

# Permanent Coexistence for Omnivory Models

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(ABSTRACT)

One of the basic questions of concern in mathematical biology is the long-term survival of each species in a set of populations. This question is particularly puzzling for a natural system with omnivory due to the fact that simple mathematical models of omnivory are prone to species extinction. Omnivory is defined as the consumption of resources from more than one trophic level. In this work, we investigate three omnivory models of increasing complexity. We use the notion of permanent coexistence, or permanence, to study the long-term survival of three interacting species governed by a mixture of competition and predation. We show the permanence of our models under certain parameter restrictions and include the biological interpretations of these parameter restrictions. Sensitivity analysis is used to obtain important information about meaningful parameter data collection. Examples are also given that demonstrate the ubiquity of omnivory in natural systems.

# Dedication

To my beautiful wife Aranda, with all my love

# Acknowledgments

I would like to thank my Lord and Saviour Jesus Christ for this wonderful life. Many thanks to my wife for all of her encouragement and patience. Without you it would not have been possible! Thanks to Dr. Russell for believing in me and this project. Special thanks to Dr. Klaus and Dr. Sun for all of the office visits and patient help. Thanks to the rest of my committee for all the advice over the years. Thanks to my family for all of the support and encouragement.

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# Chapter 1

## Introduction

The question of long-term survival of species in an ecological community should be of utmost importance to humans. Human survival depends upon biodiversity and the understanding of natural systems. However, most natural systems contain very complex multi-species food webs and when looked at as a unit are unmanageable for detailed analysis. In an attempt to gain some insight into the world around us, we must examine a small number of species and their ecological interactions in a community. This in turn can shed light on interactions in more complex systems. Of paramount importance for conservation, biological control, and nuisance control is the long-term survival or extinction of the community as a whole.

The community interactions of predation and competition have a rich history of research and analysis. However, the unique combination of predation and competition known as omnivory has a relatively recent history of mathematical and biological study. Holt et al. [40] when discussing intraguild predation (IGP), a subset of omnivory, state that “there is growing evidence for the importance of IGP in many natural communities, yet little formal ecological theory addresses this particular blend of interactions”. The mathematical theory is also lacking, especially for models with stage structure.

In order to study the long-term survival of species, we use a growing body of mathematical theory known as permanence theory. We model omnivorous systems with ordinary differential equations of species densities. Then, permanence theory is concerned only with the dynamics of the model near the boundary where densities are zeros and hence, species go extinct. Our analysis is based upon the notion of an Average Lyapunov function and we apply this theory to one linear and one non-linear model. Then, we extend the concepts to a model with stage structure. Our differential equation models depend upon model parameters that are estimated from ecological systems. Our results based on permanence theory place restrictions on the parameters.

As estimates from natural systems, the model parameters are subject to natural intrinsic variability. Since our models are deterministic, changes in the inputs cause change in the output. We will use sensitivity analysis to determine how small changes in inputs, corresponding to the natural variability, affect the population densities. This analysis in turn

will allow us to determine which parameters must be estimated with as much accuracy as possible to ensure reasonable population density estimates. Biological interpretations of the parameter restrictions are also included, so that general criteria for permanent coexistence can be achieved.

We will discuss the above topics in greater detail and explanation in the rest of this introduction and in Chapter 2.

## 1.1 Outline of Thesis

In the remainder of this introduction, we present a brief discussion on omnivory, coexistence of species, and sensitivity analysis. A cross-classification of omnivory as well as intraguild predation will provide insight into the complex array of community interactions under investigation. In the discussion of coexistence of species in deterministic models, we give an intuitive idea of what it means for a system to be permanent. This intuitive notion will set the stage for our thorough mathematical formulation. In the discussion on sensitivity analysis, we determine why we will use one of the two most often used sensitivity methods.

In Chapter 2, we review some basic ecological models and variations of these models. This will lead to a general discussion of omnivory models and their complexity. Since we need our mathematical models to have unique solutions, we review existence and uniqueness theorems for ordinary differential equations. We also discuss the general theory of permanence for differential equation models with specific emphasis on Kolmogorov models. Finally, we provide theorems to ensure differentiability with respect to parameters. From a biological perspective, this theory will allow us to determine for which parameters to obtain precise field estimates.

Chapter 3 will focus on nontrivial examples of omnivory in the wild. These examples from fish, birds, and mammals will provide the motivation for our study and provide insight into the complex array of ecological interactions that we are attempting to model. Parameter values for our differential equation models are also provided. This will allow for numerical studies as well as provide a basis for our sensitivity analysis.

Chapter 4 provides mathematical analysis for a linear response omnivory model. Existence and uniqueness of a solution to this system is proved. We then prove some results based on permanence theory that provide a straight forward check to ensure coexistence (in the mathematical sense) of three species involved in intraguild predation.

Chapter 5 provides mathematical analysis for a more complex three species omnivory model. We extend the ideas of chapter 4 to include non-linear response models for which we prove existence and uniqueness of a solution. Also, we provide a check for coexistence based on results proved from permanence theory.

Chapter 6 is a combination of mathematical analysis and deduction on a non-linear omnivory model with stage structure. We prove existence and uniqueness of a solution to the system. We use some mathematical insight as well as numerical investigations to determine under what parameter combinations coexistence of species is expected.

In Chapter 7, we apply our theorems on continuous dependence and differentiability with respect to parameters to each of our models. The resulting sensitivity equations are solved for the sensitivities by an adaptive step numerical integration method. A weighted measure is also provided to allow for a comparison of sensitivities.

In Chapter 8, we present our final results. These results include the conditions under which our three omnivory models are permanent as well as prioritized list of sensitivities. Also, we provide the biological meaning for the sensitivities and a summary of the biological meanings for the permanence conditions.

In the conclusion, we give a summary of the mathematical conditions that are derived for permanence and the biological restrictions that these conditions imply. A look at future directions for research is also included.

## 1.2 Omnivory

Ecologists usually classify species interactions according to their effects on population growth rates. Competition (-,-) is defined as a negative effect on both species. Mutualism (+,+) is a positive effect on both species. Predation (+,-) is one species gaining, while the other species loses. However, we cannot always classify species interactions in this simple way. The natural history of many species dictates that they are both “predator” and “prey”. Other species can be classified as “predators” and “competitors”. Competition and predation will be discussed in further detail in Sections 2.1.1 and 2.1.2, respectively.

**Omnivory** is defined as the act of feeding on resources at different trophic levels [76]. A **trophic level** is a step in a nutritive series or food chain of an ecosystem. Examples of trophic levels are producers, herbivores, carnivores, etc. Ecological interactions involving omnivory can become very complicated (see [2],[78],[84]). A simple example of omnivory is intraguild predation. **Intraguild predation** or IGP is the ecological interaction in which two competing species also interact as predator and prey [28]. This constellation of three species (see figure 2.2a): a predator (top), a consumer (middle), and a resource (bottom) is the simplest form of omnivory. To better understand intraguild predation we give the following definitions. A **guild** is a group of species that exploit the same class of environmental resources in a similar way [83]. **Intraguild** means within the same guild. So, IGP involves species that compete for resources in a similar way, but also engage in direct predator-prey interactions [77], [78].

Omnivory differs from classical competition because of the immediate gain of the top predator from feeding on the consumer. It differs from classical predation since the act reduces potential competition. Clearly, the interplay of competition and predation can affect population dynamics in a complex and interesting way. Communities where competing species in one trophic level are preyed upon by a species or species at a higher trophic level have been well studied (for example see [39], [62]). However, omnivory is a distinct combination of competition and predation and the search for robust mechanisms that can explain persistence of tightly linked omnivory systems remains an important challenge [58],[34].

Polis et al. [78] cross-classify intraguild predation in two ways. The first classification is symmetry (symmetric vs. asymmetric). Symmetric IGP occurs when there is mutual predation between two species. Asymmetric IGP occurs when one species is the predator of another species but not vice versa. The second classification is stage structure (important vs. relatively unimportant). Stage structure is important when IGP is influenced by changes in size or vulnerability of an individual organism as it matures from embryo to adult. For example, a species may be subject to a class of predators as a juvenile and subject to a completely different class of predators as an adult. In IGP with relatively unimportant stage structure, the stage of the organism only weakly influences the dynamics of IGP. We will use the same classifications when referring to IGP as well as omnivory.

### 1.3 Coexistence of Species in Deterministic Models

One of the most important questions in mathematical biology concerns the long-term survival or coexistence of all the species in a multi-species community governed by deterministic models. We consider dynamical systems in the form of differential equations that are approximations to ecological communities of interacting populations. Two of the most widely used conditions to define the notion of long-term survival are asymptotic (local) stability and global asymptotic stability. Another term in the ecological literature for asymptotic stability is neighborhood stability (see [60] and references therein). The idea behind neighborhood stability is to find equilibrium points and investigate the properties of orbits in a small region of the phase space around the equilibrium in which a linear approximation is valid. This requires that the Jacobian evaluated at equilibrium has all eigenvalues with negative real parts [50]. For global asymptotic stability, the idea is to determine conditions guaranteeing that all solutions to a system approach an equilibrium.

Although asymptotic stability is mathematically tractable, it is not a satisfactory condition for the long-term survival of interacting species. For many natural systems we have no reason to believe that the system starts near equilibrium. Also, the dynamics near an equilibrium do not determine the coexistence of species, but rather the dynamics of the system when one or more of the species is close to extinction. The concept of global stability is insufficient in many cases because species may coexist indefinitely without approaching equilibrium. Many systems have periodic or even chaotic attractors. Jansen et al. [49] take a quote from Lewontin [64] that we feel is worth noting: “The presence or absence of species is sometimes the point of interest regardless of some variation in their numbers”.

We therefore, want to allow any asymptotic behavior of orbits as long as they do not remain too close to the boundary. We will consider the notion of permanent coexistence or permanence in order to achieve this more satisfactory concept for long-term species survival. We will use the terms permanent coexistence and permanence interchangeably throughout this work. We feel that the term “permanent coexistence” better encompasses the ecological importance of species coexistence as given by Hutson et al. [46]. However, the term “permanent” or “permanence” has been more widely used throughout the literature (see the review by [45]).

The idea is for the boundary (where one or more species goes extinct) to be a repeller in some sense. To visualize this idea, consider a “skin” of thickness  $\delta > 0$  around the boundary such that orbits not initially in the boundary come to lie at a distance  $d > \delta$  from the boundary [46]. For biological realism, we will also require that no orbits should tend to infinity [36]. This is a global criterion because it applies to orbits starting from every point not on the boundary. We do not claim that permanent coexistence is the “best” concept in some absolute sense or that mathematically permanent communities would exist forever in the real world [60], [45]. However, we feel that (to date) permanence theory provides the most ecologically sound and mathematically tractable criterion for long-term species coexistence.

## 1.4 Sensitivity Analysis

Models are developed to approximate natural systems. This fact imposes a limitation on the confidence we place on the model outcome or model response. Since we are approximating natural systems with deterministic models there is a certain amount of natural intrinsic variability that our model inputs should be subject to. Also, model parameters are limited by measurement error. As stated by Andrea Saltelli [86], “Good modelling practice requires that the modeller provide an evaluation of the confidence in the model”. We will use sensitivity analysis to achieve this goal.

**Sensitivity analysis** involves the use of analytical and/or computational tools to evaluate how changes in inputs affect model response variables. The inputs may be initial conditions or model parameters. The model response variables may be population densities, state variables, population growth rates, etc. There are many variations and applications of sensitivity analysis (see [3], [85], [93] for examples).

One of the most important questions from our perspective is, how do small changes in model parameter values affect the population densities. This will help us determine which parameter estimates are sufficiently precise for our models to give reliable predictions based upon the dynamics of the models. Also, we will be able to prioritize the parameters to help biologists determine which parameter values should be most closely estimated from empirical data. This in turn should dictate an increase in precision and accuracy with which biologists collect data for specific parameter estimates.

There are basically two approaches to sensitivity analysis. The first is known as “manual perturbation” [3] or “conventional sensitivity” [9] and according to Mills et al. (Chapter 16 of [3]) is probably the most common approach in the ecological literature. This is a computational method in which one parameter at a time is altered by an amount deemed relevant to the system. Typically, the population growth rate is computed for each proportional change and is used to measure how sensitive the model is to the given parameter. This type of analysis tells which parameters have the most impact on population growth and which parameters to measure with extreme accuracy in the field in order to avoid incorrect population projections. However, there are issues with this method. First, there is no standardized metric or measure with which to compare across species or studies. Second, since in our

case we would like to determine the parameter values for which coexistence is ensured, the whole range of variation on the determining set of parameters must be investigated. Manual perturbation in this case is very time consuming and “as a rule, the use of this approach appears to be inexpedient or impossible due to the huge amounts of required computation” [85].

Instead, we use an analytical approach that depends on measures of how infinitesimal changes in parameter values will affect the population densities. As the value of a parameter changes, the solution to the system of ordinary differential equations changes. So our goal is to mathematically describe how small changes in a parameter affect the solution.

# Chapter 2

## Basic Concepts

In order to acquaint the reader with the basic concepts and terminology, we discuss several ecological and mathematical topics. We will give a general discussion of competition, predation, and omnivory. Some general ecological interactions and models will also be discussed. The theorems we will use to show the existence and uniqueness of solutions to our systems of differential equations will be presented as well as a general framework for permanence theory. Lastly, we will give the general criteria for the use of sensitivity analysis as a mathematical tool to provide insight on model sensitivities and parameters.

### 2.1 Modeling Omnivory

In order to model omnivory a basic understanding of competition and predation is necessary. Also, an understanding of the array of community interactions that influence individual population dynamics is imperative.

#### 2.1.1 Competition

The general term “competition” encompasses a variety of competitive interactions. **Exploitative competition** occurs when populations depress one another through use of a shared resource [28]. Examples include bears and birds competing for native fruits and nuts as well as fish in your local pond competing for algae. **Interference competition** occurs when an individual or population behaves in a way (typically aggressively) that reduces the exploitative efficiency of another individual or population [28]. Feral burros and big horn sheep aggressively competing for water holes in the deserts of the western United States is an example of interference competition.

We need to consider the forms of competition that are typically included in population models. We will use  $N$  to denote the size of a population, or group of animals of the same species that live together and reproduce. Then,  $dN/dt$  is the population growth rate. We define the **intrinsic rate of increase** of the population, denoted  $r$ , as the birth rate minus the death rate of the population. Since resources for growth and reproduction of populations

are limited, we can define  $K$ , the **carrying capacity**, as the maximum population size that the environment can support.  $K$  encompasses the limitations on space, food, shelter, etc. This form of competition for resources is known as **intraspecific competition** which is defined as competition that occurs among members of the same species.

The **logistic growth model**,

$$\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right), \quad (2.1)$$

is a model of intraspecific competition because the population growth rate decreases as the population becomes more crowded. In this case, the **density dependence** is linear.

Another form of competition is **interspecific competition** defined as competition between individuals of two or more different species. In the 1920s and 1930s, Alfred J. Lotka (1880-1949) and Vito Volterra (1860-1940) described a simple mathematical model of interspecific competition [28]. The two competing species are denoted as  $N_1$  and  $N_2$ . Each population has its respective intrinsic rates of increase and carrying capacities. Each population's growth is reduced by intraspecific competition as well as competition from the opposing species. The simplest way to express the interspecific competition is in a linear fashion.

The **Lotka-Volterra competition model** is given by

$$\begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \left( 1 - \frac{N_1}{K_1} - \frac{\alpha_{12} N_2}{K_1} \right) \\ \frac{dN_2}{dt} &= r_2 N_2 \left( 1 - \frac{N_2}{K_2} - \frac{\alpha_{21} N_1}{K_2} \right), \end{aligned} \quad (2.2)$$

where  $\alpha_{12}$  is a measure of the effect of species 2 on the growth of species 1. Similarly,  $\alpha_{21}$  is a measure of the effect of species 1 on the growth of species 2. Competition models have been studied widely in ecology [28].

## 2.1.2 Predation

Competitive interactions in nature are often indirect and subtle. In contrast, predation is a direct and conspicuous ecological interaction [28]. We will use  $P$  to denote the predator population and  $R$  to denote the prey population. For the simplest models, we assume that prey populations grow exponentially at rate  $r$  in the absence of the predator population. This increase in the prey population is diminished by losses due to the presence of the predator population. For the Lotka-Volterra predation model, losses to predation are proportional to the product of predator and prey numbers. We will denote this proportional constant called the **capture efficiency** as  $\alpha$ . The capture efficiency measures the effect of a predator on the per capita growth rate  $\left( \frac{1}{R} \frac{dR}{dt} \right)$  of a prey population.

The predator is assumed to only feed on one prey species and in the absence of prey the predator population decreases exponentially. We denote the death rate of predators by  $q$ . Only when the prey population is present can the predator population have positive growth.

We use  $\beta$  to denote the **conversion efficiency** or the ability of predators to convert each new prey into additional per capita growth rate ( $\frac{1}{P} \frac{dP}{dt}$ ) for the predator population.

**The Lotka-Volterra predation model,**

$$\begin{aligned} \frac{dP}{dt} &= (\beta R - q)P \\ \frac{dR}{dt} &= (r - \alpha P)R, \end{aligned} \quad (2.3)$$

was derived independently by Alfred J. Lotka and Vito Volterra [28].

The product  $\alpha R$  is called the **functional response** of the predator. Gotelli [28] gives the definition of the functional response as the rate of prey capture by a predator as a function of victim abundance as defined by Solomon [89]. In model (2.3), the functional response is linear. The product  $\beta R$  is called the **numerical response** and is defined as the per capita growth rate of the predator population as a function of the prey abundance [28]. Again, the numerical response is linear in the above model. We will discuss non-linear functional and numerical responses in Section 2.1.4.

### 2.1.3 Three Species Interactions

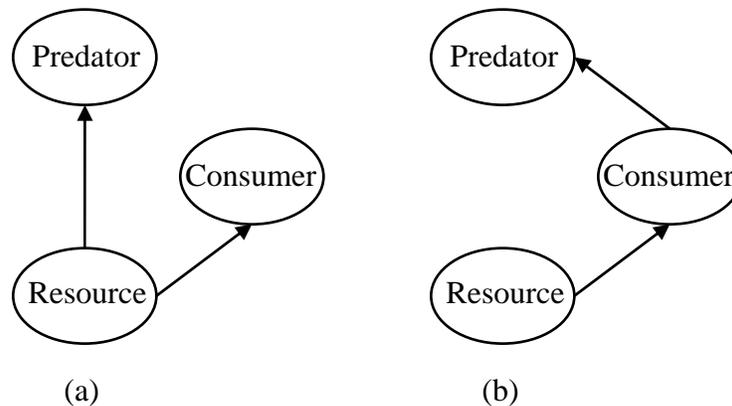


Figure 2.1: Two forms of ecological interactions discussed in this work. Arrows indicate that one species (base of arrow) is eaten by another species (point). (a) A purely competitive food web. The predator and consumer feed on the resource. (b) A linear food chain. The predator feeds on the consumer and the consumer feeds on the resource.

Three species can interact in a variety of ways. The ecological interaction in which two predators compete for a shared resource without any predation between the predators is called a **purely competitive food web** (see figure 2.1a). If we assume the resource grows logistically and the functional and numerical responses are linear, then we can model a purely

competitive food web as follows:

$$\begin{aligned}
 \frac{dP}{dt} &= P[e_{RP}\alpha_{RP}R - m_P] \\
 \frac{dC}{dt} &= C[e_{RC}\alpha_{RC}R - m_C] \\
 \frac{dR}{dt} &= R[r(1 - R/K) - \alpha_{RC}C - \alpha_{RP}P].
 \end{aligned}
 \tag{2.4}$$

The parameters  $e_{RP}$  and  $e_{RC}$  are the efficiency rates at which resources are converted to new offspring of the predator and consumer respectively.  $\alpha_{RP}$  and  $\alpha_{RC}$  are the capture rates of the resource by the predator and consumer respectively.  $m_P$  and  $m_C$  are the respective mortality rates of the predator and consumer species.

A **linear food chain** (see figure 2.1b and reference [31]) is a three species interaction in which there is no competition between species, but predation from a higher trophic level exists. Again, we assume that the resource grows logistically and the functional and numerical responses are linear.

$$\begin{aligned}
 \frac{dP}{dt} &= P[e_{CP}\alpha_{CP}C - m_P] \\
 \frac{dC}{dt} &= C[e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_C] \\
 \frac{dR}{dt} &= R[r(1 - R/K) - \alpha_{RC}C].
 \end{aligned}
 \tag{2.5}$$

The parameters  $e_{CP}$  and  $e_{RC}$  are the efficiency rates at which consumers and resources are converted to new offspring of the predator and consumer respectively.  $\alpha_{CP}$  and  $\alpha_{RC}$  are the capture rates of the consumer and resource by the predator and consumer respectively.  $m_P$  and  $m_C$  are the respective mortality rates of the predator and consumer species.

Omnivory as a combination of predation and competition may be very complex and intricate. **Asymmetrical intraguild predation** is the simplest form of omnivory (see 2.2a). This form of community interaction involves a predator feeding on a consumer (intermediate predator, [40]) and a basal resource. The consumer feeds solely on the basal resource. This is an asymmetric interaction since the consumer does not feed on the top predator. Holt et al. [40] developed a conceptual framework to analyze the population and community level implications of asymmetric IGP under Lotka-Volterra dynamics. The model,

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

is a standard Lotka-Volterra model for a food chain (2.5) with IGP added (see [40], [31]). The parameters  $e_{RP}$  and  $e_{RC}$  are the efficiency rates at which resources are converted to

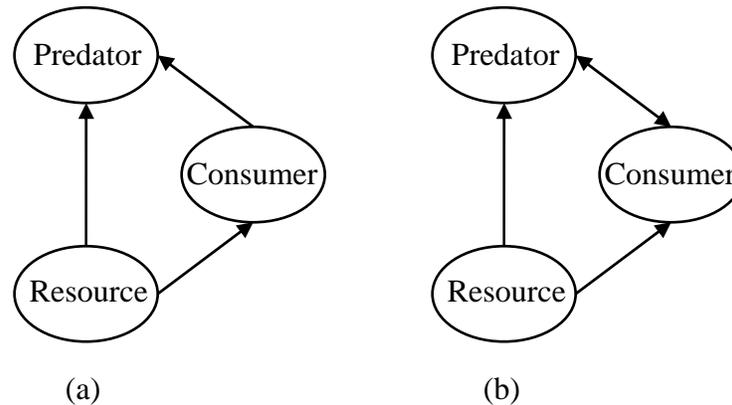


Figure 2.2: Two forms of ecological interactions discussed in this work. Arrows indicate that one species (base of arrow) is eaten by another species (point). (a) Asymmetrical intraguild predation. IGP in which the consumer feeds on the resource only, not on the predator. (b) Symmetrical intraguild predation. IGP in which the consumer feeds on the resource as well as on the predator.

new offspring of the predator and consumer respectively.  $e_{CP}$  is the efficiency rate at which consumers are converted to new offspring of the predator.  $\alpha_{RP}$  and  $\alpha_{RC}$  are the capture rates of the resource by the predator and consumer respectively.  $\alpha_{CP}$  is the capture rate of the consumer by the predator.  $m_P$  and  $m_C$  are the respective mortality rates of the predator and consumer species.

Holt et al. [40] suggested a general criterion for coexistence under model (2.6) as follows:

- 1) The consumer should be superior at exploitative competition for the shared resource.
- 2) The predator should gain significantly from its consumption of the consumer.
- 3) Along gradients in environmental productivity, coexistence is most likely at intermediate levels of productivity.

**Symmetrical intraguild predation** involves a predator feeding on a consumer and a basal resource. The consumer feeds not only on the resource but also on the predator (see 2.2b). Symmetry does not imply equal strength of interaction between the predator and consumer. This form of omnivory is “surprisingly common and often dynamically important” [78] (see also [79]).

Another variation of omnivory is **adaptive omnivory**. Up to this point, we have only discussed fixed omnivory. That is, the interactions were always in a fixed direction. Diehl et al. [58] explore how adaptive behavior by the predator affects coexistence. They assume the predator forages adaptively according to the diet rule, i.e. feeds on the less profitable of its two prey species (the consumer and resource) only if the more profitable one is sufficiently rare [58].

When the resource is more profitable for the predator and the consumer and resources become rare, then the interaction switches from omnivory (figure 2.2a) to a purely competi-

itive food web (figure 2.1a). When the consumer is more profitable for the predator and the resource and the consumer becomes rare, then the interaction switches from omnivory (figure 2.2a) to a linear food chain (figure 2.1b). They concluded that the positive effect of adaptive omnivory on coexistence of the three species is small [58].

**Important stage structure IGP models** represent ecological interactions in which adult and/or juvenile predators and consumers feed on the same resource, and also feed on each other. Obviously, there are many combinations of interactions under this categorization. Mylius et al. [71] looked at two forms of stage structures in IGP models. They incorporated size structure into the predator population by dividing the population into two classes: an initial class of small individuals that do not prey on the consumer population and a class of larger predatory individuals (see figure 2.3a).

They incorporated structure into the consumer population by means of the introduction of an invulnerable consumer life stage (see figure 2.3b). That is, only small consumer individuals were subject to predation. This, in essence, formed a size refuge for larger consumers. Looking at the attractors of the systems, they concluded that the addition of stage structure did not change the tendency of the predator to drive the consumer species extinct over a surprisingly large range of productivities [71].

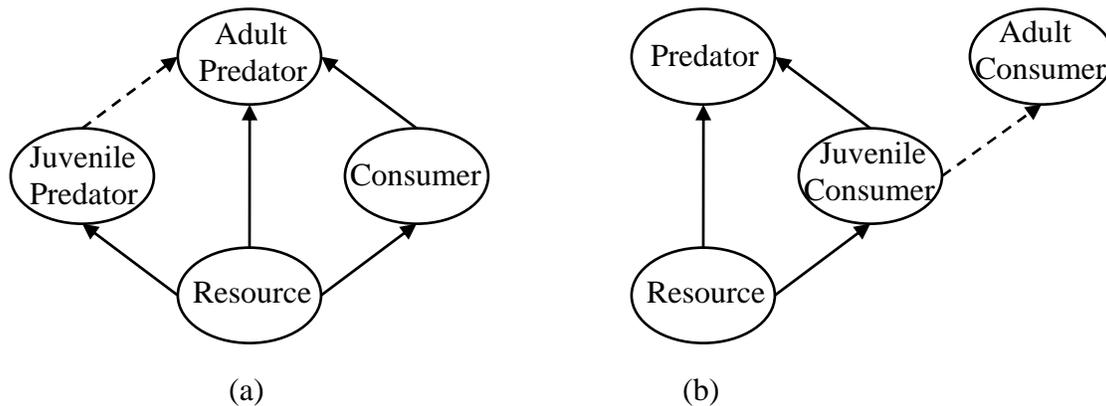


Figure 2.3: Two forms of stage structured ecological interactions discussed in this work. Solid arrows indicate that one species (base of arrow) is eaten by another species (point). Dashed arrows indicate growth transitions. (a) Stage structure in predator population. The juvenile predator stage feeds only on the resource. (b) Stage structure in consumer population. An adult consumer population that is invulnerable to predation.

#### 2.1.4 Non-linear Functional and Numerical Responses

Up to this point, we have only considered differential equation models that involve linear functional and numerical responses. The Lotka-Volterra models assume that individual

predators can always increase their consumption as the victim population increases. Linear functional responses are considered **Type I functional responses**. Type I functional responses are unrealistic for two reasons. First, the predators are limited by the **handling time** needed to catch and consume victims. Second, predators will eventually become satiated and stop feeding.

A **Type II functional response** assumes that predator consumption increases to a maximum and constant rate of victim consumption per predator. That is, the rate of consumption becomes saturated as victim densities increase. The following non-linear functional responses are known as **Holling Type II functional responses**. For a species, P, that feeds on only one other species, R, we use

$$f(R) = \frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R} \quad (2.7)$$

as our Holling Type II functional response.  $\lambda_{RP}$  is the attack rate of species P on species R.  $h_{RP}$  is the time spent by species P handling species R.

For a species, P, that feeds on two species, C and R, we use

$$f(C, R) = \frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \quad (2.8)$$

as the species R functional response and we use

$$f(C, R) = \frac{\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \quad (2.9)$$

as the species C functional response. The parameters  $h_{RP}$  and  $h_{CP}$  are the handling times corresponding to species R being eaten by species P and species C being eaten by species P, respectively. Species P feeds on species R with attack rate  $\lambda_{RP}$  and species P feeds on species C with attack rate  $\lambda_{CP}$ .

For our non-linear numerical responses involving species P and species R, we use

$$n(R) = e_{RP} \cdot f(R) \quad (2.10)$$

for our species P numerical response. For species P that feeds on species R and species C, we use

$$n(R, C) = \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \quad (2.11)$$

as our species P non-linear numerical response.  $e_{RP}$  is the conversion efficiency of species R into species P and  $e_{CP}$  is the conversion efficiency of species C into species P.

**Type III functional** responses are sometimes used in models where the feeding rate is accelerated at low victim density but decreases at high victim density as an asymptote is reached (see [28] and [69]). We will not consider models with Type III functional responses in this work.

In order to better determine the parameter space in which there is species coexistence, several authors have looked at a variety of modifications to models as well as alternate models.

Revilla [82] looked at the effects of IGP on resource competition by applying nullcline analysis to Lotka-Volterra models as well as saturating functional response models of three interacting species. Křivan [57] explored the effects of adaptive IGP on species coexistence using Lotka-Volterra models and stability analysis. In a 2003 paper, Diehl [11] explored the role of food quality on the evolution and maintenance of omnivory. Diehl et al. [12] studied the effects of enrichment (increasing growth rate or carrying capacity of basal resource) on omnivory models with three species. A numerical bifurcation study of a three species food web with omnivory under chemostat conditions was conducted by Kooi et al. [56] in 2002.

## 2.2 Existence and Uniqueness of Solutions

Consider a first order system of differential equations of the form

$$\begin{aligned} \frac{dx_1}{dt} &= f_1(t, x_1, \dots, x_n) \\ &\vdots \\ \frac{dx_n}{dt} &= f_n(t, x_1, \dots, x_n). \end{aligned} \tag{2.12}$$

The functions  $f_1(t, x_1, \dots, x_n), \dots, f_n(t, x_1, \dots, x_n)$  are defined on a  $(n + 1)$  – dimensional set  $D$  of the  $(t, x_1, \dots, x_n)$  – space,  $\mathbb{R}^{n+1}$ .

In order to show global existence and uniqueness of solutions we need some definitions. The following definitions were taken from Walter’s book on Ordinary Differential Equations [95].

**Definition 1** A vector function  $(x_1(t), \dots, x_n(t))$  is a **solution** of (2.12) in the interval  $J$  if the functions  $x_i(t)$ ,  $i = 1, \dots, n$  are differentiable in  $J$  and if (2.12) is satisfied identically when they are substituted into the equation.

We require  $(t, x_1(t), \dots, x_n(t)) \in D$  for  $t \in J$ .

