that are present within the ratio-dependent predator-prey model, recalling the mechanics of constructing RSMs of from scattered data. It will be shown that this scattered data may be assembled into continuous and differentiable mathematical models. By varying c, the analyst may estimate ecological parameters accurately by monitoring the "consistency" and "sensitivity" of the created models.

3.1 Cubic Response Surface Models

In this subsection, we construct two RSMs based upon $F(\mathbf{x})$. The parameter c is quite different for each model. This is undertaken to demonstrate how c results in very different function, gradient, and Hessian matrix models of $F(\mathbf{x})$. The crucial implication is that widely varying models, mindful of the analytic gradients and Hessians (10, 11), produce much different estimates for ecological parameters.

In order to easily compare the present results with those from the literature, we consider the dynamic system (1) with the following values for the "actual" parameters. That is, we let $r = 1.5$, $K = 200$, $\beta = 0.1$, $\alpha = 10$, $q = 0.01$, $s = 1.2$, and $v = 5$. Also, we sample $F(\mathbf{x})$ over the same space as in (McDonald 2013); given by $x_1 = 1, 1.05, 1.1, \ldots, 3$, and $x_2 = 1, 1.05, 1.1, \ldots, 3$. From these points, an RSM is created so that we may compute gradients and Hessian matrix values. We will consider the cubic radial basis function (McDonald et al. 2007)

$$\phi(r) = (r + c)^3 \tag{12}$$

and consider the interpolation parameter c taking multiple values.

3.1.1 RSMs via Multiple "c" Values

Let all constants found in (1) be given by the values listed in the text immediately preceding (12). First, let c satisfy $c = 0.1$. Following the procedure outlined in (McDonald et al. 2007, McDonald 2013), given the grid of points, a numerical simulation was executed which created a response surface model $f(x)$.

The gradient and Hessian matrix of $f(x)$ was evaluated (again for consistency with the literature) at $x_1 = 1.513$ and $x_2 = 2.513$. The gradient and Hessian matrix values at this point are displayed in Table 1. Now, let c satisfy $c = 3.0$. The gradient and Hessian matrix of $f(x)$ was evaluated at $x_1 = 1.513$ and $x_2 = 2.513$. The gradient and Hessian matrix values at this point are displayed in Table 2. The analytic gradient and Hessian matrix values are clearly different. This underscores the point that parameter estimation must be supported by similar gradient and Hessian matrix evaluations, despite the value of c. That is, a fundamental characteristic of such systems is that ecological parameters are insensitive to changes in the interpolation parameter c.

Now, we let $c = 0.6$. As before, a numerical simulation was executed which created a response surface model $f(x)$. The gradient and Hessian matrix of $f(x)$ was evaluated at $x_1 = 1.513$ and $x_2 = 2.513$. The gradient and Hessian matrix values at this point are displayed in Table 3.

Finally, let $c = 2.5$. As before, a numerical simulation was executed which created a response surface model $f(x)$. The gradient and Hessian matrix of $f(x)$ was evaluated at $x_1 = 1.513$ and $x_2 = 2.513$. The gradient and Hessian matrix values at this point are displayed in Table 4. These four tables illustrate interesting phenomena. Clearly, variation is seen in both the gradient vector and the Hessian matrix. This variance is a phenomenon that may be exploited to discern information regarding parameter estimates of ecological systems.

3.1.2 Example: Two Ecological Parameter Estimates for Varying "c" values

Note that in the analytical expressions for the gradient and the Hessian matrix of $F(\mathbf{x})$ (10, 11) involve only two unknowns for a given level of prey biomass x_1 and predator biomass x_2, s and v. Therefore, we may set the two "bold" numerical values in Tables 1-4 equal to the corresponding gradient and Hessian matrix entry in (10) and (11) respectively. This allows for parameter estimation. For example, from the gradient of $F(\mathbf{x})$ in Table 1 we may set $0.426 = s - (2sx_2)/(vx_1)$ in (10) and from the Hessian of $F(\mathbf{x})$ in Table 1 we may set $-1.20234 = -2s/vx_1$ in (11). This was executed for RSMs generated by the interpolation values represented in Tables 1-4; the results are shown in Table 5 and represent ecological parameter estimates derived from response surface models. In particular note that two pairs of the interpolation parameter c each differ in magnitude by 0.5.

