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Sensitivity Analysis of Wolf Restoration in Yellowstone Nation Park Using Omnivory Models

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SENSITIVITY ANALYSIS OF WOLF RESTORATION IN YELLOWSTONE NATION PARK USING OMNIVORY MODELS

A thesis submitted to
the Graduate College of
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In partial fulfillment of
the requirements for the degree of
Master of Arts
in
Mathematics
by
Derek Fields
Approved by
Dr. Bonita Lawrence, Committee Chairperson
Dr. Clayton Brooks
Dr. Basant Karna
Dr. James Vance

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APPROVAL OF THESIS/DISSERTATION

We, the faculty supervising the work of [DEREK PAUL FIELDS], affirm that the thesis, [SENSITIVITY ANALYSIS OF WOLF RESTORATION IN YELLOWSTONE NATIONAL PARK USING OMNIVORY MODELS], meets the high academic standards for original scholarship and creative work established by the Department of Mathematics and the College of Science. This work also conforms to the editorial standards of our discipline and the Graduate College of Marshall University. With our signatures, we approve the manuscript for publication.

Dr. Bonita Lawrence, Department of Mathematics   Committee Chairperson   Date

Dr. Clayton Brooks, Department of Mathematics   Committee Member   Date

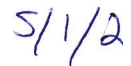Dr. Bassant Karna, Department of Mathematics   Committee Member   Date

Dr. James Vance, Department of Mathematics, UVA Wise   Committee Member   Date

ACKNOWLEDGEMENTS

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ABSTRACT

In the ever-changing world of ecology, species survival often depends on approximations and measurements taken by biologists. These approximations help to ensure and predict the future of that given species. Our ecological community of interest involves wolves, elk, and berry producing shrubs within Yellowstone National Park. We use two different systems of ordinary differential equations, each increasing in complexity to model our community. In each model the predator (wolves) and consumers (elk) compete for a common resource, berry producing shrubs. We call this consumption of resources, from more than one trophic level, omnivory. We approximate each system with parameter values from field biologist and wildlife reports. We then use a process called sensitivity analysis to determine how small changes in parameter values affect the solution to each respective system. This process allows us to determine which values biologists should take more care in monitoring to prevent extinction. Both our models offer similar results. The predator (wolf) mortality rate is the most sensitive to small changes. The least sensitive of our parameter values were the carrying capacity of the resource and the handling time of resources by wolves.

CHAPTER 1

Introduction

Living in a world surrounded by thousands of biological species, human beings are not always aware of how these complex organisms affect our world. Whether we realize it or not, our biological well-being depends a lot on other species for survival. The most obvious reason is food, but there are many more key elements that other species provide us with for survival. This dependence is worldwide for almost all species.

Interests in how populations grow or maintain stability is not a new trend. It was stimulated in the late 18th century when Thomas Malthus published, *An Essay on the Principle of Population as it Affects the Future of Society* [9].

Malthus' model used exponential growth to model human population, which he determined would exceed the carrying capacity of the earth's food supply, which in turn would cause widespread starvation. This is obviously a concern for any population, so it sparked an increase in modeling population dynamics [9]. However, until modern day, complex models have been limited due to the inherent nature of solving systems of differential equations. Without modern day computers and software that can handle intricate algorithms it was nearly impossible to solve complex systems that accurately depict population sizes at any time, t. Thankfully, the twenty-first century brought forth a huge increase in technology and software that could solve these coupled sets of differential equations used to model populations of increasing complexity. The software used to solve our coupled sets of differential equations will be Matlab, a very powerful program with built in algorithms such as the Runge-Kutta method. We will use Matlab's 4th and 5th order adaptive step size algorithm known as ODE45 to solve our coupled sensitivity differential equations.

This work will focus on a very familiar population within a vastly elaborate ecosystem, wolves in Yellowstone National Park. Since the establishment of Yellowstone National Park, wolves have had an overwhelming impact on the entire community of over two-hundred species. Wolves inside the park were the apex predator which kept coyote populations down, thus raising the population

of foxes, rabbits, beavers and other small predators that fall victim to large populations of coyotes [22]. Hence, making the wolf a very important topic when discussing population dynamics for the park. From the middle of the 1800's until 1926 the wolves of Yellowstone National Park were hunted and killed as a nuisance for preying on elk and deer, the parks most beloved animals [12]. In 1926 wolves were completely exterminated from the park [33]. Sadly, it was not until the the wolf was considered an endangered species that the government took action. Thankfully, in 1974 the U.S. government listed the wolf on the endangered species list, thus protecting them from being hunted [33]. It was not until January of 1995 that wolves trapped in Canada were released into Yellowstone National Park [28] [33] [32]. The reintroduction of wolves sparked a huge debate because of predation outside of the park, where wolves would prey on livestock and other domesticated animals.

Park researchers and others were also concerned that the wolves would prey so heavily on elk, that the elk population would drop below the threshold the park's ecosystem needs. Therefore, only 23 wolves were released into the park in 1995 [28] [27]. The wolves began to flourish along with nearly every other species in their food chain because of the rich ecosystem [28]. This promoted the release of 22 more wolves in 1996 [28] [30].

The reintroduction of the wolf into Yellowstone National Park is considered one of the most successful wildlife projects in U.S. history [22] [33]. This is mainly due to the overpopulation of elk and other species that could not be controlled without the presence of wolves. Elk populations were increasing at nearly an exponential rate and one year it was estimated that Yellowstone National Park contained approximately twenty-thousand elk [32]. We also note that not only were the elk increasing in density, but so were coyotes. Which in turn nearly exterminated beavers, foxes, and other small predators from the park[22].

Consequently, the misunderstood wolf became a savior to the Yellowstone ecosystem, once on the brink of losing several other species, including the wolf. We ask ourselves, how does such an alpha predator reduce the elk population from such a large growth rate, but also stop predation on smaller predators by other species? This is what we intend to answer by using omnivory models and finding the sensitivity of parameter values that effect each system. We will use three different omnivory models, each increasing in complexity with additional parameters. We will try

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to find which parameter values are most critical to the system and which have very little impact.

Moreover, will use coupled sets of differential equations to model wolves and their primary prey, elk, and one of the primary resources elk and wolves use for food, berry producing shrubs. We model these three species over time and use a process called sensitivity analysis to determine which parameter values effect the system the most. We will discuss how small changes in these parameters can change the entire ecosystem, forcing biologists to take extreme care when taking measurements in the field. We will also discuss which parameter values are the least sensitive to change, making them not as vital to the system. We will define and discuss our definitions and parameter values in Chapters 2 and 3.

1.1 Wolves and Their Impact on the Yellowstone Ecosystem

Before the reintroduction of the wolf into Yellowstone National Park (1995), the Aspen tree and various other berry-producing shrubs were suffering due to the overpopulation of elk [22] [2]. Naturally, one would think that elk are good for any ecosystem. However, each species in the ecosystem has its own impact on the others. We will discuss this intertwined ecosystem in more detail using omnivory models in Chapter 3.

Due to the large population of elk and overgrazing of the resources, small berry producing shrubs and aspens, the resources that support the livelihood of these animals began to diminish. This caused wildlife officials to be concerned about the aspen tree and small berry-producing shrubs which provide the basic diet for over twenty other species in the park, setting off a chain of events causing several other species to have trouble finding food: e.g. beavers, squirrels, other small mammals and various birds [22]. This was alarming to biologists and park officials. It was noted in *When the wolves returned : restoring nature's balance in Yellowstone* [22] that the once abundant foliage, shrubs, and aspen trees were now dying off, depleted, or in the process of being grazed upon by the over population of elk. Thus beavers, squirrels, and other small mammals were dying off from the depletion of these plants which they rely on for food and their habitat. It became so difficult for beavers to find live aspen trees that they were unable to build dams and raise families [22]. Another problem that resulted from the absence of the wolf was the drastic increase in the coyote population [22]. It was unknown that the absence of wolves would result in

the near extinction of several species as well as stunting the growth of the pronghorn elk population due to predation by coyotes [22]. With wolves missing from this complex ecosystem, the coyotes became the alpha predator and began killing off smaller species and ultimately shrinking the population of smaller mammals inside Yellowstone National Park. Hence, we see the massive impact the wolves, an alpha predator, make in even a large ecosystem such as Yellowstone National Park. Moroever, our interest and dynamic modeling will contain a top predator, the wolf, an intermediate consumer, the elk, and a resource vital to the park, berry producing shrubs. This ecosystem model will give us the best results since elk are the primary prey of wolves. We use berry producing shrubs as our resource because it is a shared between both populations and is directly affected by overgrazing of elk in absence of wolf predation.

Finally, in 1995-1996, park officials and biologist reintroduced the wolf, the apex predator, back into the pwark [33] [28] [27]. The results over the next decade were remarkable. A bar graph of wolf populations over the first decade of reintroduction is given in Figure 1.1, which was taken from the Yellowstone Wolf Project Annual Report [27]. Figure 1.2 depicts wolf predation statistics at elk feeding grounds [37].

Note how the change in wolf population in Figure 1.1 assumes a bell like curve. Peak population levels occur during the years 2003 and 2004. The years from 2007 to 2014 show that the wolf population settles down and assumes a very consistent population with no rapid increase in growth or decline. This offers our first evidence that the wolf population will not grow out of control, but taper off after a couple of decades. From Figure 1.2 we see a direct correlation between elk feeding grounds and wolf activity until the years 2003-2004. This suggests that elk may finding new feeding areas away from wolves. The bar graph clearly shows the number of feeding grounds increasing over the years, which spreads out elk predation on vital park resources. Hence, Figure 1.2 offers clear evidence that wolves are changing the way elk go after food and where they feed. Elk feeding in various areas allows more foliage and berry producing shrubs to survive from over consumption, making us wonder if the wolf truly is the key to restoring balance in the Park.
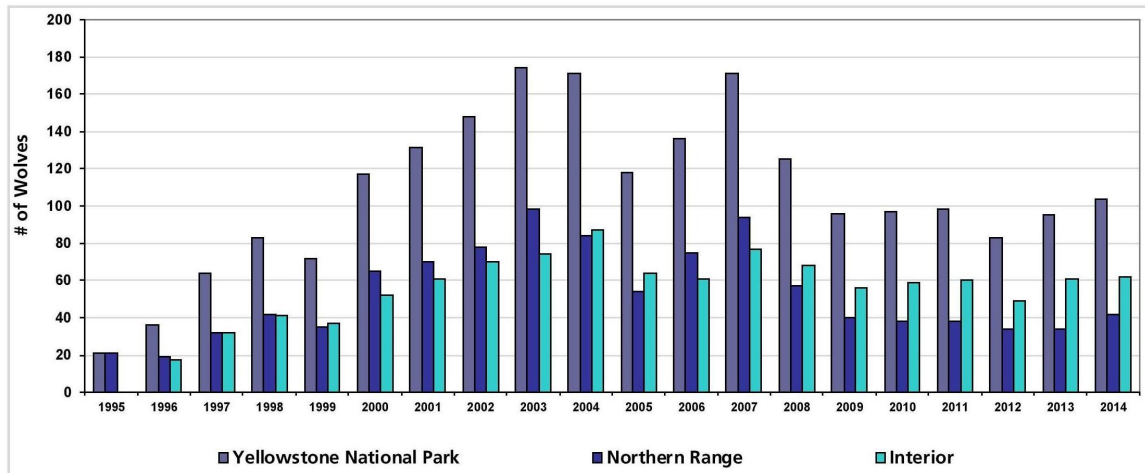
Figure 1.1: Wolf Population Density After Restoration
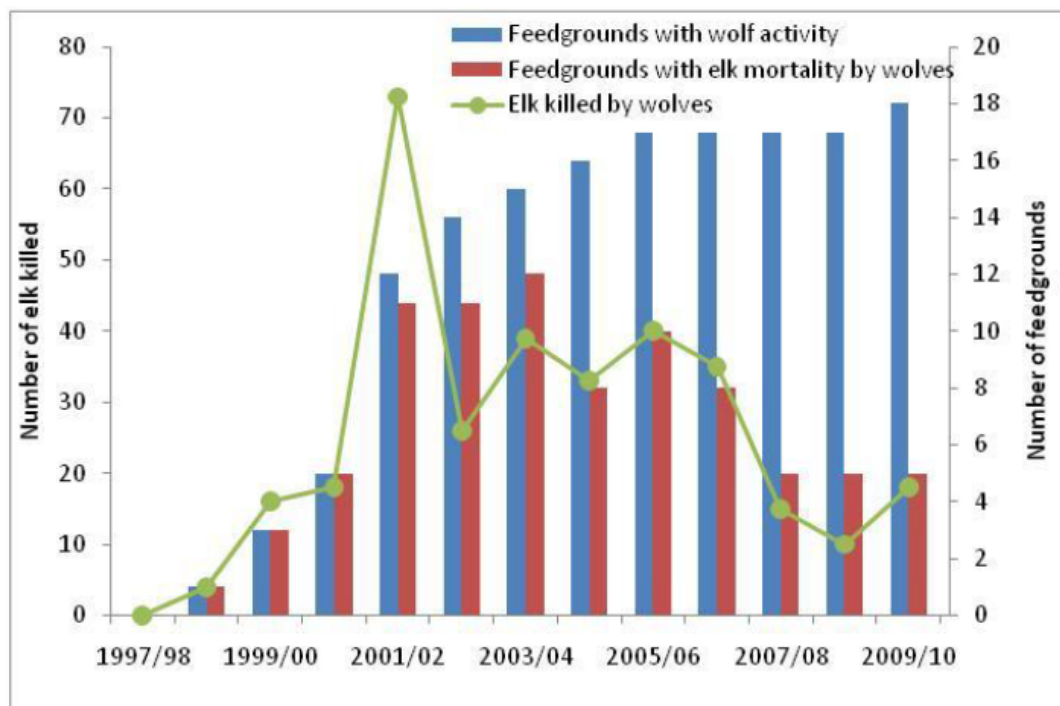
Figure 1.2: Wolf Predation on Elk Based on Number of Feedgrounds

1.2 Outline of Thesis

In Chapter 1 we have offered relevant information and time lines about wolf restoration and its impact on the Yellowstone National Park's ecosystem. Information and graphs about the wolves' impact on the population density of elk, their primary prey, is presented. We discussed problems that the massive elk population was creating for other species in the park. Finally, we reviewed the possible resolution to the ecosystems problem, the absence of the wolf. For the remainder of this introduction, we offer a brief discussion of the content in each chapter.

Chapter 2 is a general discussion about modeling competition and predation. We introduce the logistic growth equation and a standard Lotka-Voltera competition model based on logistic growth. A brief discussion of predation with two species is also given. We give a quick analysis of competition with three species and a linear food chain where the resource is governed by logistic growth.

In Chapter 3 we define a more complicated ecosystem consisting of three species where the interactions include both predation and competition. We discuss two different types of functional responses and calculate associated parameter values for each species in each of our omnivory models. Finally, we introduce two mathematical models with increasing complexity. We give an overview of each model and define parameters and give them numerical values calculated from biological sources.

In Chapter 4 we focus on definitions, lemmas, and theorems so that we can show the two systems introduced in Chapter 3 are capable of providing solutions. We provide theorems for continuous dependence and differentiability and theorems to ensure differentiability with respect to parameter values which will be used in later chapters.

Chapter 5 provides mathematical analysis for a linear response omnivory model. We reference theorems and lemmas from Chapter 4 to prove existence and uniqueness of a solution.

In Chapter 6 we reintroduce our predator stage structured model from Chapter 3. We offer mathematical analysis for this model and discuss its likelihood to offer better results than our previous model. Finally, we once again reference theorems from Chapter 4 to prove existence and uniqueness of solutions.

In Chapter 7, we apply our theorems on continuous dependence and differentiability with respect to parameters to each model. We then form sensitivity equations which will be solved by numerical integration in Matlab. We provide sensitivity equations for each model. A weighted norm is used to allow us to compare sensitivities.

Chapter 8 gives our final results. This includes graphs of each parameter's sensitivity with respect to time. We present the final sensitivity measure in a prioritized table with numbers to represent rank from most sensitive to least sensitive. Lastly, we provide biological meaning to each sensitivity measure.

In Chapter 9, our Conclusion, we discuss the impact each parameter could have in our ecosystem and Yellowstone National Park. We discuss which parameters are vital for biologists to monitor correctly and which have hardly any bearing on the system. We then look at future directions for continued research. Such examples include this same work, but on a different time continuum, such as time scales.

CHAPTER 2

MODELING PREDATION AND COMPETITION
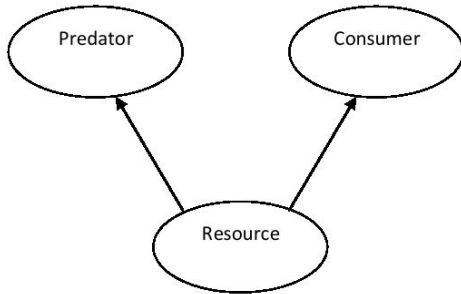
Figure 2.1: Competition
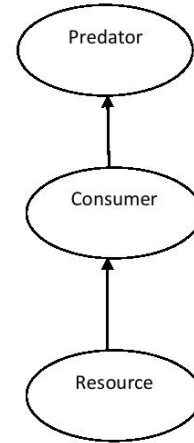
Figure 2.2: Linear Food Chain

Omnivory modeling has increased in the field of biological mathematics over the past decade and will form the foundation for all our work. Omnivory, our area of interest, consists of both predation and competition, so it is imperative for us to discuss them in this chapter. Each of our models will consist of at least three species. We will give an overview of how we combine these from a logistic growth model to the constellation of three species in an omnivory model.

2.1 Competition

To better understand omnivory models we must know a few basic things about three species interactions. First, we define competition in a three species interaction. This is just as it sounds; both the predator and consumer are competing for the same resource [10]. This model is more simplistic than our omnivory model. However, it is imperative we understand the significance behind it because the omnivory models we will be using includes competition, but from different trophic levels. We define trophic levels as steps in a nutritive food chain [10]. Figure 2.1 gives an example of a competitive food web in a three species interaction. Arrows indicate that one species (base of arrow) is eaten by another species (point).

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Since our main focus is wolves in Yellowstone National Park, we know their prey, elk, are limited by resources and other means. The confines of a national park gives us a more realistic model due to its relative size compared to a study of, for example, the entirety of North America. Our resource, the third species involved in the interaction, will be small berry-producing shrubs and aspen trees. Thus we introduce our first equation, the Logistic Growth Equation:

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}).$$

(2.1)

In this model $\frac{dN}{dt}$ represents the rate of change, or growth rate, of a population N, and r represents the intrinsic rate of increase of the population, which is merely the birth rate minus the death rate of the population. Finally, we define K as the carrying capacity, the maximum population size that the given environment can support. We will use this model and build on it to describe changes in our community of wolves and elk.

We now introduce the Lotka-Volterra competition model. The following model was first introduced in the 1920's by Alfred J. Lotka and Vito Volterra [10] [34]. The model is given below:

$$\frac{dN_1}{dt} = r_1 N_1 (1 - \frac{N_1}{K_1} - \frac{\alpha_{12} N_2}{K_1})$$

(2.2)

$$\frac{dN_2}{dt} = r_2 N_2 (1 - \frac{N_2}{K_2} - \frac{\alpha_{21} N_1}{K_2}).$$

(2.3)

This model has two competing populations, N_1 and N_2. The definitions of r_1, r_2, K_1 and K_2 are the same as in our logistic growth model with the addition of subscripts to denote the particular population. The parameter α_{12} represents the measure of effect of species 2 on the growth of species 1. Similarly, α_{21} is the measure of effect of species 1 on the growth of species 2 [10]. This model is a type of interspecific competition, defined as an environment where multiple species are competing for a particular food resource [34].

Although we will be using logistic growth to describe our resource for omnivory models, it is important to specify that our resource will be consumed by two different species, elk, our

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intermediate consumer, and wolves, our alpha predator.

2.2 Predation

We now move to another interaction in which there is no competition between species, but only predation from a higher trophic level. This means only consumers eat food resources, and only predators eat consumers. This is may seem simplistic in nature, but will prove to be vital in the development of our models for omnivory. Figure 2.2 gives a visual description of a linear food chain of three species depicted as a predator, consumer, and resource.

We note that a single wolf cannot search for, kill, eat, and convert food from a single elk instantaneously. Hence, we use parameters to help us make our models as realistic and accurate as possible. We will use parameters such as consumption rates, conversion efficiencies, and various others to get as close to a real life model as possible. We will construct two omnivory models of increasing complexity. Units on our parameter values are provided by Gotelli [10]. These are calculated and provided in Chapter 3.

The population density of the wolf is denoted as P. In all of our work we will let P represent the predator population. Likewise we denote the population density of elk as C. We now introduce a Lotka-Volterra model containing only two species and offer an analysis of the relationships between the two populations before we move on to a three species interaction. The general model has the form:

$$\frac{dP}{dt} = (\beta R - q)P \tag{2.4}$$

$$\frac{dR}{dt} = (r - \alpha P)R. \tag{2.5}$$

Here, we define R as the prey population. Our new parameters α and β represent capture efficiency and conversion efficiency, respectively. Again, we use definitions from Gotelli [10] and Vance [34] to define our new terms. The capture efficiency α measures the effect of a predator on the per capita growth rate $[(1/R)\frac{dR}{dt}]$ of the prey population R. The conversion efficiency is the

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ability of predators to convert each new prey into additional per capita growth rate $[(1/P)\frac{dP}{dt}]$ for the predator population P [34].

It is important to note that wolves do prey on other animals besides elk. However, in our model we will limit wolf predation to elk and one of their primary resources, berry-producing shrubs. This makes up the largest percentage of predation by wolves and was one of main concerns of biologists and researchers before restoration: How will wolves affect the elk population [28] [30]. Predation and competition from other animals will not be considered due to the complex nature of the park and the number of mammals involved in this large ecosystem. Hence, in all future models, the wolf population P will only consume elk C and berry-producing shrubs R.

2.3 Competition Food Web

Our next model is a competitive food web with three species: a predator population denoted P, an intermediate consumer C, and a basal resource R. The parameters m_P and m_C represent the mortality rates of the predator and consumer, respectively. While e_{RP} and e_{RC} represent the conversion efficiencies at which resources are converted into additional off spring for predators and consumers, respectively. Finally we use α_{RP} and α_{RC} to represent the capture rate of the resources by predators and the capture rate of resources by consumers [10] [34]. Now consider:

Competitive Food Web With Three Species

$$
\begin{aligned}
\frac{dP}{dt} &= P[e_{RP}\alpha_{RP}R - m_p] \\
\frac{dC}{dt} &= C[e_{RC}\alpha_{RC}R - m_c] \\
\frac{dR}{dt} &= R[r(1 - R/K) - \alpha_{RC}C - \alpha_{RP}P].
\end{aligned}
\tag{2.6}
$$

In our model (2.6) we notice that both the predator and consumer have conversion efficiencies of resources which add to their respective populations. We also have capture rates of the resource by both populations, C and P. We do not have any predation on the consumer by the predator. Hence, we only have competition between the consumer and predator for the resource, R.

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2.4 Linear Food Chain

We now model a linear food chain where there is only predation from higher trophic levels. We use the same notation for the variables as the model above, but with different parameters. We use e_{CP} to denote the conversion efficiency of the consumers into predators and e_{RC} to denote the conversion efficiency of resources into consumers. The parameters α_{CP} is the capture rate of the consumer by the predator. Likewise, α_{RC}, is the capture rate of resources by predator. This model has top down predation and is absent of competition. Figure 2.2 gives us a visual analysis of a food chain with three species.