We denote  $n$  – dimensional column vectors with boldface letters as follows:

$$\mathbf{c} = \begin{pmatrix} c_1 \\ \vdots \\ c_n \end{pmatrix}, \quad \mathbf{x}(t) = \begin{pmatrix} x_1(t) \\ \vdots \\ x_n(t) \end{pmatrix}, \quad \mathbf{f}(t, \mathbf{x}) = \begin{pmatrix} f_1(t, \mathbf{x}) \\ \vdots \\ f_n(t, \mathbf{x}) \end{pmatrix}.$$

Derivatives of a vector function  $\mathbf{x}$  are also defined component-wise:

$$\dot{\mathbf{x}}(t) = \begin{pmatrix} \frac{dx_1}{dt}(t) \\ \vdots \\ \frac{dx_n}{dt}(t) \end{pmatrix}$$

Using this notation, when we say “ $\mathbf{x}$  is continuous” or “ $\mathbf{x}$  is differentiable” we mean that each component  $x_i$  ( $i = 1, \dots, n$ ) is continuous or differentiable, respectively. In vector notation, system (2.12) is

$$\dot{\mathbf{x}} = \mathbf{f}(t, \mathbf{x}) \quad (2.13)$$

**Definition 2** *The initial value problem for (2.12) includes the initial conditions*

$$x_i(t_0) = c_i, \quad (i = 1, \dots, n) \quad \text{or} \quad \mathbf{x}(t_0) = \mathbf{c} \quad (\text{in vector form}). \quad (2.14)$$

*That is, a solution for (2.12) passes through a given point  $(t_0, \mathbf{c}) \in D$ .*

We will use the notation  $\|\mathbf{x}\|$  for the norm of a vector  $\mathbf{x} \in \mathbb{R}^n$ , regardless of which norm is used, since all norms in  $\mathbb{R}^n$  are equivalent [95]. We use the notation  $(x_1, x_2, \dots, x_n)^T$  for the transpose of a row vector into a column vector and vice versa.

**Definition 3** *A vector function  $\mathbf{f}(t, \mathbf{x})$  satisfies a Lipschitz condition with respect to  $\mathbf{x}$  in  $D$  (with Lipschitz constant  $L$ ) if*

$$\|\mathbf{f}(t, \mathbf{x}) - \mathbf{f}(t, \bar{\mathbf{x}})\| \leq L\|\mathbf{x} - \bar{\mathbf{x}}\| \quad \text{for } (t, \mathbf{x}), (t, \bar{\mathbf{x}}) \in D. \quad (2.15)$$

**Definition 4** *A function  $\mathbf{f}$  satisfies in  $D$  a local Lipschitz condition with respect to  $\mathbf{x}$  if for every point  $(t, \mathbf{x}) \in D$ , there exists a neighborhood  $U : \|t - \bar{t}\| < \delta, \|\mathbf{x} - \bar{\mathbf{x}}\| < \delta$  ( $\delta > 0$ ) such that  $\mathbf{f}$  satisfies a Lipschitz condition in  $D \cap U$ .*

We will use the following Lemma and Theorem from Walter [95] to show local existence and uniqueness of solutions to our initial value problems.

**Lemma 1** [95] *If  $\mathbf{f}$  and  $\frac{\partial \mathbf{f}}{\partial \mathbf{x}}$  are continuous in  $D$ , then  $\mathbf{f}$  satisfies in  $D$  a local Lipschitz condition with respect to  $\mathbf{x}$ .*

This allows us to achieve existence and uniqueness without delving into the cumbersome Lipschitz conditions.

The following theorem gives the conditions under which we have local existence and uniqueness of solutions to the initial value problem.

**Theorem 1 (Existence and Uniqueness)** [95] *Let  $\mathbf{f}(t, \mathbf{x})$  be continuous in a domain  $D \subset \mathbb{R}^{n+1}$  and satisfy a local Lipschitz condition with respect to  $\mathbf{x}$  in  $D$  (this hypothesis is satisfied, if  $\frac{\partial \mathbf{f}}{\partial \mathbf{x}}$  is continuous in  $D$ ). If  $(t_0, \mathbf{c}) \in D$ , then the initial value problem*

$$\dot{\mathbf{x}} = \mathbf{f}(t, \mathbf{x}), \quad \mathbf{x}(t_0) = \mathbf{c} \quad (2.16)$$

*has exactly one solution. The solution can be extended to the left and right up to the boundary of  $D$ .*

Thus, we can find a solution to the initial value problem (2.16) in a neighborhood of the initial point, but to extend a local solution to a larger interval of the independent variable  $t$ , we use the following Lemma from Hsieh [41].

**Lemma 2** [41] *Assume that  $\mathbf{f}(t, \mathbf{x})$  is continuous for  $J = \{t \in \mathbb{R} : t_0 < t < t_1\}$  and for all  $\mathbf{x} \in \mathbb{R}^n$ . Assume also that a function  $\hat{\mathbf{x}}(t)$  satisfies the following conditions:*

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

(b)  $\frac{d\hat{\mathbf{x}}}{dt} = \mathbf{f}(t, \hat{\mathbf{x}})$  in  $I$ .

Then, either

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

$$\frac{d\mathbf{x}}{dt} = \mathbf{f}(t, \mathbf{x}),$$

or

(ii)

$$\lim_{t \rightarrow \tau} \|\hat{\mathbf{x}}(t)\| = \infty$$

for some  $\tau$  in  $J$ .

This lemma simply says that the solution to (2.16) either goes to infinity or the solution can be extended to all of  $J$ . We will use this lemma to show global existence and uniqueness of solutions to our initial value problems.

In order to show that solutions to our initial value problems do not go to infinity, we use the following theorem and lemma from Hale [29].

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

$$D_r y(t) \leq w(t, y(t)) \tag{2.17}$$

on  $[a, b)$ , if  $y(t)$  is continuous on  $[a, b)$  and has a right hand derivative on  $[a, b)$  that satisfies (2.17).

**Theorem 2** *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*

$$\dot{u} = w(t, u) \tag{2.18}$$

has a unique solution. If  $u(t)$  is a solution of (2.18) on  $a \leq t \leq b$  and  $y(t)$  is a solution of (2.17) on  $a \leq t < b$  with  $y(a) \leq u(a)$ , then  $y(t) \leq u(t)$  for  $a \leq t \leq b$ .

**Lemma 3** Suppose  $w(t, u)$  satisfies the conditions of Theorem 2 for  $a \leq t < b$ ,  $u \geq 0$ , and let  $u(t) \geq 0$  be a solution of (2.18) on  $a \leq t < b$ . If  $\mathbf{f} : [a, b) \times \mathbb{R}^n \rightarrow \mathbb{R}^n$  is continuous and

$$\|\mathbf{f}(t, \mathbf{x})\| \leq w(t, \|\mathbf{x}\|), \quad a \leq t < b, \quad \mathbf{x} \in \mathbb{R}^n,$$

then the solutions of

$$\dot{\mathbf{x}} = \mathbf{f}(t, \mathbf{x}), \quad \|\mathbf{x}(a)\| \leq u(a)$$

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

We use the following Lemma on differential inequalities, similar to the one used by Birkhoff [4], in several of our proofs.

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

Part A: If  $S$  satisfies the differential inequality

$$\dot{S}(t) \leq \lambda S(t), \quad a \leq t \leq b \quad (2.19)$$

where  $\lambda > 0$  is a constant, then

$$S(t) \leq S(a)e^{\lambda(t-a)} \quad \text{for } a \leq t \leq b. \quad (2.20)$$

Part B: If  $S$  satisfies the differential inequality

$$\dot{S}(t) + \lambda S(t) \leq M_1, \quad a \leq t \leq b \quad (2.21)$$

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

$$S(t) \leq \frac{M_1}{\lambda} + \left( S(a) - \frac{M_1}{\lambda} \right) e^{\lambda(a-t)} \quad \text{for } a \leq t \leq b. \quad (2.22)$$

Part C: If  $S$  satisfies the differential inequality

$$\dot{S}(t) \leq (M_1 + M_2 e^{\lambda t}) S(t), \quad a \leq t \leq b \quad (2.23)$$

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

$$S(t) \leq S(a) e^{M_1(t-a) + \frac{M_2}{\lambda}(e^{\lambda t} - e^{\lambda a})} \quad \text{for } a \leq t \leq b. \quad (2.24)$$

*Proof.* The first result is proved similar to the second result except by multiplying both sides of (2.19) by  $e^{-\lambda t}$ . For the second result, multiply both sides of (2.21) by  $e^{\lambda t}$  to get

$$[\dot{S} + \lambda S]e^{\lambda t} \leq e^{\lambda t} M_1.$$

Rearranging, we get

$$0 \geq e^{\lambda t} [\dot{S} + \lambda S - M_1] = \frac{d}{dt} \left\{ S(t) e^{\lambda t} - \frac{M_1}{\lambda} e^{\lambda t} \right\}.$$

Thus, the function  $(S(t) - \frac{M_1}{\lambda}) e^{\lambda t}$  has a non-positive derivative and so is non-increasing for  $a \leq t \leq b$ . Therefore,

$$\left(S(t) - \frac{M_1}{\lambda}\right) e^{\lambda t} \leq \left(S(a) - \frac{M_1}{\lambda}\right) e^{\lambda a}$$

and rearranging yields

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

For Part C, multiply both sides of (2.23) by

$$e^{-(M_1 t + \frac{M_2}{\lambda} e^{\lambda t})}$$

to get

$$\begin{aligned} 0 &\geq e^{-(M_1 t + \frac{M_2}{\lambda} e^{\lambda t})} [\dot{S} - (M_1 + M_2 e^{\lambda t}) S(t)] \\ &= \frac{d}{dt} \{e^{-(M_1 t + \frac{M_2}{\lambda} e^{\lambda t})} S(t)\}. \end{aligned}$$

Hence,

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

completing the proof.

## 2.3 Permanence Theory

The idea behind permanent coexistence or permanence for dynamical systems, specifically differential equations, is to allow arbitrary asymptotic behavior of orbits as long as the orbits do not remain too close to the boundary. To meet this requirement, several mathematical concepts have been introduced in the literature.

Consider an ensemble of  $n$  population densities at time  $t$  given by

$$\mathbf{x}(t) = \{x_i(t)\}_{i=1}^n. \quad (2.25)$$

Let  $D = \{\mathbf{x} : x_1, \dots, x_n \geq 0\}$ , and let  $\text{int}(D)$ ,  $\partial D$  denote the interior and boundary of  $D$  respectively. The curve  $\gamma^+ = \{\mathbf{x}(t) : t \geq 0\}$  is known as an orbit. We denote the distance between two sets  $X$  and  $Y$  by  $d(X, Y)$ .

The  $\Omega$ -limit set  $\Omega(\mathbf{x})$  for  $\mathbf{x} \in D$  is defined to be

$$\Omega(\mathbf{x}) = \{\mathbf{y} : \exists \text{ a sequence } \{t_n\} \text{ with } t_n \rightarrow \infty \text{ such that } \mathbf{x}(t_n) \rightarrow \mathbf{y}\}. \quad (2.26)$$

For a subset  $X \subset D$

$$\Omega(X) = \bigcup_{\mathbf{x} \in X} \Omega(\mathbf{x}). \quad (2.27)$$

Freedman and Waltman [20] introduced the idea of **(weak) persistence**, that is

$$\limsup_{t \rightarrow \infty} x_i(t) > 0 \quad (2.28)$$

for all  $i$ , whenever  $x_i(t_0) > 0$  for some  $t_0$ . Gard et al. [26] constructed a Lyapunov-like function to obtain weak persistence criteria for food chain models of Lotka-Volterra type (see also [24], [25]). However, although weakly persistent, May and Leonard's system [66] spirals out toward the boundary in a heteroclinic cycle [44]. Weak persistence "guarantees only that extinction is not certain" [5].

Freedman and Waltman [21] formulated the notion that each orbit should be asymptotically at a non-zero distance from the boundary in order for the system to be **(strongly) persistent** (see also [22]):

$$\liminf_{t \rightarrow \infty} x_i(t) > 0 \quad (2.29)$$

for all  $i$ , whenever  $x_i(t_0) > 0$  for some  $t_0$ . In this case, the distance depends on the particular orbit and so is not a global criterion.

A stronger condition of permanence that avoids this difficulty is known as **uniform persistence**. Uniform persistence of the model means that for sufficiently large  $t$ , all orbits remain some fixed distance away from zero whenever all components are positive at some previous time  $t_0$ . This distance is not dependent upon the initial value  $\mathbf{x}(t_0) = \mathbf{x}_0$ . Mathematically, uniform persistence of the system means that for any positive initial condition  $\mathbf{x}(t_0) = \mathbf{x}_0$  there exists a positive constant  $m$  such that

$$\liminf_{t \rightarrow \infty} x_i(t) \geq m \quad (2.30)$$

for all  $i$ . A dynamical system describing the evolution of  $\mathbf{x}(t)$  is said to be **dissipative** if trajectories are **uniformly bounded** in positive  $t$ , that is, there exists a constant  $M$  such that

$$\limsup_{t \rightarrow \infty} \|\mathbf{x}(t)\| \leq M. \quad (2.31)$$

If 2.30 and 2.31 hold, then there are numbers  $m, M$  with  $0 < m \leq M < \infty$  such that given any initial condition in  $D$  there is a  $T = T(\mathbf{x})$  such that

$$m \leq x_i(t) \leq M \quad (t > T, i = 1, \dots, n). \quad (2.32)$$

If this condition holds, then the system is known as **permanently coexistent** or **permanent**. Hutson et al. [44], [45], [46] use the term permanently coexistent, but Hofbauer and Sigmund [36] and Kirlinger [52] use the term permanent (see also [37], [53], [54], [60], [61], [49]). Butler et al. [5], [6] use the analogous term uniformly persistent when talking about dissipative systems. The term cooperativity has been used to indicate uniform persistence in the analysis of models of hypercycles (see [87], [35]).

An equivalent mathematical formulation for a permanently coexistent system is as follows: a system is **permanently coexistent** or **permanent** if and only if there is a compact region

$D_1 \subset D$ , and thus with  $\delta = d(D_1, \partial D) > 0$ , such that given any  $\mathbf{x}(t_0) = \mathbf{x}_0 \in D$  there is a  $T = T(\mathbf{x})$  such that  $\mathbf{x}(t) \in D_1$  for  $t > T$ . As noted earlier in this work, this definition encompasses the idea that the boundary should repel orbits. The system is said to be **impermanent** if and only if there is an  $\mathbf{x} \in D$  such that

$$\lim_{t \rightarrow \infty} d(\mathbf{x}(t), \partial D) = 0. \quad (2.33)$$

For an investigation of the connections between the concepts presented above see the paper by Freedman and Moson [19].

There are many advantages to using the concept of permanent coexistence over asymptotic (local) stability, global stability, weak persistence, and strong persistence. First, if such a  $D_1$  exists, it is a global attractor under the dynamics of the system. Second, no solutions can approach the boundary. Thirdly, only the behavior of the dynamics governing the system near the boundary is relevant. Lastly, any asymptotic behavior consistent with the dynamics of the system is allowed. One clear disadvantage to this concept is that nothing is said about how close (how small  $\delta$ ) the compact set can be to the boundary. This could allow for extinction of species since “environmental perturbations are often vigorous shake-ups, rather than gentle stirrings” [49].

The notion of  **$\theta$ -persistence** where the  $\delta$  should be specified in advance was presented by Levin [63]. However, it is extremely difficult to discover when  $\theta$ -persistence holds [27]. The slightly weaker condition, that some such  $\delta$  exists, is easier to treat mathematically [46].

Much of the development of permanence theory has revolved around increasing the range of applicability to different models. Waltman [96] noted that “much of the interest has been focused on three-population models”. Three species models of Kolmogorov type have been studied by Hutson and Law [44], Hutson and Vickers [46] and Butler and Waltman [6]. The book of Hofbauer and Sigmund [36] is a good reference for models of Lotka-Volterra type. Kirlinger [52],[53], [54], and Mukherjee et al. [70] have had some success with models for four or more species. Gard [23] developed an approximate method for multi-species Kolmogorov models.

There are two distinct mathematical approaches in the literature for investigating permanent systems:

- 1) Analysis of the flow on the boundary
- 2) Use of a Lyapunov-like function.

The first approach was introduced by Freedman and Waltman [21] in 1984. Subsequent work [5] showed that permanence (uniform persistence in the terminology of the authors) held under an acyclicity condition. Most of the work on the analysis of the flow on the boundary has been done in a dynamical systems setting rather than in the restricted setting of differential equations (see [6], [96]). We will not be using this approach in this work. Instead, we concentrate on the second method listed above.

The key article by Schuster, Sigmund, and Wolff in 1979 initiated the second approach. A considerable body of literature has been devoted to this technique over the past 25 years. Some of the works deal with differential equations and others deal with dynamical systems. Hofbauer’s 1981 work [35] is one of the key references that made explicit use of the features

of a Lyapunov-like function in a differential equations setting. An extension to dynamical systems was put forward in 1984 by Hutson [43].

For a wide variety of ordinary differential equation models the two techniques produce identical results [43]. Hutson and Schmitt [43] give examples where one approach works, but the other approach does not work. Still further, some authors (see [54], [38]) use a combination of both approaches.

In order to understand the Lyapunov function approach, we define what a Lyapunov function and an Average Lyapunov function are. The latter is sometimes called a persistence function (see [23]).

**Definition 6** *We say that a real-valued function  $P \in C^1(D)$  is a **Lyapunov function** if it satisfies the relations*

$$P(\mathbf{x}) = 0 \text{ for } \mathbf{x} \in \partial D, \quad P(\mathbf{x}) > 0 \text{ for } \mathbf{x} \in \text{int}(D), \quad \text{and } \dot{P}(\mathbf{x}) > 0 \text{ for } \mathbf{x} \in D.$$

Here  $\dot{P}(\mathbf{x})$  is defined as  $\dot{P}(\mathbf{x}) := P(\mathbf{x})\Psi(\mathbf{x})$  where  $\Psi$  is a continuous function on  $D$ .  $\dot{P}(\mathbf{x})$  is called the **derivative of P along trajectories**.

Note that the last inequality above is reversed, that is  $\dot{P}(\mathbf{x}) \leq 0$ , when defining a Lyapunov function in the context of stability of equilibria [95]. For our definition we can think of  $P(\mathbf{x})$  as a surface with height zero when one or more species have zero density and with a positive height when all species have positive densities. So solutions  $\mathbf{x}(t)$  projected onto the surface  $P$  are moving away from the boundary in the positive direction.

Since we want the boundary to repel orbits it is enough to require that  $\dot{P}(\mathbf{x}) > 0$  close to the boundary. Notice that for  $\dot{P}(\mathbf{x}) = P(\mathbf{x})\Psi(\mathbf{x}) > 0$  near the boundary, it is enough to show that  $\Psi > 0$  at all points on the boundary since  $\Psi$  is a continuous function. However, it may be difficult to check all points in the boundary to see if they satisfy  $\Psi > 0$ . In fact, it is unlikely that the inequality would hold throughout the boundary [60].

A weaker version in which the time average behaves as a Lyapunov function can be used in some circumstance to overcome this drawback. In the long run, the boundary still repels orbits that are not in the boundary. To put it the way Jansen et al. [49] said it, “if one waits for a sufficiently long time, one can be sure to be further away from the boundary than one was before”.

**Definition 7** *We say that a real-valued function  $P \in C^1(D)$  is an **Average Lyapunov function** [36] or **Persistence function** [23] if it satisfies the following properties:*

1) *We have*

$$P(\mathbf{x}) = 0 \text{ for } \mathbf{x} \in \partial D \text{ and } P(\mathbf{x}) > 0 \text{ for } \mathbf{x} \in \text{int}(D) \quad (2.34)$$

and

2) *there exists a continuous function  $\Psi$  on  $D$  such that the following two conditions hold:*

i) *We have*

$$\Psi(\mathbf{x}) = \frac{\dot{P}(\mathbf{x})}{P(\mathbf{x})} \text{ for } \mathbf{x} \in \text{int}(D) \quad (2.35)$$

and

ii) for  $\mathbf{x} \in \partial D$ ,

$$\int_0^T \Psi(\mathbf{x}(t)) dt > 0 \text{ for some } T > 0. \quad (2.36)$$

### 2.3.1 Kolmogorov Type Models

We now turn our attention to a specific form of ordinary differential equation that is typically used in modeling the population densities of interacting species. The general  $n$ -species Kolmogorov type model has the form

$$\frac{dx_i}{dt} = x_i f_i(x), \quad 1 \leq i \leq n, \quad (2.37)$$

where  $\mathbf{x} = \{x_i\}$ . We assume the per capita net growth rates  $f_i$ ,  $i = 1, \dots, n$  are such that they guarantee a unique solution. We define the non-negative cone in  $\mathbb{R}^n$  as

$$\mathbb{R}_+^n = \{\mathbf{x} \in \mathbb{R}^n : x_i \geq 0, 1 \leq i \leq n\}. \quad (2.38)$$

We define each bounding hypersurface as

$$H_i = \{\mathbf{x} \in \mathbb{R}_+^n : x_i = 0\} \quad 1 \leq i \leq n. \quad (2.39)$$

**Definition 8** A region  $R$  is **invariant** for (2.37) if  $\mathbf{x}_0 \in R$  and  $\mathbf{x}(t)$  is the solution of (2.37) with  $\mathbf{x}(t_0) = \mathbf{x}_0$ , then  $\mathbf{x}(t) \in R$  for all  $t > t_0$ .

**Lemma 5** For  $n = 3$ , the bounding hypersurfaces  $H_i, 1 \leq i \leq 3$  are invariant for (2.37).

*Proof.* First, we will show that  $H_1$  is invariant. By assumption,  $f_2$  and  $f_3$  are such that

$$\begin{aligned} \frac{dx_2}{dt} &= x_2 f_2(0, x_2, x_3) \\ \frac{dx_3}{dt} &= x_3 f_3(0, x_2, x_3) \\ x_2(t_0) &= c_2 \\ x_3(t_0) &= c_3 \end{aligned}$$

has a unique solution  $\{x_2(t), x_3(t)\}$ . Also,  $\mathbf{x} = \{0, x_2(t), x_3(t)\}$  is a solution of the system

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 f_1(x_1, x_2, x_3) \\ \frac{dx_2}{dt} &= x_2 f_2(x_1, x_2, x_3) \\ \frac{dx_3}{dt} &= x_3 f_3(x_1, x_2, x_3) \\ x_1(t_0) &= 0 \\ x_2(t_0) &= c_2 \\ x_3(t_0) &= c_3. \end{aligned}$$

Since

$$\frac{dx_i}{dt} = x_i f_i(\mathbf{x}), \quad x_i(t_0) = c_i, \quad i = 1, 2, 3 \quad (2.40)$$

has a unique solution for all time, by uniqueness  $\mathbf{x} = \{0, x_2(t), x_3(t)\}$  must be the unique solution to (2.40). That is, a solution starting in the  $x_2x_3$  plane, cannot leave that plane. Therefore,  $H_1$  is invariant for (2.37). A similar argument holds for  $H_2$  and  $H_3$ , completing the proof.

### 2.3.2 Other Models

Consider a model of the form

$$\frac{dp_1}{dt} = a(x_1, x_2)p_2 - bp_1 \quad (2.41a)$$

$$\frac{dp_2}{dt} = a'p_1 - b'p_2 \quad (2.41b)$$

$$\frac{dx_1}{dt} = x_1 f_1(\mathbf{x}) \quad (2.41c)$$

$$\frac{dx_2}{dt} = x_2 f_2(\mathbf{x}) \quad (2.41d)$$

where  $\mathbf{x} = \{p_1, p_2, x_1, x_2\}$ ,  $a(x_1, x_2) > 0$  if  $x_1, x_2 > 0$ , and  $a', b$  and  $b'$  are positive constants.

**Lemma 6** *Solutions to the system (2.41) are pointing into  $\mathbb{R}_+^4$  on the bounding hypersurfaces  $H_i, 1 \leq i \leq 4$ .*

*Proof.*  $H_3 = \{\mathbf{x} \in \mathbb{R}_+^4 : x_1 = 0\}$  and  $H_4 = \{\mathbf{x} \in \mathbb{R}_+^4 : x_2 = 0\}$  are invariant for (2.41c) and (2.41d) since the last two equations are of Kolmogorov type. Thus, solutions are pointed in the positive direction on these hypersurfaces.

If  $p_1(t_0) = 0$ ,  $p_2(t_0) > 0$ ,  $x_1(t_0) > 0$ , and  $x_2(t_0) > 0$ , then

$$\frac{dp_1}{dt}(t_0) = a(x_1, x_2)p_2(t_0) > 0$$

since  $x_1(t_0) > 0$ , and  $x_2(t_0) > 0$  implies that  $a(x_1, x_2) > 0$  by invariance of  $H_3$  and  $H_4$ . Since the time derivative is strictly positive at  $t_0$ , then  $p_1$  is increasing near zero. So, solutions are pointed in the positive direction on the  $H_1$  hypersurface.

If  $p_2(t_0) = 0$ ,  $p_1(t_0) > 0$ ,  $x_1(t_0) > 0$ , and  $x_2(t_0) > 0$ , then

$$\frac{dp_2}{dt}(t_0) = a'p_1(t_0) > 0$$

since  $a' > 0$ . Since the time derivative is strictly positive at  $t_0$ , then  $p_2$  is increasing near zero. So, solutions are pointing into  $\mathbb{R}_+^4$  on the  $H_2$  hypersurface, completing the proof.

## 2.4 Sensitivity Analysis

Consider a first order system of differential equations of the form

$$\begin{aligned} \frac{dx_1}{dt} &= f_1(t, x_1, \dots, x_n) \\ &\vdots \\ \frac{dx_n}{dt} &= f_n(t, x_1, \dots, x_n). \end{aligned} \tag{2.42}$$

Written as a vector equation, the system takes the form

$$\dot{\mathbf{x}} = \mathbf{f}(t, \mathbf{x}). \tag{2.43}$$

Assume that with a given initial condition a unique solution exists for all  $t \geq t_0$ .

Since our differential equations come from modeling ecological systems, numerical values known as parameters appear in the equations. These parameters are obtained by measurements in the field and are thus only approximations. So a very important question is whether the solutions are “insensitive” to small changes in these parameter values. We will denote these parameters by  $\alpha_i$ ,  $i = 1 \dots m$ . We can write the parametric model in expanded form:

$$\begin{aligned} \frac{dx_1}{dt} &= f_1(t, x_1, \dots, x_n, \alpha_1, \dots, \alpha_m) \\ &\vdots \\ \frac{dx_n}{dt} &= f_n(t, x_1, \dots, x_n, \alpha_1, \dots, \alpha_m). \end{aligned} \tag{2.44}$$

For a parameter vector  $\boldsymbol{\alpha} \in \mathbb{R}^m$ , the vector equation is

$$\dot{\mathbf{x}} = \mathbf{f}(t, \mathbf{x}, \boldsymbol{\alpha}). \tag{2.45}$$

One of the main tasks of sensitivity analysis is the investigation of properties of a solution to 2.45 under small changes in  $\boldsymbol{\alpha}$ .

### 2.4.1 Continuous Dependence and Differentiability

We use the following theorems by Rosenwasser et al. [85] to show that the solution  $\mathbf{x}(t)$  to the system 2.45 depends continuously upon the parameter vector  $\boldsymbol{\alpha}$ , and the solution can be differentiated with respect to  $\boldsymbol{\alpha}$ . Let  $D_\alpha$  be a region in  $\mathbb{R}^m$  of possible variations of the vector  $\boldsymbol{\alpha}$ .

**Theorem 3** *Assume that for any  $\boldsymbol{\alpha} \in D_\alpha$ , equation 2.45 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  $(t, \mathbf{x}, \boldsymbol{\alpha})$ -space in which  $\mathbf{f}(t, \mathbf{x}, \boldsymbol{\alpha})$  is continuous with respect to  $t$  and  $\mathbf{x}$  for all  $\boldsymbol{\alpha} \in D_\alpha$ . Also, assume that the partial derivatives

$$\frac{\partial f_i}{\partial x_j}(t, \mathbf{x}, \boldsymbol{\alpha}), \quad \text{for } i, j = 1, \dots, n \quad (2.46)$$

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

$$\mathbf{x}(t, \boldsymbol{\alpha}_0) = \mathbf{x}_0 \quad (2.47)$$

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

**Theorem 4** *Let the conditions of the previous theorem hold. If in addition, the right hand sides of 2.44 have continuous partial derivatives in  $D$  with respect to  $x_1, \dots, x_n, \alpha_1, \dots, \alpha_m$ , then the solution  $\mathbf{x}(t, \boldsymbol{\alpha})$  satisfying*

$$\mathbf{x}(t, \boldsymbol{\alpha}_0) = \mathbf{x}_0 \quad (2.48)$$

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

## 2.4.2 Sensitivities

For our study, we define sensitivities as the partial derivatives of population densities with respect to model parameters.

**Definition 9** *The partial derivative*

$$\frac{\partial \mathbf{x}(t, \boldsymbol{\alpha})}{\partial \alpha_i} \quad (2.49)$$

is a vector and is called the **sensitivity of the solution** with respect to  $\alpha_i$ . In expanded form we define

$$S_{j,i} := \frac{\partial x_j(t, \boldsymbol{\alpha})}{\partial \alpha_i}. \quad (2.50)$$

We now obtain a system of differential equations that determines the derivative of the solution with respect to parameters. The result is formulated as a theorem also by Rosenwasser et al. [85].

**Theorem 5** *Let the conditions of Theorem 4 hold. Then, derivatives of solutions with respect to parameters are defined by differential equations*

$$\frac{d}{dt} \frac{\partial x_j}{\partial \alpha_i} = \sum_{k=1}^n \left( \frac{\partial f_j}{\partial x_k} \frac{\partial x_k}{\partial \alpha_i} \right) + \frac{\partial f_j}{\partial \alpha_i} \quad (2.51)$$

$$j = 1, \dots, n, \quad i = 1, \dots, m,$$

with initial conditions

$$\frac{\partial x_j}{\partial \alpha_i}(t = t_0) = 0, \quad j = 1, \dots, n, \quad i = 1, \dots, m. \quad (2.52)$$

or written according to the definition given in equation 2.50,

$$\frac{d}{dt} S_{j,i} = \sum_{k=1}^n \left( \frac{\partial f_j}{\partial x_k} S_{k,i} \right) + \frac{\partial f_j}{\partial \alpha_i} \quad (2.53)$$

$$j = 1, \dots, n, \quad i = 1, \dots, m,$$

with initial conditions

$$S_{j,i}(t = t_0) = 0, \quad j = 1, \dots, n, \quad i = 1, \dots, m. \quad (2.54)$$

Equation 2.51 is obtained from 2.44 by means of formal differentiation with respect to  $\alpha_i$  and is called the **sensitivity equations**. The sensitivity equations are linear with respect to the corresponding sensitivities.

# Chapter 3

## Examples

The purpose of this chapter is to show the ubiquity of omnivory in natural systems and to give parameter values for use in our differential equation models. Polis et al. [78] state that “as a taxonomically widespread interaction, intraguild predation significantly affects the distribution, abundance, and evolution of many species”. However, after some general observations from a plethora of taxa, we will restrict ourselves to examples mainly involving fish, birds, and mammals.