3.2 Sensitivity of Parameter Estimates with Respect to "c"

Sensitivity may be defined in a number of ways (Grantham and Vincent 1993, Figliola and Beasley 2006). Here we take sensitivity of ecological parameters as a (discrete) change in the parameter with respect to the (discrete) change in c. Considering (1), and the above discussion, recall that the "real" values of s and v are 1.2 and 5.0 respectively. Table 5 illustrates estimates for these ecological parameters based upon response surface models created with differing values for c. Clearly, c values of 2.5 and 3.0, for the cubic RBF, result in better estimates as compared to the "real" values. It is significant and curious to note that more accurate estimates are less sensitive to changes in the interpolation parameter. Let the sensitivity of the parameter s with respect to c be given by

$$S_{sc} = \left|\frac{change\ in\ s}{change\ in\ c}\right| = \left|\frac{\Delta s}{\Delta c}\right| \tag{13}$$

And the sensitivity of the parameter v with respect to c be given by

$$S_{vc} = \left|\frac{change\ in\ v}{change\ in\ c}\right| = \left|\frac{\Delta v}{\Delta c}\right| \tag{14}$$

Given this definition, consider sensitivity of s and v as c is varied from $c = 0.6$ to $c = 0.1$. Given (13) we have

$$S_{sc} = \left|\frac{1.81-3.9}{0.6-0.1}\right| = 4.18 \tag{15}$$

and with (14) we have

$$S_{vc} = \left|\frac{4.29-3.73}{0.6-0.1}\right| = 1.12 \tag{16}$$

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Next, consider the sensitivity of s and v as c is varied from $c = 3.0$ and $c = 2.5$. Given (13) we have

$$S_{sc} = \left|\frac{1.1-1.17}{3.0-2.5}\right| = 0.14 \qquad (17)$$

and with (14) we have

$$S_{vc} = \left|\frac{4.71-5.05}{3.0-2.5}\right| = 0.68 \qquad (18)$$

From (15, 17) it is clear that for a poorer estimate of s ($c = 0.6, 0.1$) the parameter s is much more sensitive, in fact $4.18/0.14 = 29.9$ is more sensitive than its counterpart ($c = 3.0, 2.5$). Furthermore, the parameter v, from (16, 18) is also more sensitive as reflected by $1.12/0.68 = 1.65$ when comparing (16, 18). As noted prior c plays a fundamental role in accurate parameter estimation. A fundamental conclusion of this treatment is that it appears sensitivity as defined in (13, 14) is a concrete measure by which the analyst may create multiple models, calculate the sensitivity, and feel confident as to the ecological parameter estimates.

4. Sensitivity of Parameter Estimates Compared to the Literature

Now compare the results presented in this treatment with those given in the literature (for the presented biomass levels in relevant tables). In (McDonald 2013) for a value of the interpolation parameter $c = 1.25$, which produced estimates of ecological parameters. In that work, it was reported that

$$\frac{\partial f}{\partial x_2} = 0.4024 \qquad (19)$$

and

$$\frac{\partial^2 f}{\partial x_2^2} = -0.3043 \qquad (20)$$

A similar process as executed above led to estimates $s = 1.167$ and $v = 5.07$ for the biomass levels (as in Tables 1-5). These are, of course, quite close to the "real" parameter values of $s = 1.2$ and $v = 5.0$. Let us compare these values from the literature with the results in Table 5 ($s = 1.17, v = 5.05, c = 2.5$), while considering sensitivity. This yields

$$S_{sc} = \left|\frac{1.17-1.167}{2.5-1.25}\right| = 0.0024 \qquad (21)$$

and

$$S_{vc} = \left|\frac{5.05-5.07}{2.5-1.125}\right| = 0.016 \qquad (22)$$

Now, we compare these values from the literature with the results in Table 5 ($s = 3.9, v = 3.73, c = 0.1$), while considering sensitivity. This yields

$$S_{sc} = \left|\frac{3.9-1.167}{0.1-1.25}\right| = 2.38 \qquad (23)$$

and

$$S_{vc} = \left|\frac{3.73-5.07}{0.1-1.125}\right| = 1.31 \qquad (24)$$

It is clear from the present treatment given (15-22) that more accurate ecological parameter estimates (for s and v) are less sensitive to changes in the interpolation parameter c as opposed to less accurate estimates. In fact the "distance" from $c = 0.1$ to $c = 1.125$ is, of course, 1.025 and the "distance" from $c = 1.125$ to $c = 2.5$ is 1.375. Even though the "distance" between values of c is greater (from $c = 1.125$ and $c = 2.5$, the sensitivity is smaller in magnitude. This indicates more accurate parameter estimates.