<div align="center">Linear Food Chain With Three Speices</div>

$$
\begin{aligned}
\frac{dP}{dt} &= P[e_{CP}\alpha_{CP}C - m_p] \\
\frac{dC}{dt} &= C[e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_c] \\
\frac{dR}{dt} &= R[r(1 - R/K) - \alpha_{RC}C].
\end{aligned}
\tag{2.7}
$$

A quick analysis of our Linear Food Chain (2.7) and Competition Model (2.6), shows various parameter differences. Our competition model (2.6) has the consumer C absent from predation. However, in our food chain model we see the parameter e_{CP} and α_{CP} which denote the conversion efficiency and capture rate of consumers by the predator population (2.7). The capture rate by the predator directly affects the consumer population in a negative way, thus we have the factor α_{CP} reducing the consumer population and adding to the predator population. In Chapter 3 (Modeling Omnivory) we use a combination of both predation and competition to help us make our models more realistic.

CHAPTER 3

Modeling Omnivory With Three Species
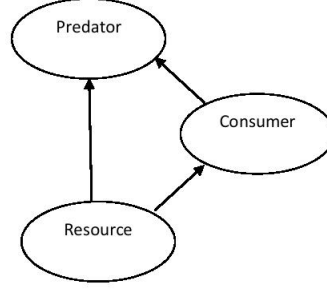
Figure 3.1: Omnivory

Now that we have defined and modeled predation and competition with three species we build our ominvory model using similar parameters and notation. Recall, omnivory includes competition and predation, where predation comes from more that one trophic level. Here we have predation from two trophic levels, and competition between the predator and consumer for the basal resource. We use previous work from Holt et al. [13], and Vance [34], to develop and combine models (2.6) and (2.7) into one that is governed by Lotka-Volterra dynamics. Hence, our new, more complex, omnivory model is given by the following system of differential equations:

Lotka - Volterra Omnivory Model

$$
\begin{aligned}
\frac{dP}{dt} &= P[e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_p] \\
\frac{dC}{dt} &= C[e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_c] \\
\frac{dR}{dt} &= R[r(1 - R/K) - \alpha_{RC}C - \alpha_{RP}P].
\end{aligned}
\tag{3.1}
$$

This model is a standard Lotka-Volterra Omnivory Model which is constructed from a linear food chain (2.7), with competition (2.6) integrated into the system [34]. Analyzing the model, we see how each trophic level is dependent on the other two. The predator, consumer, and resources are all intertwined and depend on one another, hence the differential equation associated with each of P, C, and R are functions of the other two. This makes us aware that any change in the

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Parameter	Definition
r	Resource intrinsic rate of increase
K	Environmental carrying capacity of the resource
α_{RC}	Consumption rate of resources by consumers
α_{RP}	Consumption rate of resources by predators
α_{CP}	Consumption rate of consumers by predators
e_{RC}	Conversion efficiency of resources into consumers
e_{RP}	Conversion efficiency of resources into predators
e_{CP}	Conversion efficiency of consumers into predators
m_c	Natural mortality rate of consumers
m_P	Natural mortality rate of predators

Table 3.1: Linear Model: Parameter Definitions and Values

population of $P, C,$ or R will directly affect the other populations. We see that $\frac{dR}{dt}, \frac{dC}{dt},$ and $\frac{dP}{dt}$ represent the rates of change of the resource, consumer, and predator, respectively. In our case these values represent population densities of wolves, elk, and berry-producing shrubs. Looking more in depth at the differential equation for the basal resource, we notice it is governed by logistic growth, which is expected when dealing with populations and carrying capacities. Here r is the intrinistic rate of increase and K is the carrying capacity of the resource. The two minus signs associated with parameters α_{RC} and α_{RP} are the consumptions rates of predators and consumers relative to resources. Thus it makes sense to multiply each consumption parameter by the population associated with it. For example, we know two predators eat more than one predator, so the consumption rate would be scaled by two.

Moving to the differential equation representing the consumer, we notice each parameter is also scaled by the population density C. The parameter e_{RC} is the conversion efficiency of resources into consumers. The two negative terms associated with the rate of change of the consumer is the consumption rate of resources by predators α_{CP} and the natural mortality rate of the consumer m_P. The differential equation representing our predator has only one negative term, as its death can only result from a natural mortality and not predation. We let m_P represent the natural mortality rate of the predator. Since this model has the predator feeding on two trophic levels, we have the following conversion efficiencies, e_{CP}, and e_{RP}. These represent the conversion efficiencies of consumers and resources into predators, respectively. Table 3.1 defines each parameter value in our system.

In this chapter we have introduced a Lotka-Volterra Omnivory model with ten parameter values. It is important to note that model (3.1) assumes that predators can continue to eat, even past saturation as the victim population continues to grow. This is unrealistic in our ecosystem because we know wolves and elk can only consume a certain amount or biomass before they become saturated. We also note that this model does not incorporate the handling time needed to catch and consume victims [10] [23] [17]. From a biological standpoint it is easy to justify that an entire adult elk cannot be consumed by a single wolf in one meal. We call this type of prey intake a Type I functional response. It is characterized by the constant increase of prey intake by predators as prey density increases. In Section 3.1 we discuss two different types of functional responses where we define a functional response as the intake rate of a consumer/predator as a function of food density [10]. These will help us develop a more accurate system of equations to model our omnivory system of wolves, elk, and berry-producing shrubs.

3.1 Functional Responses

Figures 3.2 and 3.3 depict two different functional responses graphically.
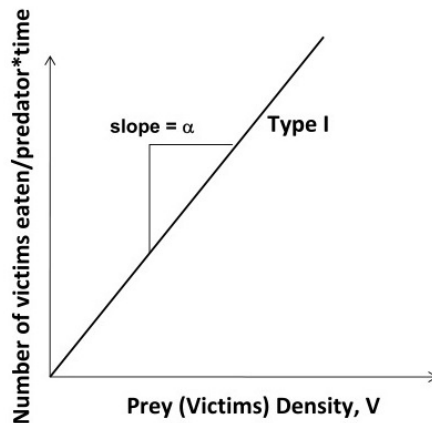
Figure 3.2: Type I Functional Response

In a Type 1 functional response the predator continues to consume more and more prey as prey abundance increases. Gotelli [10] stresses the unrealistic nature of a Type I functional response; He notes that predators are limited by handling times and attack rates which limit victim

consumption. This is why a Type II functional response is typically better when modeling larger animals [10]. Larger animals are associated with larger amounts of edible biomass. However, it takes more time to hunt, kill, and eat larger amounts of biomass. This is why we develop a model with Type II functional responses later in this chapter.

For our predator stage structured model we will use a Type II functional response, which includes components that contribute to feeding rates. Gotelli [10] states, "the total amount of time that a predator spends feeding t is the time spent searching for prey t_s, plus the time spent handling or consuming the prey t_h." Gotelli, from *A Primer of Ecology* [10], provides us with the following equations:

$$t = t_s + t_h, \tag{3.2}$$

which gives us the total time a predator spends feeding. We need to go more in depth with both t_s and t_h. We need to know total handling time, t_h, which is calculated using the number of prey items captured in time t, and h, which is the handling time per prey item. If we choose n to be the number of prey items captured in time t, then our total handling time is

$$t_h = hn. \tag{3.3}$$

We do the same for the search time/ search rate. The number of victims n, captured by a predator is the product of the victim abundance V, the capture efficiency α, and search time t_s, which yields the following equation to represent the number of prey items captured in time t:

$$n = V \alpha t_s. \tag{3.4}$$

Rearranging equation (3.4) we get,

$$t_s = \frac{n}{\alpha V}, \tag{3.5}$$

which denotes our search time. Thus, if we substitute equations (3.3) and (3.5) into (3.2), we obtain

$$t = hn + \frac{n}{\alpha V}. \tag{3.6}$$

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Or, equivalently,

$$t = n\left(\frac{1 + \alpha V h}{\alpha V}\right). \tag{3.7}$$

Since we are looking for the feeding rate (n/t), we simply divide (3.7) by n to get the feeding rate per predator as a function of the capture efficiency, victim abundance, and handling time, or:

$$\frac{n}{t} = \frac{\alpha V}{(1 + \alpha V h)}. \tag{3.8}$$

Gotelli [10] gives us that equation (3.8)," is the feeding rate per predator as a function of the capture efficiency, the victim abundance, and the handling time."

So far in this chapter we have discussed a Lotka-Volterra Omnivory Model (3.1) with a Type I function response. We discussed the natural limitations associated a Type I response and offered graphical representation. Thus our next step in creating a more realistic model is to discuss a Type II functional response. We characterize a Type II functional response as follows: As prey density increases, the number of prey each predator eats per unit of time reaches a constant value. Units for both functional responses is $victims/(predator \cdot time)$.
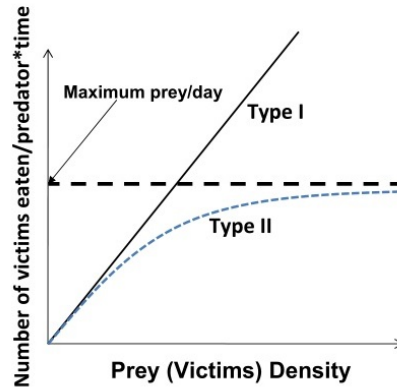
Figure 3.3: Type II Functional Response

Hence, we will use a Type II functional response in our predator stage structured model, which assumes that predator consumption increases to a maximum and constant rate of victim consumption per predator. Vance simplifies this and states,"the rate of consumption becomes

saturated as victim densities increase"[34]. This type of functional response is known as a Holling Type II functional response. Figure 3.3 depicts the differences in varying functional responses.

Vance provides us with more information about Type II responses in (3.9), (3.10), and (3.11), [34]. These can all be derived from Equation (3.8) and are provided by Gotelli and Vance [10] [34]. Parameter definitions are contained in Table 3.2. We will use these for our stage structure model.

We use $f : \mathbb{R}_+ \to \mathbb{R}_+$, defined by

$$f(R) = \frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R} \tag{3.9}$$

as our Holling Type II function response. This is for a species P, feeding on only one other species R. The parameter λ_{RP} is the search rate for species R by P. The parameter h_{RP} is the time spent by species P handling species R. For our stage structure model we will use the following functional responses provided by Vance [34]. For our predator species, P that feeds on consumers and resources,

we use $f : \mathbb{R}_+ \times \mathbb{R}_+ \to \mathbb{R}_+$, defined by

$$f(C, R) = \frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \tag{3.10}$$

as the resources functional response.

We use $f : \mathbb{R}_+ \times \mathbb{R}_+ \to \mathbb{R}_+$, defined by

$$f(C, R) = \frac{\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \tag{3.11}$$

as the functional response of species C [34]. The parameter values denoted λ_{ij} represent the search rate of species i, by species j. We let h_{ij} represent the handling time of species i, by species j, where $i = C$ or R and $j = P$ or C [34]. Table 3.2 lists all the parameter values and definitions associated with our Stage Structure Model.

After our discussion of two different functional responses we introduce a more complex model which can accommodate larger mammals due to predator stage structure with Type II functional responses. This model will likely give us more accurate results because a newborn wolf-pup is not

Parameter	Parameter Definition
e_{RP}	Conversion efficiency of resource into predators
e_{CP}	Conversion efficiency of consumers into predators
e_{RC}	Conversion efficiency of resources into consumers
λ_{RP}	Search rate of predator for resource
λ_{CP}	Search rate of predator for consumer
λ_{RC}	Search rate of consumer for resource
h_{RP}	Time spent by predator handling resource
h_{CP}	Time spent by predator handling consumer
h_{RC}	Time spent by consumer handling resource
m_{P_2}	Natural mortality rate for adult predator
m_{P_1}	Natural mortality rate for juvenile predator
m_C	Natural mortality rate of consumer
μ_P	Predator maturation rate
r	Resource intrinsic rate of increase
K	Environmental carrying capacity of the resource

Table 3.2: Stage Structure Model: Definitions of Parameters and Variables

capable of taking down full grown elk or participating in a hunt of large game. We include new parameters in this model which are handling times, search rates, and maturation rate of the predator. Vance [34] provides us with the following system of differential equations:

Stage Structured Omnivory Model

$$
\begin{aligned}
\frac{dP_2}{dt} &= \mu_P P_1 - m_P P_2. \\
\frac{dP_1}{dt} &= \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}P_2 - (\mu_P + m_P)P_1. \\
\frac{dC}{dt} &= C[\frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_C]. \\
\frac{dR}{dt} &= R[r(1 - \frac{R}{K}) - \frac{\lambda_{RC}C}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{RP}P_1}{1 + \lambda_{RP}h_{RP}R} - \frac{\lambda_{RP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}].
\end{aligned}
\tag{3.12}
$$

Our parameter definitions are given in Table 3.2. Since our model includes predator age structure we are careful to separate the population densities of adult wolves from juvenile wolves. The population density of juvenile wolves is denoted as P_1 and the population density of adult wolves is denoted as P_2. This model is more complex (4 variables and 15 parameters), but should offer a more realistic model of our three species ecosystem in Yellowstone National Park.

3.2 Data Sources

Yellowstone National Park is an enormous national park, making it nearly impossible to know the exact size of any certain species population. Animals are constantly being born and are dying off, thus our data will have to rely on reports from wildlife population conservationists, data from GPS trackers and field biologists. The majority of our data will come from the northern range of Yellowstone National Park during the early winter when wolves are most active. We will utilize data from studies of Gray Wolves in certain parts of Canada and various other regions where the wolves are secluded but not captive. It is important to note that our model parameter values can vary from year to year and are extremely difficult to accurately calculate without constant surveillance from airplanes or GPS trackers. Hence our calculations of parameter values will have to depend on the availability of published work on wolf-elk interactions. In some cases, we will rely on similar calculations done by omnivorous lab experiments to justify parameter values.

Dr. Douglas W. Smith (along with writer Gary Ferguson) provide us with valuable insight on wolf behavior in their book, *Decade of the Wolf* [28]. Smith uses a lot of information provided by Mark S. Boyce [5] from the University of Wyoming-National Park Service Research Center which we will interpret and use to calculate some of our eventual parameter values. Another familiar issue when modeling wolf behavior is their various roles within their packs. Over 90% of the wolves in Yellowstone National Park live in packs. There are currently ten packs living withing the park [30]. Within these packs, each member has its own role, whether it be the female giving birth, or the alpha male hunting the prey [30]. In our linear response model, we will assume each wolf can hunt, kill, and take down an elk unless otherwise stated. We do not incorporate pack size or age-structure in our linear response model. However, in our predator stage structure model we will separate the populations of adult wolves from juvenile wolves to help us better model this complex system.

We will also use data gathered from publications such as: *Survival of Adult Female Elk in Yellowstone Following Wolf Restoration* [8], and *Yellowstone wolf (Canis lupus) density predicted by elk (Cervus elaphus) biomass* [20]. Although, these publications may correlate to a specific gender or may be density dependent we can use the information and scale our parameters to be as

realistic as possible.

In our next section, we utilize available publications and current research work on wolf-elk relationships to calculate our parameter values.

3.2.1 Calculating Parameter Values

A huge amount of stochastic data is available on wolf restoration and elk populations from the reintroduction of the wolf into Yellowstone National Park. However, the data in these reports do not give us all the proper parameter values we need for our models. For conversion efficiencies, we need the required level of biomass of the species eaten that will produce new offspring each year. From Smith [28], we know a wolf can consume approximately 10.0 kg of biomass in one setting. However, that is not the required intake each day. Mech and Barber-Meyer [25] estimate the daily intake needed as approximately 3.5 kg/wolf/day. These values let us know that when elk densities are up, wolves can consume biomass until saturation occurs. At lower prey densities wolves are more likely to be around the 3.2 kg/day mark given by Yellowstone Park Service [32] [29].

As we already noted, it is difficult and expensive to obtain the data we need for our model. Thus we look for another method to calculate our missing parameter values. Palomares and Caro [23] stated, "collecting data from mammalian carnivores is low because they are scarce, difficult to see and to catch, move over large areas, and may be threatened" [23]. This is why Vance and Fields [17] used values from laboratory experiments on omnivorous ciliates (protozoans) in *"Sensitivity Analysis of a Linear Response Omnivory Model"*. Although these parameters may work for simplistic bacteria models, we can not assume large mammals have close to the same values. Hence, we will use information on biomass, kill rates, death rates, consumption rates, and conversion efficiencies from other sources when available. We will use the intrinsic rate of increase and environmental carrying capacity from Diehl [6] because our resource, berry producing shrubs, has relatively no research and represents a similar resource in his laboratory experiments [6]. We will also use values from Kirivan and Diehl [18] when we lack sufficient research and data for particular values. When needed, we convert units of time into one week to balance our equations in each system. We note each instance of this in the text.

We started with information from park officials and game wardens, then used other publications

to help find appropriate data to approximate each parameter value. Smith and Ferguson [28] give us that 88% of wolf kills during winter months were elk. This validates that our predators main prey is elk. Wolves are known to kill buffalo and deer, but on a much lower level. We will assume that all elk mortalities in our model are caused by wolves or from a natural death. Additionally we have wolves and elk both competing for a common resource, berry producing shrubs.

We are given the mortality rates for wolves and elk by field biologists in a 2014 winter report from *Wolf Management and Restoration* [27]. Data in 2013 estimates show there were approximately 95 wolves living within the park, those with radio collar GPS accounting for 22% of them. This gives us approximately 21 GPS tracked wolves within the park. However, in 2014, biologists installed GPS collars on another 16 wolves, making the total 37 GPS tracked wolves. We also note that the population of wolves increased from 95 to 104 in the 2013-2014 calendar year. The report indicates that out of the 37 collared wolves, 3 adults and 2 pups were killed by natural causes and not harvested (taken by humans, trappers, or other means). We want our system to solely rely on the natural mortality rates, this is why we do not include any harvested deaths. The information above gives us the wolf's natural mortality rate, m_P, as $\frac{5}{90}$ which is approximately .056 for the year 2014. We note this is not the instantaneous kill rate, but the change in number of deaths in a population measured over a period of time. Units on our mortality rates will all be in the form: $deaths/(individual \cdot time)$. Hence using the unit of time of one week gives our parameter m_P a value of .00062. For our stage structured model we need the mortality rates of adult wolves and juvenile wolves. Massey [19] gives us this value in his thesis, *Survival of an Exploited Grey Wolf Population in the Northern Rocky Mountains: Density Dependence and Licensed Hunting*. He estimates juvenile wolf survival rate at 0.671 for pups in Yellowstone National Park. This gives us the mortality rate of juvenile wolves as 0.329. Converting to our unit of time, one week, we have m_{P_1} as 0.00365. From the same report we also have the adult predator mortality rate given as .069. We convert this unit to per week and get the value of .00076. This is the value we assign to the mortality rate of adult wolves in our stage structured model. The parameter is denoted as m_{P_2}. Units remain the same for each mortality rate.

We now focus on the mortality rate of elk within the park. From *Survival of Adult Female Elk*

in Yellowstone Following Wolf Restoration [8], we are given that the female mortality rate of elk taken by wolves is .07, however, we need the natural mortality rate. Thus from Meyer [3], we are given overall elk survival rate of 0.89, providing us with a mortality rate of 0.11. The mortality rate of our elk is expressed with the same units as the predator mortality rate, $deaths/(individual \cdot time)$. We denote the elk mortality rate as m_C and assign its value as 0.00122 for both models.

The units on our consumption rates are similar to that of feeding rates, the units we use are $victims/(time \cdot predator)$. From the National Park Service [32], we are given the consumption rate of elk by wolves as .061. This relates to 1.83 elk taken/wolf/month. Hence we assign α_{CP} the value of .01525 [33] to adjust for one week.

We note that consumption of berry producing shrubs by wolves and elk is not something that has been researched heavily, leaving us without data to use. We do know from previous research [22] that young aspen trees and berry-producing shrubs were being over consumed, nearly to the brink of extinction before wolf restoration. This offers the possibility that the consumption of berries by elk is likely much higher than for wolves [2]. Because we have no formal numerical values on the consumption rates of berry-producing shrubs, we use values from Diehl et al. [6] to help us for the following two parameters. We use Diehl's value of 0.1 for each, but convert them to weeks. Thus for the consumption rate of resources by predators, denoted α_{RP} we have 1.68. Likewise we assign α_{RC} the value of 1.68, where the units on all consumption rates rates are $victims/(time \cdot predator)$ where time units are represented in weeks.

Oregon State University Researcher James Ayre gives the following statement [2],"Yellowstone has a wide variety of nutritious berries - serviceberry, chokecherry, buffaloberry, twinberry, huckleberry and others that are highly palatable to wolves. These shrubs are also eaten by elk and thus likely declined as elk populations grew over time." This assures us that the predation on berries by elk affected not only the berries, but also the availability of berries for wolves.

Our numerical value r, the intrinsic rate of increase, is equal to the per capita rate of population increase $\frac{1}{R}\frac{dR}{dt}$ with units of $individuals/(individuals \cdot time)$. Here individuals are our resources, so we use values from Vance [34]. He estimates the parameter r with the value of 0.3. The parameter K represents the maximum number of individuals that can be supported in a

population that is growing according to the logistic growth equation. Because the northern range of Yellowstone National Park accounts for only 10% of the 4,000 square mile area of the entire park, we are required to adjust K. Out of the 400 square miles in the northern range we estimate that 1% of it is capable of allowing berry-producing shrubs to live due to drastic climate changes. This gives us a maximum area of 4 square miles of berry producing shrubs. Within that 4 square mile area we estimate the maximum number of berry producing shrubs it can support is 4 hectares. With no means to count all the berry-producing shrubs in our area, we group them according to hectares. Thus we assign K to be 4 resources for simplicity.

Finally we focus on conversion efficiencies. Gotelli [10] defines the measure of conversion efficiency as the ability of predators to convert each prey item captured into additional per capita growth rate for the predator population. Gotelli states that, "when a single prey item is particularly valuable, such as when an elk is captured by wolves, we expect the conversion efficiency to be very high." The conversion efficiency of elk into wolves will be much higher than in the study done by Vance and Fields [17] due to the biomass of an elk compared to that of a berry or any small mammal. We modify values provided by Vance in *Sensitivity Analysis of a Linear Response Omnivory Model* . The value of 0.5 is given by Vance in his dissertation, *Permanent Coexistence of Ominvory Models* [34]. Due to the overwhelming biomass of an elk, compared to the needs of a wolf, we scale the value of 0.5 up to 0.8 for a more realistic model. Thus we assign e_{CP} the value 0.8. The units on all conversion efficiencies are dimensionless as noted by Diehl et. al [6]. We use the values from *Permanent Coexistence of Ominvory Models* [34] for the parameters e_{RC} and e_{RP} which are 0.8 and 0.1, respectively. Values for our linear response model are contained in Table 3.3.

Now that we have all the parameter values filled for our linear response model, we must assign values to our stage structured parameters. We use conversion of elk taken per year by the population of wolves and divide it by 365 days to give us an estimated search rate of elk by wolves for a parameter value of .02, labeled λ_{CP}. Search rate of wolves on berry-producing shrubs is again not something that is readily available and not of great nutritional value to wolves, so we will use parameters given by Mylius et al. [21], and Persson et al. [24], which are from a similar omnivorous system. We use the value of 0.025 as the search rate of resources by predators and we

assign the value of 0.037 to the search rate of resources by consumers [21] [24]. Because we are assuming search rates stay consistent, we assume all these values are taken per week. It is a broad assumption, but without data we are forced to estimate using other methods. We note that these values will not be converted to per week because we assume constant search rates throughout.

It may be unrealistic to give handling time in weeks, but we are forced by our equations to do so. We first give the value in hours then covert it to weeks. Handling times for small-berries is very short, so we will use the value of 1 hour for the handling time of resources by consumers and resources by predators, denoted as h_{RC} and h_{RP}. However, we divide by 168 to get the units in weeks. This yields the values of 0.00595 for the handling times of resources by consumers and predators. The handling time of consumers by predators will be much higher. We assign its value as 6 hours or 0.03571 weeks. For the predator maturation rate μ_P, we use the value 0.00222 since it takes nearly 20% of the wolf's expected life to mature into an adult who can hunt elk. We note this is the maturation rate per week. Table 3.4 gives us a summary of our stage structured parameter values.