A vast majority of predators eat food types in a particular size range regardless of the prey’s trophic level. Typically, larger predators attack general prey species of smaller size. This is common in insects, arthropods, and plankton [78]. In fact, omnivory is “so frequent among spiders, scorpions, and ants that each are often considered their own worst enemy” [78]. Larger consumers that eat carrion, fruit, seeds, etc. where many microorganisms and small metazoa live are involved is what is called “coincidental omnivory” [78].

Age/stage structure can also be important. Many predators take relatively small prey as juveniles and larger prey as adults. This leads to stage dependent omnivory. This type of omnivory is frequent among terrestrial insects, lizards, copepods, mysids, rotifers, freshwater insects, amphibians, and fish (see [78] and references therein). Symmetric omnivory is widespread among granivores, arthropods, parasitoids, hyperparasitoids, and benthic marine communities (see [78] and references therein). For example, adult killifish eat adult and juvenile grass shrimp and adult shrimp eat young killifish [78], [55]. Now, we will go through specific examples of fish, birds, and mammals to show that omnivory is a widespread ecological interaction.

### 3.1 Fish

Hall et al. state that “aquatic predators apparently select prey primarily on the basis of size and...thus do not recognize their food as taxonomic entities nor members of a trophic level” [30]. Polis et al. state that “IGP by larger fish on smaller fish is widespread” and when referring to stage dependent IGP among freshwater fish they state, “these complex interactions often include competition and IGP” [78].

Paul Lake in British Columbia was fishless until it was stocked with rainbow trout (*Salmo gairdneri*) in 1909. There, trout feed on a mixture of plankton, benthos, and terrestrial insects. In 1949, a smaller species, the redbreast shiner (*Richardsonius balteatus*), entered the lake from upstream. The shiner also fed on plankton and benthos. The growth of large trout increased in response to the availability of shiners as food. In contrast, it took small trout a full year longer to reach a given size due to competition with the shiners. This is a classic example of IGP in fish (see figure 3.1a) given by Werner et al. [98].

Werner [97] sampled five small lakes in southwest Michigan where bluegill sunfish (*Lepomis macrochirus*) had a considerable depressive effect on the growth and survivorship of young largemouth bass (*Micropterus salmoides*) due to competition for plankton and insects. He concluded that the bluegill form an important part of the adult largemouth bass diet. Thus, we see size dependent omnivory (see figure 3.1b). This form of omnivory determined the habitat shifts in this community [99].

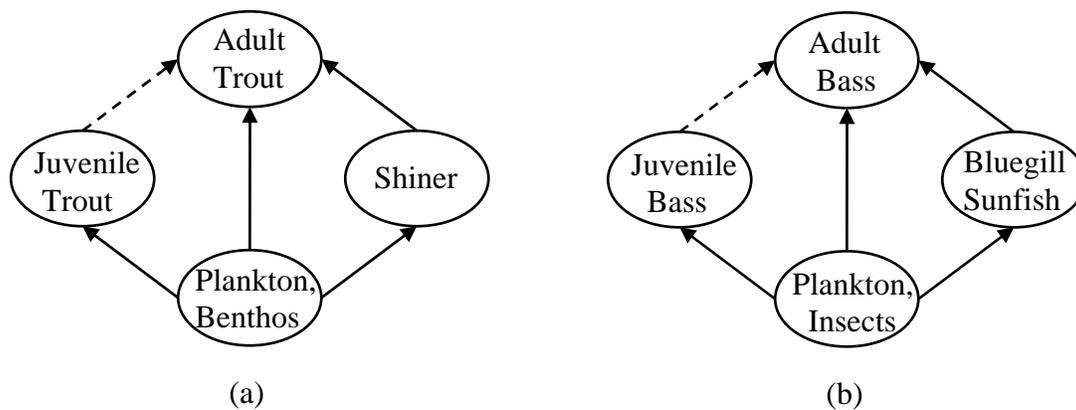


Figure 3.1: Two examples of omnivory in fish. Arrows indicate that one species (base of arrow) is eaten by another species (point). (a) Adult rainbow trout feed on redbreast shiner. Both trout and shiner compete for plankton and benthos. (b) Adult largemouth bass feed on bluegill sunfish. Both bass and bluegill compete for plankton and insects.

Clady [8] documented the food habits of yellow perch (*Perca flavescens*) and largemouth bass (*Micropterus salmoides*) in two unproductive lakes in northern Michigan. He observed that juvenile perch and juvenile bass ate mostly small crustaceans and insects. As adults, perch fed on bass and juvenile perch (cannibalism). Adult bass fed mostly (70%-80%) on juvenile perch. Here, we see asymmetric IGP as well as competition within adult stages and within juvenile stages (see figure 3.2). Again, nature has provided us with a complex interaction which we can only hope to one day model.

Other examples of omnivory in fish are walleye and sauger [91], anchovies and sardines [1], and yellow perch and walleye [18].

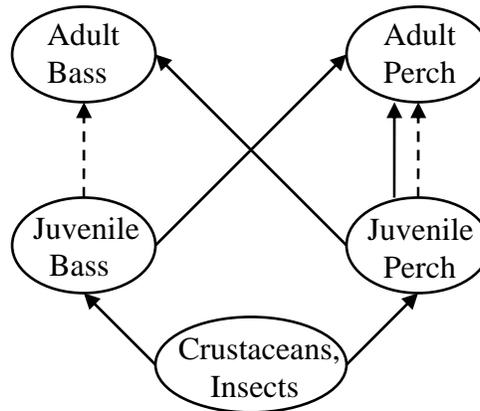


Figure 3.2: An example of asymmetric omnivory in fish. Solid arrows indicate that one species (base of arrow) is eaten by another species (point). Dashed arrows indicate growth transitions. Adult bass eat juvenile perch. Adult perch eat juvenile bass and juvenile perch. Both juvenile bass and juvenile perch compete for crustaceans and insects.

## 3.2 Birds

Sergio et al. [88] state that “studies on vertebrate predators have focused mainly on aquatic communities or on mammals. Few studies have been made on avian predators”. However, we do find IGP involving birds in the literature. The lack of studies could be due to the fact that predatory birds are often elusive and many species are under some form of conservation status.

Wright [100] analyzed stomach content for nine insectivorous bird species and six anole (lizard) species from the West Indian island Puerto Rico. He showed that the birds and anoles compete for their arthropod prey. He also suggested that anoles experience ecological release upon the extinction of an avian predator. As much as 79% of the stomach content of some of the avian species consisted of anoles. This suggests a strong IGP connection between the birds, anoles, and arthropods of Puerto Rico (see figure 3.3a).

Sergio et al. [88] studied the impact of IGP by large eagle owls (*Bubo bubo*) on diurnal black kites (*Milvus migrans*) in eight populations in the Italian Alps. “Similar preference of eagle owls and black kites for low-elevation areas in the proximity of wetlands generates potential for conflict between the two species in the Alps” [88]. The eagle owl preyed mostly on mammals and the black kite preyed mostly on fish. However, they had a dietary overlap of 23.3% by mass. Eagle owls preyed on both nestling and adult black kites (see figure 3.3b). The mean black kite productivity (number of young fledged per pair) was negatively related to eagle owl density. This shows a negative effect on the black kite population due to the predation risk of eagle owls. In this example the IGP is weak, yet present. Sergio et al. [88] state that “detection of IGP systems is complicated by the fact that observed predation

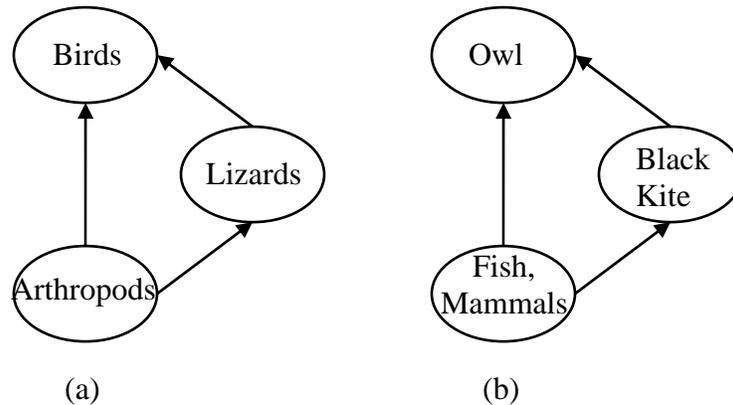


Figure 3.3: Two examples of omnivory in birds. Arrows indicate that one species (base of arrow) is eaten by another species (point). (a) Birds of the West Indies feed on anoles (lizards) as well as arthropods. Anoles feed on arthropods. (b) Eagle owls feed mostly on mammals and black kites feed mostly on fish, but they have a dietary overlap of 23.3% by mass. Eagle owl prey on black kites.

rates are often low. However, predation pressure on a prey may be intense even when actual mortality by predation is low”.

Polis [79] studied the trophic relations of biota in the sand community of the Coachella Valley desert in California. In this study he documents asymmetrical IGP between gopher snakes (*Pituophis*) and burrowing owls (*Athene cunicularia*) (see figure 3.4a). The gopher snake is a nest predator. Gopher snakes eat eggs and nestlings of burrowing owls. However, the burrowing owls are predators upon the gopher snakes. Gopher snakes and burrowing owls are both resource generalists preying on many vertebrates including arthropods, rodents, and lizards. The subwebs in the Coachella Valley are “complex because of the large number of interactive species, age structure, and high omnivory” [79].

Jaksic [47] studied diurnal (Falconiform) and nocturnal (Strigiform) raptors to determine if the difference in activity time reduced competition for food. Jaksic [47] states that diurnal and nocturnal raptors share prey of the transition time between day and night. Many prey species also become prey for both diurnal and nocturnal raptors by extending their feeding times. Jaksic [47] indicates that there are “records of interspecific territoriality, predation, and interference competition” between diurnal and nocturnal raptors. Although IGP in this system may be weak, it is none the less present (see figure 3.4b).

Other examples of omnivory in birds are great horned owl and red-tailed hawk [67] and screech owl and golden eagle [79].

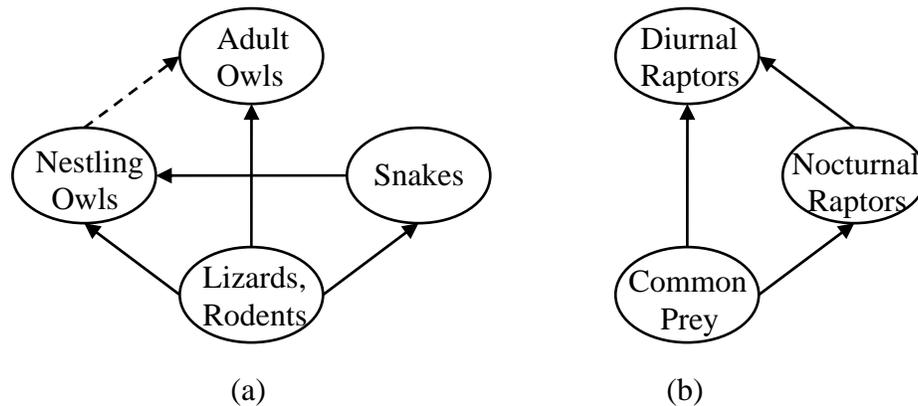


Figure 3.4: Two examples of omnivory in birds. Solid arrows indicate that one species (base of arrow) is eaten by another species (point). Dashed arrows indicate growth transitions. (a) Gopher snakes prey on burrowing owl eggs and nestlings. Burrowing owls prey on gopher snakes. Both species are resource generalists feeding on rodents, lizards, etc. (b) Both diurnal and nocturnal raptors prey on species that feed during transition periods between day and night. Records also show that there is some predation between diurnal and nocturnal raptors.

### 3.3 Mammals

Palomares et al. [73] state that “the importance of interspecific interactions among large vertebrate predators has been long recognized. However, estimation of the strength of such interactions ... has been rarely tackled, in spite of its known importance for a better knowledge of community structure”. Palomares et al. [72] also state that “interspecific killing among mammalian carnivores is common in nature and accounts for up to 68% of known mortalities in some species”. Generally, larger solitary killer species prey on smaller victim species. However, grouping species kill larger victims than solitary species. Palomares et al. [72] uncovered 97 different interspecific killings among mammalian carnivores involving 54 different victims and 27 killer species. The dietary overlap of the species was not considered in their paper. We will restrict ourselves to species with significant dietary overlap since we are modeling omnivory.

The three-species system (see figure 3.5a) involving the Iberian lynx (*Felis pardina*), Egyptian mongoose (*Herpestes ichneumon*), and European rabbit (*Oryctolagus cuniculus*) was studied by Palomares et al. [74]. The study was conducted along the Doñana National Park border in the Iberian Peninsula of southwestern Spain. The Iberian lynx is the top terrestrial predator in this ecosystem and is the most endangered carnivore in Europe. The lynx mainly feeds on adult rabbits which consists of 75% to 95% of the biomass they consume throughout the year. The study showed that rabbits represent between 33% and 87% of the biomass consumed by mongooses throughout the year. Juvenile rabbits were the most

commonly consumed. Lynx kill mongoose and mongoose avoid use of otherwise suitable areas where lynx are at high density due to the high predation risk [73]. However, the predatory link is not a strong link since lynx do not significantly gain energetically from feeding on mongoose.

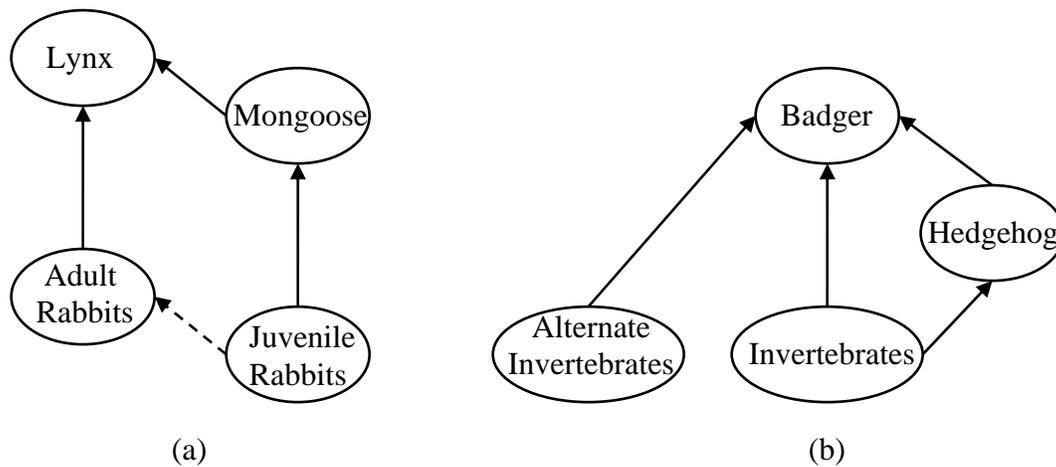


Figure 3.5: Two examples of omnivory in mammals. Solid arrows indicate that one species (base of arrow) is eaten by another species (point). Dashed arrows indicate growth transitions. (a) Iberian lynx feed on adult rabbits and Mongoose feed on juvenile rabbits. Lynx kill mongoose. (b) Badgers feed on common invertebrates with hedgehog. Badgers also feed on alternate invertebrates. Badgers have a negative effect on hedgehog survival through intraguild predation.

Doncaster [13] studied hedgehog (*Erinaceus europeaus*) and badger (*Meles meles*) populations on two sites in England (see figure 3.5b). The hedgehog consumes a variety of invertebrates which also make up a large proportion of the badger diet. Badgers may also consume alternate invertebrate prey [13]. “The study was designed to test whether hedgehogs were excluded from apparently suitable habitats through intraguild predation with badgers” [32]. Doncaster found that the density of badgers negatively affected hedgehog survival and positively affected hedgehog dispersal to microhabitats that were not accessible to badgers. The presence of alternative resources seems to be important in determining the abundance of both the badger and hedgehog [32].

Coyotes (*Canis latrans*), bobcats (*Felis rufus*), gray foxes (*Urocyon cinereoargenteus*), and red foxes (*Vulpes vulpes*) are sympatric over a large portion of their ranges in North America [10], [17] (see figure 3.6). All four of these species have been photographed (via remote cameras) going under the same fence within weeks and often days of each other [92]. Fedriani et al. [17] studied the effect of competition and IGP on local abundances of coyotes, bobcats, and gray foxes at three sites in the Santa Monica Mountains of Los Angeles County, California. They recorded that 7 of 12 gray fox deaths and 2 of 5 bobcat deaths were due to

coyote predation and 2 of 12 gray fox deaths were due to bobcats. In addition, remains of gray foxes and bobcats were found in coyote feces. They suggested that gray foxes avoided habitats of high coyote predation risk. However, they did not find a correlation between the number and distribution of bobcats and coyotes. Average seasonal food overlap for the coyote, bobcat, and gray fox were “high due to the importance of small mammals in all carnivore diets” [17]. Coyotes and gray foxes did consume a significant amount of fruit, whereas bobcats were solely carnivorous. Cypher [10] studied the food use of coyotes, gray foxes, and red foxes in Southern Illinois and found that “the high dietary overlap among [these] species results in the potential for resource competition” [10]. Red foxes were also noted to consume significant amounts of fruit. He also noted that reports of coyotes killing red foxes are common and reports of coyotes killing gray foxes are less common. Also noted was that gray foxes are reportedly more aggressive than red foxes. The energetic gain of the top predator on the intermediate prey was not addressed in either paper.

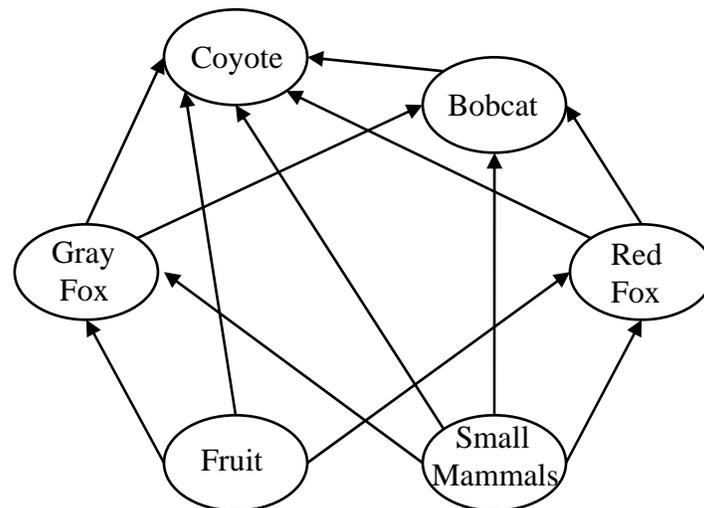


Figure 3.6: An example of omnivory in mammals. Solid arrows indicate that one species (base of arrow) is eaten by another species (point). Coyotes kill (eat) bobcats, gray foxes, and red foxes as well as feeding on small mammals and fruit. Bobcats are strictly carnivorous feeding on gray foxes, red foxes, and small mammals. Gray foxes are omnivorous, feeding on gray foxes, red foxes, and small mammals. Gray foxes are omnivorous, feeding on fruit and small mammals. Red foxes are omnivorous, feeding on fruit and small mammals.

Another complex example of omnivory comes from Africa. In this system, lions (*Panthera leo*) are the largest species of predator, but do not hold the status of “top predator”. Groups of hyenas (*Crocuta crocuta*) prey on single lions [78]. Also, packs of wild dogs (*Lycaon pictus*) will kill and eat solitary lions [78]. However, lions are common predators of wild dogs and account for about 39% of wild dog pup deaths and at least 43% of adult deaths [32], [68]. Individual lions prey on individual hyenas and groups of lions prey on groups of hyenas [78]. Lions also prey on cheetah cubs (*Acinonyx jubatus*). Kelly et al. [51] state

that “reproductive rates of cheetahs were negatively correlated with the presence of lions while cheetahs had cubs”. Durant et al. [14] state that the “negative association between recruitment and numbers of lions, demonstrate that the high rates of predation observed in previous studies have implications for the dynamics of cheetah populations”. In fact, the chief source of mortality on cheetah cubs is predation by lions, which accounts for nearly 75% of known cub mortality [59]. Cheetah densities also show an inverse relationship to hyena densities [7]. The food overlap of the above predators varies. The primary prey species of lions are wildebeest (*Connochaetes taurinus*), buffalo (*Syncerus caffer*), and zebra (*Equus burchelli*) [68]. Lions will also feed on other ungulates such as impala (*Aepyceros melampus*) and kudu (*Tragelaphus strepsiceros*), which are the main prey species of wild dogs [68]. Lions and hyenas do kleptoparasitize (steal food from) wild dogs [33], [68]. Although hyenas will scavenge for almost half of their food, they will hunt for such prey as buffalo, warthogs (*Phacochoerus aethiopicus*), kudu, and impala [33]. Thomson’s gazelle (*Gazella thomsoni*), is the main prey species for cheetahs [7]. This conglomeration of predation and competition defines a system where species have little to moderate dietary overlap and are subject to a varying degree of predation from rare to extreme. Therefore, the degree and ubiquity of omnivory have an effect on the dynamics of this ecosystem.

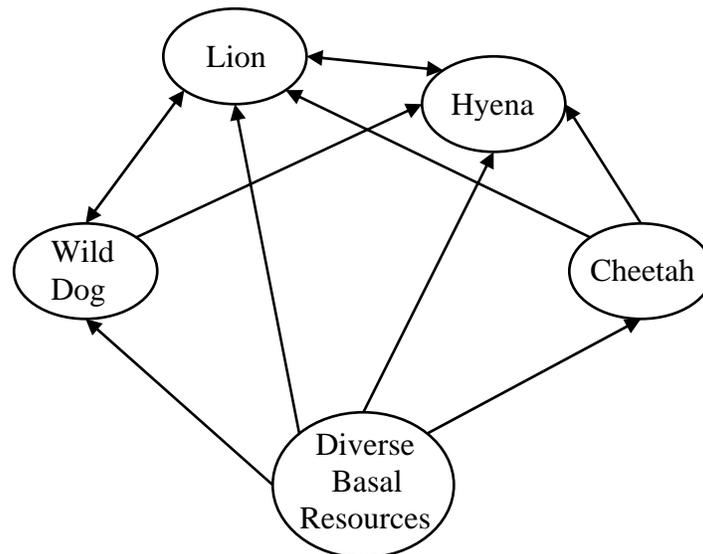


Figure 3.7: An example of omnivory in mammals. Solid arrows indicate that one species (base of arrow) is eaten by another species (point). Lions prey on cheetahs, wild dogs, and hyenas. Hyenas prey on lions, wild dogs and cheetahs. Packs of wild dogs prey on solitary lions. Lions, hyenas, wild dogs, and cheetahs feed on a variety of ungulates. The amount of dietary overlap between the predatory species varies from low to high.

Other examples of omnivory in mammals are Iberian lynx and red fox [74],[16] and coyotes and kit fox [65], [80], [79].

### 3.4 Model Parameter Values

In order to provide parameter values for our differential equation models we obtain data from three omnivorous systems. Since 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” [72], we will use data from ciliates (protozoans) instead for our linear response model. Also, since the same holds true for birds [88], we will use data from a previous study by Křivan et al. [58] for our non-linear response model and our stage structure model. In addition we use a maturation rate from Persson et al. [75].

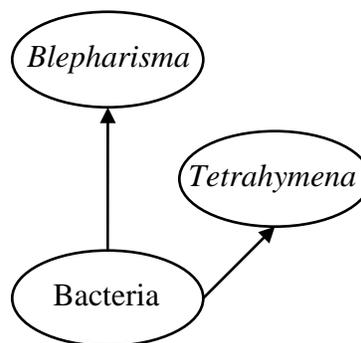


Figure 3.8: An omnivorous system used to determine parameter values. Solid arrows indicate that one species (base of arrow) is eaten by another species (point). Dashed arrows indicate growth transitions. Two ciliates *Blepharisma* and *Tetrahymena* compete for bacteria. *Blepharisma* feed on *Tetrahymena*.

For our linear response omnivory model we obtain model parameter values from a laboratory system of mixed bacteria and ciliates. Our data is taken from Diehl et al. [12]. The system consists of two ciliates *Tetrahymena pyriformis* and *Blepharisma* which coexist with heterotrophic bacteria. *Tetrahymena pyriformis* feed on bacteria and *Blepharisma* feed on bacteria and *Tetrahymena*. Diehl et al. [12] selected the *Blepharisma-Tetrahymena*-bacteria system (see figure 3.8a) to investigate the effects of enrichment on a simple three-trophic level community with omnivory. The parameter values are given in Table 3.1. The resource carrying capacity was determined from the stable coexistence regions given by Diehl et al..

For our non-linear response omnivory model we obtain model parameter values from Křivan et al. [58]. Křivan et al. made minor modifications to parameter values given by Kooi et al. [56]. Kooi et al. studied the dynamic behavior of a three species microbial food web under chemostat conditions. The parameter values taken from Křivan et al. are given in Table 3.2. In our case, we chose the resource carrying capacity according to the regions where 3-species coexistence occurs as given by Křivan et al..

For our stage structure omnivory model we parameterize the model with the same data from Křivan et al. [58]. However, Křivan et al. do not compute a maturation rate. The

Table 3.1: Parameter values for our linear response omnivory model taken from Diehl et al. [12].

Parameter	Value
$r$	0.4
$K$	2
$\alpha_{RC}$	0.1
$\alpha_{RP}$	0.1
$\alpha_{CP}$	0.05
$e_{RC}$	0.8
$e_{RP}$	0.2
$e_{CP}$	0.5
$m_C$	0.06
$m_P$	0.04

Table 3.2: Parameter values for our non-linear response omnivory model taken from Krivan et al. [58].

Parameter	Value
$r$	0.3
$K$	3
$\lambda_{RC}$	0.037
$\lambda_{RP}$	0.025
$\lambda_{CP}$	0.025
$h_{RC}$	3
$h_{RP}$	4
$h_{CP}$	4
$e_{RC}$	0.6
$e_{RP}$	0.36
$e_{CP}$	0.6
$m_C$	0.03
$m_P$	0.0275

Table 3.3: Parameter values for our stage structure omnivory model taken with slight modifications from Mylius et al. [71] and Persson et al. [75].

Parameter	Value
$r$	0.3
$K$	4
$\lambda_{RC}$	0.037
$\lambda_{RP}$	0.025
$\lambda_{CP}$	0.025
$h_{RC}$	3
$h_{RP}$	4
$h_{CP}$	4
$e_{RC}$	0.6
$e_{RP}$	0.36
$e_{CP}$	0.6
$m_C$	0.03
$m_P$	0.0275
$\mu_P$	0.1

parameter values that we will use are given in Table 3.3. We chose the resource carrying capacity according to the regions where 3-species coexistence occurs as given by Křivan et al..

# Chapter 4

## Linear Response Omnivory Model

Our first model for investigation is a three species omnivory model in which the functional and numerical responses are all linear functions of the resource or consumer densities and are thus governed by Lotka-Volterra dynamics. The model involves the resource density (R), the consumer density (C), and the predator density (P). The predator feeds on the consumer and the resource. The consumer only feeds on the resource. The population dynamics are described by the following system of differential equations

$$\frac{dP}{dt} = P[e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_P] \quad (4.1a)$$

$$\frac{dC}{dt} = C[e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_C] \quad (4.1b)$$

$$\frac{dR}{dt} = R[r(1 - R/K) - \alpha_{RC}C - \alpha_{RP}P]. \quad (4.1c)$$

You will notice that this model is an asymmetrical intraguild predation (see Section 2.1.3) model of Kolmogorov type.

According to this model, the resource population grows according to logistic growth in the absence of consumers and predators. Parameter  $r$  represents the intrinsic rate of increase of the resource, and  $K$  is the resource carrying capacity in the absence of consumers and predators. The resource declines due to predation by the consumer as well as the predator. The parameters  $\alpha_{RC}$  and  $\alpha_{RP}$  are the consumption rates of the resource by the consumer and predator respectively. Both the predator and the consumer decline by natural mortality,  $m_P$  and  $m_C$  respectively, and the consumer experiences additional mortality (in the form of a consumption rate  $\alpha_{CP}$ ) due to the predator. The efficiencies with which the predator and consumer convert resources into new offspring are given by  $e_{RP}$  (for the predator) and  $e_{RC}$  (for the consumer). In addition, the predator converts consumers into new offspring with efficiency  $e_{CP}$ . All of the above parameters are assumed to be positive. A summary of the variables and parameters is given in Table 4.1.

This is a somewhat simplistic model involving Type I functional and numerical responses. The limitations of such a model are discussed in Section 2.1.4. However, some very interesting results from permanence theory can be applied to Lotka-Volterra systems and thus will be

Table 4.1: Definitions of variables and parameters in the linear response omnivory model.

Parameter	Definition
R	Resource density
C	Consumer density
P	Predator density
r	Resource intrinsic rate of increase
K	Environmental carrying capacity of the resource
$\alpha_{RC}$	Consumption rate of resources by consumers
$\alpha_{RP}$	Consumption rate of resources by predators
$\alpha_{CP}$	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

the basis of our study. Also, some general criteria with biological significance can be derived from this model.

## 4.1 Solution to System

In order to investigate the long-term survival of the resource, consumer, and predator species we need to ensure that in fact a unique solution to our differential equation model exists for all non-negative time. We will first show that solutions which start positive will remain positive for all time. Next, we will show that a unique solution exists on a finite time interval. Lastly, we will prove that this solution can be extended uniquely for all  $t \geq 0$ .

Since 4.1 is of Kolmogorov type, we know that the bounding hypersurfaces are invariant by Lemma 5. Invariance indicates that solutions cannot cross the hypersurfaces, and thus solutions that start positive must remain positive for all time.

Now assume that the initial population densities of the resource, consumer, and predator are such that

$$P(0) = c_1 > 0, \quad C(0) = c_2 > 0, \quad \text{and} \quad R(0) = c_3 > 0. \quad (4.2)$$

Then the initial value problem is:

$$\begin{aligned}
\frac{dP}{dt} &= f_1(P, C, R) \\
\frac{dC}{dt} &= f_2(P, C, R) \\
\frac{dR}{dt} &= f_3(P, C, R) \\
P(0) &= c_1 \\
C(0) &= c_2 \\
R(0) &= c_3
\end{aligned} \tag{4.3}$$

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

$$\begin{aligned}
f_1(P, C, R) &= P[e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_P] \\
f_2(P, C, R) &= C[e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_C] \\
f_3(P, C, R) &= R[r(1 - R/K) - \alpha_{RC}C - \alpha_{RP}P].
\end{aligned}$$

The partial derivative of

$$\mathbf{f} = \begin{pmatrix} f_1 \\ f_2 \\ f_3 \end{pmatrix} \tag{4.4}$$

with respect to the predator, consumer, and resource densities are

$$\begin{aligned}
\frac{\partial \mathbf{f}}{\partial P} &= \begin{pmatrix} e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_P \\ -\alpha_{CP}C \\ -\alpha_{RP}R \end{pmatrix} \\
\frac{\partial \mathbf{f}}{\partial C} &= \begin{pmatrix} e_{CP}\alpha_{CP}P \\ e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_C \\ -\alpha_{RC}R \end{pmatrix} \\
\frac{\partial \mathbf{f}}{\partial R} &= \begin{pmatrix} e_{RP}\alpha_{RP}P \\ e_{RC}\alpha_{RC}C \\ r(1 - 2R/K) - \alpha_{RC}C - \alpha_{RP}P \end{pmatrix}.
\end{aligned}$$

Notice that  $\mathbf{f}$  and its partial derivatives are all continuous with respect to  $P$ ,  $C$ , and  $R$  for all positive  $t$ ,  $P$ ,  $C$ , and  $R$ . So by Lemma 1,  $\mathbf{f}$  satisfies in  $D$  a local Lipschitz condition with respect to

$$\mathbf{x} = \begin{pmatrix} P \\ C \\ R \end{pmatrix}. \tag{4.5}$$

Then using the Existence and Uniqueness Theorem 1, our initial value problem 4.3 has exactly one solution and that solution can be extended to the left and right up to the boundary of  $D$ .