5. Discussion

The divide between theoretical pursuits and field data observations remains one of the greatest challenges to understanding and appropriately managing natural resource systems. Building upon (McDonald 2013) it was demonstrated that multiple RSMs may be used to cross-validate models and provide the analyst with the mathematical and modeling background to generalize the results to field concerns (estimates of parameters such as s and v).

Note that it is significant that a well-known RBF, the cubic, was used in the present analysis. Therefore, we have demonstrated that within a single class of RBFs parameter estimation is possible. This work extends that of (McDonald 2013) in that multiple models (varying c values) generated by the cubic function were shown to be less sensitive to changes in this interpolation parameter as the estimates for s and ν became more precise. The fundamental message is that the analyst may use this cross-validation strategy via RSMs with differing c values with the sensitivity measure to be confident in parameter estimates. Immediate future work will explore the use of additional well-known interpolation functions $\phi(r)$ which are not of cubic form (such as the multiquadric, etc.) found in (McDonald et al., 2007).

6. Conclusion

Through the use of response surface models based upon the cubic radial basis function an effort to close the gap between strictly theoretical models of predator-prey interactions, and data which presents (in discrete form) has been established. It was shown that for the ratio-dependent predator-prey system studied here, discrete data provides a suitable basis from which continuous and differentiable models may be constructed. This is a fundamental point; discrete data is not in a suitable form, of course, in which analytic gradients and Hessian matrix may be produced. Through application of RSM, we are able to evaluate a response surface model, at a given level of prey and predator biomass, which may then be leveraged against the existing form of the dynamic system model for the purposes of parameter estimation. In addition to a constructive means by which parameters may be estimated, it is felt that the notion of sensitivity is unique; if the analyst constructs multiple models that produce similar estimates, this treatment suggests that accurate parameter estimates will follow.

7. References

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Table 1: RSM Model Data ($c = 0.1$)

x_1	x_2	$\dfrac{\partial f}{\partial x_1}$	$\dfrac{\partial f}{\partial x_2}$	$\dfrac{\partial^2 f}{\partial x_1^2}$	$\dfrac{\partial^2 f}{\partial x_1 \partial x_2}$	$\dfrac{\partial^2 f}{\partial x_2^2}$
1.513	2.513	0.67349	**0.426**	-1.3291	-0.27354	**-1.20234**

Table 2: RSM Model Data ($c = 3.0$)

x_1	x_2	$\dfrac{\partial f}{\partial x_1}$	$\dfrac{\partial f}{\partial x_2}$	$\dfrac{\partial^2 f}{\partial x_1^2}$	$\dfrac{\partial^2 f}{\partial x_1 \partial x_2}$	$\dfrac{\partial^2 f}{\partial x_2^2}$
1.513	2.513	0.66186	**0.40245**	-0.86689	0.54912	**-0.3064**

Table 3: RSM Model Data ($c = 0.6$)

x_1	x_2	$\dfrac{\partial f}{\partial x_1}$	$\dfrac{\partial f}{\partial x_2}$	$\dfrac{\partial^2 f}{\partial x_1^2}$	$\dfrac{\partial^2 f}{\partial x_1 \partial x_2}$	$\dfrac{\partial^2 f}{\partial x_2^2}$
1.513	2.513	0.66817	**0.40933**	-1.094	0.0234	**-0.5577**

Table 4: RSM Model Data ($c = 2.5$)

x_1	x_2	$\dfrac{\partial f}{\partial x_1}$	$\dfrac{\partial f}{\partial x_2}$	$\dfrac{\partial^2 f}{\partial x_1^2}$	$\dfrac{\partial^2 f}{\partial x_1 \partial x_2}$	$\dfrac{\partial^2 f}{\partial x_2^2}$
1.513	2.513	0.66185	**0.40244**	-0.86656	0.5498	**-0.3061**

Table 5: Ecological Parameter Estimates

c	x_1	x_2	$\dfrac{\partial f}{\partial x_2}$	$\dfrac{\partial^2 f}{\partial x_2^2}$	s	v
0.1	1.513	2.513	0.426	-1.20234	3.9	3.73
0.6	1.513	2.513	0.40933	-0.5577	1.81	4.29
2.5	1.513	2.513	0.40244	-0.3061	1.17	5.05
3.0	1.513	2.513	0.40245	-0.3064	1.1	4.71