Parameter	Value	Units
r	0.3	$\frac{resources}{resources \cdot time}$
K	4.0	$number\,of\,resources$
α_{RC}	1.68000	$\frac{resources}{week \cdot consumers}$
α_{RP}	1.68000	$\frac{resources}{week \cdot predator}$
α_{CP}	.01525	$\frac{consumers}{week \cdot predators}$
e_{RC}	0.8	$Dimensionless$
e_{RP}	0.1	$Dimensionless$
e_{CP}	0.8	$Dimensionless$
m_C	0.00122	$deaths/week$
m_P	0.00062	$deaths/week$

Table 3.3: Linear Model: Parameter Values

Parameter	Parameter Value	Units
m_{P_2}	0.00076	$deaths/week$
m_{P_1}	0.00365	$deaths/week$
m_C	0.00122	$deaths/week$
e_{RP}	0.8	$Dimensionless$
e_{CP}	0.1	$Dimensionless$
e_{RC}	0.8	$Dimensionless$
λ_{RP}	.025	$kills/unit\,of\,time$
λ_{CP}	.02	$kills/unit\,of\,time$
λ_{RC}	.037	$kills/unit\,of\,time$
h_{RP}	0.00595	$time-weeks$
h_{CP}	0.03571	$time-weeks$
h_{RC}	0.00595	$time-weeks$
μ_P	0.00222	
r	0.3	$\frac{resources}{resources \cdot time}$
K	4	$number\,of\,resources$

Table 3.4: Stage Structure Model: Parameter Values

CHAPTER 4

Existence and Uniqueness of Solutions of n-th Order Systems

Throughout this section we will concern ourselves with definitions, theorems, and lemmas to help us prove that each system we use is capable of providing a solution defined on $[0, \infty)$. All of our models rely on time t, so it is worthy to note we restrict our values of t to be non-negative. We use Vance's approach in *Permanent Coexistence for Ominvory Models* [34] this, with theorems, definitions, and lemmas from Walter's book, *Ordinary Differential Equations* [35] [34].

All of our models consist of at least three species and their population values depend on time, denoted t, so we use the following notation to start this section and consider a first order system of differential equations of the form:

$$\frac{dy_1}{dt} = f_1(t, y_1, \ldots, y_n)$$
$$\frac{dy_2}{dt} = f_2(t, y_1, \ldots, y_n)$$
$$\vdots \qquad \qquad \qquad (4.1)$$
$$\frac{dy_n}{dt} = f_n(t, y_1, \ldots, y_n).$$

"Where the n function:

$$f_1(t, y_1, \ldots, y_n), \ldots f_n(t, y_1, \ldots, y_n)$$

are defined on a set D of $(n + 1)-$ dimensional - space $\mathbb{R}^{n+1}$." [35] .

In order to show global existence and uniqueness of solutions, we provide readers with the following definitions. Again, these definitions are directly from Walter:

Definition 1. *[35] A vector function $(y_1(t), \ldots, y_n(t))$ is a solution of (4.1) in the interval J given the functions $y_v(t), v = 1, \ldots, n$ are differentiable in J and if (4.1) is satisfied identically when they are substituted into the equation. We require $(t, y_1(t), \ldots, y_n(t)) \in D$ for all $t \in J$.*

Thus, we can rewrite the system (4.1) using vector notation, where we denote n-dimensional column vectors with boldface letters. The system is given by (4.2),

$$\boldsymbol{y}(t) = \begin{pmatrix} y_1(t) \\ \vdots \\ y_n(t) \end{pmatrix}, \qquad \mathbf{f}(t, \boldsymbol{y}) = \begin{pmatrix} f_1(t, \boldsymbol{y}) \\ \vdots \\ f_n(t, \boldsymbol{y}) \end{pmatrix}. \qquad (4.2)$$

From Stewart [31], we know derivatives and integrals of a vector function $\boldsymbol{y}(x)$ are defined component-wise, hence:

$$\boldsymbol{y}'(t) = \begin{bmatrix} y_1'(t) \\ \vdots \\ y_n'(t) \end{bmatrix}. \qquad (4.3)$$

In vector notation our system (4.1) can be represented by

$$\boldsymbol{y}' = f(t, \boldsymbol{y}). \qquad (4.4)$$

All of our models are represented by systems of ordinary differential equations with initial conditions. We present more definitions from Walter's Book, *Ordinary Differential Equations* [35] to help us verify the existence and uniqueness of solutions. We will reference the definitions below in the remaining chapters to aid us in proving a unique solution exists for each model:

Definition 2. *[35] (Initial Value Problem)*

Our initial value problem for (4.1) asks for a solution that passes through a given point $(t_0, \boldsymbol{c}) \in D$, *that is, one that satisfies our initial conditions below,*

$$y_i(t_0) = c_i, \quad (i = 1, \ldots, n) \quad \text{or in vector form} \quad \boldsymbol{y}(t_0) = \boldsymbol{c}, \tag{4.5}$$

where

$$\boldsymbol{c} = \begin{pmatrix} c_1 \\ \vdots \\ c_n \end{pmatrix}.$$

We will call $\| \boldsymbol{y} \|$ the norm of the vector $\boldsymbol{y} \in \mathbb{R}^n$. We also note that all norms in $\mathbb{R}^n$ are equivalent, [35], [31].

Definitions 3 and 4 will be used indirectly to help us prove several theorems. We do not formally calculate a Lipschitz constant, but for our proofs we feel the need to point out what it means for a vector function to satisfy a Lipschitz condition in a certain domain.

Definition 3. *[35] A vector function $\boldsymbol{f}(t, \boldsymbol{y})$ satisfies a Lipschitz condition with respect to $\boldsymbol{y}$ in D (with Lipschitz constant L) if:*

$$\| \boldsymbol{f}(t, \boldsymbol{y}) - \boldsymbol{f}(t, \hat{\boldsymbol{y}}) \| \leq L \| \boldsymbol{y} - \hat{\boldsymbol{y}} \| \quad \text{for } (t, \hat{\boldsymbol{y}}), (t, \hat{\boldsymbol{y}}) \in D. \tag{4.6}$$

Definition 4. *[35] A function $\boldsymbol{f}$ is said to satisfy in D a local Lipschitz condition with respect to $\boldsymbol{y}$ if for every point $(t, \boldsymbol{y})$ in D, there exists a neighborhood*

$$U : \| t - \hat{t} \| < \delta, \| y - \hat{y} \| < \delta, \quad for \ \delta > 0, \tag{4.7}$$

such that $\boldsymbol{f}$ satisfies a Lipschitz condition in $D \cap U$.

We will use the next Lemma in proofs for both of our systems. We will attempt to satisfy the hypothesis by showing that each vector, **f**, has continuous partial derivatives with respect to

population densities denoted by $\boldsymbol{y}$. It is an extremely useful tool for us and will allow us to verify existence and uniqueness without finding the Lipschitz constant.

Lemma 1. *[35] If D is a domain and if $\boldsymbol{f}$ and $\frac{\partial \boldsymbol{f}}{\partial \boldsymbol{y}}$ are continuous in D, then $\boldsymbol{f}$ satisfies in D a local Lipschitz condition with respect to $\boldsymbol{y}$.*

We now introduce our first theorem, which gives us the conditions under which we have local existence and uniqueness of solutions to our initial value problem. In each model, we verify that the condition $\frac{\partial \mathbf{f}}{\partial \boldsymbol{y}}$ is continuous. This allows us to say that our initial value problem representing the system has exactly one solution and that it can be extended to the left and right up to the boundary of our domain.

Theorem 1. *[35] (Existence and Uniqueness) Let $\boldsymbol{f}\,(t, \boldsymbol{y})$ be continuous in a domain $D \subset \mathbb{R}^{n+1}$ and satisfy a local Lipschitz condition with respect to $\boldsymbol{y}$ in D (which is satisfied, if $\frac{\partial \boldsymbol{f}}{\partial \boldsymbol{y}}$ is continuous in D). If $(t_0, \boldsymbol{c}) \in D$, then the initial value problem*

$$\boldsymbol{y}' = \boldsymbol{f}(t, \boldsymbol{y}), \quad \boldsymbol{y}(t_0) = \boldsymbol{c} \tag{4.8}$$

has exactly one solution, which can be extended to the left and right up to the boundary of D.

The next Lemma, provided by Hsieh [15] will allow us to extend a local solution to larger intervals for the independent variable t.

Lemma 2. *[15] [34] Assume that $\boldsymbol{f}(t, \boldsymbol{y})$ is continuous for $J = \{t \in \mathbb{R} : t_0 < t < t_1\}$ and for all $\boldsymbol{y} \in \mathbb{R}^n$. Assume also that a function $\hat{\boldsymbol{y}}(t)$ satisfies the following conditions:*

(1) $\hat{\boldsymbol{y}}$ and $\frac{d\hat{\boldsymbol{y}}}{dt}$ are continuous in a subinterval I of J,

(2) $\frac{d\hat{\boldsymbol{y}}}{dt} = \boldsymbol{f}(t, \boldsymbol{y})$ in I.

Then, either

(a) $\hat{\boldsymbol{y}}$ can be extended to the entire interval J as a solution of the differential equation

$$\frac{d\boldsymbol{y}}{dt} = \boldsymbol{f}(t, \boldsymbol{y}),$$

or

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(b)

$$\lim_{t \to \tau} \| \; \hat{\boldsymbol{y}}(t) \; \| = \infty$$

for some τ in J.

Lemma 2 allows us to say that the solution to (4.8) either goes to infinity as t approaches τ or the solution can be extended to all of J. The main purpose for Lemma 2 is for us to be able to show global existence and uniqueness of solutions to our models by saying the solutions to our initial value problems do not go to infinity in time.

To do this, we use the following lemmas and theorem provided by Vance and Hale [11] [34]:

Definition 5. *[11] Let D_r denote the right hand derivative of a function. If $w(t, y)$ is a scalar function of the scalars t and y in some open connected set D, we say a function $y(t)$, with $a \le t \le b$, is a solution of the differential inequality,*

$$D_r y(t) \le w(t, (y(t))) \tag{4.9}$$

on [a,b), if $y(t)$ is continuous on [a, b) and has a right hand derivative on [a, b) that satisfies (4.9).

Theorem 2. *[11],[34] Let $w(t, u)$ be continuous on an open connected set $D \subset \mathbb{R}^2$ and be such that the initial value problem for the scalar equation,*

$$u' = w(t, u) \tag{4.10}$$

has a unique solution. If $u(t)$ is a solution of (4.10) on $a \le t \le b$ and $y(t)$ is a solution of (4.9) on $a \le t \le b$ with $y(a) \le u(a)$, then $y(t) \le u(t)$ for $a \le t \le b$.

Lemma 3. *[11],[34] Suppose $w(t, u)$ satisfies the conditions of Theorem 2 such that, $a \le t \le b$, with $u \ge 0$, and let $u(t) \ge 0$ be a solution of (4.10) on $a \le t < b$. If $\boldsymbol{f} : [a, b) \times \mathbb{R}^n \to \mathbb{R}^n$ is continuous and*

$$\| \; \boldsymbol{f}(t, \boldsymbol{y}) \; \| \le w(t, \| \; \boldsymbol{y} \; \|), \qquad a \le t < b, \qquad \boldsymbol{y} \in \mathbb{R}^n, \tag{4.11}$$

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then the solutions of

$$\mathbf{y}' = \mathbf{f}(t, \mathbf{y}), \qquad \| \mathbf{y}(a) \| \leq u(a) \tag{4.12}$$

exist on $[a, b)$ *and* $\| \mathbf{y}(t) \| \leq u(t)$, *with* $t \in [a, b)$.

The following lemma will be used for our differential inequalities. That is, we will use it to help us prove that we can extend our solutions to the boundary values. We will use certain parts of this lemma in our proofs. We credit Vance [34] and Birkhoff [4] for this.

Lemma 4. *[4],[34] Let S be a differentiable function on [a, b].*

Part A: If S satisfies the differential inequality

$$S'(t) \leq \lambda S(t), \qquad a \leq t \leq b \tag{4.13}$$

where λ *is a constant and* $\lambda > 0$, *then*

$$S(t) \leq S(a)e^{\lambda(t-a)} \ for \ a \leq t \leq b. \tag{4.14}$$

Part B: If S satisfies the differential inequality

$$S'(t) + \lambda S(t) \leq M_1, \qquad a \leq t \leq b. \tag{4.15}$$

where $M_1 > 0$ *and* $\lambda > 0$ *are constants, then*

$$S(t) \leq \frac{M_1}{\lambda} + (S(a) - \frac{M_1}{\lambda})e^{\lambda(a-t)} \ for \ a \leq t \leq b. \tag{4.16}$$

Part C: If S satisfies the differential inequality

$$S'(t) \leq (M_1 + M_2 e^{\lambda t})S(t), \qquad a \leq t \leq b \tag{4.17}$$

where $M_1 > 0, M_2 > 0$, *and* $\lambda > 0$ *are constants, then*

$$S(t) \leq S(a)e^{M_1(t-a)+\frac{M_2}{\lambda}(e^{\lambda t}-e^{\lambda a})} \ \ for \ a \leq t \leq b. \tag{4.18}$$

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We prove each Part of Lemma 4 separately. Vance [34] provides an outline of each proof in:

Proof of Part A.

Let S be a differentiable function on [a,b] where λ is a constant and $\lambda > 0$.

Then for part A, we suppose

$$S'(t) \leq \lambda S(t), \qquad a \geq t \geq b. \tag{4.19}$$

Rearranging (4.19) we have,

$$0 \geq S'(t) - \lambda S(t). \tag{4.20}$$

Similar to an ordinary differential equation we multiply both sides of (4.20) by the integrating factor $e^{-\lambda t}$. This gives us,

$$0 \geq S'(t)e^{-\lambda t} - \lambda S(t)e^{-\lambda t} \tag{4.21}$$

Notice that the right hand side of (4.21) is the derivative of the product

$$S(t)e^{-\lambda t}.$$

Hence we can say,

$$0 \geq S'(t)e^{-\lambda t} - \lambda S(t)e^{-\lambda t} = \frac{d}{dt}(S(t)e^{-\lambda t}) \tag{4.22}$$

We can now form the definite integral from a to t on each side of (4.22) to obtain

$$\int_a^t 0 \geq \int_a^t \frac{d}{dt}(S(t)e^{-\lambda t})dt. \tag{4.23}$$

Evaluating both integrands yields,

$$0 \geq S(t)e^{-\lambda t} - S(a)e^{-\lambda a}. \tag{4.24}$$

Isolating $S(t)$ offers the desired result,

$$S(t) \leq S(a)e^{\lambda(t-a)}. \tag{4.25}$$

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This completes the proof of Part A.

Proof of Part B.

Let S be a differentiable function on [a,b] where $\lambda > 0$ and $M_1 > 0$ are constants. Then we suppose

$$S'(t) + \lambda S(t) \leq M_1, \qquad a \geq t \geq b, \tag{4.26}$$

is satisfied. Rearranging we have,

$$0 \geq [S'(t) + \lambda S(t) - M_1]. \tag{4.27}$$

Again, this is similar to an ODE, so we multiply both sides of (4.27) by the integrating factor $e^{\lambda t}$. This gives us,

$$0 \geq e^{\lambda t}[S'(t) + \lambda S(t) - M_1]. \tag{4.28}$$

Note that the right hand side of (4.28) is

$$\frac{d}{dt}[S(t)e^{\lambda t} - \frac{M_1}{\lambda}e^{\lambda t}]. \tag{4.29}$$

Thus we can rewrite (4.28) as

$$0 \geq \frac{d}{dt}[S(t)e^{\lambda t} - \frac{M_1}{\lambda}e^{\lambda t}]. \tag{4.30}$$

We now form the definite integral from a to t on each side of (4.30),

$$\int_a^t 0 \geq \int_a^t \frac{d}{dt}[S(t)e^{\lambda t} - \frac{M_1}{\lambda}e^{\lambda t}]dt. \tag{4.31}$$

Evaluating the definite integrals in (4.31), we obtain,

$$0 \geq (S(t) - \frac{M_1}{\lambda})e^{\lambda t} - (S(a) - \frac{M_1}{\lambda})e^{\lambda a}. \tag{4.32}$$

Isolating $S(t)$ gives the desired result,

$$S(t) \leq \frac{M_1}{\lambda} + (S(a) - \frac{M_1}{\lambda})e^{\lambda(a-t)}. \tag{4.33}$$

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This completes the proof of part B.

Proof of Part C.

Let S be a differentiable function on [a,b] where $\lambda > 0$, $M_1 > 0$, and $M_2 > 0$ are constants. Then we suppose,

$$S'(t) \leq (M_1 + M_2 e^{\lambda t}) S(t), \qquad a \leq t \leq b \tag{4.34}$$

is satisfied. Rearranging (4.34) we have,

$$0 \geq S'(t) - (M_1 + M_2 e^{\lambda t}) S(t). \tag{4.35}$$

Multiplying both sides of (4.35) by the integrating factor $e^{-(M_1 t + \frac{M_2}{\lambda} e^{\lambda t})}$ we have,

$$0 \geq e^{-(M_1 t + \frac{M_2}{\lambda} e^{\lambda t})} [S'(t) - (M_1 + M_2 e^{\lambda t}) S(t)] \tag{4.36}$$

Note that the right hand side of (4.36) is the derivative of the product

$$[e^{-(M_1 t + \frac{M_2}{\lambda} e^{\lambda t})} S(t)]. \tag{4.37}$$

Thus we can rewrite (4.36) as

$$0 \geq \frac{d}{dt} [e^{-(M_1 t + \frac{M_2}{\lambda} e^{\lambda t})} S(t)]. \tag{4.38}$$

We now form the definite integral from a to t on each side of (4.39) to obtain

$$\int_a^t 0 \geq \int_a^t \frac{d}{dt} [e^{-(M_1 t + \frac{M_2}{\lambda} e^{\lambda t})} S(t)] dt \ . \tag{4.39}$$

Evaluating both integrands gives us

$$0 \geq [e^{-(M_1 t + \frac{M_2}{\lambda} e^{\lambda t})} S(t)] - [e^{-(M_1 a + \frac{M_2}{\lambda} e^{\lambda a})} S(a)]. \tag{4.40}$$

Isolating $S(t)$ offers the desired result,

$$S(t) \leq S(a) e^{M_1(t-a) + \frac{M_2}{\lambda}(e^{\lambda t} - e^{\lambda a})}. \tag{4.41}$$

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This completes the proof of Lemma 4 Part C.

4.1 Sensitivity Analysis

We have already established that all of our systems take the form,

$$
\begin{aligned}
\frac{dy_1}{dt} &= f_1(t, y_1, \ldots, y_n) \\
\frac{dy_2}{dt} &= f_2(t, y_1, \ldots, y_n) \\
&\vdots \\
\frac{dy_n}{dt} &= f_n(t, y_1, \ldots, y_n).
\end{aligned}
\tag{4.42}
$$

Written in vector form gives us:

$$
\boldsymbol{y}' = \mathbf{f}(t, \boldsymbol{y}).
\tag{4.43}
$$

In chapters 5 and 6 we prove that given initial conditions, a unique solution exists for all $t \geq t_0$.

Dealing with ecological systems that can be very sensitive to changes, we are interested in how each parameter plays a role in the livelihood of all the species involved. Parameter values we will use were taken in the field by biologists or estimated by other means, thus an important question is: Are the solutions "insensitive" to small changes in our parameter values? We denote our parameters by $\alpha_i, i = 1 \ldots m.$, and now write the parametric system in expanded form:

$$
\begin{aligned}
\frac{dy_1}{dt} &= f_1(t, y_1, \ldots, y_n, \alpha_1, \ldots, \alpha_m) \\
\frac{dy_2}{dt} &= f_2(t, y_1, \ldots, y_n, \alpha_1, \ldots, \alpha_m) \\
&\vdots \\
\frac{dy_n}{dt} &= f_n(t, y_1, \ldots, y_n, \alpha_1, \ldots, \alpha_m)
\end{aligned}
\tag{4.44}
$$

Hence for a parameter $\boldsymbol{\alpha} \in R^m$, our corresponding vector equation is

$$
\boldsymbol{y}' = \mathbf{f}(t, \boldsymbol{y}, \boldsymbol{\alpha}).
\tag{4.45}
$$

We want to investigate the properties of a solution to (4.45) under small changes in $\boldsymbol{\alpha}$. This will allow us to see how extremely small changes in a certain parameter value may or may not affect

our ecosystem. It will also help us to determine which parameter values need more attention in the field when measuring. If a value is extremely sensitive, it means it affects our ecosystem greatly even with the slightest change. Insensitive changes to a parameter value correlates to a parameter that can vary somewhat before the ecosystem feels the effects, or it may not even affect the system at all.

4.2 Continuous Dependence and Differentiability

We want to show that the solution $\boldsymbol{y}(\boldsymbol{t})$ to the system (4.45) depends continuously upon the parameter vector $\boldsymbol{\alpha}$. We also need the solutions to be differentiable with respect to $\boldsymbol{\alpha}$. Thus we use the following theorems by Rosenwasser [26] [34]. Let D_α be a region in $\mathbb{R}^m$ of possible variations of the vector $\boldsymbol{\alpha}$.

Theorem 3. *[26] (Continuous Dependence) Assume that for any $\boldsymbol{\alpha} \in D_\alpha$, equation (4.45) satisfies conditions of existence and uniqueness of solutions and this solution can be continued for $t \geq t_0$. This yields the existence of an open set D in the $(t, \boldsymbol{y}, \boldsymbol{\alpha})$-space in which $\boldsymbol{f}(t, \boldsymbol{y}, \boldsymbol{\alpha})$ is continuous with respect to t and $\boldsymbol{y}$ for all $\boldsymbol{\alpha} \in D_\alpha$. Also, assume that the partial derivatives*

$$\frac{\partial f_i}{\partial y_j}(t, \boldsymbol{y}, \boldsymbol{\alpha}), \qquad for \qquad i, j = 1, \ldots, n \tag{4.46}$$

are continuous with respect to t and $\boldsymbol{y}$ for all $\boldsymbol{\alpha} \in D_\alpha$. Then the solution $\boldsymbol{y}(t, \boldsymbol{\alpha})$ satisfying

$$\boldsymbol{y}(t, \boldsymbol{\alpha}_0) = \boldsymbol{y}_0 \tag{4.47}$$

is continuous with respect to $\boldsymbol{\alpha}$ for all $\boldsymbol{\alpha} \in D_\alpha$ and $t \geq t_0$.

Theorem 4. *[26] (Differentiability in D) Let the conditions of Theorem 3 hold. If in addition, the right hand sides of (4.44) have continuous partial derivatives in D with respect to $y_1, \ldots, y_n, \alpha_1, \ldots, \alpha_m$, then the solution $\boldsymbol{y}(t, \boldsymbol{\alpha})$ satisfying:*

$$\boldsymbol{y}(t, \boldsymbol{\alpha}_0) = \boldsymbol{y}_0 \tag{4.48}$$

has continuous partial derivatives with respect to $\alpha_1, \ldots, \alpha_m$.

4.2.1 Parameter Sensitivities

The goal of this work is to investigate parameter value sensitivity for an ecosystem involving three species: wolves, elk, and berry producing shrubs. We define the sensitives as the partial derivatives of population densities with respect to model parameters. We use the following definition from Rosenwasser [26] and Vance [34] to give us a more formal approach to parameter sensitivities:

Definition 6. *[34] [26] The partial derivative*

$$\frac{\partial \boldsymbol{y}(t, \boldsymbol{\alpha})}{\partial \alpha_i} \tag{4.49}$$

is a vector and we call it the "sensitivity of the solution" with respect to α_i, where $i = 1, 2, \ldots, m$ denotes parameter values in each respective model. In expanded form we define

$$S_{j,i} = \frac{\partial y_j(t, \boldsymbol{\alpha})}{\partial \alpha_i}. \tag{4.50}$$

where $S_{j,i}$ represents the sensitivity of population j with respect to parameter i.

The bounds on j and i change for each model. In our linear response model $i = 1, 2, \ldots, 10$ and $j = 1, 2, 3$. For our stage structured model we have 15 parameters and 4 trophic levels, hence $i = 1, 2, \ldots, 15$ and $j = 1, 2, 3, 4$.