We will now show that we have a unique solution for all  $t \geq 0$ .

**Theorem 6** *The initial value problem 4.3 has a unique solution in  $\mathbb{R}_+^3$  for all  $t \geq 0$ .*

*Proof.* Recall from above that  $P(t), C(t), R(t) \geq 0$  for all  $t \geq 0$ . Then

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

So we have the differential inequality

$$\frac{dR(t)}{dt} \leq R(t)r(1 - R(t)/K). \quad (4.6)$$

However, the initial value problem

$$\frac{du(t)}{dt} = u(t)r(1 - u(t)/K), \quad u(0) = u_0 \quad (4.7)$$

has the unique solution

$$u(t) = \frac{K}{1 + \left(\frac{K}{u_0} - 1\right) e^{-rt}}. \quad (4.8)$$

Then applying Theorem 2 and Lemma 3, we have that  $R(t) \leq u(t)$  for  $0 \leq t \leq \infty$ . If in addition, we let  $K_{max} = \max(u_0, K)$ , then  $u(t) \leq K_{max}$  and we have

$$R(t) \leq K_{max} \text{ for } 0 \leq t \leq \infty. \quad (4.9)$$

Also,

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

Since  $R(t) \leq K_{max}$ , we have that

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

If we define

$$\Gamma = e_{RC}\alpha_{RC}K_{max}$$

then by Lemma 4 Part A

$$\begin{aligned} C(t) &\leq C(0)e^{\Gamma(t-0)} \\ &= c_2e^{\Gamma t}. \end{aligned} \quad (4.10)$$

This exponential function does not reach infinity in finite time.

Finally,

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

Since  $R(t) \leq K_{max}$  and  $C(t) \leq c_2 e^{\Gamma t}$ , we have that

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

If we define

$$\Phi = e_{CP}\alpha_{CP}c_2$$

and

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

then by Lemma 4 Part C

$$P(t) \leq c_1 e^{\Gamma t + \Lambda(e^{\Gamma t} - 1)}. \quad (4.11)$$

This exponential function does not reach infinity in finite time. So by Lemma 2 and inequalities (4.9), (4.10), and (4.11) a unique solution for the initial value problem (4.3) exists for all  $t \geq 0$ . This completes the proof.

## 4.2 Permanent Coexistence

In this section we will show that our linear response omnivory model is permanently coexistent under certain parameter restrictions. To make the analysis simpler, we redefine the third vector component,  $R(t)$ , in the following way:

$$\bar{R}(t) = \frac{R(t)}{K}. \quad (4.12)$$

Then, we take  $(x_1(t), x_2(t), x_3(t))^T = (P(t), C(t), \bar{R}(t))^T$  to form the classical Lotka-Volterra equations for three populations,

$$\dot{x}_i(t) = x_i(t)f_i(\mathbf{x}(t)) = x_i(t) \left( r_i + \sum_{j=1}^3 a_{ij}x_j(t) \right) \quad i = 1, 2, 3 \quad (4.13)$$

where  $r_1 = -m_P$ ,  $r_2 = -m_C$ , and  $r_3 = r$ . We define the **interaction matrix** to be

$$A = (a_{ij}) = \begin{pmatrix} 0 & e_{CP}\alpha_{CP} & e_{RP}\alpha_{RP} \\ -\alpha_{CP} & 0 & e_{RC}\alpha_{RC} \\ -\alpha_{RP} & -\alpha_{RC} & -1 \end{pmatrix}. \quad (4.14)$$

In order to use available theory from Hofbauer et al. [37], we need the following definitions. We define the **replicator equation** as

$$\dot{x}_i = x_i((A\mathbf{x})_i - \mathbf{x} \cdot A\mathbf{x})$$

defined on the simplex

$$S_n = \{\mathbf{x} = (x_1, \dots, x_n)^T \in \mathbb{R}^n : x_i \geq 0 \text{ and } \sum_{i=1}^n x_i = 1\}$$

where

$$(A\mathbf{x})_i = \sum_{j=1}^n a_{ij}x_j. \quad (4.15)$$

We say that an equilibrium point  $\bar{\mathbf{x}}$  is **saturated** if

$$f_i(\bar{\mathbf{x}}) \leq 0 \text{ for all } i \text{ with } \bar{x}_i = 0. \quad (4.16)$$

Note that every equilibrium point in the interior of the state space is saturated. For an equilibrium point on the boundary, saturated means that the dynamics do not “call for” the missing species [37].

We use the following theorem from Hofbauer et al. [37] to show that the replicator equation in  $n$  variables is equivalent to the Lotka-Volterra equation in  $n - 1$  variables.

**Theorem 7** *There exists a differentiable, invertible map from  $\hat{S}_n = \{\mathbf{x} \in S_n : x_n > 0\}$  onto  $\mathbb{R}_+^{n-1}$  mapping the orbits of the replicator equation*

$$\dot{x}_i = x_i((A\mathbf{x})_i - \mathbf{x} \cdot A\mathbf{x}) \quad (4.17)$$

*onto the orbits of the Lotka-Volterra equation*

$$\dot{y}_i(t) = y_i(t) \left( r_i + \sum_{j=1}^3 a'_{ij}y_j(t) \right) \quad i = 1, \dots, n - 1 \quad (4.18)$$

where  $r_i = a_{in} - a_{nn}$  and  $a'_{ij} = a_{ij} - a_{nj}$ .

Then, we use the following two theorems on Average Lyapunov functions also from Hofbauer et al. [37] to show that a dynamical system on  $S_n$  is permanent.

**Theorem 8** *Consider a dynamical system on  $S_n$  that leaves the boundary invariant. Let  $P : S_n \rightarrow \mathbb{R}$  be a differentiable function vanishing on  $\partial S_n$  and strictly positive in  $\text{int}(S_n)$ . If there exists a continuous function  $\Psi$  on  $S_n$  such that the following two conditions hold:*

$$\text{for } \mathbf{x} \in \text{int}(S_n), \quad \frac{\dot{P}(\mathbf{x})}{P(\mathbf{x})} = \Psi(\mathbf{x}) \quad (4.19)$$

$$\text{for } \mathbf{x} \in \partial(S_n), \quad \int_0^T \Psi(\mathbf{x}(t)) dt > 0 \text{ for some } T > 0, \quad (4.20)$$

*then the dynamical system is permanent.*

Note that this is the definition of an Average Lyapunov function given in Chapter 2.

**Theorem 9** *It is sufficient to verify (4.20) for all  $\mathbf{x} \in \Omega(\partial S_n)$ , the  $\Omega$ -limit set of orbits on the boundary of  $S_n$ .*

From the proceeding three theorems, we can now state a theorem on Average Lyapunov functions for a Lotka-Volterra equation on  $\mathbb{R}_+^n$ . An extended version for autonomous differential equations is given by Hutson [43].

**Theorem 10** *Consider a Lotka-Volterra equation with uniformly bounded orbits on  $\mathbb{R}_+^n$  that leaves the boundary invariant. Let  $P : \mathbb{R}_+^n \rightarrow \mathbb{R}$  be a differentiable function vanishing on  $\partial\mathbb{R}_+^n$  and strictly positive in  $\text{int}(\mathbb{R}_+^n)$ . If there exists a continuous function  $\Psi$  on  $\mathbb{R}_+^n$  such that the following two conditions hold:*

$$\text{for } \mathbf{x} \in \text{int}(\mathbb{R}_+^n), \quad \frac{\dot{P}(\mathbf{x})}{P(\mathbf{x})} = \Psi(\mathbf{x}) \quad (4.21)$$

$$\text{for } \mathbf{x} \in \Omega(\partial\mathbb{R}_+^n), \quad \int_0^T \Psi(\mathbf{x}(t)) dt > 0 \text{ for some } T > 0, \quad (4.22)$$

*then the Lotka-Volterra equation is permanent.*

We now present a theorem that provides a sufficient condition for permanence for Lotka-Volterra systems that is a very useful strengthening of Theorem 10 on Average Lyapunov functions. A similar result for a replicator equation is given by Hofbauer et al. [37] and also by Jansen [48].

**Theorem 11** *If there exists a  $\mathbf{p} \in \text{int}(\mathbb{R}_+^n)$  such that*

$$\mathbf{p} \cdot (\mathbf{r} + A\mathbf{x}) > 0 \quad (4.23)$$

*for all equilibrium points  $\mathbf{x} \in \partial\mathbb{R}_+^n$ , then the Lotka-Volterra equation with uniformly bounded orbits on  $\mathbb{R}_+^n$  that leaves the boundary invariant is permanent.*

Notice that only equilibrium points on the boundary of  $\mathbb{R}_+^n$  are involved. Since the  $\Omega$ -limit set on the boundary may be considerably more complicated, this is a very helpful result.

*Proof.* We will use Theorem 10 on Average Lyapunov functions with the function

$$P(\mathbf{x}) = \prod_{i=1}^n x_i^{p_i} \quad (4.24)$$

to show permanence. Clearly,  $P(\mathbf{x}) = 0$  for  $\mathbf{x} \in \partial\mathbb{R}_+^n$  and  $P(\mathbf{x}) > 0$  for  $\mathbf{x} \in \text{int}(\mathbb{R}_+^n)$ . Also,

$$\begin{aligned}\dot{P}(\mathbf{x}) &= p_1 x_1^{p_1-1} \dot{x}_1 \left( \prod_{i=2}^n x_i^{p_i} \right) + x_1^{p_1} \left( p_2 x_2^{p_2-1} \dot{x}_2 \left( \prod_{i=3}^n x_i^{p_i} \right) + \dots \right) \\ &= \left( \prod_{i=1}^n x_i^{p_i} \right) p_1 \left( \frac{\dot{x}_1}{x_1} \right) + \left( \prod_{i=1}^n x_i^{p_i} \right) p_2 \left( \frac{\dot{x}_2}{x_2} \right) + \dots \\ &= P(\mathbf{x}) \cdot (\mathbf{p} \cdot (\mathbf{r} + A\mathbf{x})) = P(\mathbf{x})\Psi(\mathbf{x})\end{aligned}$$

where

$$\Psi(\mathbf{x}) = \mathbf{p} \cdot (\mathbf{r} + A\mathbf{x}). \quad (4.25)$$

Next, we must show that for every  $\mathbf{y} \in \Omega(\partial\mathbb{R}_+^n)$  there is a  $T > 0$  such that

$$\int_0^T \Psi(\mathbf{y}(t)) dt > 0. \quad (4.26)$$

We use proof by math induction on the number  $k$  of positive components of  $\mathbf{y}$ . For  $k = 1$ ,  $\mathbf{y}$  has only one positive component and thus lies on one of the positive axes of  $\mathbb{R}_+^n$ . Since each axis is invariant, the form of the equations requires that the  $\Omega$ -limit set of orbits on each axis contains only the equilibrium points on that axis. Then, (4.26) is an immediate consequence of our assumption (4.23).

We proceed with math induction by assuming that (4.26) is valid for  $k = 2, \dots, m-1$ . Define the index set

$$I = \{i : 1 \leq i \leq n \text{ and } y_i > 0\} \quad (4.27)$$

with cardinality  $m$ . Notice that  $I$  is a proper subset of  $\{1, \dots, n\}$ . Also, define

$$H(I) = \{\mathbf{x} \in \mathbb{R}_+^n : x_i = 0 \text{ for all } i \notin I\} \quad (4.28)$$

a subset of  $\mathbb{R}_+^n$ .

Now we must distinguish two cases:

- 1)  $\mathbf{y}(t)$  converges to the boundary of the hypersurface  $H(I)$  or
- 2)  $\mathbf{y}(t)$  does not converge to the boundary of the hypersurface  $H(I)$ .

For case 1), since  $\mathbf{y}(t)$  converges to the boundary of the hypersurface  $H(I)$ , the  $\Omega(\mathbf{y})$  is contained in a union of hypersurfaces of dimension  $m-1$ . Thus by the inductive assumption, (4.26) holds for all  $\mathbf{z} \in \Omega(\mathbf{y})$ .

For case 2), since  $\mathbf{y}(t)$  does not converge to the boundary of the hypersurface  $H(I)$ , there exists an  $\epsilon > 0$  and a sequence  $T_s \rightarrow +\infty$  such that

$$y_i(T_s) > \epsilon \text{ for all } i \in I \text{ and } s = 1, 2, \dots \quad (4.29)$$

Now, we define a sequence of  $T$ ,

$$\bar{y}_i(T) = \frac{1}{T} \int_0^T y_i(t) dt.$$

Since the orbits of our states are uniformly bounded, the sequence  $\bar{y}_i(T_s)$  is bounded. So we may obtain a subsequence, which we will again denote by  $T_s$ , such that  $\bar{y}_i(T_s)$  converges. We will denote the limit by  $\bar{x}_i$ .

For  $i \in I$ , using (4.29), we have

$$\frac{d}{dt}(\log y_i(t)) = \frac{\dot{y}_i(t)}{y_i(t)} = r_i + (A\mathbf{y})_i.$$

Integrating from 0 to  $T_s$  and dividing by  $T_s$ , we obtain

$$\begin{aligned} \frac{1}{T_s} \int_0^{T_s} \frac{d}{dt}(\log y_i(t)) dt &= \frac{1}{T_s} \int_0^{T_s} r_i + (A\mathbf{y}(t))_i dt \\ &= \frac{1}{T_s}(r_i T_s - 0) + \frac{1}{T_s} \int_0^{T_s} \sum_{j=1}^n a_{ij} y_j(t) dt \\ &= r_i + \sum_{j=1}^n a_{ij} \frac{1}{T_s} \int_0^{T_s} y_j(t) dt \\ &= r_i + \sum_{j=1}^n a_{ij} \bar{y}_j(T_s) \\ &= r_i + (A\bar{\mathbf{y}}(T_s))_i. \end{aligned}$$

So we get,

$$\frac{1}{T_s}((\log y_i(T_s)) - \log y_i(0)) = r_i + (A\bar{\mathbf{y}}(T_s))_i. \quad (4.30)$$

Since  $\log y_i(T_s)$  is bounded, the left hand side converges to zero. Hence,

$$r_i + (A\bar{\mathbf{x}}(T_s))_i = 0 \text{ for all } i \in I. \quad (4.31)$$

Note that  $\bar{x}_i \geq 0$  for all  $i$  and  $\bar{x}_i = 0$  for  $i \notin I$ , because the boundary is invariant. Hence,  $r_i + (A\bar{\mathbf{x}}(T_s))_i = 0$  for  $i \in I$  and  $\bar{x}_i = 0$  for  $i \notin I$ . Thus,  $\bar{\mathbf{x}}$  is an equilibrium point in  $S(I)$ . Now,

$$\frac{1}{T_s} \int_0^{T_s} \Psi(\mathbf{y}(t)) dt = \sum_{i=1}^n p_i \frac{1}{T_s} \int_0^{T_s} [r_i + (A\mathbf{y})_i] dt$$

converges to

$$\sum_{i=1}^n p_i [r_i + (A\bar{\mathbf{x}})_i] = \mathbf{p} \cdot (\mathbf{r} + A\mathbf{x})$$

which is positive by our assumption (4.23). Thus, we have proved (4.26) holds for all  $\mathbf{y} \in \Omega(\partial\mathbb{R}_+^n)$  with  $m$  components strictly positive. So by math induction, (4.26) holds for all  $\mathbf{y} \in \Omega(\partial\mathbb{R}_+^n)$ . Hence our system is permanent, completing the proof.

To apply the above theorems, our system must have uniformly bounded orbits. Note that if the original system (4.1) has uniformly bounded orbits, then the Lotka-Volterra system (4.13) with  $K = 1$ , has uniformly bounded orbits. The condition for the system (4.1) to have uniformly bounded orbits is given in the following theorem.

**Theorem 12** *Provided that  $e_{RP} < e_{CPE_{RC}}$ , all solutions of the system (4.3) that initiate in  $\mathbb{R}_+^3$  are uniformly bounded and enter a certain region  $B$  defined by*

$$B = \{(P, C, R) \in \mathbb{R}_+^3 : 0 \leq P + C + R \leq M\} \quad (4.32)$$

where

$$M = \max \left\{ \frac{M_1}{\lambda}, \frac{M_1}{e_{CP}\lambda}, \frac{M_1}{e_{CPE_{RC}}\lambda} \right\},$$

$$M_1 = \frac{Ke_{CPE_{RC}}(r + \lambda)^2}{4r},$$

and

$$0 < \lambda < \min(m_C, m_P).$$

That is, the system (4.1) is dissipative with the asymptotic bound  $M$ .

*Proof.* Recall that we have already shown that the components of all solutions of the system that initiate in  $\mathbb{R}_+^3$  are bounded below by zero. Now, define

$$S(t) = e_{CPE_{RC}}R + e_{CP}C + P.$$

The time derivative along a solution of the system is

$$\begin{aligned} \dot{S}(t) &= e_{CPE_{RC}}R[r(1 - R/K) - \alpha_{RC}C - \alpha_{RP}P] + e_{CP}C[e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_C] \\ &\quad + P[e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_P] \\ &= e_{CPE_{RC}}rR - (e_{CPE_{RC}}r/K)R^2 + (e_{RP}\alpha_{RP} - e_{CPE_{RC}}\alpha_{RP})RP - e_{CP}m_C C \\ &\quad - m_P P. \end{aligned}$$

For each  $\lambda > 0$  the following inequality is fulfilled:

$$\begin{aligned} \dot{S}(t) + \lambda S(t) &= (e_{CPE_{RC}}r + e_{CPE_{RC}}\lambda)R - (e_{CPE_{RC}}r/K)R^2 \\ &\quad + (e_{RP}\alpha_{RP} - e_{CPE_{RC}}\alpha_{RP})RP + (\lambda e_{CP} - e_{CP}m_C)C + (\lambda - m_P)P \\ &\leq (e_{CPE_{RC}}r + e_{CPE_{RC}}\lambda)R - (e_{CPE_{RC}}r/K)R^2 \end{aligned}$$

since  $e_{RP} < e_{CPE_{RC}}$  and we choose  $\lambda < \min(m_C, m_P)$ . Because the right hand side is a parabola that opens downward, it is bounded for all  $(P, C, R) \in \mathbb{R}_+^3$ . Specifically, the right hand side is bounded by  $M_1 = \frac{Ke_{CPE_{RC}}(r+\lambda)^2}{4r}$ . Thus, we find an  $M_1 > 0$  with

$$\dot{S} + \lambda S \leq M_1.$$

Applying Lemma 4, we obtain

$$0 \leq S(P, C, R) \leq \frac{M_1}{\lambda} + \left( S(P(0), C(0), R(0)) - \frac{M_1}{\lambda} \right) e^{-\lambda t}$$

and as  $t \rightarrow \infty$ ,  $0 \leq e_{CP}e_{RC}R + e_{CP}C + P \leq M_1/\lambda$ .

Now let  $M = \max \left\{ \frac{M_1}{\lambda}, \frac{M_1}{e_{CP}\lambda}, \frac{M_1}{e_{CP}e_{RC}\lambda} \right\}$ , then

$$0 \leq P + C + R \leq M.$$

Hence, system (4.1) is dissipative with the asymptotic bound  $M$ .

Thus, there is a compact neighborhood  $B \subseteq \mathbb{R}_+^3$  such that for sufficiently large  $T = T(c_1, c_2, c_3)$ ,  $(P(t), C(t), R(t)) \in B$  for all  $t \geq T$ , where  $(P(t), C(t), R(t))$  is a solution to (4.1) that initiates in  $\mathbb{R}_+^3$ . This completes the proof.

Now, we use Theorem 11 to determine conditions that guarantee permanence of the system (4.1).

**Theorem 13** *If the system (4.1) has uniformly bounded orbits ( $e_{RP} < e_{CP}e_{RC}$ ) and no boundary equilibrium is saturated, then the system is permanent. The conditions for no saturated boundary equilibria are:*

$$1) \ a, b, b', c, \text{ and } d \text{ hold or} \tag{4.33}$$

$$2) \ a, b, \text{ and } d \text{ hold, but not } b' \text{ or} \tag{4.34}$$

$$3) \ a, b', \text{ and } c \text{ hold, but not } b \tag{4.35}$$

where

$$a) \ r > 0 \tag{4.36}$$

$$b) \ e_{RP}\alpha_{RP}K - m_P > 0, \tag{4.37}$$

$$b') \ e_{RC}\alpha_{RC}K - m_C > 0, \tag{4.38}$$

$$c) \ m_C \left( \frac{e_{RP}\alpha_{RP}}{e_{RC}\alpha_{RC}} \right) + r \left( \frac{e_{CP}\alpha_{CP}}{\alpha_{RC}} \right) \left( 1 - \frac{m_C}{e_{RC}\alpha_{RC}K} \right) - m_P > 0, \tag{4.39}$$

$$d) \ m_P \left( \frac{e_{RC}\alpha_{RC}}{e_{RP}\alpha_{RP}} \right) - r \left( \frac{\alpha_{CP}}{\alpha_{RP}} \right) \left( 1 - \frac{m_P}{e_{RP}\alpha_{RP}K} \right) - m_C > 0. \tag{4.40}$$

*Proof.* We break the proof up into three parts. In Part I, we find the equilibria of the system (4.1). In this part of the proof, our results do not change for any  $K > 0$ . For Part II, we use Theorem 11 to show permanence for the Lotka-Volterra system (4.13) with  $K = 1$ . In Part III, we extend these results to include the case for any  $K > 0$ .

*Part I:* From the form of the equations in (4.1), we see that  $\mathbf{F}_0 = (0, 0, 0)^T$  is a boundary equilibrium point in  $\mathbb{R}_+^3$ . The only possible one species equilibrium is  $\mathbf{F}_R = (0, 0, K)^T$ .

The two species equilibria involve the resource and consumer,  $F_{RC}$ , and the resource and predator,  $F_{RP}$ :

$$\mathbf{F}_{RC} = \left( 0, \frac{r}{\alpha_{RC}} \left( 1 - \frac{m_C}{e_{RC}\alpha_{RC}K} \right), \frac{m_C}{e_{RC}\alpha_{RC}} \right)^T \quad (4.41)$$

$$\mathbf{F}_{RP} = \left( \frac{r}{\alpha_{RP}} \left( 1 - \frac{m_P}{e_{RP}\alpha_{RP}K} \right), 0, \frac{m_P}{e_{RP}\alpha_{RP}} \right)^T. \quad (4.42)$$

The equilibrium with the resource absent is never positive and thus does not exist. For the interior equilibrium,  $(\bar{x}_1, \bar{x}_2, \bar{x}_3)^T$ , of the system, we must solve the system

$$\begin{pmatrix} 0 & e_{CP}\alpha_{CP} & e_{RP}\alpha_{RP} \\ -\alpha_{CP} & 0 & e_{RC}\alpha_{RC} \\ -\alpha_{RP} & -\alpha_{RC} & -\frac{r}{K} \end{pmatrix} \begin{pmatrix} \bar{x}_1 \\ \bar{x}_2 \\ \bar{x}_3 \end{pmatrix} = \begin{pmatrix} m_P \\ m_C \\ -r \end{pmatrix} \quad (4.43)$$

to get

$$\mathbf{F}_{RCP} = (\bar{P}_1, \bar{C}_1, \bar{R}_1)^T \quad (4.44)$$

where

$$\begin{aligned} \bar{P}_1 &= \frac{Ke_{RP}\alpha_{RC}\alpha_{RP}m_C + rKe_{RC}\alpha_{RC}e_{CP}\alpha_{CP} - Ke_{RC}(\alpha_{RC})^2m_P - re_{CP}\alpha_{CP}m_C}{\alpha_{CP}\beta} \\ \bar{C}_1 &= \frac{Ke_{RP}\alpha_{RC}\alpha_{RP}m_C + r\alpha_{CP}m_P - Ke_{RP}(\alpha_{RP})^2m_C - rKe_{RP}\alpha_{RP}\alpha_{CP}}{\alpha_{CP}\beta} \\ \bar{R}_1 &= \frac{K(re_{CP}\alpha_{CP} + e_{CP}\alpha_{RC}m_C - \alpha_{RC}m_P)}{\beta} \end{aligned}$$

and

$$\beta = K\alpha_{RC}\alpha_{RP}(e_{RC}e_{CP} - e_{RP}) + re_{CP}\alpha_{CP}. \quad (4.45)$$

Notice that boundary equilibrium  $\mathbf{F}_{RC}$  exists in  $\mathbb{R}_+^3$  if and only if b' holds, and boundary equilibrium  $\mathbf{F}_{RP}$  exists in  $\mathbb{R}_+^3$  if and only if b holds.

*Part II:* Note that the equilibria for the Lotka-Volterra system are the same as for the system in Part I with  $K = 1$ . Now we apply Theorem 11 to the Lotka-Volterra system 4.13. We have to find  $p_1, p_2, p_3 > 0$  such that

$$\sum_{i:\bar{x}_i=0} p_i \left( r_i + \sum_{j=1}^3 a_{ij}\bar{x}_j \right) > 0 \quad (4.46)$$

at each boundary equilibria  $\bar{\mathbf{x}}$ .

For  $\mathbf{F}_{RC}$ , (4.46) becomes,

$$p_1(r_1 + a_{12}\bar{x}_2 + a_{13}\bar{x}_3) > 0. \quad (4.47)$$

But, we assumed that  $\mathbf{F}_{RC}$  is not saturated. That is,

$$f_1(\mathbf{F}_{RC}) = m_C \left( \frac{e_{RP}\alpha_{RP}}{e_{RC}\alpha_{RC}} \right) + r \left( \frac{e_{CP}\alpha_{CP}}{\alpha_{RC}} \right) \left( 1 - \frac{m_C}{e_{RC}\alpha_{RC}} \right) - m_P > 0 \quad (4.48)$$

since  $\bar{x}_1 = 0$ . However, (4.48) is the condition  $r_1 + a_{12}\bar{x}_2 + a_{13}\bar{x}_3 > 0$ . Thus, we have that (4.47) holds for any  $p_1 > 0$ .

Similarly, for  $\mathbf{F}_{RP}$  we need that

$$p_2(r_2 + a_{11}\bar{x}_1 + a_{13}\bar{x}_3) > 0. \quad (4.49)$$

$\mathbf{F}_{RC}$  not saturated means that

$$f_2(\mathbf{F}_{RP}) = m_P \left( \frac{e_{RC}\alpha_{RC}}{e_{RP}\alpha_{RP}} \right) - r \left( \frac{\alpha_{CP}}{\alpha_{RP}} \right) \left( 1 - \frac{m_P}{e_{RP}\alpha_{RP}} \right) - m_C > 0. \quad (4.50)$$

Thus, we have that (4.49) holds for any  $p_2 > 0$ .

At  $\mathbf{F}_0$  and  $\mathbf{F}_R$ , (4.46) yields:

$$p_1 r_1 + p_2 r_2 + p_3 r_3 > 0 \quad (4.51)$$

$$p_1(r_1 + a_{13}\bar{x}_3) + p_2(r_2 + a_{23}\bar{x}_3) > 0. \quad (4.52)$$

Since  $r > 0$  we have that  $\mathbf{F}_0$  is not saturated. In order for  $\mathbf{F}_R$  not to be saturated, we need either

$$f_1(0, 0, 1) = e_{RP}\alpha_{RP} - m_P > 0 \quad (4.53)$$

or

$$f_2(0, 0, 1) = e_{RC}\alpha_{RC} - m_C > 0 \quad (4.54)$$

or both, since  $\bar{x}_1 = \bar{x}_2 = 0$ . But,

$$r_1 + a_{13}\bar{x}_3 = e_{RP}\alpha_{RP} - m_P \quad (4.55)$$

and

$$r_2 + a_{23}\bar{x}_3 = e_{RC}\alpha_{RC} - m_C. \quad (4.56)$$

So in either case, we can first choose  $p_1$  and  $p_2$  such that (4.52) holds. Then for large  $p_3$ , (4.51) holds too. Thus, we have found a positive solution of (4.46). Hence by Theorem 11 the system 4.13 is permanent.

*Part III:* In all of the above calculations, the presence of a  $K > 0$  with  $K \neq 1$ , does not change the existence of a positive solution of (4.46) under the conditions set forth in the theorem. Hence, the system 4.1 is permanent. This completes the proof.

# Chapter 5

## Non-linear Response Omnivory Model

As noted in Section 2.1.4, Type I functional responses are unrealistic in most cases. To make our model more realistic, we use the non-linear Holling Type II functional responses defined in Section 2.1.4. This adds to the complexity of the model in a meaningful way, but we can no longer use the theory dealing with Lotka-Volterra models. However, the model is still of Kolmogorov type. Again, we assume that all parameters are positive.

Our non-linear response omnivory model is given by the system of differential equations

$$\frac{dP}{dt} = P \left[ \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_P \right] \quad (5.1a)$$

$$\frac{dC}{dt} = C \left[ \frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_C \right] \quad (5.1b)$$

$$\frac{dR}{dt} = R \left[ r \left( 1 - \frac{R}{K} \right) - \frac{\lambda_{RC}C}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{RP}P}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right] \quad (5.1c)$$

with initial conditions

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

This forms an initial value problem

$$\frac{d\mathbf{f}}{dt} = \mathbf{f}(\mathbf{x}), \quad \mathbf{f}(0) = \mathbf{c} \quad (5.3)$$

on  $D = \mathbb{R}_+ \times \mathbb{R}_+^3$  with the understood definitions for  $\mathbf{f}$ ,  $\mathbf{x}$ , and  $\mathbf{c}$ .

Parameter  $\lambda_{ij}$  is the search rate of species  $j$  for species  $i$ ,  $e_{ij}$  is the efficiency with which species  $i$  is converted to new offspring of species  $j$ , and  $h_{ij}$  is the time spent by species  $j$  handling species  $i$ .  $K$  is the resource carrying capacity and  $r$  is the intrinsic rate of increase of the resource. The natural mortality rates of the predator and consumer are  $m_P$  and  $m_C$ , respectively. A summary of the variables and parameters is given in Table 5.1.

With this more complicated model we hope to better approximate the natural omnivory system and obtain less stringent criteria for permanent coexistence that have some biological meaning. The fact that this system is of Kolmogorov type ensures that the boundary is invariant. This allows for more mathematically tractable analysis and satisfactory results.