From Vance [34] and Rosenwasser [26], we know by using Definition 6 we can obtain a system of differential equations that determines the derivative of the solution with respect to each each parameter, α_i. Rosenwasser [26] formulates this as a theorem below.

Theorem 5. *[26] [34] Let the conditions of Theorem 4.1 hold. Then, the derivatives of solutions with respect to parameters are defined by the following differential equations:*

$$\frac{d}{dt}\frac{\partial y_j}{\partial \alpha_i} = \sum_{k=1}^{n}\left(\frac{\partial f_j}{\partial y_k}\frac{\partial y_k}{\partial \alpha_i}\right) + \frac{\partial f_j}{\partial \alpha_i} \tag{4.51}$$

with

$$j = 1, \ldots, n \qquad and \qquad i = 1, \ldots, m,$$

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and initial conditions

$$\frac{\partial y_j}{\partial \alpha_i}(t = t_0) = 0, \qquad j = 1, \ldots, n, \qquad i = 1, \ldots, m. \tag{4.52}$$

Note that equation (4.51) is obtained from (4.44) by formal means of differentiation with respect to α_i and we call these the sensitivity equations. Vance [34] also notes, "the sensitivity equations are linear with respect to the corresponding sensitivities."

To see this more easily, we can rewrite (4.51) using Definition 6 given by Rosenwasser [26] as

$$\frac{d}{dt} S_{j,i} = \sum_{k=1}^{n} \left(\frac{\partial f_j}{\partial y_k} S_{k,i} \right) + \frac{\partial f_j}{\partial \alpha_i} \tag{4.53}$$

$$j = 1, \ldots, n \qquad \text{and} \qquad i = 1, \ldots, m,$$

with initial conditions,

$$S_{j,i}(t = t_0) = 0, \qquad j = 1, \ldots, n, \qquad i = 1, \ldots, m.$$

CHAPTER 5

Linear Response Omnivory Model

We will first attempt to model our ecosystem using a linear response model. From previous research and information provided in Chapter 3, we are aware a Type II non-linear response model may offer better results. However, we use this model as a baseline to develop intuition, then use a stage-structured model with Type II functional responses in the next chapter to model our complex system of wolves, elk, and berry-producing shrubs. The model containing Type I functional responses is given below by the following set of differential equations:

Lotka - Volterra Omnivory Model

$$
\begin{aligned}
\frac{dP}{dt} &= P[e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_p] \\
\frac{dC}{dt} &= C[e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_c] \\
\frac{dR}{dt} &= R[r(1 - R/K) - \alpha_{RC}C - \alpha_{RP}P].
\end{aligned}
\tag{5.1}
$$

We assume that the initial population densities of all species(P, C, R) are such that,

$$
P(0) = c_1 > 0, C(0) = c_2 > 0, R(0) = c_3 > 0.
\tag{5.2}
$$

Then we have the following initial value problem:

$$
\begin{aligned}
\frac{dP}{dt} &= f_1(t, P, C, R) \\
\frac{dC}{dt} &= f_2(t, P, C, R) \\
\frac{dR}{dt} &= f_3(t, P, C, R)
\end{aligned}
\tag{5.3}
$$

$$
P(0) = c_1, C(0) = c_2, R(0) = c_3.
$$

defined on $D = \mathbb{R}_+ \times \mathbb{R}_+^3$.

That is,

$$f_1(P, C, R) = P[e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_p]$$

$$f_2(P, C, R) = C[e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_c] \tag{5.4}$$

$$f_3(P, C, R) = R[r(1 - R/K) - \alpha_{RC}C - \alpha_{RP}P].$$

Thus we can represent our system by the following initial value problem,

$$\frac{d\mathbf{f}}{dt} = \mathbf{f}(\boldsymbol{y}), \qquad \mathbf{f}(0) = \boldsymbol{c}, \tag{5.5}$$

defined on $D = \mathbb{R}_+ \times \mathbb{R}_+^3$, where boldface letters represent our vectors.

5.1 Solution to system

In order to use the system (5.3) we need to know that it can provide a solution and that the solution is unique. Thus we attempt to satisfy Lemma 1 to show that $\mathbf{f}$ satisfies in $D = \mathbb{R}_+ \times \mathbb{R}_+^3$ a local Lipschitz condition with respect to $\boldsymbol{y}$. To do this, we need to show that $\mathbf{f}$ and its partial derivatives are all continuous with respect to our population densities (P, C, R) for all positive t, P, C, R. We calculate the derivatives below and provide them in Table 5.1.

We calculate all the partial derivatives of $\mathbf{f}$ with respect to each population density, (P, C, R) using vector form. We show the calculations of $\mathbf{f}$ with respect to population densities below:

$$\frac{\partial \mathbf{f}}{\partial P} = \begin{pmatrix} \frac{\partial f_1}{\partial P} \\ \frac{\partial f_2}{\partial P} \\ \frac{\partial f_3}{\partial P} \end{pmatrix} = \begin{pmatrix} e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_p \\ -\alpha_{CP}C \\ -\alpha_{RP}R \end{pmatrix}$$

$$\frac{\partial \mathbf{f}}{\partial C} = \begin{pmatrix} \frac{\partial f_1}{\partial C} \\ \frac{\partial f_2}{\partial C} \\ \frac{\partial f_3}{\partial C} \end{pmatrix} = \begin{pmatrix} e_{CP}\alpha_{CP}P \\ e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_C \\ -\alpha_{RC}R \end{pmatrix}$$

$$\frac{\partial \mathbf{f}}{\partial R} = \begin{pmatrix} \frac{\partial f_1}{\partial R} \\[2mm] \frac{\partial f_2}{\partial R} \\[2mm] \frac{\partial f_3}{\partial R} \end{pmatrix} = \begin{pmatrix} e_{RP}\alpha_{RP}P \\[2mm] e_{RC}\alpha_{RC}C \\[2mm] r(1 - R/K) - \alpha_{RC}C - \alpha_{RP}P \end{pmatrix}.$$

The partials of $\mathbf{f}$ are given in Table 5.1.

Population	Partial of f_1	Partial of f_2	Partial of f_3
P	$e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_c$	$-\alpha_{CP}C$	$-\alpha_{RP}R$
C	$e_{CP}\alpha_{CP}P$	$e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_C$	$-\alpha_{RC}R$
R	$e_{RP}\alpha_{RP}P$	$e_{RC}\alpha_{RC}C$	$r(1 - 2R/K) - \alpha_{RC}C - \alpha_{RC}P$

Table 5.1: Partials with respect to Population Densities

We see that all our derivatives contained in Table 5.1 are continuous with respect to our population densities (P, C, R), for all positive t, P, C, R in $D = \mathbb{R}_+ \times \mathbb{R}^3_+$. Hence we have satisfied the hypothesis of Lemma 1. Thus by the conclusion of Lemma 1, we can say the vector $\mathbf{f}$ satisfies in $D = \mathbb{R}_+ \times \mathbb{R}^3_+$ a local Lipschitz condition with respect to

$$\boldsymbol{y} = \begin{bmatrix} P \\ C \\ R \end{bmatrix}. \tag{5.6}$$

We now use Theorem 1 to show we have both existence and uniqueness of solutions of (5.3). The hypothesis of Theorem 1 is satisfied if $\frac{\partial \mathbf{f}}{\partial \boldsymbol{y}}$ is continuous in some set D. We already have this hypothesis satisfied by the calculations in Table 5.1, hence, we conclude the initial value problem,

$$\boldsymbol{y} = \mathbf{f}(t, \boldsymbol{y}), \qquad \boldsymbol{y}(t_0) = \boldsymbol{c}, \tag{5.7}$$

has exactly one solution in $D = \mathbb{R}_+ \times \mathbb{R}^3_+$. Theorem 1 also allows us to extend this solution to left and right up to the boundary of $D = \mathbb{R}_+ \times \mathbb{R}^3_+$.

Since we are dealing with time and populations, we need to show that a unique solution is available for all $t \geq 0$. Vance provides us with this proof in, "Permanent Coexistence for Omnivory Models,"[34], but we will include it for the reader. Our goal in this proof is to conclude

that our initial value problem (5.5) has a unique solution for all $t \geq 0$. We give the proof in the form of a lemma, as we will reference it in the next chapter.

Lemma 5. *The initial value problem 5.3 has has a unique solution in $\mathbb{R}_+^3$ for all $t \geq 0$.*

Proof. Assume that the population densities are such that,

$$P(t), C(t), R(t) \geq 0 \qquad \text{for all} \qquad t \geq 0. \tag{5.8}$$

Recall,

$$\frac{dR(t)}{dt} = R[r(1 - R/K) - \alpha_{RC}C - \alpha_{RP}P]. \tag{5.9}$$

From (5.8), we know that $-\alpha_{RC}C - \alpha_{RP}P \leq 0$. Hence, we can form the differential inequality,

$$\frac{dR(t)}{dt} \leq R[r(1 - R/K)]. \tag{5.10}$$

We want to use Definition 1 and Theorem 2 in order apply Lemma 3 to show our differential inequality in (5.10) holds for $0 \leq t \leq \infty$. Hence, we form the following initial value problem,

$$\frac{du(t)}{dt} = u(t)r(1 - u(t)/K), \qquad u(0) = u_0. \tag{5.11}$$

This is a first order non-linear differential equation that is separable. Solving, we begin by dividing by sides of (5.11) by $u(t)(1 - \frac{u(t)}{K})$ to obtain,

$$\frac{\frac{u(t)}{dt}}{(-\frac{u(t)}{K} + 1)u(t)} = r. \tag{5.12}$$

We now integrate both sides with respect to t,

$$\int \frac{u'(t)}{1 - \frac{u(t)}{K}u(t)} dt = \int r dt. \tag{5.13}$$

Integration of the right hand side yields,

$$\int r dt = rt + b_1 \tag{5.14}$$

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where b_1 is an arbitrary constant. Now focusing on the left hand side of (5.13), we have

$$\int \frac{u'}{u(1 - \frac{u}{K})} dt. \tag{5.15}$$

We note that $u' = \frac{du}{dt}$. This gives us

$$\int \frac{1}{u(1 - \frac{u}{K})} du = \int \frac{-K}{u(u - K)} du. \tag{5.16}$$

Using the method of partial fractions for the integrand in (5.16), this results in,

$$- K \int \left(\frac{1}{Ku - K^2} - \frac{1}{Ku} \right) du. \tag{5.17}$$

Factoring out the constant $\frac{1}{K}$, we have

$$\frac{-K}{K} \left[\int \frac{1}{u - K} du + \int \frac{1}{u} du \right] = - \int \frac{1}{u - K} du + \int \frac{1}{u} du. \tag{5.18}$$

Using the method of substitution for the first integral in (5.18), we let $s = (u - K)$ and $ds = 1du$. This gives us,

$$- \int \frac{1}{s} ds + \int \frac{1}{u} du. \tag{5.19}$$

Integration yields,

$$- \int \frac{1}{s} ds + \int \frac{1}{u} du = - \ln(s) + \ln(u) + b_2, \tag{5.20}$$

where b_2 is an arbitrary constant. Substituting $s = (u - K)$ back into (5.20) gives us,

$$- \int \frac{1}{s} ds + \int \frac{1}{u} du = - \ln(s) + \ln(u) + b_2 = - \ln(u - K) + \ln(u) + b_2. \tag{5.21}$$

Then substituting back for $u = u(t)$ gives us,

$$\ln(u(t)) - \ln(u(t) - K) + b_2. \tag{5.22}$$

Hence,

$$\int \frac{u'(t)}{u(t)(1 - \frac{u(t)}{K})} dt = \ln\left(u(t) - \ln\left(u(t) - K\right) + b_2\right). \tag{5.23}$$

Equating (5.23) to the right hand side, (5.14), we have that,

$$\ln\left(u(t) - \ln\left(u(t) - K\right) + b_2 = \int r dt,$$

$$\ln(u(t)) - \ln(u(t) - K) + b_2 = rt + b_1,$$

$$\ln(u(t)) - \ln(u(t) - K) = rt + b_3,$$

$$\ln\left(\frac{u(t)}{(u(t) - K)}\right) = rt + b_3, \tag{5.24}$$

$$\frac{u(t)}{(u(t) - K)} = e^{rt+b_3} \quad \text{or equivalently,}$$

$$u(t) = e^{rt+b_3}(u(t) - K)$$

$$= e^{rt+b_3}u(t) - (Ke^{rt+b_3}),$$

$$\text{where } b_3 = b_1 - b_2.$$

Solving for $u(t)$ gives us,

$$u(t) - u(t)e^{rt+b_3} = -Ke^{rt+b_3},$$

$$u(t)(1 - e^{rt+b_3}) = -(Ke^{rt+b_3}),$$

$$u(t) = \frac{-Ke^{rt+b_3}}{1 - e^{rt+b_3}}, \tag{5.25}$$

$$= \frac{Ke^{rt+b_3}}{e^{rt+b_3} - 1}.$$

Thus our general solution is,

$$u(t) = \frac{Ke^{rt+b_3}}{e^{rt+b_3} - 1}. \tag{5.26}$$

Substituting our initial conditions $u(0) = u_0$ into the general solution, gives us;

$$u_0 = \frac{Ke^{b_3}}{e^{b_3} - 1}. \tag{5.27}$$

We now solve (5.27) for b_3. This gives us,

$$b_3 = -ln(\frac{u_0 - K}{u_0}) = ln(\frac{u_0}{u_0 - K}).$$ (5.28)

Then plugging (5.28) into our general solution (5.26), gives us the unique solution,

$$u(t) = \frac{Ku_0e^{rt}}{K + u_0(e^{rt} - 1)}.$$ (5.29)

Finally, (5.29) can be rewritten as,

$$u(t) = \frac{K}{1 + (\frac{K}{u_0} - 1)e^{-rt}}.$$ (5.30)

Thus we have satisfied the conditions of Definition 5 and the hypothesis of Theorem 2 by showing (5.11) has a unique solution. Moreover, by satisfying the conditions of Theorem 2, and since $\mathbf{f}$ is continuous we apply Lemma 3 to the differential inequality to say that,

$$R(t) \leq u(t),$$ (5.31)

for $0 \leq t \leq \infty$.

Additionally, if we let $K_{max} = max(u_0, K)$, then we have $u(t) \leq K_{max}$ and thus,

$$R(t) \leq K_{max} \quad \text{for} \quad 0 \leq t \leq \infty.$$ (5.32)

Similarly we consider,

$$\frac{dC}{dt} = C[e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_c].$$ (5.33)

Once again noting the negative terms, we can rewrite the differential inequality as,

$$\frac{dC}{dt} \leq e_{RC}\alpha_{RC}CR.$$ (5.34)

From (5.32), we know $R(t) \leq K_{max}$, thus we have that,

$$\frac{dC}{dt} \leq e_{RC}\alpha_{RC}K_{max}C \text{ for } 0 \leq t \leq \infty. \tag{5.35}$$

Recall that $e_{RC}\alpha_{RC}K_{max}$ is a constant. Hence, if we define

$$\Gamma = e_{RC}\alpha_{RC}K_{max}, \tag{5.36}$$

we can rewrite (5.35) as,

$$\frac{dC(t)}{dt} \leq \Gamma C(t) \text{ for } 0 \leq t \leq \infty. \tag{5.37}$$

Hence the inequality in (5.37) satisfies the hypothesis of Lemma 4 Part A. So by the conclusion of Lemma 4 Part A we have that,

$$C(t) \leq C(0)e^{\Gamma(t-0)}. \tag{5.38}$$

From our initial value problem (5.3), we have $C(0) = c_2$, so we can say

$$\begin{aligned} C(t) \leq &C(0)e^{\Gamma(t-0)} \\ =&c_2 e^{\Gamma t}. \end{aligned} \tag{5.39}$$

This exponential function does not approach infinity in finite time.

Finally we have,

$$\frac{dP(t)}{dt} = P[e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_p]. \tag{5.40}$$

Dropping the negative terms as in our previous calculations, we can form the following differential inequality,

$$\frac{dP(t)}{dt} \leq P[e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C]. \tag{5.41}$$

Plugging in $\Gamma = e_{RC}\alpha_{RC}K_{max}$ into (5.41) gives us,

$$\frac{dP(t)}{dt} \leq P[\Gamma + e_{CP}\alpha_{CP}C]. \tag{5.42}$$

Since we know $C(t) \leq c_2 e^{\Gamma t}$, we now have,

$$\frac{dP(t)}{dt} \leq (\Gamma + e_{CP} \alpha_{CP} c_2 e^{\Gamma t}) P \text{ for } 0 \leq t \leq \infty. \tag{5.43}$$

Defining

$$\Phi = e_{CP} \alpha_{CP} c_2, \tag{5.44}$$

and using $[e_{RC} \alpha_{RC} K_{max}] = \Gamma$ gives us,

$$\frac{dP(t)}{dt} \leq (\Gamma + \Phi e^{\Gamma t}) P \text{ for } a \leq t \leq b. \tag{5.45}$$

Note that (5.45) satisfies the hypothesis of Lemma 4 Part C where Γ and Φ represent M_1 and M_2 respectively. The conclusion of Lemma 4 Part C gives us,

$$P(t) \leq P(a) e^{M_1(t-a) + \frac{M_2}{\lambda}(e^{\lambda t} - e^{\lambda a})} \text{ for } a \leq t \leq b. \tag{5.46}$$

From (5.3) we have

$$P(t) \leq c_1 e^{M_1(t-0) + \frac{M_2}{\lambda}(e^{\lambda t} - e^{\lambda 0})},$$
$$\leq c_1 e^{M_1(t) + \frac{M_2}{\lambda}(e^{\lambda t} - 1)}. \tag{5.47}$$

Using the constants defined in (5.45) yields

$$P(t) \leq c_1 e^{\Gamma + \frac{\Phi}{\lambda}(e^{\lambda t} - 1)}. \tag{5.48}$$

Defining

$$\Lambda = \frac{\Phi}{\Gamma}, \tag{5.49}$$

gives use the desired result of

$$P(t) \leq c_1 e^{\Gamma t + \Lambda(e^{\Gamma t} - 1)}. \tag{5.50}$$

Thus the exponential function (5.50) does not reach infinity in finite time. Moreover, by all the inequalities acquired in (5.32), (5.38), and (5.50) we have shown a unique solution exists for the

initial value problem (5.3) for all $t \geq 0$, [15], [34]. Hence we have a unique solution for all $t \geq 0$.

This completes the proof.

CHAPTER 6

Stage Structured Omnivory Model

To better model our complex system of wolves, elk, and resources we use a stage structured approach with non-linear functional responses. Vance [34] uses a similar model in, "Permanent Coexistence for Omnivory Models." However, in his model he assumes the mortality rate of both predator classes to be the same. In our case, the mortality rate of our juvenile wolf is much greater than that of an adult wolf. Separating the mortality rates into two different parameters will likely give us better results. This model separates the predator into two classes, adults and juveniles. As Gotelli [10] notes, this can make a huge difference in the accuracy of a model. By separating the predator into two classes, we have to include the maturation rate μp, the time it takes a juvenile wolf to become an adult wolf. We assume the juvenile predator, denoted P_1, feeds solely on the resource, while the adult predator, P_2, feeds on both the consumer and resource. The model is given below with the following set of differential equations:

Predator Stage Structured Omnivory Model

$$
\begin{aligned}
\frac{dP_2}{dt} &= \mu_P P_1 - m_{P_2} P_2. \\
\frac{dP_1}{dt} &= \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} P_2 - (\mu_P + m_{P_1})P_1. \\
\frac{dC}{dt} &= C[\frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_C]. \\
\frac{dR}{dt} &= R[r(1 - \frac{R}{K}) - \frac{\lambda_{RC}C}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{RP}P_1}{1 + \lambda_{RP}h_{RP}R} - \frac{\lambda_{RP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}].
\end{aligned}
\tag{6.1}
$$

We assume that the initial population densities of all species (P_2, P_1, C, R) are such that,

$$
P_2(0) = c_1 > 0, P_2(0) = c_2 > 0, C(0) = c_3 > 0, R(0) = c_4 > 0.
\tag{6.2}
$$

Then we have the following initial value problem:

$$\frac{dP_2}{dt} = f_1(t, P_2, P_1, C, R)$$

$$\frac{dP_1}{dt} = f_2(t, P_2, P_1, C, R)$$

$$\frac{dC}{dt} = f_3(t, P_2, P_1, C, R) \tag{6.3}$$

$$\frac{dR}{dt} = f_4(t, P_2, P_1, C, R)$$

$$P_2(0) = c_1, P_1(0) = c_2, C(0) = c_3, R(0) = c_4.$$

defined on $D = \mathbb{R}_+ \times \mathbb{R}_+^4$.

From (6.1) and (6.3), we have

$$f_1(t, P_2, P_1, C, R) = \mu_P P_1 - m_{P_2} P_2$$

$$f_2(t, P_2, P_1, C, R) = \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}P_2 - (\mu_P + m_{P_1})P_1$$

$$f_3(t, P_2, P_1, C, R) = C\left[\frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_C\right]$$

$$f_4(t, P_2, P_1, C, R) = R\left[r(1 - \frac{R}{K}) - \frac{\lambda_{RC}C}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{RP}P_1}{1 + \lambda_{RP}h_{RP}R} - \frac{\lambda_{RP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}\right].$$

$$\tag{6.4}$$

Thus we can represent our system by the following initial value problem,

$$\frac{d\mathbf{f}}{dt} = \mathbf{f}(t, \mathbf{y}) \qquad \mathbf{f}(0) = \mathbf{c} \tag{6.5}$$

defined on $D = \mathbb{R} \times \mathbb{R}_+^4$, with the understood definitions for $\mathbf{f}$, $\mathbf{y}$, and $\mathbf{c}$ where boldface letters represent our vectors.