Table 5.1: Definitions of variables and parameters in the non-linear response omnivory model.

Parameter	Definition
R	Resource density
C	Consumer density
P	Predator density
r	Resource intrinsic rate of increase
K	Environmental carrying capacity of the resource
$\lambda_{RC}$	Search rate of consumers for resources
$\lambda_{RP}$	Search rate of predators for resources
$\lambda_{CP}$	Search rate of predators for consumers
$h_{RC}$	Time spent by consumers handling resources
$h_{RP}$	Time spent by predators handling resources
$h_{CP}$	Time spent by predators handling consumers
$e_{RC}$	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

## 5.1 Solution to System

Again, we need to show that a unique solution exists for all  $t \geq 0$  in order to investigate long-term species survival. We will use an approach similar to the approach in the previous chapter.

Notice that  $\mathbf{f}$  and its partial derivatives

$$\begin{aligned} \frac{\partial \mathbf{f}}{\partial P} &= \begin{pmatrix} \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_P \\ -\frac{\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \\ -\frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \end{pmatrix} \\ \frac{\partial \mathbf{f}}{\partial C} &= \begin{pmatrix} \frac{e_{CP}\lambda_{CP}P(1 + \lambda_{RP}h_{RP}R) - e_{RP}\lambda_{RP}\lambda_{CP}h_{CP}RP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \\ \frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P(1 + \lambda_{RP}h_{RP}R)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} - m_C \\ -\frac{\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} + \frac{\lambda_{RP}\lambda_{CP}h_{CP}RP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \end{pmatrix} \\ \frac{\partial \mathbf{f}}{\partial R} &= \begin{pmatrix} \frac{e_{RP}\lambda_{RP}P(1 + \lambda_{CP}h_{CP}C) - e_{CP}\lambda_{RP}\lambda_{CP}h_{RP}CP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \\ \frac{e_{RC}\lambda_{RC}C}{(1 + \lambda_{RC}h_{RC}R)^2} + \frac{\lambda_{CP}\lambda_{RP}h_{RP}CP}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \\ r \left(1 - \frac{2R}{K}\right) - \frac{\lambda_{RC}C}{(1 + \lambda_{RC}h_{RC}R)^2} - \frac{\lambda_{RP}P(1 + \lambda_{CP}h_{CP}C)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \end{pmatrix} \end{aligned}$$

are all continuous with respect to P, C, and R for all positive t, P, C, and R. So by the Existence and Uniqueness Theorem 1 our initial value problem 5.3 has exactly one solution in D.

We will now show by means of a theorem that a unique solution exists for all  $t \geq 0$ .

**Theorem 14** *The initial value problem 5.3 has a unique solution in  $\mathbb{R}_+^3$  for all  $t \geq 0$ .*

*Proof.* Since the initial value problem is of Kolmogorov type,  $P(t), C(t), R(t) \geq 0$  for all  $t \geq 0$ . Then

$$R(t) \leq K_{max} \text{ for } 0 \leq t \leq \infty \quad (5.4)$$

by the exact argument in the proof of Theorem 6.

Also,

$$\frac{dC(t)}{dt} \leq \frac{e_{RC}\lambda_{RC}R(t)}{1 + h_{RC}\lambda_{RC}R(t)}C(t) \leq e_{RC}\lambda_{RC}R(t)C(t).$$

Since  $R(t) \leq K_{max}$ , we have that

$$\frac{dC(t)}{dt} \leq e_{RC}\lambda_{RC}K_{max}C(t) \text{ for } 0 \leq t \leq \infty.$$

If we define

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

then by Lemma 4 Part A

$$C(t) \leq c_2 e^{\Gamma t}. \quad (5.5)$$

This exponential function does not reach infinity in finite time.

Finally,

$$\frac{dP(t)}{dt} \leq \frac{e_{RP}\lambda_{RP}R(t) + e_{CP}\lambda_{CP}C(t)}{1 + \lambda_{RP}h_{RP}R(t) + \lambda_{CP}h_{CP}C(t)}P(t) \leq (e_{RP}\lambda_{RP}R(t) + e_{CP}\lambda_{CP}C(t))P(t).$$

Since  $R(t) \leq K_{max}$  and  $C(t) \leq c_2 e^{\Gamma t}$ , we have that

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

If we define

$$\Phi = e_{CP}\lambda_{CP}c_2$$

and

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

then by Lemma 4 Part C

$$P(t) \leq c_1 e^{\Gamma t + \Lambda(e^{\Gamma t} - 1)}. \quad (5.6)$$

This exponential function does not reach infinity in finite time. So by Lemma 2 and inequalities (5.4), (5.5), and (5.6) a unique solution for the initial value problem 5.3 exists for all  $t \geq 0$ . This completes the proof.

## 5.2 Permanent Coexistence

In this section we will show that our non-linear response omnivory model is permanently coexistent under certain parameter restrictions. We cannot expect criteria as precise as in the linear response omnivory model. In order to use available theory from Hutson et al. [43], we need the following definitions. Consider a system of three equations of Kolmogorov type:

$$\frac{dx_i}{dt} = x_i f_i(x), \quad 1 \leq i \leq 3, \quad (5.7)$$

where the  $f_i : \mathbb{R}_+^3 \rightarrow \mathbb{R}$  are  $C^1$ . We say that an orbit of (5.7) is **ultimately in**  $M \subset \mathbb{R}_+^3$  if and only if there exists  $T(\mathbf{x}) < \infty$  such that  $\mathbf{x}(t) \in M$  for  $t \geq T(\mathbf{x})$ . We use the notation  $A - B$  to denote set difference for two sets A and B. Recall from Chapter 2, that the system (5.7) is **permanently coexistent** if and only if there exists a compact set  $M \subset \mathbb{R}_+^3$  such that orbits are ultimately in M for all  $\mathbf{x} \in \mathbb{R}_+^3$ .

Our proof on permanent coexistence will be based on the following theorem from Hutson et al. [43] which is an extension of a result by Hofbauer [35].

**Theorem 15** *Let  $B \subseteq \mathbb{R}_+^3$  be compact and  $S$  a compact subset of  $B$ . Assume that  $S$  and  $B - S$  are invariant. Suppose that there is a  $C^1$  function  $P : B \rightarrow \mathbb{R}_+$  which is such that  $P(\mathbf{x}) = 0$  if and only if  $\mathbf{x} \in S$ . Take  $\Psi(\mathbf{x}) = \dot{P}(\mathbf{x})/P(\mathbf{x})$  and assume that  $\Psi$  is bounded below on  $B - S$ . Define its (lower semicontinuous) extension to  $S$ , still denoted by  $\Psi$ , by setting*

$$\Psi(\mathbf{x}) = \liminf_{\mathbf{y} \rightarrow \mathbf{x}, \mathbf{y} \in B - S} \Psi(\mathbf{y}) \quad (\mathbf{x} \in S) \quad (5.8)$$

and assume that for

$$\mathbf{x} \in \overline{\Omega(S)}, \quad \sup_{t \geq 0} \int_0^t \Psi(\mathbf{x}(t)) dt > 0. \quad (5.9)$$

Then there is a compact invariant set  $M$  with  $d(M, S) > 0$  which is such that every orbit generated by (5.7) with  $\mathbf{x} \in \mathbb{R}_+^3$  is ultimately in  $M$ . That is the system (5.7) is permanently coexistent.

The function P is an extension of our Average Lyapunov function given in Definition 7 and is also known as an Average Lyapunov function [43]. Note that (5.9) holds if  $\Psi > 0$  on  $\overline{\Omega(S)}$ .

We begin our analysis by showing that our non-linear system (5.1) has uniformly bounded orbits and enters a compact region of  $\mathbb{R}_+^3$ .

**Theorem 16** *Provided that  $e_{RP} < e_{CP}e_{RC}$ , all solutions of the system (5.1) that initiate in  $\mathbb{R}_+^3$  are uniformly bounded and enter a certain region  $B$  defined by*

$$B = \{(P, C, R) \in \mathbb{R}_+^3 : 0 \leq P + C + R \leq M\} \quad (5.10)$$

where

$$M = \max \left\{ \frac{M_1}{\lambda}, \frac{M_1}{e_{CP}\lambda}, \frac{M_1}{e_{CP}e_{RC}\lambda} \right\},$$

$$M_1 = \frac{Ke_{CPE_{RC}}(r + \lambda)^2}{4r},$$

and

$$0 < \lambda < \min(m_C, m_P).$$

That is, the system (5.1) is dissipative with the asymptotic bound  $M$ .

*Proof.* This proof is similar to the one given in Chapter 4, so we will not present the details. Define

$$S(t) = e_{CPE_{RC}}R + e_{CPC} + P.$$

The time derivative along a solution of the system is

$$\begin{aligned} \dot{S}(t) &= e_{CPE_{RC}}rR - (e_{CPE_{RC}}r/K)R^2 + (e_{RP} - e_{CPE_{RC}}) \left( \frac{\lambda_{RP}}{1 + \lambda_{RP}h_{RP}R + \lambda_{CPh_{CPC}}} \right) RP \\ &\quad - e_{CP}m_eC - m_P P. \end{aligned}$$

For each  $\lambda > 0$  the following inequality is fulfilled:

$$\begin{aligned} \dot{S}(t) + \lambda S(t) &= (e_{CPE_{RC}}r + e_{CPE_{RC}}\lambda)R - (e_{CPE_{RC}}r/K)R^2 \\ &\quad + (e_{RP} - e_{CPE_{RC}}) \left( \frac{\lambda_{RP}}{1 + \lambda_{RP}h_{RP}R + \lambda_{CPh_{CPC}}} \right) RP \\ &\quad + (\lambda e_{CP} - e_{CP}m_e)C + (\lambda - m_P)P \\ &\leq (e_{CPE_{RC}}r + e_{CPE_{RC}}\lambda)R - (e_{CPE_{RC}}r/K)R^2. \end{aligned}$$

Again, this is a parabola that opens downward. Following the argument in Chapter 4, we have that there is a compact neighborhood  $B \subseteq \mathbb{R}_+^3$  such that for sufficiently large  $T = T(c_1, c_2, c_3)$ ,  $(P(t), C(t), R(t)) \in B$  for all  $t \geq T$ , where  $(P(t), C(t), R(t))$  is a solution to (5.1) that initiates in  $\mathbb{R}_+^3$ . This completes the proof.

Since we have global existence and uniqueness of a solution,  $\mathbb{R}_+^3$  and the compact set  $B$  from Theorem 16 are invariant. Now define the set  $S = B \cap \partial\mathbb{R}_+^3$ .

**Lemma 7** *The sets  $S$  and  $B - S$  are invariant.*

*Proof.* Assume that  $\mathbf{x}_0 \in S$  and  $\mathbf{x}(t)$  is a solution of the system (5.1) with  $\mathbf{x}(t_0) = \mathbf{x}_0$ . Since  $B$  and  $\partial\mathbb{R}_+^3$  are invariant, then  $\mathbf{x}(t) \in B$  and  $\mathbf{x}(t) \in \mathbb{R}_+^3$  for all  $t > t_0$ . Thus,  $S = B \cap \partial\mathbb{R}_+^3$  is invariant. Now assume that  $\mathbf{x}_0 \in B - S$  and  $\mathbf{x}(t)$  is a solution of the system (5.1) with  $\mathbf{x}(t_0) = \mathbf{x}_0$ . Since  $S$  and  $B$  are invariant we have global existence and uniqueness of solutions, then  $\mathbf{x}(t) \in B$  and  $\mathbf{x}(t) \notin S$  for all  $t > t_0$ . Hence,  $B - S$  is invariant. This completes the proof.

Now, we use Theorem 15 to determine conditions that guarantee permanence of the system (5.1).

**Theorem 17** *Assume that the following conditions hold:*

(H1) *The solutions of (5.1) in  $\mathbb{R}_+^3$  are uniformly bounded.*

(H2) *The  $\Omega$ -limit of every orbit on  $\partial\mathbb{R}_+^3$  consists of equilibrium points.*

(H3) *No boundary equilibrium is saturated.*

*Then the system (5.1) is permanent. The conditions for no saturated boundary equilibria are:*

$$1) \ a, b, b', c, \text{ and } d \text{ hold } \mathbf{or} \quad (5.11)$$

$$2) \ a, b, \text{ and } d \text{ hold, but not } b' \ \mathbf{or} \quad (5.12)$$

$$3) \ a, b', \text{ and } c \text{ hold, but not } b \quad (5.13)$$

where

$$a) \ r > 0 \quad (5.14)$$

$$b) \ \frac{e_{RP}\lambda_{RP}K}{1 + \lambda_{RP}h_{RP}K} - m_P > 0, \quad (5.15)$$

$$b') \ \frac{e_{RC}\lambda_{RC}K}{1 + \lambda_{RC}h_{RC}K} - m_C > 0, \quad (5.16)$$

$$c) \ \frac{\lambda_{RC}K\xi_1(\lambda_{RPe_{RPM_C} + \lambda_{CPe_{CPe_{RC}r}}) - \lambda_{CPe_{CPe_{RC}m_Cr}}}{K(\lambda_{RC})^2\xi_1^2 - \lambda_{CPe_{RC}h_{CPm_Cr}} + \lambda_{RC}K\xi_1\nu} - m_P > 0, \quad (5.17)$$

$$d) \ \frac{\lambda_{RCe_{RC}m_P}{\lambda_{RPe_{RP}} + \lambda_{RC}h_{RC}m_P - \lambda_{RP}h_{RPM_P}} \quad (5.18)$$

$$+ \frac{r\lambda_{CP}(\lambda_{RP}h_{RP}Km_P + m_p - \lambda_{RPe_{RP}K})}{K(\lambda_{RP})^2\xi_2} - m_C > 0 \quad (5.19)$$

and

$$\xi_1 = e_{RC} - m_Ch_{RC}$$

$$\xi_2 = e_{RP} - m_Ph_{RP}$$

$$\xi_3 = e_{CP} - m_Ph_{CP}$$

$$\nu = \lambda_{RP}h_{RPM_C} + r\lambda_{CP}h_{CPe_{RC}}.$$

*Proof.* We break the proof up into two parts. In Part I, we find the equilibria of the system (5.1). For Part II, we use Theorem 15 to show permanence.

*Part I:* From the form of the equations in (5.1), we see that  $\mathbf{F}_0 = (0, 0, 0)^T$  is a boundary equilibrium point in  $\mathbb{R}_+^3$ . The only possible one species equilibrium is  $\mathbf{F}_R = (0, 0, K)^T$ . The two species equilibria involve the resource and consumer,  $F_{RC}$ , and the resource and predator,  $F_{RP}$ :

$$\mathbf{F}_{RC} = \left( 0, \frac{re_{RC}[K\lambda_{RC}(e_{RC} - m_Ch_{RC}) - m_C]}{K(\lambda_{RC})^2(e_{RC} - m_Ch_{RC})^2}, \frac{m_C}{\lambda_{RC}(e_{RC} - m_Ch_{RC})} \right)^T \quad (5.20)$$

$$\mathbf{F}_{RP} = \left( \frac{re_{RP}[K\lambda_{RP}(e_{RP} - m_Ph_{RP}) - m_P]}{K(\lambda_{RP})^2(e_{RP} - m_Ph_{RP})^2}, 0, \frac{m_P}{\lambda_{RP}(e_{RP} - m_Ph_{RP})} \right)^T. \quad (5.21)$$

The equilibrium with the resource absent is never positive and thus does not exist. Notice that boundary equilibrium  $\mathbf{F}_{RC}$  exists in  $\mathbb{R}_+^3$  if and only if b' holds. This is due to the fact that

$$\frac{e_{RC}\lambda_{RC}K}{1 + \lambda_{RC}h_{RC}K} - m_C > 0 \Rightarrow e_{RC} > m_C \left( h_{RC} + \frac{1}{K\lambda_{RC}} \right) > m_C h_{RC}. \quad (5.22)$$

Similarly, boundary equilibrium  $\mathbf{F}_{RP}$  exists in  $\mathbb{R}_+^3$  if and only if b holds.

*Part II:* Let  $\mathbf{x}(t) = (P(t), C(t), R(t))^T$  and

$$P(\mathbf{x}) = x_1^{p_1} x_2^{p_2} x_3^{p_3} (x_1 + x_2)^\epsilon. \quad (5.23)$$

Clearly,  $P(\mathbf{x}) = 0$  for  $\mathbf{x} \in \partial\mathbb{R}_+^3$  and  $P(\mathbf{x}) > 0$  for  $\mathbf{x} \in \text{int}(\mathbb{R}_+^3)$ . Also,

$$\begin{aligned} \dot{P}(\mathbf{x}) &= p_1 x_1^{p_1-1} \dot{x}_1 (x_2^{p_2} x_3^{p_3} (x_1 + x_2)^\epsilon) + x_1^{p_1} (p_2 x_2^{p_2-1} \dot{x}_2 x_3^{p_3} (x_1 + x_2)^\epsilon \\ &\quad + x_2^{p_2} (p_3 x_3^{p_3-1} \dot{x}_3 (x_1 + x_2)^\epsilon + x_3^{p_3} \epsilon (x_1 + x_2)^{\epsilon-1} (\dot{x}_1 + \dot{x}_2))) \\ &= x_1^{p_1} x_2^{p_2} x_3^{p_3} (x_1 + x_2)^\epsilon \left( p_1 f_1(\mathbf{x}) + p_2 f_2(\mathbf{x}) + p_3 f_3(\mathbf{x}) + \epsilon \left( \frac{x_1 f_1(\mathbf{x}) + x_2 f_2(\mathbf{x})}{x_1 + x_2} \right) \right) \\ &= P(\mathbf{x}) \Psi(\mathbf{x}) \end{aligned}$$

where

$$\Psi(\mathbf{x}) = \sum_{i=1}^3 p_i f_i(\mathbf{x}) + \epsilon (x_1 f_1(\mathbf{x}) + x_2 f_2(\mathbf{x})) / (x_1 + x_2) \quad (5.24)$$

in  $\text{int}(\mathbb{R}_+^3)$ . However, the last term in  $\Psi$  does not admit a continuous extension to the  $x_3$ -axis. To correct this, we take the lower semicontinuous extension and the last term in (5.24) becomes

$$\Psi(0, 0, x_3) = \epsilon \min(f_1(0, 0, x_3), f_2(0, 0, x_3)). \quad (5.25)$$

By (H2), condition (5.9) reduces to

$$\Psi(\mathbf{x}) > 0 \quad (5.26)$$

for all equilibrium points in  $\partial\mathbb{R}_+^3$ , for a suitable choice of  $\epsilon \geq 0, p_1, p_2, p_3 > 0$ . For  $\mathbf{F}_{RC}$  and  $\mathbf{F}_{RP}$ , (5.26) becomes,

$$p_1 f_1(0, \bar{C}, \bar{R}) > 0 \quad (5.27)$$

$$p_2 f_2(\bar{P}, 0, \bar{R}) > 0 \quad (5.28)$$

respectively. But, we assumed that no boundary equilibria are saturated. That is,

$$f_1(\mathbf{F}_{RC}) = \frac{\lambda_{RC} K \xi_1 (\lambda_{RP} e_{RP} m_C + \lambda_{CP} e_{CP} e_{RC} r) - \lambda_{CP} e_{CP} e_{RC} m_C r}{K (\lambda_{RC})^2 \xi_1^2 - \lambda_{CP} e_{RC} h_{CP} m_C r + \lambda_{RC} K \xi_1 \nu} - m_P > 0 \quad (5.29)$$

$$f_2(\mathbf{F}_{RP}) = \frac{\lambda_{RC} e_{RC} m_P}{\lambda_{RP} e_{RP} + \lambda_{RC} h_{RC} m_P - \lambda_{RP} h_{RP} m_P} \quad (5.30)$$

$$+ \frac{r \lambda_{CP} (\lambda_{RP} h_{RP} K m_P + m_p - \lambda_{RP} e_{RP} K)}{K (\lambda_{RP})^2 \xi_2} - m_C > 0. \quad (5.31)$$

Thus, we have that (5.27) and (5.28) hold for any  $p_1, p_2 > 0$ .

At  $\mathbf{F}_0$  and  $\mathbf{F}_R$ , (5.26) yields:

$$p_1 f_1(\mathbf{0}) + p_2 f_2(\mathbf{0}) + p_3 f_3(\mathbf{0}) + \epsilon \min(f_1(\mathbf{0}), f_2(\mathbf{0})) > 0 \quad (5.32)$$

$$p_1 f_1(0, 0, K) + p_2 f_2(0, 0, K) + \epsilon \min(f_1(0, 0, K), f_2(0, 0, K)) > 0. \quad (5.33)$$

Since  $r > 0$  we have that  $\mathbf{F}_0$  is not saturated. In order for  $\mathbf{F}_R$  not to be saturated, we need either

$$f_1(0, 0, K) = \frac{e_{RP}\lambda_{RP}K}{1 + \lambda_{RP}h_{RP}K} - m_P > 0 \quad (5.34)$$

or

$$f_2(0, 0, K) = \frac{e_{RC}\lambda_{RC}K}{1 + \lambda_{RC}h_{RC}K} - m_C > 0 \quad (5.35)$$

or both, since  $\bar{P} = \bar{C} = 0$ . So in either case, we can first choose  $p_1 > 0$ ,  $p_2 > 0$ , and  $\epsilon = 0$  such that (5.33) holds. Since  $f_3(\mathbf{0}) > 0$ , then for large  $p_3$ , (5.32) holds too. Hence, by Theorem 15 the system 5.1 is permanent.

Finally, we show that the  $\Omega$ -limit set of every orbit in  $\partial\mathbb{R}_+^3$  is an equilibrium point. The zero equilibrium is unstable due to the fact that  $r$  and  $K$  are positive. Also, it is well known that solutions to the logistic equation quickly reach the fixed carrying capacity  $K$  [28]. For the predator-prey subsystems, there may be periodic orbits.

We use a Lemma from Hsu [42] which is based on an application of the Poincaré-Bendixson Theorem and the Dulac Criterion [50] to show that a positive stable equilibrium of a predator-prey system is globally stable. Consider the predator-prey model

$$\frac{dx}{dt} = xg(x) - yp(x) \quad (5.36)$$

$$\frac{dy}{dt} = y[e_{xy}p(x) - m_y] \quad (5.37)$$

where  $x$  represents the prey density and  $y$  represents the predator density and

$$g(x) = r \left(1 - \frac{x}{K}\right) \quad (5.38)$$

$$p(x) = \frac{\lambda_{xy}x}{1 + x} \quad (5.39)$$

To investigate global stability, we compute the variational matrix evaluated at the positive equilibrium  $(x^*, y^*)$ ,

$$H(x^*) = x^* g'(x^*) + g(x^*) - \frac{x^* g(x^*) p'(x^*)}{p(x^*)}. \quad (5.40)$$

Then the equilibrium is (locally) asymptotically stable if  $H(x^*) \leq 0$  [42]. Graphically, this means that if the prey isocline  $y = \frac{xg(x)}{p(x)}$  is decreasing at  $x^*$ , then  $(x^*, y^*)$  is asymptotically stable. To give conditions under which local stability of  $(x^*, y^*)$  implies global stability of  $(x^*, y^*)$  we give the following Lemma without proof from Hsu [42].

**Lemma 8** Assume the equilibrium  $(x^*, y^*)$  of (5.36) is stable and

$$\frac{d^2}{dx^2} \left( \frac{xg(x)}{p(x)} \right) < 0 \text{ for } 0 \leq x \leq K. \quad (5.41)$$

Then  $(x^*, y^*)$  is globally stable.

Thus, we can prove the following theorem on the  $\Omega$ -limit set of every orbit in  $\partial\mathbb{R}_+^3$ .

**Theorem 18** Let the conditions of Lemma 8 hold for the two equilibria  $(\bar{C}, \bar{R})$  and  $(\bar{P}, \bar{R})$  of the appropriate subsystems of (5.1), that is

$$H(\bar{R}) = \frac{rm_C(\lambda_{RC}(K-1)\xi_1 - 2m_C)}{\lambda_{RC}K\xi_1(m_C + \lambda_{RC}\xi_1)} \leq 0 \quad (5.42)$$

$$\frac{d^2}{dx^2} \left( \frac{xg(x)}{p(x)} \right) = -\frac{2r}{\lambda_{RC}K} < 0 \quad (5.43)$$

and

$$H(\bar{R}) = \frac{rm_P(\lambda_{RP}(K-1)\xi_2 - 2m_P)}{\lambda_{RP}K\xi_2(m_P + \lambda_{RP}\xi_2)} \leq 0 \quad (5.44)$$

$$\frac{d^2}{dx^2} \left( \frac{xg(x)}{p(x)} \right) = -\frac{2r}{\lambda_{RP}K} < 0 \quad (5.45)$$

respectively, where

$$\xi_1 = e_{RC} - m_C h_{RC} \quad (5.46)$$

$$\xi_2 = e_{RP} - m_P h_{RP} \quad (5.47)$$

Then for the system (5.1), the  $\Omega$ -limit set of every orbit in  $\partial\mathbb{R}_+^3$  is an equilibrium point.

*Proof.* From the above comments, we see that the  $\Omega$ -limit set of every orbit on each axis is an equilibrium point. Since the conditions of Theorem 8 hold, then each stable equilibrium in the bounding hyperplanes is globally stable. That is, the  $\Omega$ -limit set of every orbit in each bounding hyperplane is an equilibrium point, completing the proof.

Notice that conditions on the curvature are trivially satisfied for our system because we assume  $r, K, \lambda_{RC}, \lambda_{RP} > 0$ .

# Chapter 6

## Stage Structured Omnivory Model

In an attempt to better model the real world, we expand our non-linear response omnivory model to take into account a form of stage structure. As noted by Gotelli [28], “for most plants and animals, birth and death rates depend on the age [stage] of an individual... [and] age [stage] structure of an individual has the potential to affect population growth”. Ebenman et al. [15] state that size is “no doubt, one of the most important characteristics of any organism”. Mylius et al. [71] add that “intraguild predation is especially likely to occur in systems with stage- or size- structured populations”. Therefore, we feel that adding stage structure to our existing omnivory model is a natural and important extension. The stage structure of the predator species will be investigated in this chapter.

We consider a non-linear response omnivory model with top predator stage structure. We model the natural system with a system of ordinary differential equations

$$\frac{dP_2}{dt} = \mu_P P_1 - m_P P_2 \quad (6.1a)$$

$$\frac{dP_1}{dt} = \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} P_2 - (\mu_P + m_P) P_1 \quad (6.1b)$$

$$\frac{dC}{dt} = C \left[ \frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} - m_C \right] \quad (6.1c)$$

$$\frac{dR}{dt} = R \left[ r \left( 1 - \frac{R}{K} \right) - \frac{\lambda_{RC}C}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{RP}P_1}{1 + \lambda_{RP}h_{RP}R} - \frac{\lambda_{RP}P_2}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right] \quad (6.1d)$$

and initial conditions

$$P_2(0) = c_1 > 0, \quad P_1(0) = c_2 > 0, \quad C(0) = c_3 > 0, \quad \text{and} \quad R(0) = c_4 > 0. \quad (6.2)$$

In this model the predator population is divided into two stage classes. The initial class consists of small individuals (with density  $P_1$ ) and the second class consists of larger individuals (with density  $P_2$ ). The initial class matures at rate  $\mu_P$  and does not prey upon the consumer population. However, both classes prey upon the resource population at the

Table 6.1: Definitions of variables and parameters in the stage structure omnivory model.

Parameter	Definition
$R$	Resource density
$C$	Consumer density
$P_1$	Young/Small Predator density
$P_2$	Mature/Large Predator density
$r$	Resource intrinsic rate of increase
$K$	Environmental carrying capacity of the resource
$\lambda_{RC}$	Search rate of consumers for resources
$\lambda_{RP}$	Search rate of predators for resources
$\lambda_{CP}$	Search rate of predators for consumers
$h_{RC}$	Time spent by consumers handling resources
$h_{RP}$	Time spent by predators handling resources
$h_{CP}$	Time spent by predators handling consumers
$e_{RC}$	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 for both predator classes
$\mu_P$	Predator maturation rate

same rate. The second class preys on both the resource and consumer populations. Notice that our model assumes no reproduction by the individuals of the initial class. Both classes of predators decline by means of a natural mortality rate  $m_P$ . The density of the second class only increases due to maturation from the initial class. All other parameters are identical to those used in the non-linear response omnivory model. The additional parameters used in this model are also positive. A summary of the variables and parameters is given in Table 6.1.

The initial value problem

$$\frac{d\mathbf{f}}{dt} = \mathbf{f}(\mathbf{x}), \quad \mathbf{f}(0) = \mathbf{c} \quad (6.3)$$

is defined on  $D = \mathbb{R}_+ \times \mathbb{R}_+^4$  with the understood definitions for  $\mathbf{f}$ ,  $\mathbf{x}$ , and  $\mathbf{c}$ .

This more complicated initial value problem will better model some omnivory systems, but this model is no longer of Kolmogorov type and in fact, the boundary is not invariant. However, we have shown in Section 2.3.2, that solutions of this system are all pointing into  $\mathbb{R}_+^4$  on the bounding hypersurfaces. This fact will become useful in our analysis.

## 6.1 Solution to System

Again, an investigation of the long-term survival of species requires that a unique solution exists for all  $t \geq 0$ . We use an approach similar to the approaches used in the previous two chapters.

Since  $\mathbf{f}$  and its partial derivatives

$$\begin{aligned} \frac{\partial \mathbf{f}}{\partial P_2} &= \begin{pmatrix} -m_P \\ \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \\ -\frac{\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \\ -\frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \end{pmatrix} \\ \frac{\partial \mathbf{f}}{\partial P_1} &= \begin{pmatrix} \mu_P \\ -(\mu_P + m_P) \\ 0 \\ -\frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R} \end{pmatrix} \\ \frac{\partial \mathbf{f}}{\partial C} &= \begin{pmatrix} 0 \\ \frac{e_{CP}\lambda_{CP}P_2(1 + \lambda_{RP}h_{RP}R) - e_{RP}\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \\ \frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2(1 + \lambda_{RP}h_{RP}R)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} - m_C \\ -\frac{\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} + \frac{\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \end{pmatrix} \\ \frac{\partial \mathbf{f}}{\partial R} &= \begin{pmatrix} 0 \\ \frac{e_{RP}\lambda_{RP}P_2(1 + \lambda_{CP}h_{CP}C) - e_{CP}\lambda_{RP}\lambda_{CP}h_{RP}CP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \\ \frac{e_{RC}\lambda_{RC}C}{(1 + \lambda_{RP}h_{RP}R)^2} + \frac{\lambda_{CP}\lambda_{RP}h_{RP}CP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \\ r \left(1 - \frac{2R}{K}\right) - \frac{\lambda_{RC}C}{(1 + \lambda_{RC}h_{RC}R)^2} - \frac{\lambda_{RP}P_1}{(1 + \lambda_{RP}h_{RP}R)^2} - \frac{\lambda_{RP}P_2(1 + \lambda_{CP}h_{CP}C)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \end{pmatrix} \end{aligned}$$

are all continuous with respect to P, C, and R for all positive t, P, C, and R, our initial value problem 6.3 has exactly one solution in D.

We will now show by means of a theorem that a unique solution exists for all  $t \geq 0$ .

**Theorem 19** *The initial value problem 6.3 has a unique solution in  $\mathbb{R}_+^4$  for all  $t \geq 0$ .*

*Proof.* As noted earlier,  $P_2(t), P_1(t), C(t), R(t) \geq 0$  for all  $t \geq 0$ . Then

$$R(t) \leq K_{max} \quad \text{for } 0 \leq t \leq \infty \quad (6.4)$$

by the exact argument in the proof of Theorem 14.

Similar to the argument in the proof of Theorem 14, if we let

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

then

$$C(t) \leq c_3 e^{\Gamma t} \quad (6.5)$$

and this exponential function does not reach infinity in finite time.

Further,

$$\begin{aligned}\frac{dP_1(t)}{dt} &\leq (e_{RP}\lambda_{RP}R(t) + e_{CP}\lambda_{CP}C(t))P_2(t) \\ \frac{dP_2(t)}{dt} &\leq \mu_P P_1(t).\end{aligned}$$

Since  $R(t) \leq K_{max}$  and  $C(t) \leq c_3 e^{\Gamma t}$ , we have that

$$\begin{aligned}\frac{dP_1(t)}{dt} &\leq (\Gamma + e_{CP}\lambda_{CP}c_3 e^{\Gamma t})P_2(t) \\ \frac{dP_2(t)}{dt} &\leq \mu_P P_1(t)\end{aligned}$$

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

$$\Phi = e_{CP}\lambda_{CP}c_3$$

and rewrite these inequalities in matrix form

$$\frac{d}{dt} \begin{pmatrix} P_1(t) \\ P_2(t) \end{pmatrix} \leq \begin{bmatrix} 0 & \Gamma + \Phi e^{\Gamma t} \\ \mu_P & 0 \end{bmatrix} \begin{pmatrix} P_1(t) \\ P_2(t) \end{pmatrix}. \quad (6.6)$$

Since

$$2 \begin{pmatrix} P_1(t) & P_2(t) \end{pmatrix} \frac{d}{dt} \begin{pmatrix} P_1(t) \\ P_2(t) \end{pmatrix} = \frac{d}{dt} \left\| \begin{pmatrix} P_1(t) \\ P_2(t) \end{pmatrix} \right\|^2, \quad (6.7)$$

we can multiply both sides of (6.6) by 2 and the row vector  $(P_1(t) P_2(t))$  to get

$$\begin{aligned}\frac{d}{dt} \left\| \begin{pmatrix} P_1(t) \\ P_2(t) \end{pmatrix} \right\|^2 &\leq 2(\Gamma + \Phi e^{\Gamma t})P_1(t)P_2(t) \\ &\leq (\Gamma + \Phi e^{\Gamma t})((P_1(t))^2 + (P_2(t))^2).\end{aligned}$$

So we have

$$\frac{d}{dt} \left\| \begin{pmatrix} P_1(t) \\ P_2(t) \end{pmatrix} \right\|^2 \leq (\Gamma + \Phi e^{\Gamma t}) \left\| \begin{pmatrix} P_1(t) \\ P_2(t) \end{pmatrix} \right\|^2. \quad (6.8)$$

If we define

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

and apply Lemma 4 Part C to the scalar equation (6.8) we have

$$\frac{d}{dt} \left\| \begin{pmatrix} P_1(t) \\ P_2(t) \end{pmatrix} \right\|^2 \leq ((c_2)^2 + (c_1)^2) e^{\Gamma t + \Lambda(e^{\Gamma t} - 1)} \quad (6.9)$$

and this exponential function does not reach infinity in finite time. The above inequality ensures the  $P_1(t)$  and  $P_2(t)$  do not reach infinity in finite time.

Hence, by Lemma 2 and inequalities (6.4), (6.5), and (6.9) a unique solution for the initial value problem 6.3 exists for all  $t \geq 0$ . This completes the proof.

## 6.2 Permanent Coexistence

In this section we will investigate the permanence of our stage structure omnivory model. Model (6.1) does not leave the boundary invariant, so we cannot use the available theory on Average Lyapunov functions. However, we have already shown that solutions are nonnegative for all positive time (see Lemma 6). Again, we must require that solutions are uniformly bounded.

**Theorem 20** *Provided that*

$$e_{RP} < e_{CP}e_{RC} \quad (6.10)$$

and

$$\mu_P \leq e_{RC}e_{CP} \left( \frac{e_{RP}\lambda_{RP}K_{max}}{1 + \lambda_{RP}h_{RP}K_{max}} \right) - \lambda e_{RP}, \quad (6.11)$$

all solutions of the system (6.1) that initiate in  $\mathbb{R}_+^4$  are uniformly bounded and enter a certain region  $B$  defined by

$$B = \{(P_2, P_1, C, R) \in \mathbb{R}_+^4 : 0 \leq P_2 + P_1 + C + R \leq M\} \quad (6.12)$$

where

$$M = \max \left\{ \frac{M_1}{\lambda}, \frac{M_1}{e_{RP}\lambda}, \frac{M_1}{e_{RP}e_{CP}e_{RC}\lambda}, \frac{M_1}{e_{RP}e_{CP}\lambda} \right\},$$

$$M_1 = \frac{Ke_{RP}e_{CP}e_{RC}(r + \lambda)^2}{4r},$$

and

$$0 < \lambda < \min(m_C, \mu_P + 2m_P).$$

That is, the system (6.1) is dissipative with the asymptotic bound  $M$ .

*Proof.* From a similar argument in the other proofs on uniformly bounded orbits, we have

$$R(t) \leq K_{max} \text{ for all } t \geq 0.$$

Now, define

$$S(t) = e_{RP}e_{CP}e_{RC}R + e_{RP}e_{CP}C + e_{RP}P_1 + P_2.$$

The time derivative along a solution of the system is

$$\begin{aligned} \dot{S}(t) = & e_{RP}e_{CP}e_{RC}r \left( R - \frac{R^2}{K} \right) + (e_{RP} - e_{CP}e_{RC}) \left( \frac{e_{RP}\lambda_{RP}}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right) RP_2 \\ & + \left( \mu_P - e_{RC}e_{CP} \left( \frac{e_{RP}\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R} \right) \right) P_1 - e_{RP}e_{CP}m_C C - (\mu_P + 2m_P)P_2. \end{aligned}$$

For each  $\lambda > 0$  the following inequality is fulfilled:

$$\begin{aligned} \dot{S}(t) + \lambda S(t) &= (e_{RP}e_{CP}e_{RC}r + e_{RP}e_{CP}e_{RC}\lambda)R - (e_{RP}e_{CP}e_{RC}r/K)R^2 \\ &\quad + \left( \lambda e_{RP} + \mu_P - e_{RC}e_{CP} \left( \frac{e_{RP}\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R} \right) \right) P_1 \\ &\quad + (\lambda e_{RP}e_{CP} - e_{RP}e_{CP}m_C)C + (\lambda - (\mu_P + 2m_P))P_2 \\ &\leq (e_{RP}e_{CP}e_{RC}r + e_{RP}e_{CP}e_{RC}\lambda)R - (e_{RP}e_{CP}e_{RC}r/K)R^2 \end{aligned}$$

since

$$\begin{aligned} \mu_P &\leq e_{RC}e_{CP} \left( \frac{e_{RP}\lambda_{RP}K_{max}}{1 + \lambda_{RP}h_{RP}K_{max}} \right) - \lambda e_{RP}, \\ e_{RP} &< e_{CP}e_{RC}, \end{aligned}$$

and  $R(t) \leq K_{max}$ , and we choose  $\lambda < \min(m_C, \mu_P + 2m_P)$ . Because the right hand side is a parabola that opens downward, it is bounded for all  $(P_2, P_1, C, R) \in \mathbb{R}_+^4$ . Specifically, the right hand side is bounded by  $M_1 = \frac{Ke_{RP}e_{CP}e_{RC}(r+\lambda)^2}{4r}$ . Thus, we find an  $M_1 > 0$  with

$$\dot{S} + \lambda S \leq M_1.$$

Applying Lemma 4, we obtain

$$0 \leq S(P_2, P_1, C, R) \leq \frac{M_1}{\lambda} + \left( S(P_2(0), P_1(0), C(0), R(0)) - \frac{M_1}{\lambda} \right) e^{-\lambda t}$$

and as  $t \rightarrow \infty$ ,  $0 \leq e_{RP}e_{CP}e_{RC}R + e_{RP}e_{CP}C + e_{RP}P_1 + P_2 \leq M_1/\lambda$ .

Now let  $M = \max \left\{ \frac{M_1}{\lambda}, \frac{M_1}{e_{RP}\lambda}, \frac{M_1}{e_{RP}e_{CP}\lambda}, \frac{M_1}{e_{RP}e_{CP}e_{RC}\lambda} \right\}$ , then

$$0 \leq P_2 + P_1 + C + R \leq M.$$

Hence, system (6.1) is dissipative with the asymptotic bound  $M$ .

Thus, there is a compact neighborhood  $B \subseteq \mathbb{R}_+^4$  such that for sufficiently large  $T = T(c_1, c_2, c_3, c_4)$ ,  $(P_2(t), P_1(t), C(t), R(t)) \in B$  for all  $t \geq T$ , where  $(P_2(t), P_1(t), C(t), R(t))$  is a solution to (6.1) that initiates in  $\mathbb{R}_+^4$ . This completes the proof.

We must alter our definition of permanent coexistence since the predator is not extinct if the stage 1 (juveniles) or stage 2 (adults) go extinct, but only if both stages go extinct. We therefore require that

$$m \leq P_1(t) + P_2(t) \tag{6.13}$$

for  $t \geq T$  and some  $m > 0$ . For a graphical depiction see Figure 6.1

System (6.1) has four boundary equilibria: one with no species present, one with the resource only present, one with the resource and consumer present, and one with the resource and both stages of the predator present:

$$\mathbf{F}_0 = (0, 0, 0, 0)^T \tag{6.14}$$

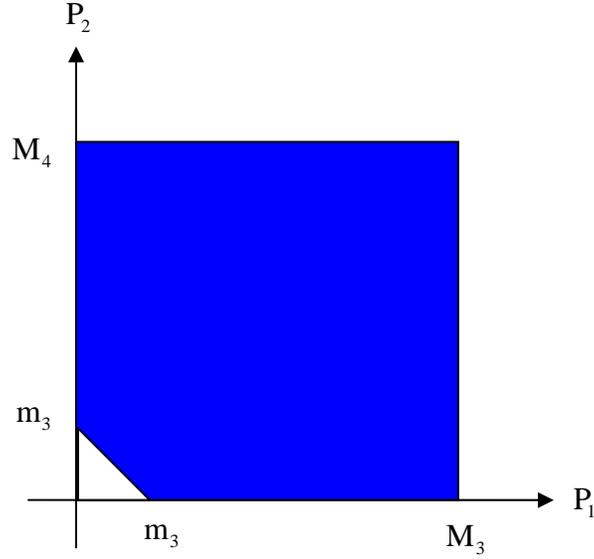


Figure 6.1: A graphical depiction of permanence for the stage predator population where  $P_1(t) \leq M_3$ ,  $P_2(t) \leq M_4$ , and  $m_3 \leq P_1(t) + P_2(t)$  for  $t \geq T$ .

$$\mathbf{F}_K = (0, 0, 0, K)^T \quad (6.15)$$

$$\mathbf{F}_{RC} = \left( 0, 0, \frac{re_{RC}[K\lambda_{RC}(e_{RC} - m_C h_{RC}) - m_C]}{K(\lambda_{RC})^2(e_{RC} - m_C h_{RC})^2}, \frac{m_C}{\lambda_{RC}(e_{RC} - m_C h_{RC})} \right)^T \quad (6.16)$$

$$\mathbf{F}_{RP} = \left( e_{RP}(\mu_P)^2 r \eta, e_{RP} \mu_P m_P r \eta, 0, -\frac{m_P(\mu_P + m_P)}{\lambda_{RP}(h_{RP} m_P(\mu_P + m_P) - e_{RP} \mu_P)} \right) \quad (6.17)$$

where

$$\eta = \frac{\lambda_{RP} e_{RP} K \mu_P - (m_P)^2 (1 + \lambda_{RP} h_{RP} K) - \mu_P m_P (1 + \lambda_{RP} h_{RP} K)}{K(\lambda_{RP})^2 (\mu_P + m_P) (e_{RP} - h_{RP} m_P (\mu_P + m_P))^2}. \quad (6.18)$$

The equilibrium with the resource missing is never positive.

The idea behind the following discussion is as follows. We first give conditions on the entire system that we see as necessary for permanence. Next, we assume that under these conditions we have that there exists  $m_1, m_2 > 0$ ,  $M_1, M_2 < \infty$ , and  $T_1 \geq 0$  such that

$$m_1 \leq R(t) \leq M_1 \text{ for } t \geq T_1 \quad (6.19)$$

$$m_2 \leq C(t) \leq M_2 \text{ for } t \geq T_1. \quad (6.20)$$

Finally, we show that under these conditions, there exists  $m_3 > 0$ ,  $M_3, M_4 < \infty$ , and  $T_2 \geq 0$  such that

$$P_1(t) \leq M_3 \quad (6.21)$$

$$P_2(t) \leq M_4 \quad (6.22)$$

$$m_3 \leq P_1(t) + P_2(t) \quad (6.23)$$

for  $t \geq T_2$ . That is, the system (6.1) is permanent.

One condition that we feel is necessary is that none of the boundary equilibria should be saturated. However, we must change our definition of saturated because of the predator stage structure. Consider the auxiliary equation

$$\frac{ds(t)}{dt} = \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}s(t) - m_Ps(t) = s(t)f_1(C, R). \quad (6.24)$$

From equations (6.1a) and (6.1b), we see that

$$\frac{d}{dt}(P_1 + P_2) \leq (P_1 + P_2)f_1(C, R). \quad (6.25)$$

Also, we write equations (6.1c) and (6.1d) as

$$\frac{dC}{dt} = Cf_2(P_2, C, R) \quad (6.26)$$

$$\frac{dR}{dt} = Rf_3(P_2, P_1, C, R). \quad (6.27)$$

Then, we say that an equilibrium  $\bar{\mathbf{x}}$  is saturated if  $f_i(\bar{\mathbf{x}}) \leq 0$  for all  $i$  with  $\bar{x}_i = 0$

Equilibrium  $\mathbf{F}_0$  is not saturated since  $r$  is positive. Equilibrium  $\mathbf{F}_K$  is not saturated if either

$$\frac{e_{RC}\lambda_{RC}K}{1 + \lambda_{RC}h_{RC}K} - m_C > 0 \quad (6.28)$$

or

$$\frac{e_{RP}\lambda_{RP}K}{1 + \lambda_{RP}h_{RP}K} - m_P > 0 \quad (6.29)$$

or both inequalities hold.

Notice that boundary equilibrium  $\mathbf{F}_{RC}$  exists in  $\mathbb{R}_+^4$  if and only if (6.28) holds. In order for  $\mathbf{F}_{RP}$  to exist in  $\mathbb{R}_+^4$  we need,

$$\lambda_{RP}e_{RP}K\mu_P - (m_P)^2(1 + \lambda_{RP}h_{RP}K) - \mu_P m_P(1 + \lambda_{RP}h_{RP}K) > 0 \quad (6.30)$$

which implies that

$$\frac{1 + \lambda_{RP}h_{RP}K}{\lambda_{RP}K\mu_P} m_P(\mu_P + m_P) < e_{RP} \quad (6.31)$$

and thus

$$e_{RP} > \left( \frac{1}{\lambda_{RP}K} + h_{RP} \right) \frac{m_P(\mu_P + m_P)}{\mu_P} > \frac{h_{RP}m_P(\mu_P + m_P)}{\mu_P} \quad (6.32)$$

That is, if equilibrium  $\mathbf{F}_{RP}$  exists, then  $\mathbf{F}_K$  is not saturated. Also, (6.32) holds if the product of the growth rates plus the product of the death rates of the predator stages is positive.

This may be reasonable alternative requirement for not being saturated. Equilibrium  $\mathbf{F}_{RC}$  is not saturated if

$$f_1(\mathbf{F}_{RC}) = \frac{\lambda_{RC}K\xi_1(\lambda_{RP}e_{RP}m_C + \lambda_{CP}e_{CP}e_{RC}r) - \lambda_{CP}e_{CP}e_{RC}m_Cr}{K(\lambda_{RC})^2\xi_1^2 - \lambda_{CP}e_{RC}h_{CP}m_Cr + \lambda_{RC}K\xi_1\nu} - m_P > 0 \quad (6.33)$$

and equilibrium  $\mathbf{F}_{RP}$  is not saturated if

$$f_2(\mathbf{F}_{RP}) = \frac{r\lambda_{CP}\mu_P(\xi_4(m_P)^2 + \mu_P m_P \xi_4 - e_{RP}\lambda_{RP}K\mu_P)}{(\lambda_{RP})^2K(\mu_P + m_P)\xi_5} \quad (6.34)$$

$$+ \frac{\lambda_{RC}e_{RC}m_P(\mu_P + m_P)}{\lambda_{RC}h_{RC}m_P(\mu_P + m_P) - \lambda_{RP}\xi_5} - m_C > 0 \quad (6.35)$$

where

$$\xi_1 = e_{RC} - m_C h_{RC} \quad (6.36)$$

$$\xi_2 = e_{RP} - m_P h_{RP} \quad (6.37)$$

$$\xi_3 = e_{CP} - m_P h_{CP} \quad (6.38)$$

$$\xi_4 = 1 + \lambda_{RP} h_{RP} K \quad (6.39)$$

$$\xi_5 = h_{RP} m_P (\mu_P + m_P) - e_{RP} \mu_P \quad (6.40)$$

$$\nu = \lambda_{RP} h_{RP} m_C + r \lambda_{CP} h_{CP} e_{RC}. \quad (6.41)$$

Finally, we assume that the  $\Omega$ -limit set of every orbit in  $\partial\mathbb{R}_+^4$  is an equilibrium point.

Notice that our stage structure omnivory model attempts to counter the consumer inferiority by decreasing predation upon the consumer. Also, the alternative stable states of omnivory models always involve the resource (see [40], [12], [71]). Therefore, the extinction of the resource is of little concern. Thus, we would expect that the consumer and resource densities of the stage structured model are uniformly bounded away from zero under conditions similar to those for the non-linear response model. We assume this is true. That is, there exists  $m_1, m_2 > 0$ , and  $T_1 \geq 0$  such that

$$m_1 \leq R(t) \quad (6.42)$$

$$m_2 \leq C(t) \quad (6.43)$$

for  $t \geq T_1$ . Our numerical simulations confirm this assumption (see also [71]).

**Lemma 9** *Suppose that  $m_1 \leq R(t)$  and  $m_2 \leq C(t)$  for  $t \geq T_1$  and*

$$\mu_P > \frac{(m_P)^2}{b - m_P} \quad (6.44)$$

where  $b > 0$  is such that

$$\frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \geq b. \quad (6.45)$$

Then, there exists  $m_3 > 0$  and  $T_2 \geq 0$  such that

$$m_3 \leq P_1(t) + P_2(t) \quad (6.46)$$

for  $t \geq T_2$ .

We will use the following Lemma from [95] in the proof of Lemma 9.

**Lemma 10** *Let  $\mathbf{f}(t, \mathbf{x}) : D \subset \mathbb{R}^2 \rightarrow \mathbb{R}^2$  satisfy a local Lipschitz condition in  $\mathbf{x}$ . Let  $\mathbf{v} : J = [\epsilon, \epsilon + a] \rightarrow \mathbb{R}^2$  be differentiable. If  $f_1(t, x_1, x_2)$  is increasing in  $x_2$  and  $f_2(t, x_1, x_2)$  is increasing in  $y_1$  and the following conditions hold:*

$$\frac{dv_1}{dt} \leq f_1(t, v_1, v_2) \quad (6.47)$$

$$\frac{dv_2}{dt} \leq f_2(t, v_1, v_2) \quad (6.48)$$

$$v_1(\epsilon) \leq \eta_1 \quad (6.49)$$

$$v_2(\epsilon) \leq \eta_2 \quad (6.50)$$

then

$$v_1 \leq x_1 \quad (6.51)$$

and

$$v_2 \leq x_2 \quad (6.52)$$

in  $J$ .

We now prove Lemma 9.

*Proof.* Since

$$m_1 \leq R(t) \quad (6.53)$$

$$m_2 \leq C(t), \quad (6.54)$$

then

$$\frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \geq b \quad (6.55)$$

for some  $b > 0$ . Consider the auxiliary equations

$$\frac{dx}{dt} = \mu_P y - m_P x \quad (6.56)$$

$$\frac{dy}{dt} = bx - (\mu_P + m_P)y \quad (6.57)$$

written in vector form

$$\frac{d}{dt} \begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \begin{bmatrix} -m_P & \mu_P \\ b & -(\mu_P + m_P) \end{bmatrix} \begin{pmatrix} x(t) \\ y(t) \end{pmatrix}. \quad (6.58)$$

This linear system has equilibrium point  $(0, 0)$ . We will show that  $(0, 0)$  is unstable along all paths in the positive  $xy$  quadrant. First, we compute the eigenvalues  $\lambda_+$  and  $\lambda_-$  of the system. The equation

$$\det \begin{bmatrix} -m_P - \lambda & \mu_P \\ b & -(\mu_P + m_P) - \lambda \end{bmatrix} = 0 \quad (6.59)$$

yields

$$\lambda^2 + (\mu_P + 2m_P)\lambda + m_P(\mu_P + m_P) - \mu_P b = 0. \quad (6.60)$$

Solving for  $\lambda$  yields

$$\lambda_+ = \frac{-(\mu_P + 2m_P) + \sqrt{\mu_P(4b + \mu_P)}}{2} \quad (6.61)$$

$$\lambda_- = \frac{-(\mu_P + 2m_P) - \sqrt{\mu_P(4b + \mu_P)}}{2}. \quad (6.62)$$

$\lambda_-$  is always negative and  $\lambda_+$  is positive if

$$\mu_P > \frac{(m_P)^2}{b - m_P}. \quad (6.63)$$

Next, we compute the eigenvectors corresponding to the eigenvalues by solving the systems

$$-(m_P + \lambda_+)x_+ + \mu_P y_+ = 0 \quad (6.64)$$

$$bx_+ - (\mu_P + m_P + \lambda_+)y_+ = 0 \quad (6.65)$$

and

$$-(m_P + \lambda_-)x_- + \mu_P y_- = 0 \quad (6.66)$$

$$bx_- - (\mu_P + m_P + \lambda_-)y_- = 0 \quad (6.67)$$

for  $(x_+, y_+)$  and  $(x_-, y_-)$ , respectively. These computations yield

$$x_+ = \frac{\mu_P + \sqrt{\mu_P(4b + \mu_P)}}{2b} y_+ \quad (6.68)$$

and

$$x_- = \frac{\mu_P - \sqrt{\mu_P(4b + \mu_P)}}{2b} y_-. \quad (6.69)$$

So if  $y_+ > 0$ , then  $x_+ > 0$  and if  $y_+ < 0$ , then  $x_+ < 0$ . Also, since  $\mu_P > 0$  by assumption, if  $y_- > 0$ , then  $x_- < 0$  and if  $y_- < 0$ , then  $x_- > 0$ . That is,  $(0, 0)$  is an unstable saddle with solutions moving away from  $(0, 0)$  along all paths in the positive  $xy$  quadrant. Thus, there exists  $m_+ > 0$  and  $T_+ \geq 0$  such that

$$m_+ \leq x(t) + y(t) \quad (6.70)$$

for  $t \geq T_+$ .

Now, we must show that the original system in  $P_2$  and  $P_1$  also has this property. We apply Lemma 10 to the original system. Clearly,

$$g_1(t, P_2, P_1) = \mu_P P_1 - m_P P_2 \quad (6.71)$$

is increasing in  $P_1$ , and

$$g_2(t, P_2, P_1) = \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C}P_2 - (\mu_P + m_P)P_1 = h(t)P_2 - (\mu_P + m_P)P_1 \quad (6.72)$$

is increasing in  $P_2$ , since we have shown that  $R, C > 0$ . Since

$$\frac{dx}{dt} = \mu_P y - m_P x = g_1(t, x, y) \quad (6.73)$$

and

$$\frac{dy}{dt} = bx - (\mu_P + m_P)y \leq h(t)x - (\mu_P + m_P)y = f_2(t, x, y) \quad (6.74)$$

then by Lemma 10

$$x \leq P_2 \quad (6.75)$$

and

$$y \leq P_1 \quad (6.76)$$

for all  $t \geq 0$ . That is, there exists  $m_3 > 0$  and  $T_2 \geq 0$  such that

$$m_3 \leq P_1(t) + P_2(t) \quad (6.77)$$

for  $t \geq T_2$ . This completes the proof.

Hence, by (6.21) and (6.19), our stage structure omnivory model (6.1) is permanent.

# Chapter 7

## Sensitivity Analysis

The first step in our sensitivity analysis method is to differentiate each right hand side of our three models with respect to each of the model parameters. The partial derivatives of the right hand sides of the linear response omnivory model with respect to each model parameter are given in Table 7.1. Also, Table 7.2 and Table 7.3 list the associated partials for the non-linear response model and stage structure model, respectively. Notice that each partial derivative is continuous with respect to  $t$ ,  $P$ ,  $C$ , and  $R$  for all positive parameter values. Hence, by Theorems 3 and 4, we can differentiate the solution to each model with respect to each model parameter.

### 7.1 Sensitivity Equations

The second step is a derivation of the sensitivity equations. The idea is to differentiate each differential equation with respect to each parameter. We then interchange the order of differentiation, and derive a linear system of equations for the sensitivities that solves

$$\frac{d}{dt}S_{x_j, \alpha_i} = \sum_{k=1}^n \left( \frac{\partial f_j}{\partial x_k} S_{x_k, \alpha_i} \right) + \frac{\partial f_j}{\partial \alpha_i}. \quad (7.1)$$

with the notation

$$S_{x_j, \alpha_i}(t) = \frac{\partial x_j(t)}{\partial \alpha_i} \quad (7.2)$$

where  $x_j$  is the  $j$ th component of the state,  $j = 1, 2, 3$  or  $j = 1, 2, 3, 4$  (stage model), and  $\alpha_i$  is the model parameter,  $i = 1, 2, \dots, 10$  (linear model) or  $i = 1, 2, \dots, 13$  (non-linear model) or  $i = 1, 2, \dots, 14$  (stage model). Notice that we must also differentiate the initial conditions with respect to each parameter. Hence, we have the initial conditions

$$S_{x_j, \alpha_i}(0) = 0, \quad \text{for each } x_j, \alpha_i. \quad (7.3)$$

Theorem 5 gives the justification for these formal mathematical manipulations.

Table 7.1: Partial derivatives of the right hand side of the linear response omnivory model with respect to the model parameters. The dependence upon time is suppressed for these calculations.

Parameter	Partial of $f_1$	Partial of $f_2$	Partial of $f_3$
$e_{RP}$	$\alpha_{RP}RP$	0	0
$e_{CP}$	$\alpha_{CP}CP$	0	0
$e_{RC}$	0	$\alpha_{RC}RC$	0
$\alpha_{RP}$	$e_{RP}RP$	0	-RP
$\alpha_{CP}$	$e_{CP}CP$	-CP	0
$\alpha_{RC}$	0	$e_{RC}RC$	-RC
$m_P$	-P	0	0
$m_C$	0	-C	0
$r$	0	0	$R(1 - R/K)$
$K$	0	0	$rR^2/K^2$

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

$$\frac{d}{dt}S_{x_j, \alpha_i} = \sum_{k=1}^n \left( \frac{\partial f_j}{\partial x_k} S_{x_j, \alpha_i} \right) \quad (7.4)$$

since the terms  $\frac{\partial f_j}{\partial x_k}$  remain the same for each parameter. However, the terms  $\frac{\partial f_j}{\partial \alpha_i}$  differ between our three models. We use the term **particular part of the equations** of the model for the terms

$$\frac{\partial f_j}{\partial \alpha_i} \quad (7.5)$$

since they change for each parameter and each model.

Due to the fact that there are ten systems of three variables for the linear response model, thirteen systems of three variables for the non-linear response model, and fourteen systems of four variables for the stage structure model that must be solved, we do not list all of these systems. However, we will list the general sensitivity equations for each of our models. Then the sensitivity equations are formed by adding the particular part of the equations. The particular part of the equations can be found on each row in Tables 7.1, 7.2, and 7.3.

We will suppress the dependence upon time for the following models. The general sensitivity equations for the linear response omnivory model are given by

$$\begin{aligned} \frac{d}{dt}(S_P) &= (e_{RP}\alpha_{RP}R + e_{CP}\alpha_{CP}C - m_P)S_P + (e_{CP}\alpha_{CP}P)S_C + (e_{RP}\alpha_{RP}P)S_R \\ \frac{d}{dt}(S_C) &= (-\alpha_{CP}C)S_P + (e_{RC}\alpha_{RC}R - \alpha_{CP}P - m_C)S_C + (e_{RC}\alpha_{RC}C)S_R \\ \frac{d}{dt}(S_R) &= (-\alpha_{RP}R)S_P + (-\alpha_{RC}R)S_C + (r(1 - 2R/K) - \alpha_{RC}C - \alpha_{RP}P)S_R \end{aligned}$$

Table 7.2: Partial derivatives of the right hand side of the non-linear response omnivory model with respect to the model parameters. The dependence upon time is suppressed for these calculations.

Parameter	Partial of $f_1$	Partial of $f_2$
$e_{RP}$	$\frac{\lambda_{RP}RP}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}$	0
$e_{CP}$	$\frac{\lambda_{CP}CP}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}$	0
$e_{RC}$	0	$\frac{\lambda_{RC}RC}{1+\lambda_{RP}h_{RP}R}$
$\lambda_{RP}$	$\frac{e_{RP}RP(1+\lambda_{CP}h_{CP}C)-e_{CP}\lambda_{CP}h_{RP}RCP}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$\frac{\lambda_{CP}h_{RP}RCP}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
$\lambda_{CP}$	$\frac{e_{CP}CP(1+\lambda_{RP}h_{RP}R)-e_{RP}\lambda_{RP}h_{CP}RCP}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$-\frac{CP(1+\lambda_{RP}h_{RP}R)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
$\lambda_{RC}$	0	$\frac{e_{RC}RC}{(1+\lambda_{RP}h_{RP}R)^2}$
$h_{RP}$	$-\frac{\lambda_{RP}RP(e_{RP}\lambda_{RP}R+e_{CP}\lambda_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$\frac{\lambda_{RP}\lambda_{CP}RCP}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
$h_{CP}$	$-\frac{\lambda_{CP}CP(e_{RP}\lambda_{RP}R+e_{CP}\lambda_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$\frac{(\lambda_{CP})^2C^2P}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
$h_{RC}$	0	$-\frac{e_{RC}(\lambda_{RC})^2R^2C}{(1+\lambda_{RP}h_{RP}R)^2}$
$m_P$	-P	0
$m_C$	0	-C
$r$	0	0
$K$	0	0
Parameter	Partial of $f_3$	
$e_{RP}$	0	
$e_{CP}$	0	
$e_{RC}$	0	
$\lambda_{RP}$	$-\frac{RP(1+\lambda_{CP}h_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	
$\lambda_{CP}$	$\frac{\lambda_{RP}h_{CP}RCP}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	
$\lambda_{RC}$	$-\frac{RC}{(1+\lambda_{RP}h_{RP}R)^2}$	
$h_{RP}$	$\frac{(\lambda_{RP})^2R^2P}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	
$h_{CP}$	$\frac{\lambda_{RP}\lambda_{CP}RCP}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	
$h_{RC}$	$\frac{(\lambda_{RC})^2R^2C}{(1+\lambda_{RP}h_{RP}R)^2}$	
$m_P$	0	
$m_C$	0	
$r$	$R(1 - R/K)$	
$K$	$rR^2/K^2$	

Table 7.3: Partial derivatives of the right hand side of the stage structure omnivory model with respect to the model parameters. The dependence upon time is suppressed for these calculations.