6.1 Solution to system

Investigating long-term survival of species requires that a unique solution exists for all $t \geq 0$. We use a similar approach as in the previous chapter for our linear response model. We first show that the f and its partial derivatives are all continuous with respect to population densities P_2, P_1, C, R for all positive t, P(t), C(t), R(t). We calculate the derivatives below and provide them in Table 6.1

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We show the components of $\mathbf{f}$ with respect to population densities below:

$$\frac{\partial \mathbf{f}}{\partial P_2} = \begin{pmatrix} \frac{\partial f_1}{\partial P_2} \\ \frac{\partial f_2}{\partial P_2} \\ \frac{\partial f_3}{\partial P_2} \\ \frac{\partial f_4}{\partial P_2} \end{pmatrix} = \begin{pmatrix} -m_{P_2} \\ \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \\ -\frac{\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \\ -\frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \end{pmatrix}$$

$$\frac{\partial \mathbf{f}}{\partial P_1} = \begin{pmatrix} \frac{\partial f_1}{\partial P_1} \\ \frac{\partial f_2}{\partial P_1} \\ \frac{\partial f_3}{\partial P_1} \\ \frac{\partial f_4}{\partial P_1} \end{pmatrix} = \begin{pmatrix} \mu_P \\ -(\mu_P + m_{P_1}) \\ 0 \\ -\frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R} \end{pmatrix}$$

$$\frac{\partial \mathbf{f}}{\partial C} = \begin{pmatrix} \frac{\partial f_1}{\partial C} \\ \frac{\partial f_2}{\partial C} \\ \frac{\partial f_3}{\partial C} \\ \frac{\partial f_4}{\partial C} \end{pmatrix} = \begin{pmatrix} 0 \\ \frac{e_{CP}\lambda_{CP}P_2(1 + \lambda_{RP}h_{RP}R) - e_{RP}\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \\ \frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2(1 + \lambda_{RP}h_{RP}R)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} - m_C \\ -\frac{\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} + \frac{\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \end{pmatrix}$$

$$\frac{\partial \mathbf{f}}{\partial R} = \begin{pmatrix} \frac{\partial f_1}{\partial R} \\ \frac{\partial f_2}{\partial R} \\ \frac{\partial f_3}{\partial R} \\ \frac{\partial f_4}{\partial R} \end{pmatrix} = \begin{pmatrix} 0 \\ \frac{e_{RP}\lambda_{RP}P_2(1 + \lambda_{CP}h_{CP}C) - e_{CP}\lambda_{RP}\lambda_{CP}h_{RP}CP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \\ \frac{e_{RC}\lambda_{RC}C}{(1 + \lambda_{RP}h_{RP}R)^2} + \frac{\lambda_{CP}\lambda_{RP}h_{RP}CP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \\ r(1 - \frac{2R}{K}) - \frac{\lambda_{RC}C}{(1 + \lambda_{RC}h_{RC}R)^2} - \frac{\lambda_{RP}P_1}{(1 + \lambda_{RP}h_{RP}R)^2} - \frac{\lambda_{RP}P_2(1 + \lambda_{CP}h_{CP}C)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \end{pmatrix}$$

We see that $\mathbf{f}$ and all our derivatives contained in Table 6.1 are continuous with respect to our four population densities. Applying Lemma 1 to our system, we see that our vector $\mathbf{f}$ satisfies, in $D = \mathbb{R} \times \mathbb{R}_+^4$, a local Lipschitz condition with respect to $\boldsymbol{y}$ where:

Pop.	Partial of f_1
P_2	$-m_{P_2}$
P_1	μ_p
C	0
R	0

Pop.	Partial of f_2
P_2	$\frac{e_{RP}\lambda_{RP}R+e_{CP}\lambda_{CP}C}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}$
P_1	$-(\mu_p + m_{p_1})$
C	$\frac{e_{CP}\lambda_{CP}P_2(1+\lambda_{RP}h_{RP}R)-e_{RP}\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
R	$\frac{e_{RP}\lambda_{RP}P_2(1+\lambda_{CP}h_{CP}C)-e_{CP}\lambda_{RP}\lambda_{CP}h_{RP}CP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$

Pop.	Partial of f_3
P_2	$-\frac{\lambda_{CP}C}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}$
P_1	0
C	$\frac{e_{RC}\lambda_{RC}R}{1+\lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2(1+\lambda_{RP}h_{RP}R)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2} - m_C$
R	$\frac{e_{RC}\lambda_{RC}C}{(1+\lambda_{RP}h_{RP}R)^2} + \frac{\lambda_{CP}\lambda_{RP}h_{RP}CP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$

Pop.	Partial of f_4
P_2	$-\frac{\lambda_{RP}R}{1+\lambda_{RP}h_{RP}R+h_{CP}\lambda_{CP}C}$
P_1	$-\frac{\lambda_{RP}R}{1+\lambda_{RP}h_{RP}R}$
C	$-\frac{\lambda_{RC}R}{1+\lambda_{RC}h_{RC}R} + \frac{\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
R	$r(1-\frac{2R}{K}) - \frac{\lambda_{RC}C}{(1+\lambda_{RC}h_{RC}R)^2} - \frac{\lambda_{RP}P_1}{(1+\lambda_{RP}h_{RP}R)^2} - \frac{\lambda_{RP}P_2(1+\lambda_{CP}h_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$

Table 6.1: Partials with respect to Population Densitites for Predator Stage Structure Model

$$\boldsymbol{y} = \begin{bmatrix} P_2 \\ P_1 \\ C \\ R \end{bmatrix}. \tag{6.6}$$

We now use Theorem 1 to show existence and uniqueness. Recall the hypothesis of Theorem 1 is satisfied if $\frac{\partial \mathbf{f}}{\partial \boldsymbol{y}}$ is continuous in D. We already have this hypothesis satisfied by the calculations (found in Table 6.1) hence, we conclude the initial value problem

$$\boldsymbol{y}' = \mathbf{f}(t, \boldsymbol{y}), \qquad \boldsymbol{y}(t_0) = \boldsymbol{c} \tag{6.7}$$

has exactly one solution in D. This solution can be extended to the left and right up to the

boundary of D.

Since we are dealing with time and populations over time, we also need to show that a unique solution is available for all $t \geq 0$. We provide the proof in the form of a theorem below. We credit Vance for this approach and proof.

Lemma 6. *[34] The initial value problem (6.3) has a unique solution in $\mathbb{R}^4_+$ for all $t \geq 0$.*

Proof. Assume the population densities are such that,

$$P_2(t), P_1(t), C(t), R(t) \geq 0 \tag{6.8}$$

for all $t \geq 0$.

In model (6.1), we have that,

$$\frac{dR}{dt} = R[r(1 - \frac{R}{K}) - \frac{\lambda_{RC}C}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{RP}P_1}{1 + \lambda_{RP}h_{RP}R} - \frac{\lambda_{RP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}]. \tag{6.9}$$

Using the fact that (6.8) and all parameter values are positive we can say,

$$-\frac{\lambda_{RC}C}{1 + \lambda_{RC}h_{RC}R} \leq 0,$$
$$-\frac{\lambda_{RP}P_1}{1 + \lambda_{RP}h_{RP}R} \leq 0, \text{ and} \tag{6.10}$$
$$-\frac{\lambda_{RP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \leq 0.$$

Likewise, from (6.10), we know the quantity,

$$[-\frac{\lambda_{RC}C}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{RP}P_1}{1 + \lambda_{RP}h_{RP}R} - \frac{\lambda_{RP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}] \leq 0. \tag{6.11}$$

Hence we can form the differential inequality,

$$\frac{dR(t)}{dt} \leq R(t)r(1 - R(t)/K). \tag{6.12}$$

Equivalently,

$$\frac{dR(t)}{dt} \leq R(t)[r(1 - R(t)/K]. \tag{6.13}$$

Note this differential inequality (6.13) is identical to (5.10) in the proof of Lemma 5. Thus from (5.32), we conclude that,

$$R(t) \leq K_{max} \quad for \quad 0 \leq t \leq \infty. \tag{6.14}$$

We use the same approach as above for the following differential equation,

$$\frac{dC}{dt} = C[\frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_C]. \tag{6.15}$$

Once again using (6.8) and knowing all parameter values are positive we can say,

$$-\frac{\lambda_{CP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \leq 0, \text{and}$$

$$-m_C \leq 0. \tag{6.16}$$

Thus we know the quantity,

$$(-\frac{\lambda_{CP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_C) \leq 0. \tag{6.17}$$

Hence we can form the differential inequality,

$$\frac{dC}{dt} \leq C\frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R}. \tag{6.18}$$

Noticing that denominator on the right hand side of (6.18) is always greater than 1 and that the numerator is always positive, we have

$$C\frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} < Ce_{RC}\lambda_{RC}R. \tag{6.19}$$

This gives us the following differential inequality,

$$\frac{dC}{dt} \leq C[e_{RC}\lambda_{RC}R]. \tag{6.20}$$

Then from the proof of Lemma 5, particularly differential inequality (5.37), we replace R with

K_{max} giving us,

$$\frac{dC}{dt} \le C[e_{RC}\lambda_{RC}K_{max}]. \tag{6.21}$$

Now we let the positive constant Γ represent the quantity of $[e_{RC}\lambda_{RC}K_{max}]$. That is,

$$\Gamma = e_{RC}\lambda_{RC}K_{max} \tag{6.22}$$

Substituting Γ into equation (6.21) gives us the exact form we need to satisfy the hypothesis of Lemma 4 Part A on the interval $\quad 0 \le t < \infty$,

$$\frac{dC(t)}{dt} \le C(t)\Gamma \quad \text{with} \quad 0 \le t < \infty. \tag{6.23}$$

Note that our independent variable t is bounded below. That is, $0 \le t < \infty$. Hence Lemma 4 Part A with our interval, $0 \le t < \infty$ (In our case $0 = a$ is our lower bound) yields the following conclusion from (4.14),

$$C(t) \le C(0)e^{\Gamma(t-0)} \text{ for } 0 \le t < \infty. \tag{6.24}$$

Recall that our initial value problem (6.3) gives us that $C(0) = c_3$. Plugging this value into (6.24) and simplifying yields,

$$\begin{aligned} C(t) &\le C(0)e^{\Gamma(t)} \\ &= c_3 e^{\Gamma(t)}. \end{aligned} \tag{6.25}$$

This exponential function does not approach infinity in finite time.

Now we focus on our predator population. Taking the negative terms away from the adult population P_2, and using the numerator of the positive term, juvenile predator population, P_1, we can form the following differential inequalities,

$$\frac{dP_1(t)}{dt} \le (e_{RP}\lambda_{RP}R(t) + e_{CP}\lambda)_{CP}C(t))P_2(t) \tag{6.26}$$

$$\frac{dP_2}{dt}(t) \le \mu P_1(t). \tag{6.27}$$

Recall that $R(t) \leq K_{max}$ from equation (6.14), and $C(t) \leq c_3 e^{\Gamma t}$ from equation (6.25).

Using that information we can say,

$$\frac{dP_1}{dt}(t) \leq (\Gamma + e_{CP}\lambda_{CP}c_3 e^{\Gamma t})P_2(t), \qquad (6.28)$$

and

$$\frac{dP_2}{dt}(t) \leq \mu P_1(t), \qquad (6.29)$$

for $0 \leq t \leq \infty$.

We now denote the product $e_{CP}\lambda_{CP}c_3$ with θ to simplify our inequalities.

That is,

$$e_{CP}\lambda_{CP}c_3 = \theta. \qquad (6.30)$$

Rewriting our inequalities for both predator populations in matrix form using θ gives us,

$$\frac{d}{dt}\begin{bmatrix} P_1(t) \\ P_2(t) \end{bmatrix} \leq \begin{bmatrix} 0 & \Gamma + \theta e^{\Gamma t} \\ \mu p & 0 \end{bmatrix} \begin{bmatrix} P_1(t) \\ P_2(t) \end{bmatrix}. \qquad (6.31)$$

Note that

$$2(P_1 \ P_2) \frac{d}{dt}\begin{bmatrix} P_1 \\ P_2 \end{bmatrix} = \frac{d}{dt}\left\| \begin{bmatrix} P_1 \\ P_2 \end{bmatrix} \right\|^2. \qquad (6.32)$$

Thus we can multiply both sides of (6.31) by 2 and the row vector $(P_1 \ P_2)$ to get

$$\frac{d}{dt}\left\| \begin{bmatrix} P_1 \\ P_2 \end{bmatrix} \right\|^2 \leq 2(\Gamma + \theta e^{\Gamma t})(P_1 \ P_2). \qquad (6.33)$$

Since $2(P_1 \ P_2) \leq ((P_1)^2 + (P_2)^2)$ we can rewrite (6.33) as

$$\frac{d}{dt}\left\| \begin{bmatrix} P_1 \\ P_2 \end{bmatrix} \right\|^2 \leq (\Gamma + \theta e^{\Gamma t})((P_1)^2 + (P_2)^2). \qquad (6.34)$$

Note,

$$\left\| \begin{array}{c} P_1 \\ P_2 \end{array} \right\|^2 = (P_1)^2 + (P_2)^2 \tag{6.35}$$

.

Using (6.35) we can rewrite (6.34) as

$$\frac{d}{dt} \left\| \begin{array}{c} P_1(t) \\ P_2(t) \end{array} \right\|^2 \leq (\Gamma + \theta e^{\Gamma t}) \left\| \begin{array}{c} P_1(t) \\ P_2(t) \end{array} \right\|^2. \tag{6.36}$$

If we define

$$\Lambda = \frac{\theta}{\Gamma}$$

then we can apply Lemma 4 part C to the scalar equation (6.36). We note that the left hand side of (6.36) matches the left hand side of the hypothesis of Lemma 4 part C because the norm of P_1 and P_2 are functions of t. The constant terms Γ and θ represent M_1 and M_2 from the right hand side of Lemma 4 Part C. Finally, because the norm on the right hand side of (6.36) is a function of t. Thus apply Lemma 4 part C to the scaler equation (6.36) gives us the desired result of

$$\frac{d}{dt} \left\| \begin{array}{c} P_1(t) \\ P_2(t) \end{array} \right\|^2 \leq ((c_2)^2 + (c_1)^2) e^{\Gamma t + \Lambda(e^{\Gamma t} - 1)}. \tag{6.37}$$

This exponential function does not approach infinity in finite time. The inequality above also ensures that $P_1(t)$ and $P_2(t)$ do not reach infinity in finite time [34]. Hence, by Lemma 2 and inequalities (6.14), (6.25), and (6.37) a unique solution for the initial value problem (6.3) exists for all $t \geq 0$. This completes the proof and allows us to say that a unique solution is available to (6.3) for all $t \geq 0$.

CHAPTER 7

Sensitivity Analysis

The first step in our method to obtain the sensitivity of each parameter value is to differentiate the right hand side of each model with respect to each model parameter. The partial derivatives for the right hand side of our linear response model (5.3) are contained in Table 7.1 . Table 7.2 lists the associated partials for our stage structured model (6.3). We note that each resulting partial in Table 7.1 and Table 7.2 are continuous with respect to the independent variable t, and all population densities P, C, and R for all positive parameter values. Thus by Theorem 3 and Theorem 4 we can differentiate the solution to each model with respect to each parameter.

7.1 Deriving Sensitivity Equations

Recall from equations (5.3) and (6.3) that both our systems take the form,

$$
\begin{aligned}
\frac{dy_1}{dt} &= f_1(y_1, \ldots, y_j) \\
\frac{dy_2}{dt} &= f_2(y_1, \ldots, y_j) \\
&\vdots \\
\frac{dy_j}{dt} &= f_j(y_1, \ldots, y_j).
\end{aligned}
\tag{7.1}
$$

where y_j, $j = 1, 2, 3$, represent the population densities (P, C, R) for our linear response model. For our stage structure model we have $j = 1, 2, 3, 4$ for our population densities (P_2, P_1, C, R). We represent each parameter value by α_i, where $i = 1, 2, \ldots, 10$ for our linear response model, and $i = 1, 2, \ldots, 15$ for our stage structure model. We define the sensitivity of the state variable y_j with respect to parameter α_i as the partial derivative of y_j with respect α_i. Using Definition 6, we can define the sensitivity of each population with respect to the parameter α_i as,

$$
S_{y_j, \alpha_i} = \frac{\partial y_j}{\partial \alpha_i}
\tag{7.2}
$$

for $j = 1, 2, 3$ with $i = 1, 2, \ldots, 10$ (linear response model) and $j = 1, 2, 3, 4$ with $i = 1, 2, \ldots, 15$

(stage sturcture model).

Since our sensitivities involve the rate of change in population densities with respect to model parameters, we need to differentiate each trophic level with respect to each model parameter. To justify these calculations we look back at Theorems 3 and 4. In chapters 5 and 6 we proved by means of Theorem 1 and Lemma 2, that each respective model satisfied the conditions of existence and uniqueness of solutions and that the solution for each model can be continued for $t \geq t_0$ (Theorems 5 and 6). We also showed, by means of Theorem 3 that the solution to each system depends continuously upon the parameter vector

$$\boldsymbol{\alpha} = \begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \vdots \\ \alpha_i \end{bmatrix}^T , \tag{7.3}$$

on the premise that the partial derivatives in Tables 5.1 and 6.1 are continuous with respect to t and $\boldsymbol{y}$ for all $t \geq 0$. The conclusion of Theorem 3 guarantees us that the solution $\boldsymbol{y}(t, \boldsymbol{\alpha})$ satisfying,

$$\boldsymbol{y}(t, \boldsymbol{\alpha}_0) = \boldsymbol{y}_0 \tag{7.4}$$

is continuous with respect to $\boldsymbol{\alpha}$ for all $\boldsymbol{\alpha} \in D_\alpha$ and $t \geq t_0$.

Hence we have we have satisfied one of the two conditions for Theorem 4. The other condition is satisfied by the calculations contained in Tables 7.1 and 7.2. That is, the right hand sides of (5.3) and (6.1) have continuous partial derivatives in D with respect to the vectors $\boldsymbol{y}$ and $\boldsymbol{\alpha}$. Hence by Theorems 3 and 4, we can differentiate the solution to each model with respect to model parameters.

7.2 Sensitivity Equations

Our next step is to obtain the sensitivity equations. We use Theorems 4 and 5 for this task. Our goal is to calculate the rate of change of the population densities with respect to each parameter value. Recall that the hypothesis of Theorem 5 is satisfied by meeting the conditions of Theorem 4. Theorem 5 allows us to differentiate each differential equation (in each model) with respect to

each model parameter. It then allows us to interchange the order of differentiation to derive a linear system of equations for the sensitivities that solves,

$$\frac{d}{dt}S_{y_j,\alpha_i} = \sum_{k=1}^{n}\left(\frac{\partial f_j}{\partial y_k}S_{y_j,\alpha_i}\right) + \frac{\partial f_j}{\partial \alpha_i}. \tag{7.5}$$

Where S_{y_j,α_i} represent the sensitivity of the population density y_j with respect to the parameter α_i. Thus, we are looking to solve each system for,

$$S_{y_j,\alpha_i}(t) = \frac{\partial y_j(t)}{\partial \alpha_i}, \tag{7.6}$$

where y_j is the j-th component of the state, $j = 1, 2, 3$ (linear response model) or $j = 1, 2, 3, 4$ (for stage structured model), and α_i are the model parameters.

Note that $i = 1, 2, \ldots, 10$ for our linear model and $i = 1, 2, \ldots 15$ for our Stage Structured Model. We must also differentiate the initial conditions with respect to each parameter, hence we have the initial conditions,

$$S_{y_j,\alpha_i(0)} = 0, \text{ for each } y_j, \alpha_i. \tag{7.7}$$

We call the equations in (7.6) the sensitivity equations and note that they require that,

$$\frac{\partial \mathbf{f}_j}{\partial y_k}, \tag{7.8}$$

be continuous with respect to each state variable y_j, where $j = 1, 2, 3$ (for our linear model) and $j = 1, 2, 3, 4$ (for our stage structure model) and the independent variable t.

7.3 Calculating Linear Response Model Sensitivity Equations

We have already established from the initial value problem in Chapter 5, particularly in (5.3), that we can represent our linear response model as,

$$\begin{aligned}
\frac{dP}{dt} &= f_1(P, C, R) \\
\frac{dC}{dt} &= f_2(P, C, R), \\
\frac{dR}{dt} &= f_3(P, C, R),
\end{aligned} \tag{7.9}$$

where f_1, f_2, and f_3 are continuous functions of more than one variable. Thus using the notation above and the result of Theorem 4 we can differentiate each differential equation with respect to our ten parameters. We start by taking the partial derivatives of each differential equation with respect to α_1 then proceed until we reach α_{10}. We show the process for each row vector denoted f_1, f_2, and f_3.

For f_1 we have,

$$\frac{\partial}{\partial \alpha_1} \frac{dP}{dt} = \frac{\partial f_1(P,C,R)}{\partial \alpha_1}$$
$$\frac{\partial}{\partial \alpha_2} \frac{dP}{dt} = \frac{\partial f_1(P,C,R)}{\partial \alpha_2}$$
$$\vdots$$
$$\frac{\partial}{\partial \alpha_{10}} \frac{dP}{dt} = \frac{\partial f_1(P,C,R)}{\partial \alpha_{10}},$$

(7.10)

for f_2 we have,

$$\frac{\partial}{\partial \alpha_1} \frac{dC}{dt} = \frac{\partial f_2(P,C,R)}{\partial \alpha_1}$$
$$\frac{\partial}{\partial \alpha_2} \frac{dC}{dt} = \frac{\partial f_2(P,C,R)}{\partial \alpha_2}$$
$$\vdots$$
$$\frac{\partial}{\partial \alpha_{10}} \frac{dC}{dt} = \frac{\partial f_2(P,C,R)}{\partial \alpha_{10}},$$

(7.11)

and, finally, for f_3 we have,

$$\frac{\partial}{\partial \alpha_1} \frac{dR}{dt} = \frac{\partial f_3(P,C,R)}{\partial \alpha_1}$$
$$\frac{\partial}{\partial \alpha_2} \frac{dR}{dt} = \frac{\partial f_3(P,C,R)}{\partial \alpha_2}$$
$$\vdots$$
$$\frac{\partial}{\partial \alpha_{10}} \frac{dR}{dt} = \frac{\partial f_3(P,C,R)}{\partial \alpha_{10}}.$$

(7.12)

7.3.1 Chain Rule Differentiation

Given the notation in equations, (7.10), (7.11), and (7.12) we can now formally differentiate the right hand side of each. We use the multi-variable chain rule for differentiation of the right hand sides of (7.10), (7.11), and (7.12) with respect to $\alpha_1, \ldots, \alpha_{10}$ to obtain our linear response sensitivity equations. The general form of the chain rule given by Stewart [31] states;

"If u is a differentiable function of n variables $y_1, y_2, y_3, \ldots, y_n$ and each y_n is a differentiable function of m variables $t_1, t_2, t_3, \ldots, t_m$. Then u is a function of $t_1, t_2, t_3, \ldots, t_m$ and

$$\frac{\partial u}{\partial t_i} = \frac{\partial u}{\partial y_1}\frac{\partial y_1}{\partial t_i} + \frac{\partial u}{\partial y_2}\frac{\partial y_2}{\partial t_i} + \ldots + \frac{\partial u}{\partial y_n}\frac{\partial y_n}{\partial t_i}$$

for each $i = 1, 2, \ldots, m$."[31]

In our differential equations $u = f_i, i \in 1, 2, 3$. Our variables, n are as follows:

$y_1 = P, y_2 = C, y_3 = R$. Our parameters are represented by, $t_i = \alpha_i, i \in 1, 2, 3, \ldots, 10$.

Applying the chain rule to the right hand side of each equation in (7.10), (7.11), and (7.12) gives us,

Predator

$$\frac{d}{dt}\frac{\partial P}{\partial \alpha_1} = \frac{\partial f_1}{\partial P}\frac{\partial P}{\partial \alpha_1} + \frac{\partial f_1}{\partial C}\frac{\partial C}{\partial \alpha_1} + \frac{\partial f_1}{\partial R}\frac{\partial R}{\partial \alpha_1} + \frac{\partial f_1}{\partial \alpha_1}$$

$$\frac{d}{dt}\frac{\partial P}{\partial \alpha_2} = \frac{\partial f_1}{\partial P}\frac{\partial P}{\partial \alpha_2} + \frac{\partial f_1}{\partial C}\frac{\partial C}{\partial \alpha_2} + \frac{\partial f_1}{\partial R}\frac{\partial R}{\partial \alpha_2} + \frac{\partial f_1}{\partial \alpha_2} \qquad (7.13)$$

$$= \vdots$$

$$\frac{d}{dt}\frac{\partial P}{\partial \alpha_{10}} = \frac{\partial f_1}{\partial P}\frac{\partial P}{\partial \alpha_{10}} + \frac{\partial f_1}{\partial C}\frac{\partial C}{\partial \alpha_{10}} + \frac{\partial f_1}{\partial R}\frac{\partial R}{\partial \alpha_{10}} + \frac{\partial f_1}{\partial \alpha_{10}},$$

Consumer

$$\frac{d}{dt}\frac{\partial C}{\partial \alpha_1} = \frac{\partial f_2}{\partial P}\frac{\partial P}{\partial \alpha_1} + \frac{\partial f_2}{\partial C}\frac{\partial C}{\partial \alpha_1} + \frac{\partial f_2}{\partial R}\frac{\partial R}{\partial \alpha_1} + \frac{\partial f_2}{\partial \alpha_1}$$

$$\frac{d}{dt}\frac{\partial C}{\partial \alpha_2} = \frac{\partial f_2}{\partial P}\frac{\partial P}{\partial \alpha_2} + \frac{\partial f_2}{\partial C}\frac{\partial C}{\partial \alpha_2} + \frac{\partial f_2}{\partial R}\frac{\partial R}{\partial \alpha_2} + \frac{\partial f_2}{\partial \alpha_2} \qquad (7.14)$$

$$= \vdots$$

$$\frac{d}{dt}\frac{\partial C}{\partial \alpha_{10}} = \frac{\partial f_2}{\partial P}\frac{\partial P}{\partial \alpha_{10}} + \frac{\partial f_2}{\partial C}\frac{\partial C}{\partial \alpha_{10}} + \frac{\partial f_2}{\partial R}\frac{\partial R}{\partial \alpha_{10}} + \frac{\partial f_2}{\partial \alpha_{10}},$$

$$\frac{d}{dt}\frac{\partial R}{\partial \alpha_1} = \frac{\partial f_3}{\partial P}\frac{\partial P}{\partial \alpha_1} + \frac{\partial f_3}{\partial C}\frac{\partial C}{\partial \alpha_1} + \frac{\partial f_3}{\partial R}\frac{\partial R}{\partial \alpha_1} + \frac{\partial f_3}{\partial \alpha_1}$$

$$\frac{d}{dt}\frac{\partial R}{\partial \alpha_2} = \frac{\partial f_3}{\partial P}\frac{\partial P}{\partial \alpha_2} + \frac{\partial f_3}{\partial C}\frac{\partial C}{\partial \alpha_2} + \frac{\partial f_3}{\partial R}\frac{\partial R}{\partial \alpha_2} + \frac{\partial f_3}{\partial \alpha_2}$$

$$= \vdots$$

$$\frac{d}{dt}\frac{\partial R}{\partial \alpha_{10}} = \frac{\partial f_3}{\partial P}\frac{\partial P}{\partial \alpha_{10}} + \frac{\partial f_3}{\partial C}\frac{\partial C}{\partial \alpha_{10}} + \frac{\partial f_3}{\partial R}\frac{\partial R}{\partial \alpha_{10}} + \frac{\partial f_3}{\partial \alpha_{10}}. \tag{7.15}$$

Visually analyzing the differential equations above, we see the term on the end of each differential equation changes for each respective parameter value. The term we are looking at is denoted as $\frac{\partial \mathbf{f}_j}{\partial \alpha_i}$ and we call this term the **particular part of the equations**. This term is located on the right hand side of (7.5) after the addition sign. We call this the particular part of the equations because it changes for every parameter α_i. We note that the term $\frac{\partial \mathbf{f}_j}{\partial y_k}$ with j and $k \in 1, 2, 3$ does not depend on the parameter α_i, hence this term does not change for each parameter. This can be seen in equations (7.13) and (7.14). We use this observation to define the **general sensitivity equations**.

Knowing that $\frac{\partial \mathbf{f}_j}{\partial y_k}$ remains the same for each parameter we can use the notation used in equation (7.6) to form our general sensitivity equations. We call the following the **general sensitivity equations** for the system of linear differential equations,

$$\frac{d}{dt}S_{y_j,\alpha_i} = \sum_{k=1}^{n}\left(\frac{\partial f_j}{\partial y_k}S_{y_j,\alpha_i}\right). \tag{7.16}$$

The partial derivatives computed from the **particular part of the sensitivity equations** are given in Tables 7.1 and 7.2 for each respective model parameter. We note that each partial derivative in the tables noted are continuous with respect to t and all respective population densities for all positive values. If we include the particular part of the equations, we have the exact form on the right hand side as provided in equation (7.5).

7.3.2 Changing Order of Differentiation

Having already noted that Theorem 5 is satisfied by meeting the conditions of Theorem 4, we can use the result of Theorem 5 which allows us to interchange the order of differentiation on the left hand side of each differential equation. We note that we have already calculated the right hand side of each equation in the previous section. Starting with the differential equation related to the predator, we have

$$\frac{dP}{dt} = f_1(P, C, R)$$

Applying the partial derivative to both sides with respect to the parameter value α_i gives,

$$\frac{\partial}{\partial \alpha_1} \frac{dP}{dt} = \frac{\partial}{\partial \alpha_1} f_1(P, C, R).$$

Now concentrating on the left hand side of the equation, we interchange the order of differentiation,

$$\frac{d}{dt} \frac{\partial P}{\partial \alpha_i} = \frac{\partial f_1(P, C, R)}{\partial \alpha_i}.$$

The same follows for the C and R:

$$\text{Consumer}$$

$$\frac{dC}{dt} \frac{\partial}{\partial \alpha_i} = \frac{\partial}{\partial \alpha_i} f_2(P, C, R), \qquad \text{is equivalent to}$$

$$\frac{d}{dt} \frac{\partial C}{\partial \alpha_i} = \frac{\partial f_2(P, C, R)}{\partial \alpha_i},$$

Resource

$$\frac{dR}{dt}\frac{\partial}{\partial \alpha_i} = \frac{\partial}{\partial \alpha_i} f_3(P, C, R), \qquad \text{is equivalent to}$$

$$\frac{d}{dt}\frac{\partial R}{\partial \alpha_i} = \frac{\partial f_3(P, C, R)}{\partial \alpha_i}.$$

We continue this process for each population and all ten parameter values. Recalling from equation (4.50) that our sensitivity for parameter α_i is defined as,

$$S_{j,i} = \frac{\partial y_j(t, \boldsymbol{\alpha})}{\partial \alpha_i}.$$

where $S_{j,i}$ represents the sensitivity of population j with respect to parameter i. Hence we can replace the term $\frac{\partial y_j}{\partial \alpha_i}$, with the notation of S_{j,α_i}, where $j = P, C, R$ and $i = 1, 2, \ldots, 10$.

7.3.3 Sensitivity Differential Equations

Since we know our sensitivities are $\frac{\partial y_j}{\partial \alpha_i}$ where $y_j = P, C, R$, $j = 1, 2, 3$ and $i = 1, \ldots, 10$ we can replace $\frac{\partial y_j}{\partial \alpha_i}$ with the notation S_{y_j,α_i}. This gives us the following sets of sensitivity differential equations.

$$\frac{d}{dt}S_{y_1,\alpha_1} = \frac{\partial f_1}{\partial P}S_{y_1,\alpha_1} + \frac{\partial f_1}{\partial C}S_{y_2,\alpha_1} + \frac{\partial f_1}{\partial R}S_{y_3,\alpha_1} + \frac{\partial f_1}{\partial \alpha_1}$$
$$\frac{d}{dt}S_{y_1,\alpha_2} = \frac{\partial f_1}{\partial P}S_{y_1,\alpha_2} + \frac{\partial f_1}{\partial C}S_{y_2,\alpha_2} + \frac{\partial f_1}{\partial R}S_{y_3,\alpha_2} + \frac{\partial f_1}{\partial \alpha_2}$$
$$\frac{d}{dt}S_{y_1,\alpha_3} = \frac{\partial f_1}{\partial P}S_{y_1,\alpha_3} + \frac{\partial f_1}{\partial C}S_{y_2,\alpha_3} + \frac{\partial f_1}{\partial R}S_{y_3,\alpha_3} + \frac{\partial f_1}{\partial \alpha_3}$$
$$\vdots$$
$$\frac{d}{dt}S_{y_1,\alpha_{10}} = \frac{\partial f_1}{\partial P}S_{y_1,\alpha_{10}} + \frac{\partial f_1}{\partial C}S_{y_2,\alpha_{10}} + \frac{\partial f_1}{\partial R}S_{y_3,\alpha_{10}} + \frac{\partial f_1}{\partial \alpha_{10}}$$

$$\frac{d}{dt}S_{y2,\alpha_1} = \frac{\partial f_2}{\partial P}S_{y1,\alpha_1} + \frac{\partial f_2}{\partial C}S_{y2,\alpha_1} + \frac{\partial f_2}{\partial R}S_{y3,\alpha_1} + \frac{\partial f_2}{\partial \alpha_1}$$

$$\frac{d}{dt}S_{y2,\alpha_2} = \frac{\partial f_2}{\partial P}S_{y1,\alpha_2} + \frac{\partial f_2}{\partial C}S_{y2,\alpha_2} + \frac{\partial f_2}{\partial R}S_{y3,\alpha_2} + \frac{\partial f_2}{\partial \alpha_2}$$

$$\frac{d}{dt}S_{y2,\alpha_3} = \frac{\partial f_2}{\partial P}S_{y1,\alpha_3} + \frac{\partial f_2}{\partial C}S_{y2,\alpha_3} + \frac{\partial f_2}{\partial R}S_{y3,\alpha_3} + \frac{\partial f_2}{\partial \alpha_3}$$

$$\vdots$$

$$\frac{d}{dt}S_{y2,\alpha_{10}} = \frac{\partial f_2}{\partial P}S_{y1,\alpha_{10}} + \frac{\partial f_2}{\partial C}S_{y2,\alpha_{10}} + \frac{\partial f_2}{\partial R}S_{y3,\alpha_{10}} + \frac{\partial f_2}{\partial \alpha_{10}}$$

$$\frac{d}{dt}S_{y3,\alpha_1} = \frac{\partial f_3}{\partial P}S_{y1,\alpha_1} + \frac{\partial f_3}{\partial C}S_{y2,\alpha_1} + \frac{\partial f_3}{\partial R}S_{y3,\alpha_1} + \frac{\partial f_3}{\partial \alpha_1}$$

$$\frac{d}{dt}S_{y3,\alpha_2} = \frac{\partial f_3}{\partial P}S_{y1,\alpha_2} + \frac{\partial f_3}{\partial C}S_{y2,\alpha_2} + \frac{\partial f_3}{\partial R}S_{y3,\alpha_2} + \frac{\partial f_3}{\partial \alpha_2}$$

$$\frac{d}{dt}S_{y3,\alpha_3} = \frac{\partial f_3}{\partial P}S_{y1,\alpha_3} + \frac{\partial f_3}{\partial C}S_{y2,\alpha_3} + \frac{\partial f_3}{\partial R}S_{y3,\alpha_3} + \frac{\partial f_3}{\partial \alpha_3}$$

$$\vdots$$

$$\frac{d}{dt}S_{y3,\alpha_{10}} = \frac{\partial f_3}{\partial P}S_{y1,\alpha_{10}} + \frac{\partial f_3}{\partial C}S_{y2,\alpha_{10}} + \frac{\partial f_3}{\partial R}S_{y3,\alpha_{10}} + \frac{\partial f_3}{\partial \alpha_{10}}$$

7.4 Chain rule differentiation for stage structure model

Recall that the differential equations in our stage structured model contains $f_j, j \in 1, 2, 3, 4$, $y_1 = P_2, y_2 = P_1, y_3 = C, y_4 = R$, and $t = \alpha_i, i \in 1, 2, \ldots, 15$. Hence, using the chain rule we have the following differential equations for our stage structure model;

Adult Predator

$$\frac{d}{dt}\frac{\partial P_2}{\partial \alpha_1} = \frac{\partial f_1}{\partial P_2}\frac{\partial P_2}{\partial \alpha_1} + \frac{\partial f_1}{\partial P_1}\frac{\partial P_1}{\partial \alpha_1} + \frac{\partial f_1}{\partial C}\frac{\partial C}{\partial \alpha_1} + \frac{\partial f_1}{\partial R}\frac{\partial R}{\partial \alpha_1} + \frac{\partial f_1}{\partial \alpha_1}$$

$$\frac{d}{dt}\frac{\partial P_2}{\partial \alpha_2} = \frac{\partial f_1}{\partial P_2}\frac{\partial P_2}{\partial \alpha_2} + \frac{\partial f_1}{\partial P_1}\frac{\partial P_1}{\partial \alpha_2} + \frac{\partial f_1}{\partial C}\frac{\partial C}{\partial \alpha_2} + \frac{\partial f_1}{\partial R}\frac{\partial R}{\partial \alpha_2} + \frac{\partial f_1}{\partial \alpha_2}$$

$$\vdots$$

$$\frac{d}{dt}\frac{\partial P_2}{\partial \alpha_{15}} = \frac{\partial f_1}{\partial P_2}\frac{\partial P_2}{\partial \alpha_{15}} + \frac{\partial f_1}{\partial P_1}\frac{\partial P_1}{\partial \alpha_{15}} + \frac{\partial f_1}{\partial C}\frac{\partial C}{\partial \alpha_{15}} + \frac{\partial f_1}{\partial R}\frac{\partial R}{\partial \alpha_{15}} + \frac{\partial f_1}{\partial \alpha_{15}}$$

Juvenile Predator

$$\frac{d}{dt}\frac{\partial P_1}{\partial \alpha_1} = \frac{\partial f_2}{\partial P_2}\frac{\partial P_2}{\partial \alpha_1} + \frac{\partial f_2}{\partial P_1}\frac{\partial P_1}{\partial \alpha_1} + \frac{\partial f_2}{\partial C}\frac{\partial C}{\partial \alpha_1} + \frac{\partial f_2}{\partial R}\frac{\partial R}{\partial \alpha_1} + \frac{\partial f_2}{\partial \alpha_1}$$

$$\frac{d}{dt}\frac{\partial P_1}{\partial \alpha_2} = \frac{\partial f_2}{\partial P_2}\frac{\partial P_2}{\partial \alpha_2} + \frac{\partial f_2}{\partial P_1}\frac{\partial P_1}{\partial \alpha_2} + \frac{\partial f_2}{\partial C}\frac{\partial C}{\partial \alpha_2} + \frac{\partial f_2}{\partial R}\frac{\partial R}{\partial \alpha_2} + \frac{\partial f_2}{\partial \alpha_2}$$

$$\vdots$$

$$\frac{d}{dt}\frac{\partial P_1}{\partial \alpha_{15}} = \frac{\partial f_2}{\partial P_2}\frac{\partial P_2}{\partial \alpha_{15}} + \frac{\partial f_2}{\partial P_1}\frac{\partial P_1}{\partial \alpha_{15}} + \frac{\partial f_2}{\partial C}\frac{\partial C}{\partial \alpha_{15}} + \frac{\partial f_2}{\partial R}\frac{\partial R}{\partial \alpha_{15}} + \frac{\partial f_2}{\partial \alpha_{15}}$$

Consumer

$$\frac{d}{dt}\frac{\partial C}{\partial \alpha_1} = \frac{\partial f_3}{\partial P_2}\frac{\partial P_2}{\partial \alpha_1} + \frac{\partial f_3}{\partial P_1}\frac{\partial P_1}{\partial \alpha_1} + \frac{\partial f_3}{\partial C}\frac{\partial C}{\partial \alpha_1} + \frac{\partial f_3}{\partial R}\frac{\partial R}{\partial \alpha_1} + \frac{\partial f_3}{\partial \alpha_1}$$

$$\frac{d}{dt}\frac{\partial C}{\partial \alpha_2} = \frac{\partial f_3}{\partial P_2}\frac{\partial P_2}{\partial \alpha_2} + \frac{\partial f_3}{\partial P_1}\frac{\partial P_1}{\partial \alpha_2} + \frac{\partial f_3}{\partial C}\frac{\partial C}{\partial \alpha_2} + \frac{\partial f_3}{\partial R}\frac{\partial R}{\partial \alpha_2} + \frac{\partial f_3}{\partial \alpha_2}$$

$$\vdots$$

$$\frac{d}{dt}\frac{\partial C}{\partial \alpha_{15}} = \frac{\partial f_3}{\partial P_2}\frac{\partial P_2}{\partial \alpha_{15}} + \frac{\partial f_3}{\partial P_1}\frac{\partial P_1}{\partial \alpha_{15}} + \frac{\partial f_3}{\partial C}\frac{\partial C}{\partial \alpha_{15}} + \frac{\partial f_3}{\partial R}\frac{\partial R}{\partial \alpha_{15}} + \frac{\partial f_3}{\partial \alpha_{15}}$$

Resource

$$\frac{d}{dt}\frac{\partial R}{\partial \alpha_1} = \frac{\partial f_4}{\partial P_2}\frac{\partial P_2}{\partial \alpha_1} + \frac{\partial f_4}{\partial P_1}\frac{\partial P_1}{\partial \alpha_1} + \frac{\partial f_4}{\partial C}\frac{\partial C}{\partial \alpha_1} + \frac{\partial f_4}{\partial R}\frac{\partial R}{\partial \alpha_1} + \frac{\partial f_4}{\partial \alpha_1}$$

$$\frac{d}{dt}\frac{\partial R}{\partial \alpha_2} = \frac{\partial f_4}{\partial P_2}\frac{\partial P_2}{\partial \alpha_2} + \frac{\partial f_4}{\partial P_1}\frac{\partial P_1}{\partial \alpha_2} + \frac{\partial f_4}{\partial C}\frac{\partial C}{\partial \alpha_2} + \frac{\partial f_4}{\partial R}\frac{\partial R}{\partial \alpha_2} + \frac{\partial f_4}{\partial \alpha_2}$$

$$\vdots$$

$$\frac{d}{dt}\frac{\partial R}{\partial \alpha_{15}} = \frac{\partial f_4}{\partial P_2}\frac{\partial P_2}{\partial \alpha_{15}} + \frac{\partial f_4}{\partial P_1}\frac{\partial P_1}{\partial \alpha_{15}} + \frac{\partial f_4}{\partial C}\frac{\partial C}{\partial \alpha_{15}} + \frac{\partial f_4}{\partial R}\frac{\partial R}{\partial \alpha_{15}} + \frac{\partial f_4}{\partial \alpha_{15}}$$

7.5 Sensitivity Differential Equations for Stage Structured Model

Since we know our sensitivities are $\frac{\partial y_j}{\partial \alpha_i}$ where $y_j = j = P_2, P_1, C, R$, $j = 1, 2, 3, 4$ and $i = 1, \ldots, 15$, we can replace $\frac{\partial y_j}{\partial \alpha_i}$ with the notation S_y, α_i. Thus we have:

Adult Predator

$$\frac{d}{dt}S_{y_1,\alpha_1} = \frac{\partial f_1}{\partial P_2}S_{y_1,\alpha_1} + \frac{\partial f_1}{\partial P_1}S_{y_2,\alpha_1} + \frac{\partial f_1}{\partial C}S_{y_3,\alpha_1} + \frac{\partial f_1}{\partial R}S_{y_4,\alpha_1} + \frac{\partial f_1}{\partial \alpha_1}$$

$$\frac{d}{dt}S_{y_1,\alpha_2} = \frac{\partial f_1}{\partial P_2}S_{y_1,\alpha_2} + \frac{\partial f_1}{\partial P_1}S_{y_2,\alpha_2} + \frac{\partial f_1}{\partial C}S_{y_3,\alpha_2} + \frac{\partial f_1}{\partial R}S_{y_4,\alpha_2} + \frac{\partial f_1}{\partial \alpha_2}$$

$$\vdots$$

$$\frac{d}{dt}S_{y_1,\alpha_{15}} = \frac{\partial f_1}{\partial P_2}S_{y_1,\alpha_{15}} + \frac{\partial f_1}{\partial P_1}S_{y_2,\alpha_{15}} + \frac{\partial f_1}{\partial C}S_{y_3,\alpha_{15}} + \frac{\partial f_1}{\partial R}S_{y_4,\alpha_1} + \frac{\partial f_1}{\partial \alpha_{15}}$$

Juvenile Predator

$$\frac{d}{dt}S_{y_2,\alpha_1} = \frac{\partial f_2}{\partial P_2}S_{y_1,\alpha_1} + \frac{\partial f_2}{\partial P_1}S_{y_2,\alpha_1} + \frac{\partial f_2}{\partial C}S_{y_3,\alpha_1} + \frac{\partial f_2}{\partial R}S_{y_4,\alpha_1} + \frac{\partial f_2}{\partial \alpha_1}$$

$$\frac{d}{dt}S_{y_2,\alpha_2} = \frac{\partial f_2}{\partial P_2}S_{y_1,\alpha_2} + \frac{\partial f_2}{\partial P_1}S_{y_2,\alpha_2} + \frac{\partial f_2}{\partial C}S_{y_3,\alpha_2} + \frac{\partial f_2}{\partial R}S_{y_4,\alpha_2} + \frac{\partial f_2}{\partial \alpha_2}$$

$$\vdots$$

$$\frac{d}{dt}S_{y_2,\alpha_{15}} = \frac{\partial f_2}{\partial P_2}S_{y_1,\alpha_{15}} + \frac{\partial f_2}{\partial P_1}S_{y_2,\alpha_{15}} + \frac{\partial f_2}{\partial C}S_{y_3,\alpha_{15}} + \frac{\partial f_2}{\partial R}S_{y_4,\alpha_1} + \frac{\partial f_2}{\partial \alpha_{15}}$$

Consumer

$$\frac{d}{dt}S_{y_3,\alpha_1} = \frac{\partial f_3}{\partial P_2}S_{y_1,\alpha_1} + \frac{\partial f_3}{\partial P_1}S_{y_2,\alpha_1} + \frac{\partial f_3}{\partial C}S_{y_3,\alpha_1} + \frac{\partial f_3}{\partial R}S_{y_4,\alpha_1} + \frac{\partial f_3}{\partial \alpha_1}$$

$$\frac{d}{dt}S_{y_3,\alpha_2} = \frac{\partial f_3}{\partial P_2}S_{y_1,\alpha_2} + \frac{\partial f_3}{\partial P_1}S_{y_2,\alpha_2} + \frac{\partial f_3}{\partial C}S_{y_3,\alpha_2} + \frac{\partial f_3}{\partial R}S_{y_4,\alpha_2} + \frac{\partial f_3}{\partial \alpha_2}$$

$$\vdots$$

$$\frac{d}{dt}S_{y_3,\alpha_{15}} = \frac{\partial f_3}{\partial P_2}S_{y_1,\alpha_{15}} + \frac{\partial f_3}{\partial P_1}S_{y_2,\alpha_{15}} + \frac{\partial f_3}{\partial C}S_{y_3,\alpha_{15}} + \frac{\partial f_3}{\partial R}S_{y_4,\alpha_1} + \frac{\partial f_3}{\partial \alpha_{15}}$$

Resource

$$\frac{d}{dt}S_{y_4,\alpha_1} = \frac{\partial f_4}{\partial P_2}S_{y_1,\alpha_1} + \frac{\partial f_4}{\partial P_1}S_{y_2,\alpha_1} + \frac{\partial f_4}{\partial C}S_{y_3,\alpha_1} + \frac{\partial f_4}{\partial R}S_{y_4,\alpha_1} + \frac{\partial f_4}{\partial \alpha_1}$$

$$\frac{d}{dt}S_{y_4,\alpha_2} = \frac{\partial f_4}{\partial P_2}S_{y_1,\alpha_2} + \frac{\partial f_4}{\partial P_1}S_{y_2,\alpha_2} + \frac{\partial f_4}{\partial C}S_{y_3,\alpha_2} + \frac{\partial f_4}{\partial R}S_{y_4,\alpha_2} + \frac{\partial f_4}{\partial \alpha_2}$$

$$\vdots$$

$$\frac{d}{dt}S_{y_4,\alpha_{15}} = \frac{\partial f_4}{\partial P_2}S_{y_1,\alpha_{15}} + \frac{\partial f_4}{\partial P_1}S_{y_2,\alpha_{15}} + \frac{\partial f_4}{\partial C}S_{y_3,\alpha_{15}} + \frac{\partial f_4}{\partial R}S_{y_4,\alpha_1} + \frac{\partial f_4}{\partial \alpha_{15}}$$

Tables 7.1 and 7.2 contain all the **particular parts** for the sensitivity equations; the partial derivatives of each population with respect to parameter values. We can now write our initial

value problem of sensitivity equations for each model. We suppress the dependence on time for these calculations. The general sensitivity equations (7.16) for our linear response model are given by,

$$\frac{d}{dt}(S_P) = (e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_P)S_P + (e_{CP}\alpha_{CP}P)S_C + (e_{RP}\alpha_{RP}P)S_R$$

$$\frac{d}{dt}(S_C) = (-\alpha_{CP}C)S_P + (e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_C)S_C + (e_{RC}\alpha_{RC}C)S_R \qquad (7.17)$$

$$\frac{d}{dt}(S_R) = (-\alpha_{CP}C)S_P + (e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_C)S_C + (e_{RC}\alpha_{RC}C)S_R$$

with initial conditions

$$S_P(0) = 0, \qquad\qquad S_C(0) = 0, \qquad\quad and\ \ S_R(0) = 0 \qquad\qquad (7.18)$$

where we define

$$S_P(t) = \frac{\partial}{\partial\alpha_i}P(t), \quad S_C(t) = \frac{\partial}{\partial\alpha_i}C(t), \quad S_R(t) = \frac{\partial}{\partial\alpha_i}R(t). \qquad (7.19)$$

Similarly, by 7.16 the general sensitivity equations for our stage structured model are:

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

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

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

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

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

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

$$+ \left(\frac{e_{RC}\lambda_{RC}C}{(1 + \lambda_{RP}h_{RP}R)^2} + \frac{\lambda_{CP}\lambda_{RP}h_{RP}CP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2}\right)S_R \qquad (7.20)$$

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

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

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

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

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

with initial conditions

$$S_{P_2}(0) = 0, S_{P_1}(0) = 0, \qquad S_C(0) = 0, \qquad and \ \ S_R(0) = 0 \qquad (7.21)$$

where we define

$$S_{P_2}(t) = \frac{\partial}{\partial \alpha_i}P_2(t), \ \ S_{P_1}(t) = \frac{\partial}{\partial \alpha_i}P_1(t), \ \ S_C(t) = \frac{\partial}{\partial \alpha_i}C(t), \ \ S_R(t) = \frac{\partial}{\partial \alpha_i}R(t). \qquad (7.22)$$

7.6 Solving the Sensitivity Equations

For each parameter that the original system has, we must solve a system of linear sensitivity equations. We note that the number of differential equations in the state system dictates how many differential equations we will have in the linear sensitivity system. For our linear response model, we have ten parameters and three variables. For our stage structured model we have fifteen parameters and four variables. Vance and Eads [16] note that, "Although the sensitivity equations are linear, they are forced by the solution to the state equations." Hence, we will need to solve one hundred and twenty equations in groups of eight (four model and four sensitivity) for our stage structure model.