Parameter	Partial of $f_1$	Partial of $f_2$
$e_{RP}$	0	$\frac{\lambda_{RP}RP_2}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}$
$e_{CP}$	0	$\frac{\lambda_{CP}CP_2}{1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C}$
$e_{RC}$	0	0
$\lambda_{RP}$	0	$\frac{e_{RP}RP_2(1+\lambda_{CP}h_{CP}C)-e_{CP}\lambda_{CP}h_{RP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
$\lambda_{CP}$	0	$\frac{e_{CP}CP_2(1+\lambda_{RP}h_{RP}R)-e_{RP}\lambda_{RP}h_{CP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
$\lambda_{RC}$	0	0
$h_{RP}$	0	$-\frac{\lambda_{RP}RP_2(e_{RP}\lambda_{RP}R+e_{CP}\lambda_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
$h_{CP}$	0	$-\frac{\lambda_{CP}CP_2(e_{RP}\lambda_{RP}R+e_{CP}\lambda_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
$h_{RC}$	0	0
$m_P$	$-P_2$	$-P_1$
$m_C$	0	0
$\mu_P$	$P_1$	$-P_1$
$r$	0	0
$K$	0	0
Parameter	Partial of $f_3$	Partial of $f_4$
$e_{RP}$	0	0
$e_{CP}$	0	0
$e_{RC}$	$\frac{\lambda_{RC}RC}{1+\lambda_{RP}h_{RP}R}$	0
$\lambda_{RP}$	$\frac{\lambda_{CP}h_{RP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$-\frac{RP_1}{1+\lambda_{RP}h_{RP}R} - \frac{RP_2(1+\lambda_{CP}h_{CP}C)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
$\lambda_{CP}$	$-\frac{CP_2(1+\lambda_{RP}h_{RP}R)}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$\frac{\lambda_{RP}h_{CP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
$\lambda_{RC}$	$\frac{e_{RC}RC}{(1+\lambda_{RP}h_{RP}R)^2}$	$-\frac{RC}{(1+\lambda_{RP}h_{RP}R)^2}$
$h_{RP}$	$\frac{\lambda_{RP}\lambda_{CP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$\frac{(\lambda_{RP})^2R^2P_1}{(1+\lambda_{RP}h_{RP}R)^2} + \frac{(\lambda_{RP})^2R^2P_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
$h_{CP}$	$\frac{(\lambda_{CP})^2C^2P_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$	$\frac{\lambda_{RP}\lambda_{CP}RCP_2}{(1+\lambda_{RP}h_{RP}R+\lambda_{CP}h_{CP}C)^2}$
$h_{RC}$	$-\frac{e_{RC}(\lambda_{RC})^2R^2C}{(1+\lambda_{RP}h_{RP}R)^2}$	$\frac{(\lambda_{RC})^2R^2C}{(1+\lambda_{RP}h_{RP}R)^2}$
$m_P$	0	0
$m_C$	$-C$	0
$\mu_P$	0	0
$r$	0	$R(1 - R/K)$
$K$	0	$rR^2/K^2$

with initial conditions

$$S_P(0) = 0, \quad S_C(0) = 0, \quad \text{and} \quad S_R(0) = 0$$

where we define

$$S_P(t) = \frac{\partial}{\partial \alpha_i} P(t), \quad (7.6)$$

$$S_C(t) = \frac{\partial}{\partial \alpha_i} C(t), \quad (7.7)$$

$$S_R(t) = \frac{\partial}{\partial \alpha_i} R(t). \quad (7.8)$$

Using this same definition, the general sensitivity equations for the non-linear response omnivory model are

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

with initial conditions

$$S_P(0) = 0, \quad S_C(0) = 0, \quad \text{and} \quad S_R(0) = 0.$$

Now with

$$S_{P_1}(t) = \frac{\partial}{\partial \alpha_i} P_1(t), \quad (7.9)$$

$$S_{P_2}(t) = \frac{\partial}{\partial \alpha_i} P_2(t), \quad (7.10)$$

the general sensitivity equations for the stage structure omnivory model are

$$\begin{aligned}
\frac{d}{dt}(S_{P_2}) &= (-m_P)S_{P_2} + (\mu_P)S_{P_1} \\
\frac{d}{dt}(S_{P_1}) &= \left( \frac{e_{RP}\lambda_{RP}R + e_{CP}\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right) S_{P_2} + (-(\mu_P + m_P)) S_{P_1} \\
&\quad + \left( \frac{e_{CP}\lambda_{CP}P_2(1 + \lambda_{RP}h_{RP}R) - e_{RP}\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \right) S_C \\
&\quad + \left( \frac{e_{RP}\lambda_{RP}P_2(1 + \lambda_{CP}h_{CP}C) - e_{CP}\lambda_{RP}\lambda_{CP}h_{RP}CP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \right) S_R \\
\frac{d}{dt}(S_C) &= \left( -\frac{\lambda_{CP}C}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right) S_{P_2} \\
&\quad + \left( \frac{e_{RC}\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} - \frac{\lambda_{CP}P_2(1 + \lambda_{RP}h_{RP}R)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} - m_C \right) S_C \\
&\quad + \left( \frac{e_{RC}\lambda_{RC}C}{(1 + \lambda_{RP}h_{RP}R)^2} + \frac{\lambda_{CP}\lambda_{RP}h_{RP}CP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \right) S_R \\
\frac{d}{dt}(S_R) &= \left( -\frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C} \right) S_{P_2} \\
&\quad + \left( -\frac{\lambda_{RP}R}{1 + \lambda_{RP}h_{RP}R} \right) S_{P_1} \\
&\quad + \left( -\frac{\lambda_{RC}R}{1 + \lambda_{RC}h_{RC}R} + \frac{\lambda_{RP}\lambda_{CP}h_{CP}RP_2}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \right) S_C \\
&\quad + \left( r \left( 1 - \frac{2R}{K} \right) - \frac{\lambda_{RC}C}{(1 + \lambda_{RC}h_{RC}R)^2} - \frac{\lambda_{RP}P_1}{(1 + \lambda_{RP}h_{RP}R)^2} \right) S_R \\
&\quad - \left( \frac{\lambda_{RP}P_2(1 + \lambda_{CP}h_{CP}C)}{(1 + \lambda_{RP}h_{RP}R + \lambda_{CP}h_{CP}C)^2} \right) S_R
\end{aligned}$$

with initial conditions

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

We feel it is necessary to point out some of the difficulties that arise when using sensitivity equation methods.

First, for each parameter that the original systems has, we must solve a system of linear differential equations. The number of differential equations in the state system dictates how many differential equations there will be in the linear sensitivity system. For example, the linear response omnivory model has ten parameters and three variables. Thus, for each parameter we must solve a first order linear system of three variables.

Second, although the sensitivity equations are linear, they are “forced” by the solution to the state equations. Therefore, as stated by Stanley [90] “the state equations must be solved as a first step in any algorithm used to compute the sensitivity”. However, the state

equations are not dependent upon the sensitivities. Thus, we can form the coupled system of states and sensitivities for the stage structure model

$$\frac{d\mathbf{y}}{dt}(t) = \mathbf{g}(t) \quad (7.11)$$

with initial condition

$$\mathbf{y}(0) = \mathbf{k} \quad (7.12)$$

where

$$\frac{d\mathbf{y}}{dt}(t) = \begin{pmatrix} \frac{dx_1}{dt}(t) \\ \vdots \\ \frac{dx_4}{dt}(t) \\ \frac{dS_{x_1}}{dt} \\ \vdots \\ \frac{dS_{x_4}}{dt} \end{pmatrix}, \quad k = \begin{pmatrix} c_1 \\ c_2 \\ c_3 \\ c_4 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix},$$

and  $\mathbf{g}(t)$  is the vector of right hand sides. Similarly, we can form the coupled system for the linear and non-linear response models.

Finally, a set of parameter values that seem appropriate for the natural system must be used in solving the sensitivity equations. The sets of parameters that we will use for each of our systems are listed in Section 3.4.

## 7.2 Sensitivities

We numerically integrate the coupled systems using *Matlab's* fourth- and fifth-order adaptive step size algorithm known as *ode45* to solve for the states and sensitivities. This is a Runge-Kutta-Fehlberg method that simultaneously obtains two solutions per step in order to monitor the accuracy of the solution and adjust the step size according to a user-prescribed tolerance on the error [81]. We use  $1 \times 10^{-3}$  for relative error tolerance and  $1 \times 10^{-6}$  for absolute error tolerance.

For our calculations we use the initial conditions  $\mathbf{c} = (1, 1, 1)^T$  for our linear system,  $\mathbf{c} = (1, 1, 2)^T$  for our non-linear system, and  $\mathbf{c} = (1, 1, 2, 3)^T$  for our stage structure system.

Now, we must consider how to measure our sensitivities. We will use a weighted norm as a performance measure of how small changes in the parameters affect the state. We use a weighted euclidean norm in three dimensions:

$$\|S_{\alpha_i}\|(t) = \|(S_{P, \alpha_i}, S_{C, \alpha_i}, S_{R, \alpha_i})^T\|(t) = \sqrt{w_1(S_{P, \alpha_i})^2 + w_2(S_{C, \alpha_i})^2 + w_3(S_{R, \alpha_i})^2}. \quad (7.13)$$

In four dimensions, there is another weight,  $w_4$ , to go with the fourth sensitivity. The weights may be used to gauge that one species is more important in your measure. For our computations, we weight each species equally with a value of one. Notice, that we now have

a performance measure that is a function of the parameter and time only. The following plots are graphs of the norms of the sensitivities over time. We have defined three classes for the sensitivities based upon the numerical values over time: smaller, medium, larger. In the linear response omnivory model there are only two classes: smaller and larger. Figures 7.1 and 7.2 are the sensitivities for the linear response omnivory model. The sensitivities for the non-linear response omnivory model are in Figures 7.3, 7.4, 7.5. Figures 7.6, 7.7, and 7.8 provide the graphs of the sensitivities for the stage structure omnivory model. The parameter values for each plot are listed in the figure captions.

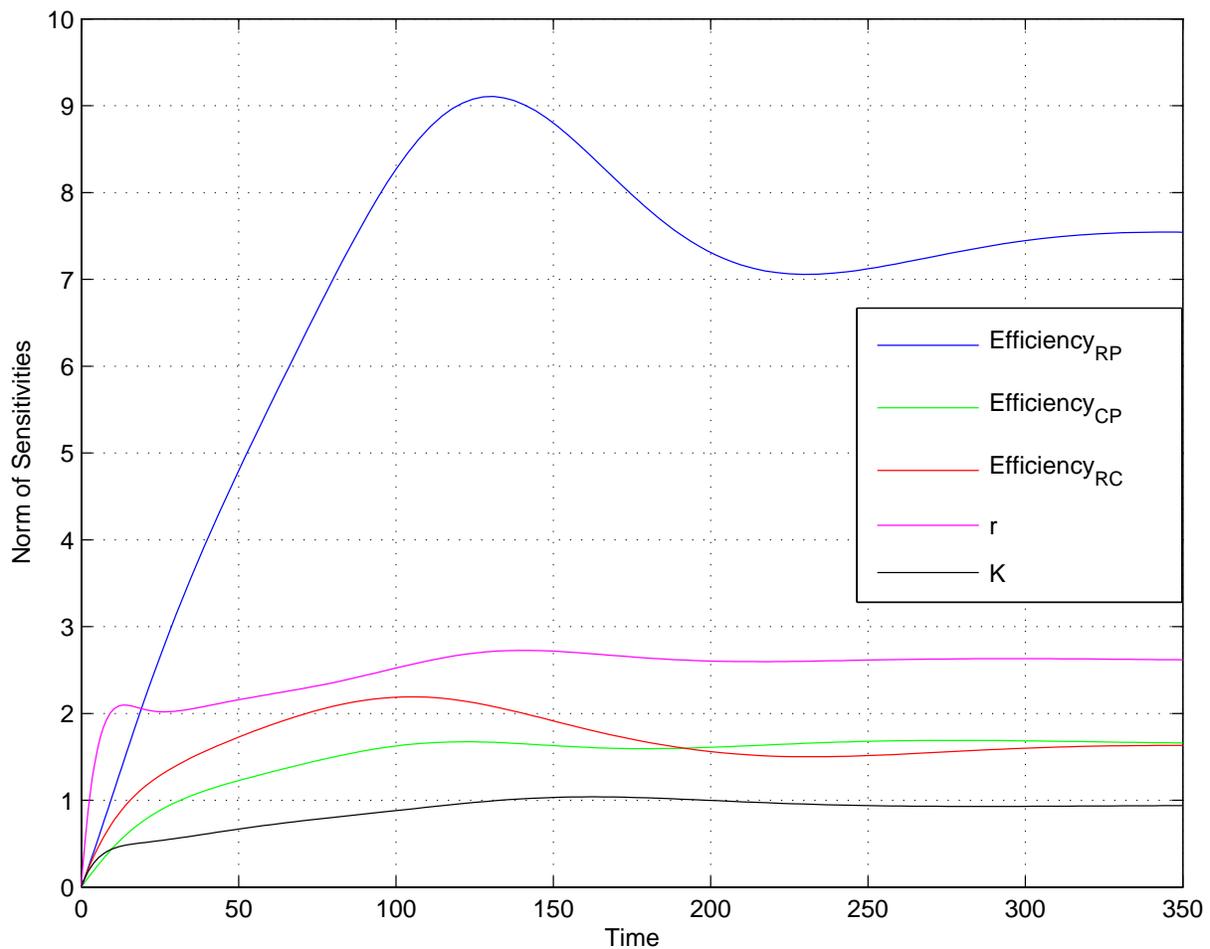


Figure 7.1: Plot of the norm of (smaller) sensitivities over time for the linear response omnivory model.  $r = 0.4$ ,  $K = 2$ ,  $\alpha_{RC} = 0.1$ ,  $\alpha_{RP} = 0.1$ ,  $\alpha_{CP} = 0.05$ ,  $e_{RC} = 0.8$ ,  $e_{RP} = 0.2$ ,  $e_{CP} = 0.5$ ,  $m_C = 0.06$ ,  $m_P = 0.04$ ,  $\mathbf{c} = (1, 1, 1)^T$ ,  $w_1 = 1$ ,  $w_2 = 1$ ,  $w_3 = 1$ .

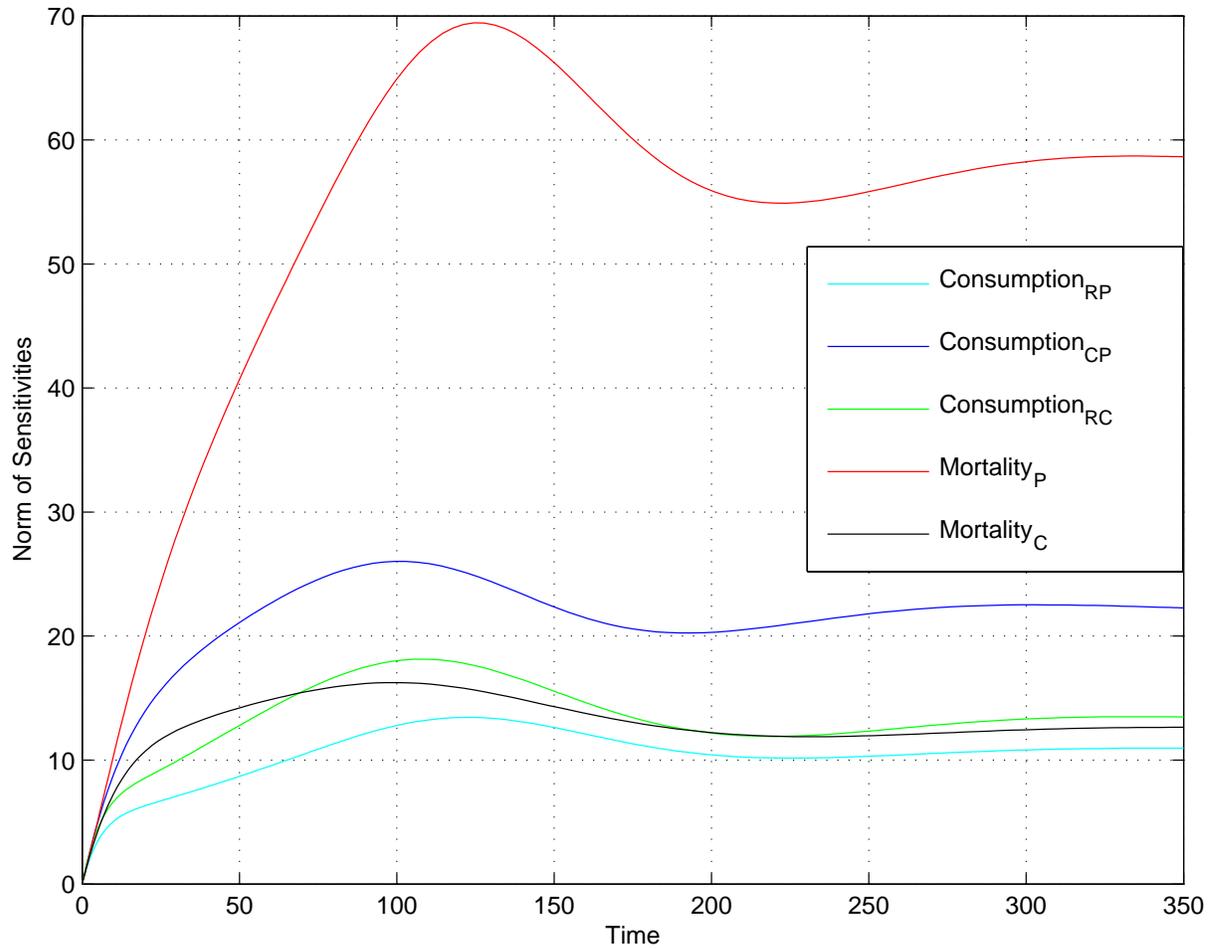


Figure 7.2: Plot of the norm of (larger) sensitivities over time for the linear response omnivory model.  $r = 0.4$ ,  $K = 2$ ,  $\alpha_{RC} = 0.1$ ,  $\alpha_{RP} = 0.1$ ,  $\alpha_{CP} = 0.05$ ,  $e_{RC} = 0.8$ ,  $e_{RP} = 0.2$ ,  $e_{CP} = 0.5$ ,  $m_C = 0.06$ ,  $m_P = 0.04$ ,  $\mathbf{c} = (1, 1, 1)^T$ ,  $w_1 = 1$ ,  $w_2 = 1$ ,  $w_3 = 1$ .

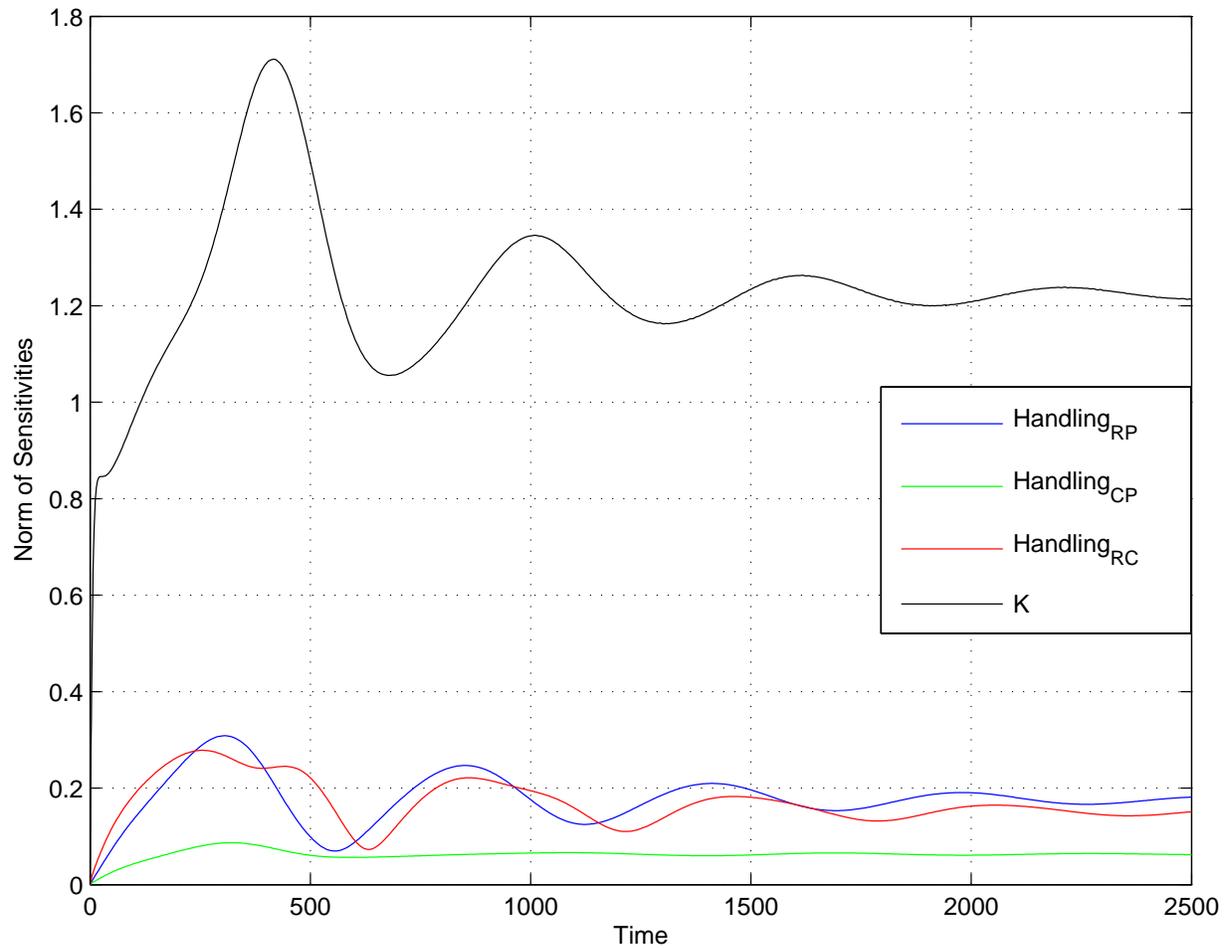


Figure 7.3: Plot of the norm of (smaller) sensitivities over time for the non-linear response omnivory model.  $r = 0.3$ ,  $K = 3$ ,  $\lambda_{RC} = 0.037$ ,  $\lambda_{RP} = 0.025$ ,  $\lambda_{CP} = 0.025$ ,  $h_{RC} = 3$ ,  $h_{RP} = 4$ ,  $h_{CP} = 4$ ,  $e_{RC} = 0.6$ ,  $e_{RP} = 0.36$ ,  $e_{CP} = 0.6$ ,  $m_C = 0.03$ ,  $m_P = 0.0275$ ,  $\mathbf{c} = (1, 1, 2)^T$ ,  $w_1 = 1$ ,  $w_2 = 1$ ,  $w_3 = 1$ .

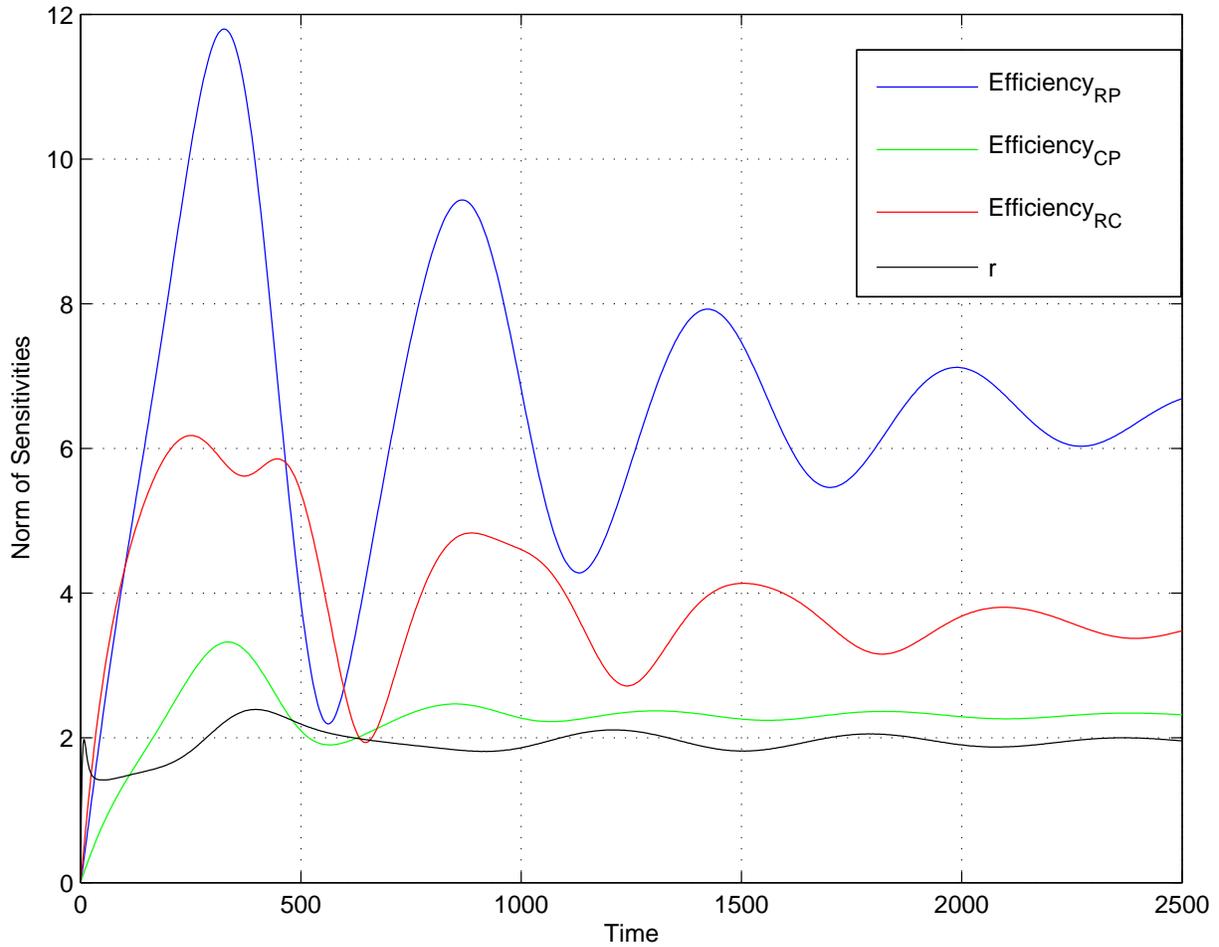


Figure 7.4: Plot of the norm of (medium) sensitivities over time for the non-linear response omnivory model.  $r = 0.3$ ,  $K = 3$ ,  $\lambda_{RC} = 0.037$ ,  $\lambda_{RP} = 0.025$ ,  $\lambda_{CP} = 0.025$ ,  $h_{RC} = 3$ ,  $h_{RP} = 4$ ,  $h_{CP} = 4$ ,  $e_{RC} = 0.6$ ,  $e_{RP} = 0.36$ ,  $e_{CP} = 0.6$ ,  $m_C = 0.03$ ,  $m_P = 0.0275$ ,  $\mathbf{c} = (1, 1, 2)^T$ ,  $w_1 = 1$ ,  $w_2 = 1$ ,  $w_3 = 1$ .

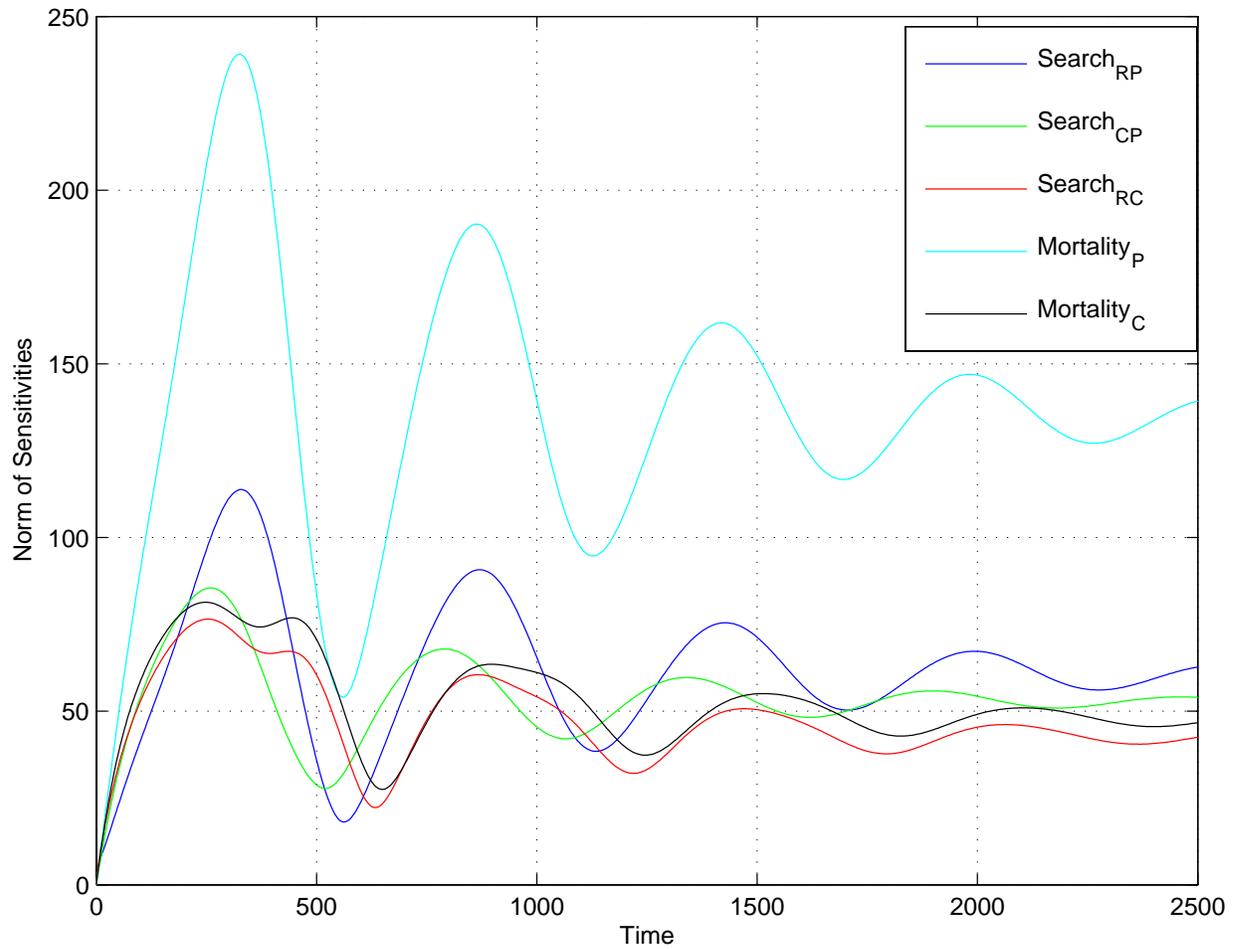


Figure 7.5: Plot of the norm of (larger) sensitivities over time for the non-linear response omnivory model.  $r = 0.3$ ,  $K = 3$ ,  $\lambda_{RC} = 0.037$ ,  $\lambda_{RP} = 0.025$ ,  $\lambda_{CP} = 0.025$ ,  $h_{RC} = 3$ ,  $h_{RP} = 4$ ,  $h_{CP} = 4$ ,  $e_{RC} = 0.6$ ,  $e_{RP} = 0.36$ ,  $e_{CP} = 0.6$ ,  $m_C = 0.03$ ,  $m_P = 0.0275$ ,  $\mathbf{c} = (1, 1, 2)^T$ ,  $w_1 = 1$ ,  $w_2 = 1$ ,  $w_3 = 1$ .