We will numerically integrate the linear sensitivity equations and the nonlinear state equations using Matlab's fourth and fifth order adaptive step-size algorithm known as ode45. This is a Runge-Kutta-Fehlberg method that will simultaneously obtain two solutions per step. This helps to monitor the accuracy of the solution and adjusts the step size.

After differentiating our linear response model with respect to our ten parameter values we obtain ten sensitivity equations for each population density. Given our three population densities, we have a total of thirty sensitivity equations to solve. That is, for each parameter in our original system we must solve a system of linear sensitivity equations. We note that the number of differential equations in the state system dictates how many differential equations there will be in the linear sensitivity system. The equations in (7.17) remain the same with only the addition of the particular part to each line. In our linear model, we have ten parameters and three variables. Vance and Eads [16] state, "although the sensitivity equations are linear, they are forced by the solution to the state equations". Hence we must solve the initial value problem for the model and the three corresponding sensitivity equations. Hence, to compute all our sensitivities (for each parameter in our linear response model) we solve ten systems of equations with six coupled equations in each system.

Our stage structure model contains four variables and fifteen parameters. Thus, to compute the sensitivities of this model, we are required to solve fifteen systems with eight coupled equations in each. We have eight equations in each group because we must solve the sensitivity equations for

each of our four populations and solve the original system simultaneously.

To solve each coupled set of equations in each model we will numerically integrate the linear sensitivity equations and the state equations using Matlab's built-in algorithm known as ode45. Ode45 is a Runge-Kutta-Fehlberg method algorithm which obtains two solutions per step to monitor accuracy of the solution. We note that the Runge-Kutta method we are using allows for adjusting the step size to desired tolerances. We set the the relative error for 1 x 10^{-3} and the absolute error at 1 x 10^{-3}. We set the initial conditions for the state equations as $(1, 1, 1, 1)^T$ and set our initial conditions for the sensitivity equations as $(0, 0, 0, 0)^T$ [34] [16].

In order to quantify or give our sensitivities a performance measure we use a weighted Euclidean norm. Our weighted norm for the linear response model will be in three dimensions while our norm for the stage structure model will be in four dimensions. We define the weighted norms for each model below and note that taking the weighted norm will be a function of the parameter value and time only. This will allow us to graph parameter sensitivities against one another to see which of these sensitivity measures rank higher and ones which rank lower. Because we are unsure if any state variable in terms of of performance measure is more important, we simply use a weight of 1 for all our calculations. We use the following weighted Euclidean norm for our linear response model,

$$\| S_{\alpha_i} \| = \| (S_{P,\alpha_i}, S_{C,\alpha_i}, S_{R,\alpha_i})^T \| \ \sqrt{w_1(S_{P,\alpha_i})^2 + w_2(S_{C,\alpha_i})^2 + w_3(S_{R,\alpha_i})^2} \qquad (7.23)$$

and likewise,

$$\| S_{\alpha_i} \| = \| (S_{P_2,\alpha_i}, S_{P_1,\alpha_i} S_{C,\alpha_i}, S_{R,\alpha_i})^T \| \ \sqrt{w_1(S_{P_2,\alpha_i})^2 + w_2 S_{P_1,\alpha_i})^2 w_3(S_{C,\alpha_i})^2 + w_4(S_{R,\alpha_i})^2}$$

$$(7.24)$$

as the norm for our stage structure model.

α_i	Parameter	Partial of f_1	Partial of f_2	Partial of f_3
α_1	e_{RP}	$\alpha_{RP}RP$	0	0
α_2	e_{CP}	$\alpha_{CP}CP$	0	0
α_3	e_{RC}	0	$\alpha_{RC}RC$	0
α_4	α_{RP}	$e_{RP}RP$	0	$-RP$
α_5	α_{CP}	$e_{CP}CP$	$-CP$	0
α_6	α_{RC}	0	$e_{RC}RC$	$-RC$
α_7	m_P	$-P$	0	0
α_8	m_C	0	$-C$	0
α_9	r	0	0	$R(1-R/K)$
α_{10}	K	0	0	rR^2/K^2

Table 7.1: Linear Response Model: Partials with respect to Parameter Values

Parameter	Partial of f_1	Partial of f_2
r	0	0
K	0	0
μ_P	P_1	$-P_1$
m_{P_2}	$-P_2$	$-P_1$
m_{P_1}	0	0
m_C	0	0
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
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
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
Parameter	Partial of f_3	Partial of f_4
r	0	$R(1-\frac{R}{K})$
K	0	$\frac{rR^2}{K^2}$
μ_P	0	0
m_{P_2}	0	0
m_{P_1}	0	0
m_C	$-C$	0
e_{RP}	0	0
e_{CP}	0	0
e_{RC}	$\frac{\lambda_{RC}RC}{1+\lambda_{RP}h_{RP}R}$	0
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}	$-\frac{e_{RC}(\lambda_{RC})^2R^2C}{(1+\lambda_{RP}h_{RP}R)^2}$	$\frac{(\lambda_{RC})^2R^2C}{(1+\lambda_{RP}h_{RP}R)^2}$
λ_{RP}	$\frac{\lambda_{CP}h_{RP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$-\frac{RP_1}{1+\lambda_{RP}h_{RP}R}-\frac{RP_2(1+\lambda_{CP}h_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
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}	$\frac{e_{RC}RC}{(1+\lambda_{RP}h_{RP}R)^2}$	$-\frac{RC}{(1+\lambda_{RP}h_{RP}R)^2}$

Table 7.2: Stage Structured Model: Partials with respect to Parameter Values

CHAPTER 8

Results

In order to quantify and do a performance measure of how small changes in parameter values dictate the state variables, we use a weighted norm (three dimensions for linear response model and 4 dimensions for stage structure model) which is a function of the parameter and time only. We use a weight of one so that the sensitivities can be weighed equally. With further research we could adjust the weights according to biological significance. However, for this initial research project we will assume an equal weight of 1 for each population. Each graph shows the norm of each sensitivity over time. We graph the linear response model's sensitivities using two graphs, one for the larger (most) sensitivities and one for the smaller (least) sensitivities. Similarly, we create graphs for the stage structured model using the same methodology. In this case we use four graphs due to the broad range in sensitivity norm values. All graphs have the norm of the sensitivities on the y-axis vs time which is located on the x-axis. The graphs are given below for each model.

We also offer two tables (one for each model) which depict the rank of the parameter sensitivity versus the other respective sensitivities. Rank 1 in our Tables represents the most sensitive parameter and increasing rank numbers means a decrease in sensitivity. We also offer an approximate sensitivity measure (value) to show the large discrepancies between parameters. Our sensitives range from a max of 750 for the adult predator mortality rate (stage model) to 0.25 for the handling time of resources by predators (stage model). Hence, Tables 8.1 and 8.2 give us an overview of which parameter is the most and least sensitive and how far apart the sensitives may be. We note that the approximate sensitivity values in the tables are taken at or near equilibrium. Figures 8.1 through 8.5 let us visualize how each function (sensitivity vs time) levels off to a nearly stable value. These values are the approximations we use in Tables 8.1 and 8.2. The peaks and valleys show how each parameter may affect the system earlier in time before they taper off to equilibrium.
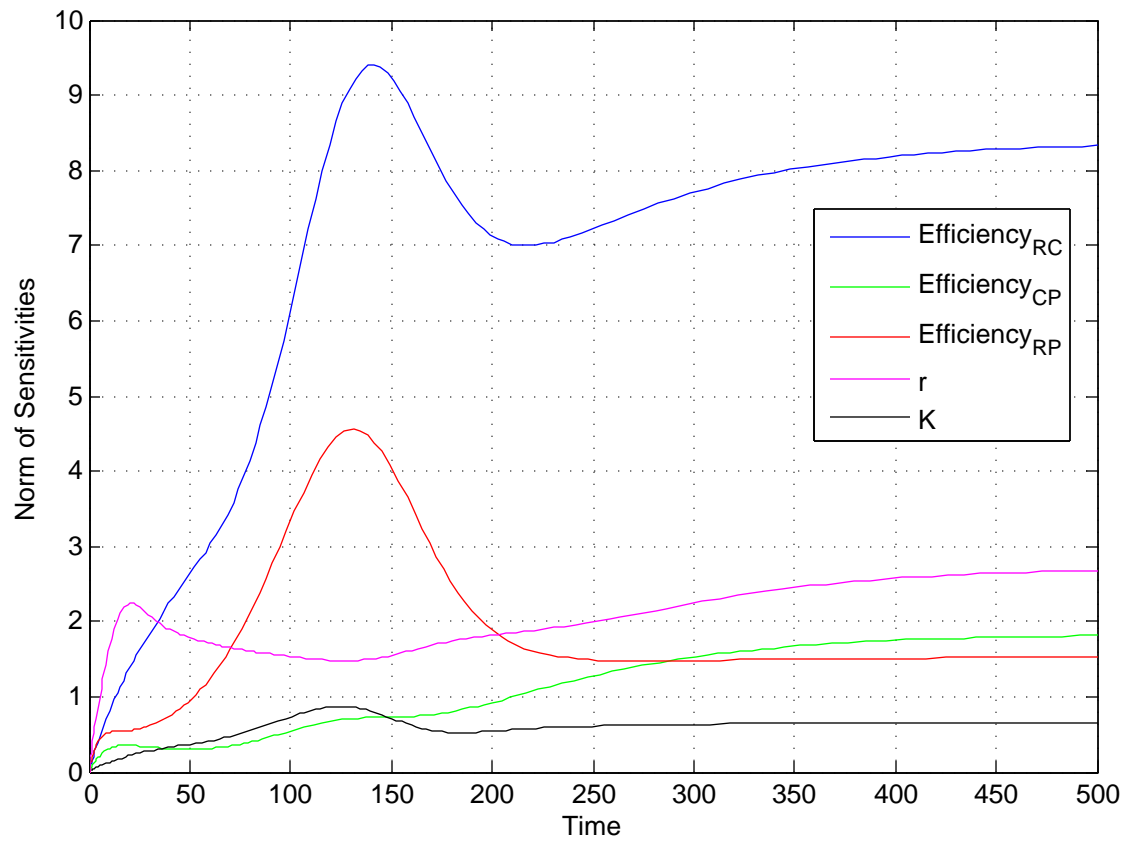
Figure 8.1: Graph of Smaller Sensitivities for Linear Response Model
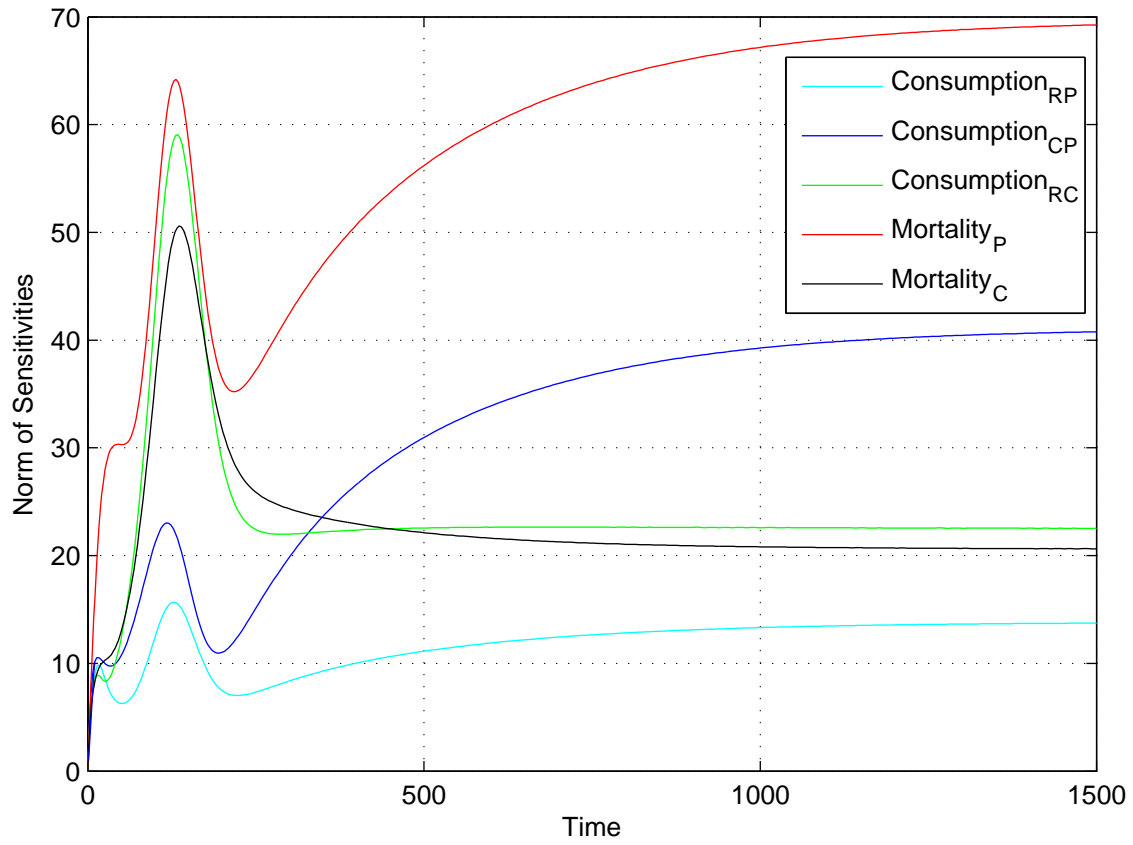
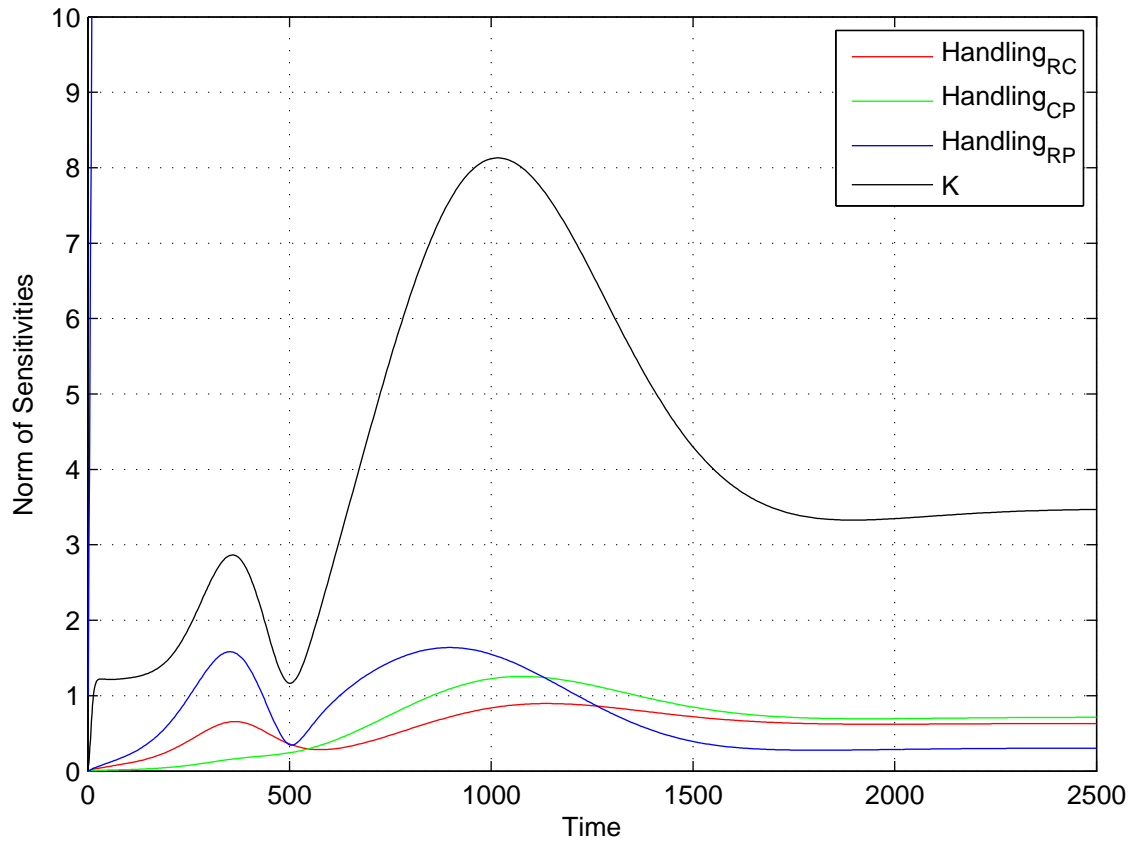Figure 8.2: Graph of Large Sensitivities for Linear Response Model

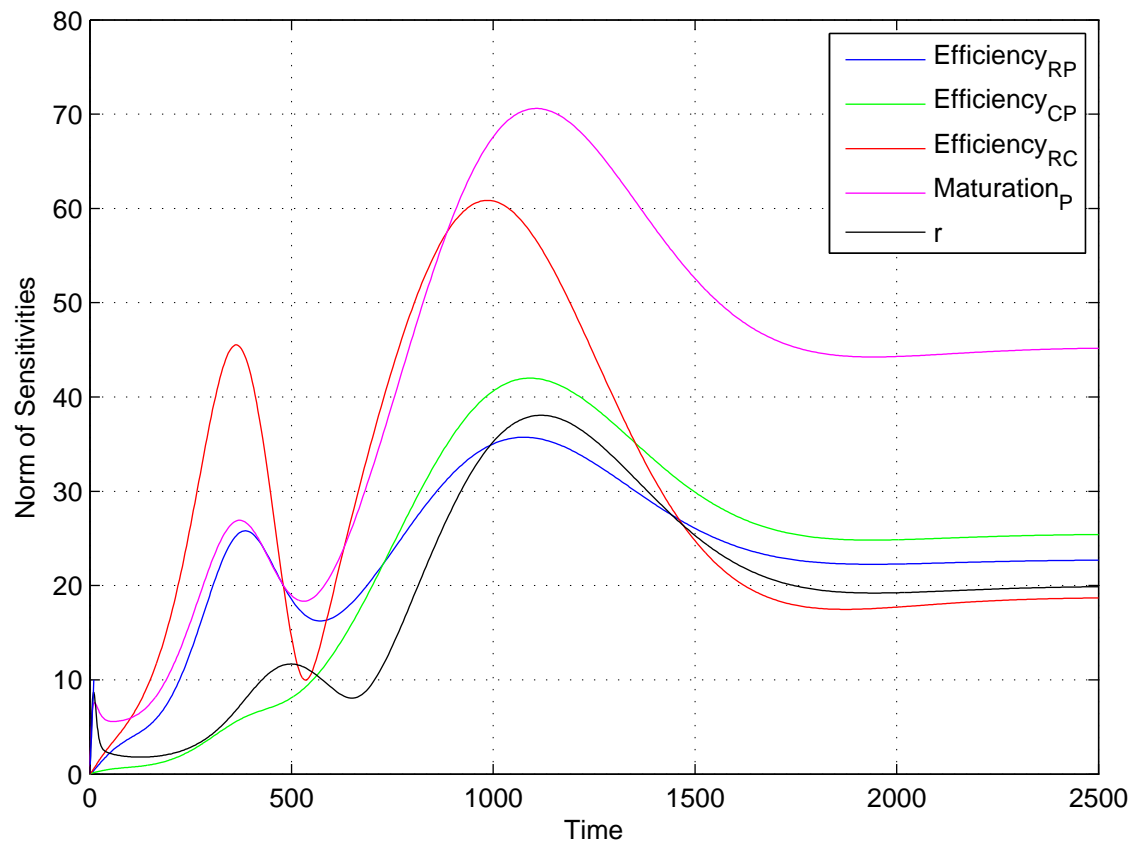Figure 8.3: Graph of Smaller Sensitivities for Stage Structure Model

Figure 8.4: Graph of Medium Sensitivities for Stage Structure Model
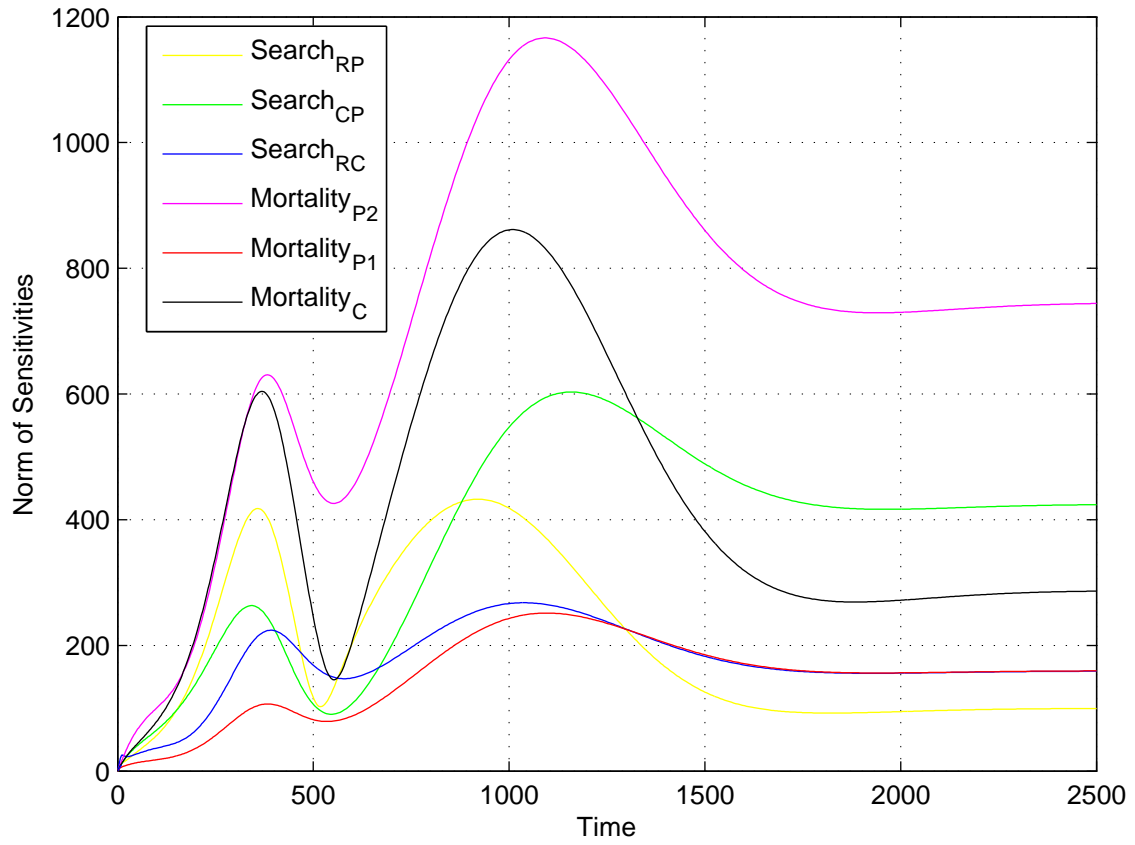
Figure 8.5: Graph of Larger Sensitivities for Stage Structure Model

Parameter	Rank	Approximate sensitivity value
m_p	1	69
α_{CP}	2	42
α_{RC}	3	23
m_C	4	21
α_{RP}	5	14
e_{RC}	6	8.4
r	7	2.75
e_{CP}	8	1.75
e_{RP}	9	1.5
K	10	0.7

Table 8.1: Sensitivity rankings of parameters for linear response model

Parameter	Rank	Approximate sensitivity value
m_{P2}	1	750
λ_{CP}	2	425
m_C	3	290
m_{P1}	4	180
λ_{RC}	5	175
λ_{RP}	6	150
μ_P	7	45
e_{CP}	8	25
e_{RP}	9	23
r	10	20
e_{RC}	11	18
K	12	3.5
h_{CP}	13	0.6
h_{RC}	14	0.5
h_{RP}	15	0.25

Table 8.2: Sensitivity rankings of parameters for stage structured model

8.1 Most Sensitive Parameters

Using Table 8.1 and Table 8.2 we see that in both models the largest norm of the sensitivities is the predator mortality rate, m_P and m_{P_2} (adult for stage model). Given the history of Yellowstone National Park and the success of wolf reintroduction, this does not come as a surprise. From previous discussions we noted how the entire ecosystem was suffering before wolf reintroduction, then flourished afterward. Thus it supports current biological understanding of the natural system that the mortality rate of the predator and adult predator are our most sensitive parameters. This means that very small changes in the mortality rate of the predator

cause the largest change to the solution of the system. Thus, biologist should take extra time and care in the field when monitoring and collecting data. Any small change in this parameter will drastically change the entire ecosystem.

8.2 Least Sensitive Parameters

Due to the enormous size of Yellowstone National Park it makes logical and biological sense that the carrying capacity of our resource, K (berry producing shrubs) is the least sensitive for our linear response model. For our stage structured model we see that the carrying capacity of the resource is ranked 12th out of 15, where the 15th ranked parameter representing our least sensitive parameter, is the handling time of resources by predators, h_{RP}. Note that in our linear response model we did not include handling times of Type II functional responses, so this is one explanation why our results from model to model vary. However, if we look at it from a biological perspective the handling time of berries by wolves is not something that takes very long. We used an approximate value of 1 hour for this parameter. We also note the nutritional effect that berries give wolves is almost negligible when compared to the biomass that an elk would give. Moreover, with the three species models we used, this value makes sense and is one that biologists need not spend as much time precisely monitoring as other values, especially when compared to mortality rates.

8.3 Overview of all sensitivities for linear response model

As previously noted, the mortality rate of the predator is the most sensitive parameter in this model. However, we do note that the consumption rate of consumers by predators α_{CP} also stands out being nearly twice as sensitive as the consumption rate of resources by consumers α_{RC}, which rank 2 and 3, respectively. The mortality rate of the consumer m_C ranks 4th which is only slightly below the consumption rate of resources by consumers. Out of all of our consumption rates, the least sensitive is the consumption rate of resources by predators α_{RP}. Ranking number 6 is the conversion efficiency of resources by consumers, e_{RC} which is the most sensitive conversion efficiency. The other conversion efficiencies, consumers into predators and resources into predators, e_{CP}, e_{RP} rank 8 and 9. Rank number 7 goes to the intrinsic rate of increase of the resource, r. Our least sensitive parameter is the carrying capacity of the resource, K.

8.4 Overview of all sensitivities for stage structured model

Again, as noted above the mortality rate of the adult predator, m_{P_2} is almost twice as sensitive as the next closest parameter, the search rate of consumers by predators, λ_{CP}. At rank 3 and 4 we have a drop off in sensitivities making the top two sensitivities stand out. Rank 3 and 4 are held by the mortality rate of the consumer m_C and the mortality rate of the juvenile predator m_{P_1}. The search rates of resources by consumers λ_{RC}, and resources by predators λ_{RP}, come in at rank 5 and 6. After mortality rates and search rates our next most sensitive parameter is the maturation rate of the predator μ_P. The conversion efficiencies of consumers by predators e_{CP} and resources by predators e_{RP} rank 8 and 9, respectively. The intrinsic rate of increase of the resource r ranks number 10 and the least sensitive conversion efficiency, the conversion efficiency of resources into consumers, e_{RC}, ranks 11th. After a drop off in sensitivity, we find the carrying capacity of the resource K ranks 12th. The least sensitive parameters are the handling times. The handling time of consumers by predators h_{CP} is the most sensitive of the three, while the handling time of resources by predators h_{RP} is the least sensitive of all parameters.

CHAPTER 9

Conclusions

In this work we discussed the reintroduction of wolves into Yellowstone National Park and how their impact has helped to save the entire ecosystem. We introduced two mathematical models, a linear response model and an age (stage) structured model to represent an ecosystem involving wolves, elk, and berries. Within these models we included various parameter values to represent real life values that were taken in the field by biologists or estimated where noted. Our linear response model consists of 10 parameters and our stage structured model contains 15 parameters.

We then mathematically proved that each system has a solution and that it is unique. Using a mathematical process called sensitivity analysis we determined which parameter values affect the solution to each respective system the most. To solve our coupled sets of differential equations we used an algorithm in Matlab to numerically solve each system and graph the norm of each sensitivity over time. Our purpose for this was to determine which parameters biologist need to be more careful about measuring or which values may not need to be as precisely monitored. It is extremely difficult to obtain data on wolves in their natural habitat. Knowing which parameter values need precise monitoring could help save valuable time, but most importantly, keep track of this ecosystem that has helped to restore more life into the park. With all the controversy over wolf reintroduction and the progress it has made, we can now say how important wolves are to this ecosystem. Results from both of our models showed that any change in the wolf mortality rate made the largest change in the entire model. In our results section, we deduced that any small change in the mortality rate of the predator (for both models) can completely change the ecosystem and cause extinction of any of the three species involved. To further this explanation, the second most sensitive parameter in our stage structured model was the search rate of elk by wolves confirming that wolf predation on elk is truly needed to keep the ecosystem in equilibrium.

Our least sensitive parameters were the carrying capacity and the handling time of resources by predators. This makes sense due to the fact that wolves do not eat a lot of berries, which are not of great value nutritionally. The carrying capacity of berry producing shrubs is huge for a park

the size of Yellowstone, making us understand why these two parameters are the least sensitive and that changes in these parameters may not affect the system very much or at all.

For our work we have used two different models to mathematically describe an ecosystem in Yellowstone National Park and considered three: species, wolves, elk, and berry producing shrubs. Although our results give valuable insight to biologists on how each parameter value affects the entire system, it would be extremely useful in future projects to include more species.

For future work, instead of determining how sensitive each parameter value is, it could be very beneficial to determine at what range of parameter values does the ecosystem maintain equilibrium. Thus we are looking for the range at which a parameter may vary before causing a species to go extinct.

APPENDIX A

Matlab Code

Here we offer the Matlab code for the Linear Response Model, [34].

```
function ode45_both
%--------------------------------------------------------------------------
% Solves the sensitivity equations for the linear

% response omnivory model.

%

% Input:     None

%

% Output:   Graphs of norms of sensitivities over time.

%--------------------------------------------------------------------------
close all
%--------------------------------------------------------------------------
%  Define "Input" Parameters

%--------------------------------------------------------------------------
tn =500;   %tn=1500 is used for one graph, we simply we run the system twice          % e

y0 = [1; 1; 1; 0; 0; 0];   % initial values

w_P = 1;                    % weight on the predator sensitivity for the norm

w_C =1;                     % weight on the consumer sensitivity for the norm

w_R = 1;                    % weight on the resource sensitivity for the norm

norm_s = zeros(500,10);    % initialize a matrix to hold the norms of

                           % sensivities (columns) at each time step

                           % (rows).

parameter = 1;             % = 1, then use parameter values from literature

                           % otherwise use my favorite parameter values
```

```
%---Parameters to be passed to rhs_both


if parameter == 1

    eRP = 0.1;

    eCP = 0.8;

    eRC = 0.8;

    aRP = 1.68;

    aCP = .01525;

    aRC = 1.68;

    mP = 0.00062;

    mC = 0.00122;

    r = 0.3;

    K = 4;

else

    eRP = 0.1;

    eCP = 0.8;

    eRC = 0.8;

    aRP = 1.68;

    aCP = .01525;

    aRC = 1.68;

    mP = 0.00062;

    mC = 0.00122;

    r = 0.3;

    K = 4;

end


%--------------------------------------------------------------------------

% Solve the state and sensitivity systems simultaniously

% y = column vector (length 6) of states and sensitivities
```

```
% y(1) = predator density, y(2) = consumer density,
% y(3) = resource density, y(4) = predator sensitivity,
% y(5) = consumer sensitivity, y(6) = resource sensitivity
%-----------------------------------------------------------------------

%For the RHS

% eRP
p = 1;
[t_1,y] = ode45('rhs_both',tn,y0,[],p,eRP,eCP,eRC,aRP,aCP,aRC,mP,mC,r,K);
L_1 = length(t_1);
norm_s(1:L_1,p) = sqrt(w_P.*(y(:,4)).^2 + w_C.*(y(:,5)).^2 + w_R.*(y(:,6)).^2);


% eCP
p = 2;
[t_2,y] = ode45('rhs_both',tn,y0,[],p,eRP,eCP,eRC,aRP,aCP,aRC,mP,mC,r,K);
L_2 = length(t_2);
norm_s(1:L_2,p) = sqrt(w_P.*(y(:,4)).^2 + w_C.*(y(:,5)).^2 + w_R.*(y(:,6)).^2);


% eRC
p = 3;
[t_3,y] = ode45('rhs_both',tn,y0,[],p,eRP,eCP,eRC,aRP,aCP,aRC,mP,mC,r,K);
L_3 = length(t_3);
norm_s(1:L_3,p) = sqrt(w_P.*(y(:,4)).^2 + w_C.*(y(:,5)).^2 + w_R.*(y(:,6)).^2);


% aRP
p = 4;
[t_4,y] = ode45('rhs_both',tn,y0,[],p,eRP,eCP,eRC,aRP,aCP,aRC,mP,mC,r,K);
L_4 = length(t_4);
```

```
norm_s(1:L_4,p) = sqrt(w_P.*(y(:,4)).^2 + w_C.*(y(:,5)).^2 + w_R.*(y(:,6)).^2);


% aCP

p = 5;

[t_5,y] = ode45('rhs_both',tn,y0,[],p,eRP,eCP,eRC,aRP,aCP,aRC,mP,mC,r,K);

L_5 = length(t_5);

norm_s(1:L_5,p) = sqrt(w_P.*(y(:,4)).^2 + w_C.*(y(:,5)).^2 + w_R.*(y(:,6)).^2);


% aRC

p = 6;

[t_6,y] = ode45('rhs_both',tn,y0,[],p,eRP,eCP,eRC,aRP,aCP,aRC,mP,mC,r,K);

L_6 = length(t_6);

norm_s(1:L_6,p) = sqrt(w_P.*(y(:,4)).^2 + w_C.*(y(:,5)).^2 + w_R.*(y(:,6)).^2);


% mP

p = 7;

[t_7,y] = ode45('rhs_both',tn,y0,[],p,eRP,eCP,eRC,aRP,aCP,aRC,mP,mC,r,K);

L_7 = length(t_7);

norm_s(1:L_7,p) = sqrt(w_P.*(y(:,4)).^2 + w_C.*(y(:,5)).^2 + w_R.*(y(:,6)).^2);


% mC

p = 8;

[t_8,y] = ode45('rhs_both',tn,y0,[],p,eRP,eCP,eRC,aRP,aCP,aRC,mP,mC,r,K);

L_8 = length(t_8);

norm_s(1:L_8,p) = sqrt(w_P.*(y(:,4)).^2 + w_C.*(y(:,5)).^2 + w_R.*(y(:,6)).^2);


% r

p = 9;

[t_9,y] = ode45('rhs_both',tn,y0,[],p,eRP,eCP,eRC,aRP,aCP,aRC,mP,mC,r,K);
```

```matlab
L_9 = length(t_9);

norm_s(1:L_9,p) = sqrt(w_P.*(y(:,4)).^2 + w_C.*(y(:,5)).^2 + w_R.*(y(:,6)).^2);


% K

p = 10;

[t_10,y] = ode45('rhs_both',tn,y0,[],p,eRP,eCP,eRC,aRP,aCP,aRC,mP,mC,r,K);

L_10 = length(t_10);

norm_s(1:L_10,p) = sqrt(w_P.*(y(:,4)).^2 + w_C.*(y(:,5)).^2 + w_R.*(y(:,6)).^2);


x = y(:,1:3);  % State variables


%---Plot the states versus time

figure(5)

plot(t_10,x)

grid;

ylabel('Species Density');

xlabel('Time');

legend('Predator','Consumer','Resource')




%---Plot the norms versus time

figure(1)

plot(t_1,norm_s(1:L_1,1),'b') %eRP

hold on

plot(t_2,norm_s(1:L_2,2),'g') %eCP

hold on

plot(t_3,norm_s(1:L_3,3),'r') %eRC

hold on
```

```
plot(t_9,norm_s(1:L_9,9),'m') %r

hold on

plot(t_10,norm_s(1:L_10,10),'k') % K

grid;

ylabel('Norm of Sensitivities');

xlabel('Time');

legend('Efficiency_{RC}','Efficiency_{CP}','Efficiency_{RP}','r','K')


figure(2)

plot(t_4,norm_s(1:L_4,4),'c') %aRP

hold on

plot(t_5,norm_s(1:L_5,5),'b') %aCP

hold on

plot(t_6,norm_s(1:L_6,6),'g') %aRC

hold on

plot(t_7,norm_s(1:L_7,7),'r') %mP

hold on

plot(t_8,norm_s(1:L_8,8),'k') %mC

grid;

ylabel('Norm of Sensitivities');

xlabel('Time');

legend('Consumption_{RP}','Consumption_{CP}','Consumption_{RC}','Mortality_P','Mortality_C')


h = 1;

plot(1:10);

set(h,'Units','Inches');

pos = get(h,'Position');

set(h,'PaperPositionMode','Auto','PaperUnits','Inches','PaperSize',[pos(3), pos(4)])

print(h,'filename','-dpdf','-r0')
```

```
function dydt = rhs_both_agea(~,y,~,p,eRP,eCP,eRC,aRP,aCP,aRC,hRP,hCP,hRC,mPA,mC,nP,r,K,mPJ)

%---------------------------------------------------------------------------
% Simultaniously computes the right hand sides of the state and sensitivity
% equations for the age structure omnivory model.
%
% Input:    t = time. Not used, but needed by ode45
%           flag = (not used) placeholder for compatibility with ode45
%           y = column vector (length 6) of states and sensitivities
%               y(1) = adult predator density,
%               y(2) = juvenile predator density
%               y(3) = consumer density,
%               y(4) = resource density,
%               y(5) = adult predator sensitivity,
%               y(6) = juvenile predator sensitivity
%               y(7) = consumer sensitivity
%               y(8) = resource sensitivity
%           p = integer that tells which parameter sensitivity to compute
%           eRP, eCP, ... , r, K are model parameters
%
% Output:   dydt = column vector (length 8) of dy/dt values
%---------------------------------------------------------------------------


%---the column vector of four zeros on top and the partials of f with
%   respect to the model parameters.
if p == 1 %eRP
    partial = [0;
               0;
               0;
               0;
```

```
                0;

                (aRP*y(4)*y(1))/(1+aRP*hRP*y(4)+aCP*hCP*y(3));

                0;

                0];
elseif p == 2 %eCP
    partial = [0;

                0;

                0;

                0;

                0;

                (aCP*y(3)*y(1))/(1+aRP*hRP*y(4)+aCP*hCP*y(3));

                0;

                0];
elseif p == 3 %eRC
    partial = [0;

                0;

                0;

                0;

                0;

                0;

                (aRC*y(4)*y(3))/(1+aRC*hRC*y(4));

                0];
elseif p == 4 %aRP
    partial = [0;

                0;

                0;

                0;

                0;

                (eRP*y(4)*y(1)*(1+aCP*hCP*y(3))-eCP*aCP*hRP*y(4)*y(3)*y(1))/((1+aRP*hRP*y(4)+aC
```

```
                        (aCP*hRP*y(4)*y(3)*y(1))/((1+aRP*hRP*y(4)+aCP*hCP*y(3))^2);

                        -(y(4)*y(2))/((1+aRP*hRP*y(4))^2)-(y(4)*y(1)*(1+aCP*hCP*y(3)))/((1+aRP*hRP*y(4)
elseif p == 5 %aCP
    partial = [0;

                0;

                0;

                0;

                0;

                (eCP*y(3)*y(1)*(1+aRP*hRP*y(4))-eRP*aRP*hCP*y(4)*y(3)*y(1))/((1+aRP*hRP*y(4)+aC

                -(y(3)*y(1)*(1+aRP*hRP*y(4)))/((1+aRP*hRP*y(4)+aCP*hCP*y(3))^2);

                (aRP*hCP*y(4)*y(3)*y(1))/((1+aRP*hRP*y(4)+aCP*hCP*y(3))^2)];
elseif p == 6 %aRC
    partial = [0;

                0;

                0;

                0;

                0;

                0;

                (eRC*y(4)*y(3))/((1+aRC*hRC*y(4))^2);

                -(y(4)*y(3))/((1+aRC*hRC*y(4))^2)];
elseif p == 7 %hRP
    partial = [0;

                0;

                0;

                0;

                0;

                -(aRP*y(4)*y(1)*(eRP*aRP*y(4)+eCP*aCP*y(3)))/((1+aRP*hRP*y(4)+aCP*hCP*y(3))^2)

                (aRP*aCP*y(4)*y(3)*y(1))/((1+aRP*hRP*y(4)+aCP*hCP*y(3))^2);

                (((aRP)^2)*((y(4))^2)*y(2))/((1+aRP*hRP*y(4))^2)+(((aRP)^2)*((y(4))^2)*y(1))/(
```

```
elseif p == 8 %hCP
    partial = [0;
                0;
                0;
                0;
                0;
                -(aCP*y(3)*y(1)*(eRP*aRP*y(4)+eCP*aCP*y(3)))/((1+aRP*hRP*y(4)+aCP*hCP*y(3))^2)
                (((aCP)^2)*((y(3))^2)*y(1))/((1+aRP*hRP*y(4)+aCP*hCP*y(3))^2);
                (aRP*aCP*y(4)*y(3)*y(1))/((1+aRP*hRP*y(4)+aCP*hCP*y(3))^2)];
elseif p == 9 %hRC
    partial = [0;
                0;
                0;
                0;
                0;
                0;
                -(eRC*((aRC)^2)*((y(4))^2)*y(3))/((1+aRC*hRC*y(4))^2);
                (((aRC)^2)*((y(4))^2)*y(3))/((1+aRC*hRC*y(4))^2)];


elseif p == 10 %mPA
    partial = [0;
                0;
                0;
                0;
                -y(1);
                0;
                0;
                0];
elseif p == 11 %mC
```

```
    partial = [0;

              0;

              0;

              0;

              0;

              0;

              -y(3);

              0];
elseif p == 12 %nP

    partial = [0;

              0;

              0;

              0;

              y(2);

              -y(2);

              0;

              0];
elseif p == 13 %r

    partial = [0;

              0;

              0;

              0;

              0;

              0;

              0;

              y(4)*(1-(y(4)/K))];
elseif p == 14 %K

    partial = [0;

              0;
```

```matlab
                        0;
                        0;
                        0;
                        0;
                        0;
                        ((r*(y(4))^2)/(K)^2)];
    elseif p == 15 %mPJ
        partial = [0;
                        0;
                        0;
                        0;
                        0;
                        -y(2);
                        0;
                        0];

end


dydt_temp = [
nP*y(2)-mPA*y(1);


((eRP*aRP*y(4)+eCP*aCP*y(3))/(1+aRP*hRP*y(4)+aCP*hCP*y(3)))*y(1)-(nP+mPJ)*y(2);


y(3)*((eRC*aRC*y(4))/(1+aRC*hRC*y(4))-(aCP*y(1))/(1+aRP*hRP*y(4)+aCP*hCP*y(3))-mC);


y(4)*(r*(1-(y(4)/K))-(aRC*y(3))/(1+aRC*hRC*y(4))-(aRP*y(2))/(1+aRP*hRP*y(4))-(aRP*y(1))/(1+aRP=


-mP*y(5)+nP*y(6);
```

99

```
((eRP*aRP*y(4)+eCP*aCP*y(3))/(1+aRP*hRP*y(4)+aCP*hCP*y(3)))*y(5)-(nP+mP)*y(6)+((eCP*aCP*y(1)*(

-((aCP*y(3))/(1+aRP*hRP*y(4)+aCP*hCP*y(3)))*y(5)+((eRC*aRC*y(4))/(1+aRC*hRC*y(4))-(aCP*y(1)*(1-

-((aRP*y(4))/(1+aRP*hRP*y(4)+aCP*hCP*y(3)))*y(5)-((aRP*y(4))/(1+aRP*hRP*y(4)))*y(6)-((aRC*y(4))

];


dydt = dydt_temp + partial;
```

<div align="center">**Derek Fields**</div>

Born   January 15, 1987 in Norton, VA

Education

- Master of Arts. Marshall University. Thesis Advisor: Bonita Lawrence.

- Bachelor of Science. University of Virginia's College at Wise, December 2009, *Education and Psychology Minor.*

Publications

1. *James Vance and Derek Fields, Sensitivity Analysis of a Three-Species Linear Response Omnivory Model, International Journal of Arts and Sciences, Volume 3, Issue 9, 2010, pp. 102-107.*

2. *Sensitivity Analysis of Wolf Restoration in Yellowstone Nation Park using Omnivory Models.* Master's thesis, Marshall University, May 2017.

Invited Workshop Presentations

1. *Sensitivity Analysis of a Three-Species Linear Response Omnivory Model, 1069th American Mathematical Society Meeting, University of Iowa, Iowa City, Iowa, March 2011* Coauthor

2. *Sensitivity Analysis of a Three-Species Linear Response Omnivory Model, International Journal of Arts and Sciences International Conference for Academic Disciplines, Las Vegas, Nevada, March 2010* Coauthor

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APPENDIX B

LETTER FROM INSTITUTIONAL RESEARCH BOARD

MARSHALL UNIVERSITY®
www.marshall.edu

Office of Research Integrity

May 4, 2017

Derek Fields
249 Lyons Station Road
New Haven, KY 40051

Dear Mr. Fields:

This letter is in response to the submitted thesis abstract entitled *"Sensitivity Analysis of Wolf Restoration in Yellowstone National Park using Omnivory Models."* After assessing the abstract, it has been deemed not to be human subject research and therefore exempt from oversight of the Marshall University Institutional Review Board (IRB). The Code of Federal Regulations (45CFR46) has set forth the criteria utilized in making this determination. Since the information in this study does not involve human subjects as defined in the above referenced instruction, it is not considered human subject research. If there are any changes to the abstract you provided then you would need to resubmit that information to the Office of Research Integrity for review and a determination.

I appreciate your willingness to submit the abstract for determination. Please feel free to contact the Office of Research Integrity if you have any questions regarding future protocols that may require IRB review.

Sincerely,

Bruce F. Day, ThD, CIP
Director

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