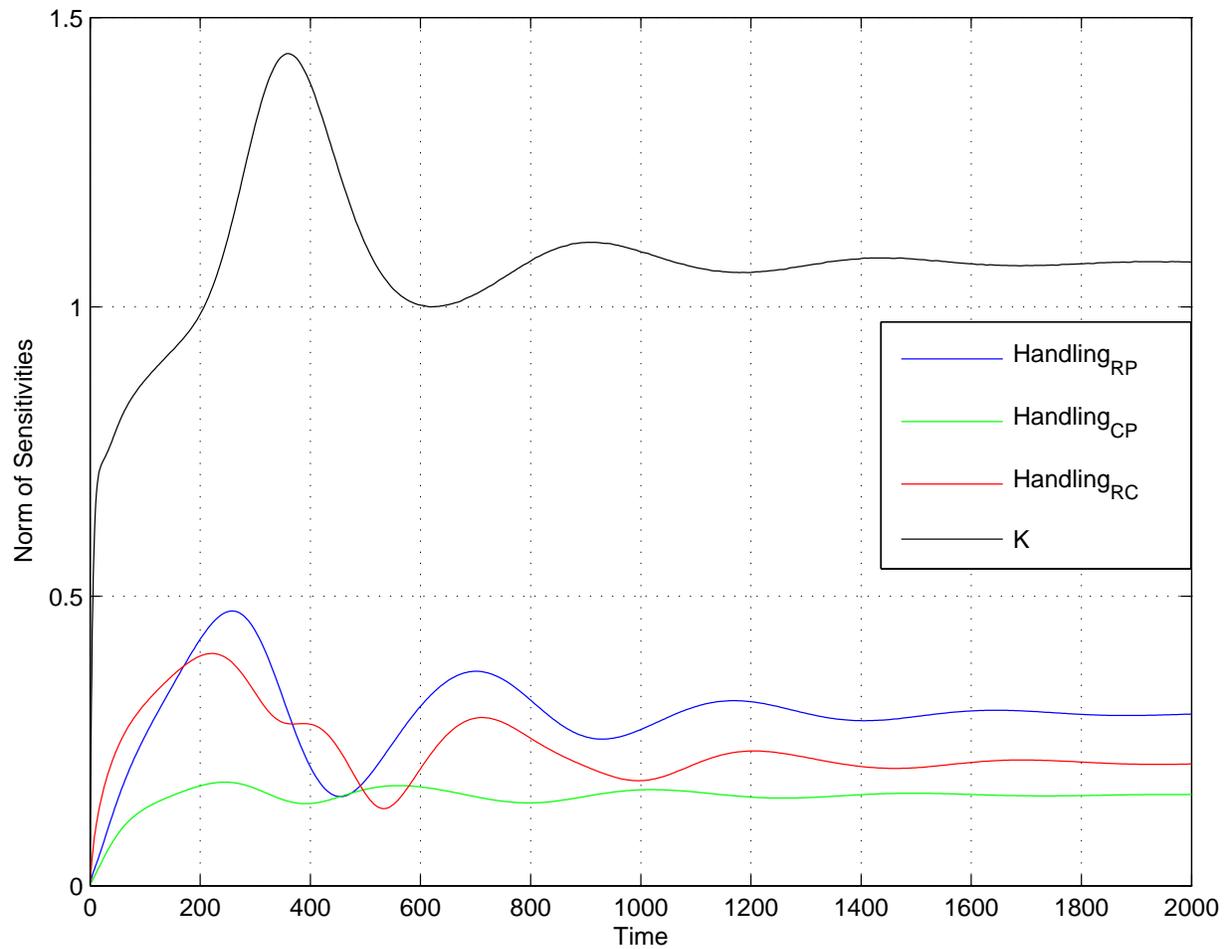


Figure 7.6: Plot of the norm of (smaller) sensitivities over time for the stage structure omnivory model.  $r = 0.3$ ,  $K = 3$ ,  $\lambda_{RC} = 0.037$ ,  $\lambda_{RP} = 0.025$ ,  $\lambda_{CP} = 0.025$ ,  $h_{RC} = 3$ ,  $h_{RP} = 4$ ,  $h_{CP} = 4$ ,  $e_{RC} = 0.6$ ,  $e_{RP} = 0.36$ ,  $e_{CP} = 0.6$ ,  $m_C = 0.03$ ,  $m_P = 0.0275$ ,  $\mu_P = 0.1$ ,  $\mathbf{c} = (1, 1, 2, 3)^T$ ,  $w_1 = 1$ ,  $w_2 = 1$ ,  $w_3 = 1$ ,  $w_4 = 1$ .

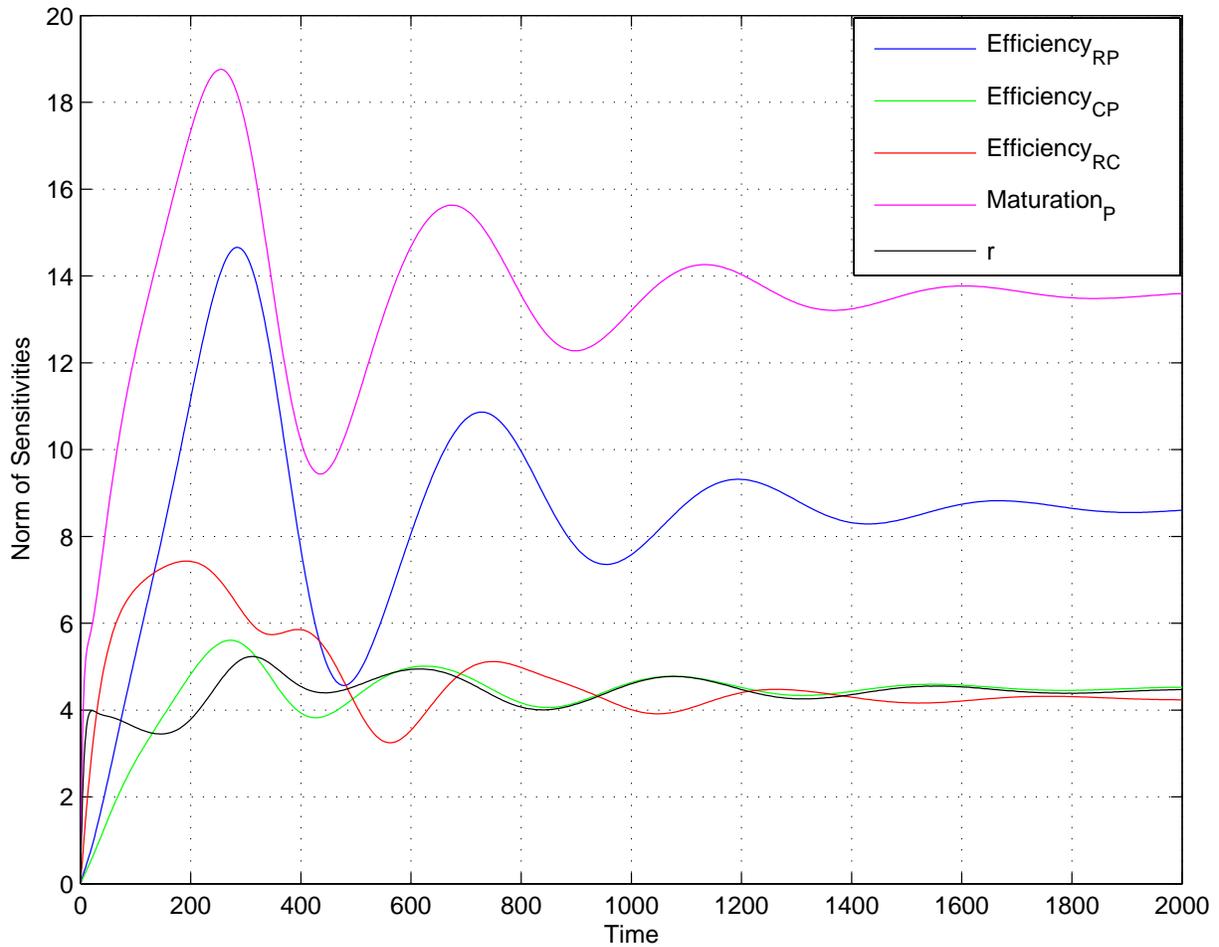


Figure 7.7: Plot of the norm of (medium) sensitivities over time for the stage structure omnivory model.  $r = 0.3$ ,  $K = 3$ ,  $\lambda_{RC} = 0.037$ ,  $\lambda_{RP} = 0.025$ ,  $\lambda_{CP} = 0.025$ ,  $h_{RC} = 3$ ,  $h_{RP} = 4$ ,  $h_{CP} = 4$ ,  $e_{RC} = 0.6$ ,  $e_{RP} = 0.36$ ,  $e_{CP} = 0.6$ ,  $m_C = 0.03$ ,  $m_P = 0.0275$ ,  $\mu_P = 0.1$ ,  $\mathbf{c} = (1, 1, 2, 3)^T$ ,  $w_1 = 1$ ,  $w_2 = 1$ ,  $w_3 = 1$ ,  $w_4 = 1$ .

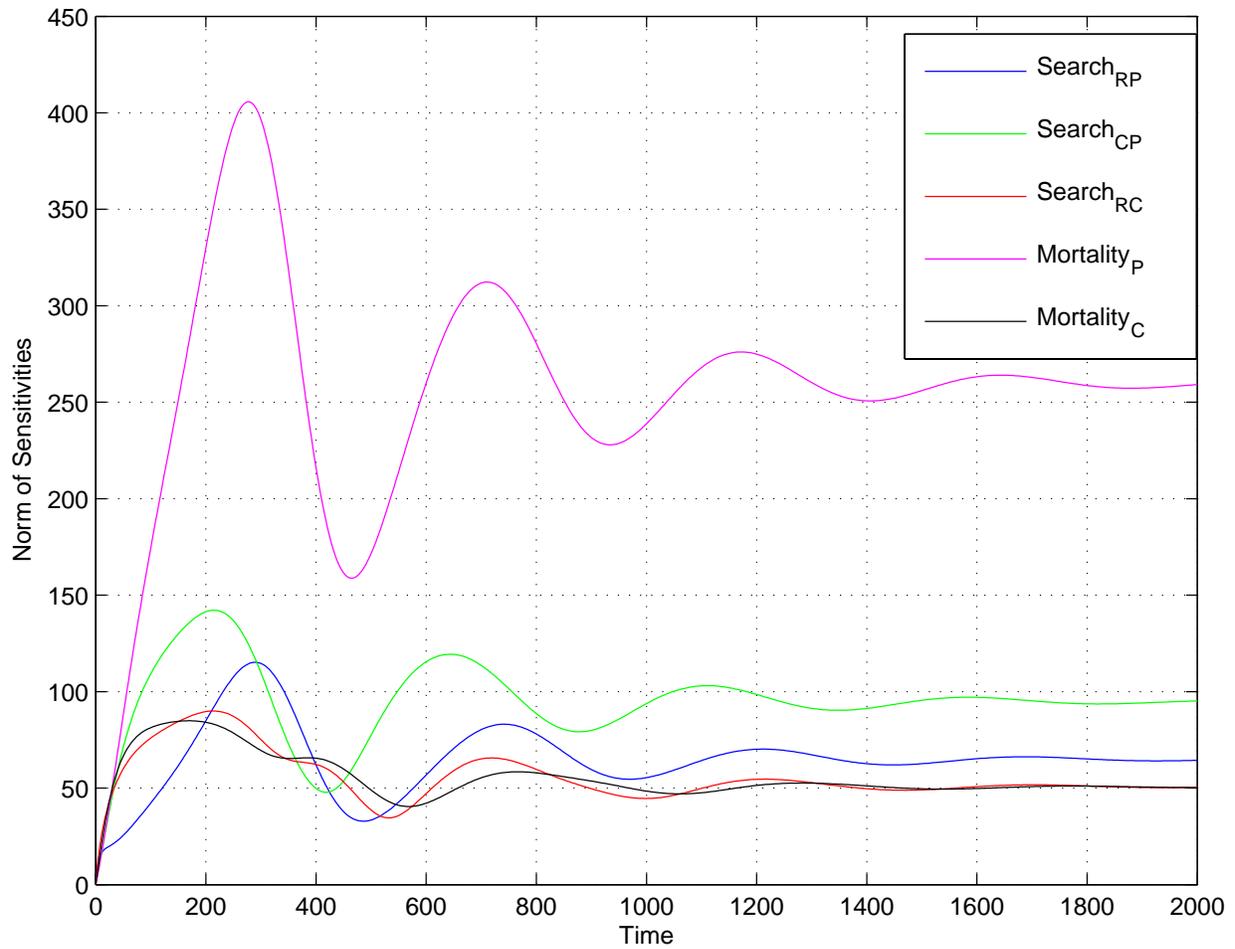


Figure 7.8: Plot of the norm of (larger) sensitivities over time for the stage structure omnivory model.  $r = 0.3$ ,  $K = 3$ ,  $\lambda_{RC} = 0.037$ ,  $\lambda_{RP} = 0.025$ ,  $\lambda_{CP} = 0.025$ ,  $h_{RC} = 3$ ,  $h_{RP} = 4$ ,  $h_{CP} = 4$ ,  $e_{RC} = 0.6$ ,  $e_{RP} = 0.36$ ,  $e_{CP} = 0.6$ ,  $m_C = 0.03$ ,  $m_P = 0.0275$ ,  $\mu_P = 0.1$ ,  $\mathbf{c} = (1, 1, 2, 3)^T$ ,  $w_1 = 1$ ,  $w_2 = 1$ ,  $w_3 = 1$ ,  $w_4 = 1$ .

# Chapter 8

## Results

### 8.1 Check for Coexistence and Biological Meaning

In this section we will summarize the restrictions that must be placed upon the model parameters to ensure permanent coexistence for our systems. This will provide an easy way to check for coexistence. Also, we will provide interpretations on what the parameter restrictions mean biologically.

The parameter conditions that guarantee our linear response omnivory model (4.1) is permanent are given by the following:

$$0 < e_{CP}e_{RC} - e_{RP} \quad (8.1)$$

$$0 < e_{RP}\alpha_{RP}K - m_P \quad (8.2)$$

$$0 < e_{RC}\alpha_{RC}K - m_C \quad (8.3)$$

$$0 < m_C \left( \frac{e_{RP}\alpha_{RP}}{e_{RC}\alpha_{RC}} \right) + r \left( \frac{e_{CP}\alpha_{CP}}{\alpha_{RC}} \right) \left( 1 - \frac{m_C}{e_{RC}\alpha_{RC}K} \right) - m_P \quad (8.4)$$

$$0 < m_P \left( \frac{e_{RC}\alpha_{RC}}{e_{RP}\alpha_{RP}} \right) - r \left( \frac{\alpha_{CP}}{\alpha_{RP}} \right) \left( 1 - \frac{m_P}{e_{RP}\alpha_{RP}K} \right) - m_C \quad (8.5)$$

Condition (8.1) can be rewritten as  $e_{RP} < e_{CP}e_{RC}$ . That is, the consumer provides a high benefit to the predator, relative to the basal resource and thus, the predator gains significantly from its consumption of the consumer.

Condition (8.2) represents a positive per capita rate of increase for the predator when the resource is at carrying capacity. That is, the predator can invade when the resource is at carrying capacity. Similarly, condition (8.3) states that the consumer can invade when the resource is at carrying capacity. Recall that only one of these two conditions must hold to ensure permanence. We can rewrite conditions (8.2) and (8.3) as

$$K > \frac{m_P}{e_{RP}\alpha_{RP}} \quad (8.6)$$

and

$$K > \frac{m_C}{e_{RC}\alpha_{RC}}, \quad (8.7)$$

respectively. So, in either case, the resource productivity (measured as  $K$ ) cannot be too low.

(8.4) is the condition for the predator to invade when the consumer and resource are present and at equilibrium and (8.5) is the condition for the consumer to invade when the predator and resource are present and at equilibrium. We rewrite condition (8.4) as

$$e_{RP} > \frac{(\alpha_{RC})^2 e_{RC} K m_P - \alpha_{RC} \alpha_{CP} e_{RC} e_{CP} K r + \alpha_{CP} e_{CP} m_C r}{\alpha_{RC} \alpha_{RP} K m_C} := M_{RC} \quad (8.8)$$

and (8.5) as

$$e_{RP} < \frac{m_P (\alpha_{RP} \alpha_{RC} e_{RC} K + \alpha_{CP} r)}{\alpha_{RP} K (\alpha_{RP} m_C + \alpha_{CP} r)} := M_{RP}. \quad (8.9)$$

So,

$$M_{RC} < e_{RP} < M_{RP}. \quad (8.10)$$

However,

$$M_{RC} = M_{RP} = \frac{\alpha_{RC} e_{RC} m_P}{\alpha_{RP} m_C} \quad (8.11)$$

if

$$K = \frac{m_C}{e_{RC} \alpha_{RC}}. \quad (8.12)$$

Define,

$$\bar{R}_{RC} = \frac{m_C}{e_{RC} \alpha_{RC}} \quad (8.13)$$

which is the resource density at equilibrium in the resource-consumer system with the predator missing. Similarly, define

$$\bar{R}_{RP} = \frac{m_P}{e_{RP} \alpha_{RP}} \quad (8.14)$$

which is the resource density at equilibrium in the resource-predator system with the consumer missing. Then the consumer is said to be the **superior competitor** [40] for the shared resource if

$$\bar{R}_{RC} < \bar{R}_{RP}. \quad (8.15)$$

Since

$$\frac{\partial M_{RC}}{\partial K} = -\frac{\alpha_{CP} m_P r}{\alpha_{RP} K^2 (\alpha_{RP} m_C + \alpha_{CP} r)} < 0, \quad (8.16)$$

$M_{RC}$  is a decreasing function of the resource carrying capacity. Then by (8.10)

$$e_{RP} < \frac{\alpha_{RC} e_{RC} m_P}{\alpha_{RP} m_C}, \quad (8.17)$$

which is equivalent to

$$\bar{R}_{RC} < \bar{R}_{RP}. \quad (8.18)$$

Thus, we see that the consumer must be the superior competitor for the shared resource.

Finally, from (8.5) we get the positive term

$$r \left( \frac{\alpha_{CP}}{\alpha_{RP}} \right) \left( \frac{m_P}{e_{RP}\alpha_{RP}K} \right). \quad (8.19)$$

Thus, increasing the productivity of the resource via  $K$ , decreases (8.19) and thereby making invasion by the consumer more difficult.

In conclusion, we have the following:

- 1) The predator should gain significantly from its consumption of the consumer.
- 2) The consumer should be superior at exploitative competition for the shared resource.
- 3) Along gradients in resource productivity, coexistence is most likely at intermediate levels of productivity.

Our results affirm the conclusions drawn by Holt et al. [40].

For the non-linear response omnivory model (5.1), the conditions that guarantee permanence are given by the following:

$$0 < e_{CP}e_{RC} - e_{RP} \quad (8.20)$$

$$0 < \frac{e_{RP}\lambda_{RP}K}{1 + \lambda_{RP}h_{RP}K} - m_P \quad (8.21)$$

$$0 < \frac{e_{RC}\lambda_{RC}K}{1 + \lambda_{RC}h_{RC}K} - m_C \quad (8.22)$$

$$0 < \frac{\lambda_{RC}K\xi_1(\lambda_{RP}e_{RP}m_C + \lambda_{CP}e_{CP}e_{RC}r) - \lambda_{CP}e_{CP}e_{RC}m_Cr}{K(\lambda_{RC})^2\xi_1^2 - \lambda_{CP}e_{RC}h_{CP}m_Cr + \lambda_{RC}K\xi_1\nu} - m_P \quad (8.23)$$

$$0 < \frac{\lambda_{RC}e_{RC}m_P}{\lambda_{RP}e_{RP} + \lambda_{RC}h_{RC}m_P - \lambda_{RP}h_{RP}m_P + \frac{r\lambda_{CP}(\lambda_{RP}h_{RP}Km_P + m_p - \lambda_{RP}e_{RP}K)}{K(\lambda_{RP})^2(e_{RP} - m_P h_{RP})}} - m_C \quad (8.24)$$

$$0 \geq \frac{rm_C(\lambda_{RC}(K-1)\xi_1 - 2m_C)}{\lambda_{RC}K\xi_1(m_C + \lambda_{RC}\xi_1)} \quad (8.25)$$

$$0 \geq \frac{rm_P(\lambda_{RP}(K-1)\xi_2 - 2m_P)}{\lambda_{RP}K\xi_2(m_P + \lambda_{RP}\xi_2)} \quad (8.26)$$

where

$$\xi_1 = e_{RC} - m_C h_{RC} \quad (8.27)$$

$$\xi_2 = e_{RP} - m_P h_{RP} \quad (8.28)$$

$$\xi_3 = e_{CP} - m_P h_{CP} \quad (8.29)$$

$$\nu = \lambda_{RP}h_{RP}m_C + r\lambda_{CP}h_{CP}e_{RC}. \quad (8.30)$$

Similar to above,

$$e_{RP} < e_{CP}e_{RC}. \quad (8.31)$$

$$(8.32)$$

Thus, the predator should gain significantly from its consumption of the consumer.

Conditions (8.21) and (8.22) can be rewritten as

$$\frac{e_{RP}}{h_{RP}} > m_P \left( 1 + \frac{h_{RP}}{\lambda_{RP}K} \right) > m_P \quad (8.33)$$

and

$$\frac{e_{RC}}{h_{RC}} > m_C \left( 1 + \frac{h_{RC}}{\lambda_{RC}K} \right) > m_C \quad (8.34)$$

respectively. Condition (8.33) states that the profitability of resources for predators (the energy return per handling time,  $e_{RC}/h_{RC}$ ) must exceed predator mortality ( $m_P$ ) by a sufficient amount. Similarly, condition (8.34) states that the profitability of resources for consumers must exceed consumer mortality by a sufficient amount. Also, we see that  $\xi_1 > 0$  and  $\xi_2 > 0$ . Conditions (8.25) and (8.26) can be rewritten as

$$\frac{e_{RC}}{h_{RC}} < m_C \left( 1 + \frac{2h_{RC}}{\lambda_{RC}(K-1)} \right) \quad (8.35)$$

and

$$\frac{e_{RP}}{h_{RP}} < m_P \left( 1 + \frac{2h_{RP}}{\lambda_{RP}(K-1)} \right) \quad (8.36)$$

respectively. That is, the profitability of resources for consumer must not be too high. Otherwise, the predator is driven to extinction. Similarly, the profitability of resources for predators must not be too high, so that the consumer is not driven to extinction.

Solving for  $K$  in equations (8.25) and (8.26) yield

$$K \leq \frac{2m_C}{\lambda_{RC}\xi_1} \quad (8.37)$$

$$K \leq \frac{2m_P}{\lambda_{RP}\xi_2}. \quad (8.38)$$

Since,  $\xi_1, \xi_2 > 0$ , these conditions state that there must be an upper bound on  $K$  for coexistence of species.

In order to simplify expressions, we set  $h_{RC} = 0$ . The general case with  $h_{RC} > 0$  can be analyzed in the same way, but with more complex formulas. Then, manipulations similar to the linear case show that the consumer must be the superior competitor for the shared resource (see also [58]). Thus, our conclusions for the non-linear response omnivory model are the same as for the linear model.

For the stage structure model (6.1), the conditions that we feel are necessary for perma-

nence are given by the following:

$$0 < e_{CP}e_{RC} - e_{RP} \quad (8.39)$$

$$0 \leq e_{RC}e_{CP} \left( \frac{e_{RP}\lambda_{RP}K_{max}}{1 + \lambda_{RP}h_{RP}K_{max}} \right) - e_{RP} \min(m_C, \mu_P + 2m_P) - \mu_P \quad (8.40)$$

$$0 > \frac{(m_P)^2}{b - m_P} - \mu_P \quad (8.41)$$

$$0 < \frac{e_{RP}\lambda_{RP}K}{1 + \lambda_{RP}h_{RP}K} - m_P \quad (8.42)$$

$$0 < \frac{e_{RC}\lambda_{RC}K}{1 + \lambda_{RC}h_{RC}K} - m_C \quad (8.43)$$

$$0 < \frac{\lambda_{RC}K\xi_1(\lambda_{RP}e_{RP}m_C + \lambda_{CP}e_{CP}e_{RC}r) - \lambda_{CP}e_{CP}e_{RC}m_C r}{K(\lambda_{RC})^2\xi_1^2 - \lambda_{CP}e_{RC}h_{CP}m_C r + \lambda_{RC}K\xi_1\nu} - m_P \quad (8.44)$$

$$0 < \frac{r\lambda_{CP}\mu_P(\xi_4(m_P)^2 + \mu_P m_P \xi_4 - e_{RP}\lambda_{RP}K\mu_P)}{(\lambda_{RP})^2 K(\mu_P + m_P)\xi_5} + \frac{\lambda_{RC}e_{RC}m_P(\mu_P + m_P)}{\lambda_{RC}h_{RC}m_P(\mu_P + m_P) - \lambda_{RP}\xi_5} - m_C \quad (8.45)$$

where

$$\xi_1 = e_{RC} - m_C h_{RC} \quad (8.46)$$

$$\xi_2 = e_{RP} - m_P h_{RP} \quad (8.47)$$

$$\xi_3 = e_{CP} - m_P h_{CP} \quad (8.48)$$

$$\xi_4 = 1 + \lambda_{RP}h_{RP}K \quad (8.49)$$

$$\xi_5 = h_{RP}m_P(\mu_P + m_P) - e_{RP}\mu_P \quad (8.50)$$

$$\nu = \lambda_{RP}h_{RP}m_C + r\lambda_{CP}h_{CP}e_{RC}. \quad (8.51)$$

Conditions (8.40) and (8.41) yield,

$$\frac{(m_P)^2}{b - m_P} < \mu_P \leq e_{RC}e_{CP} \left( \frac{e_{RP}\lambda_{RP}K_{max}}{1 + \lambda_{RP}h_{RP}K_{max}} \right) - e_{RP} \min(m_C, \mu_P + 2m_P). \quad (8.52)$$

Thus, we have restrictions on how large and how small  $\mu_P$  can be. Note that the other inequalities are similar to those for the non-linear model. In fact, Mylius et al. [71] state that “for higher values of the maturation rate (i.e., shorter initial stage), the situation is qualitatively identical to the basic [non-linear] model”. Thus, our conclusions are the same as for the linear model. See [71] for numerical confirmation.

## 8.2 Sensitivities

As seen in the figures of Chapter 7, the largest value for the norm of the sensitivities for any parameter and any model is less than 410. In fact, the most sensitive parameter in

all three models is the predator mortality rate,  $m_P$ . This means that small changes in the predator mortality rate cause the largest change in the solution. Thus, biologist should take extra care in the field to accurately collect data for the predator mortality rate.

The next most sensitive parameters are the consumption, search and consumer mortality rates. For the linear model, the most sensitive of these rates is the consumption rate,  $\alpha_{CP}$ . The other consumption rates and the consumer mortality rate have essentially the same sensitivities over time. For the non-linear model, the search rates and predator mortality rate have comparable sensitivities over time. All three of the search rates are more sensitive than the consumer mortality rate for the stage structure model.

In the stage structure model, the maturation rate,  $\mu_P$ , is more sensitive than the conversion efficiencies. For all three models the next group of comparable sensitivities are the conversion efficiencies and resource enrichment parameters,  $r$  and  $K$ . In the linear case, the least sensitive parameter is the resource carrying capacity,  $K$ . Similarly, the least sensitive parameter in the above group of sensitivities is  $K$  for the non-linear and stage structure models.

Finally, the least sensitive parameters for the non-linear and stage structure models are the handling times. Thus, biologist need not be as accurate in collecting data for these parameters since they affect the solution the least. Of the handling times, the most sensitive parameter is  $h_{RP}$  and the least sensitive is  $h_{CP}$  for both models.

# Chapter 9

## Conclusions

There were three main ideas studied in this dissertation. One was the formulation of omnivory models of increasing complexity. Incorporated in this formulation is showing the ubiquity of omnivory in natural systems of fish, birds, and mammals. The second was the analysis of the parameter conditions under which our models are permanent, or in a realistic biological sense, the coexistence of species is ensured. We used a linear response omnivory model, a non-linear response omnivory model, and a stage structure omnivory model as approximations to natural systems. We also showed that these systems have unique solutions for all non-negative time. Lastly, we used sensitivity analysis to analyze our models and provide information on meaningful parameter data collection.

Our analysis was based on a technique of developing an Average Lyapunov function for the linear and non-linear models and extending the results to gain insight on the stage structure model. In considering these models, we were led to the following conclusions for permanence:

- 1) The systems of equations should have uniformly bounded orbits.
- 2) The  $\Omega$  limit set of the boundary of the state space should consist of equilibrium points only.
- 3) The missing species should be able to invade the system when the other species are present and at equilibrium.

The sensitivity analysis provided us with a prioritization of the model parameters based upon the parameter sensitivities. We concluded that the most sensitive parameter is the predator mortality rate and the least sensitive parameter is the time spent by the predator handling the consumer.

From a biological point of view, we concluded the following general criteria for species coexistence in our omnivory models:

- 1) The predator should gain significantly from its consumption of the consumer.
- 2) The consumer should be superior at exploitative competition for the shared resource.
- 3) Along gradients in resource productivity, coexistence is most likely at intermediate levels of productivity.

The permanence of models with migration dynamics, symmetrical interactions, and ad-

ditional species is still an open question. One limiting factor is that most available theory assumes that the boundary of the state space is invariant. It would be useful to investigate these more complicated models and provide the theory to analyze the permanence of these models.

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