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Competition Effects in an Intraguild Predation Model

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Abstract

In the biological world, many interactions exist between various species. These interactions generally consist of predator-prey relationships, competition between species and beneficial relationships. One observed phenomenon, termed the fear effect, occurs when one species reacts to an increased risk of predation by another species. The fear response causes the affected species to reproduce and forage for food less. In some cases, the fear response can be beneficial, while in other times it can be harmful. In this thesis, we consider a four-compartment food-chain model in which there exists a top-level predator, a mesopredator and two types of prey who directly compete with one another. The model accounts for each lesser species' fear response to the next highest one. We aim to examine how competition and the fear effect can work together to adjust the structure of the food chain. We used some standard techniques of dynamical systems to glean some results about the long-term dynamics of the system. We found that the fear response and competition effects can play an important part in the long-term dynamics of the system and cause a restructuring in the food chain itself.

Keywords Predator-prey models, competition models, ordinary differential equations, systems of ordinary differential equations, mathematical biology, fear effect, fear response, food chains, intraguild predation models.

Summary for Lay Audience

When we consider species in the natural world, one topic that may be of interest is how species and animals interact with each other and their environment. There are three basic interaction types termed predation, competition and mutualism. Predation occurs when a member of one species eats a member of another species. Competition occurs when individual entities fight among the same species, or other species for some sort basic needs which are required for sustenance. Competition can have a negative effect. Mutualism occurs when one species interacting with another has a beneficial or helpful effect. This usually culminates when both species are coexisting peacefully, and their interactions are mutually beneficial. An interesting biological result shows that the threat of predation can have an indirect effect on prey. This phenomenon is known as the fear effect. Put simply, when a species is being eaten more by a predator, or when a species perceives an increased likelihood of being eaten, it will trigger a self-preservation response driven by fear. The fear response manifests itself as the species at risk reproducing less and foraging for food less, thus reducing its interaction with predators. This response can have a beneficial effect, although if too strong a response occurs, it can significantly reduce the population of the affected species. We can use a food chain to represent the various interactions between species. It is possible to devise mathematical models that encode the details of a food chain. We can use these models to study the long-term effects of the various sorts of interactions. In our model, we study the long-term behaviours of a specific food chain model. The food chain consists of a top predator which predate on a mid-level predator who in turn predate on two distinct types of prey. Both preys are in direct competition with each other, and our model accounts for the fear response driven by the next highest member on the food chain. We were able to study the long-term behaviours of this system and study how competition and the fear effect could impact the structure of the food chain.

Epigraph

”Competition is a sin.”

—John D. Rockefeller

Dedication

I would like to dedicate this work to my predecessors. Their derivation of useful theorems sure makes my job a lot easier.

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Chapter 1

Introduction

1.1 Population Dynamics of Interacting Species

The usage of differential equations in mathematical biology to study population dynamics is nothing new, nor an exact science given the countless different modelling approaches. One common application is the study of dynamics of a hierarchical relationship between predator and prey. We've all heard of the classic rabbits and foxes scenario, and could easily think of countless others. One such model is the well-known Lotka-Volterra equations. This famous model has served, and still serves as a useful frame work for building predator-prey models in the literature. As discussed in [12] the original model was developed separately by A.J. Lotka and V. Volterra during the 1920s. Volterra showed that the equations admit periodic solutions. In the context of population dynamics, this explains certain boom-and-bust cycles one sees in predator-prey systems. In [13], Lotka presents the classic model. In his analysis, he proposes the model:

$$\frac{dN_i}{dt} = N_i F_i(N_1, N_2, N_3, \dots, N_i), \quad i = 1, 2, 3, \dots, \quad (1.1)$$

where N_i describes the density of each species in the model, F_i describes the per-capita growth rate, and t represents the time variable. By choosing a suitable F_i function, this model can serve as a framework to describe population dynamics of interacting species. Predator-prey interactions, competition and mutualism can all be encoded into a suitable F_i function. The basic Lotka-Volterra framework has been extensively covered in the literature, including the books [5], [1], [8], [4].

1.2 Predator-Prey Models

The general Lotka-Volterra equation can be used to represent a whole host of predator-prey interactions. The most basic form is the special case where $i = 2$, studied by Lotka and Volterra. Lotka suggests the scenario could be used to describe a plant and herbivore relationship, i.e. a specific predator-prey relationship. It is proposed that the rate of change of each N_i is given by the benefit minus the cost affecting each N_i . This leads to the equations:

$$\begin{aligned}\frac{dN_1}{dt} &= N_1(a_1 - b_1N_2), \\ \frac{dN_2}{dt} &= N_2(a_2N_1 - b_2),\end{aligned}\tag{1.2}$$

where a_1 describes the benefit to N_1 , and b_1 describes the cost to N_1 by interacting with N_2 . a_2 describes the benefit N_2 gains by interacting with N_1 and b_2 describes the costs affecting N_2 . When thinking about the possible equilibria, there are four possible cases. These are extinction, two forms of invasion and coexistence. (1.2) only has two possible solutions eliminating the invasion cases. The equilibria consist of an extinction case and a coexistence case. Lotka goes on to show that the extinction case is unstable for positive model parameters. It is then shown that the coexistence equilibrium is a center, and so admits periodic solutions.

The basic idea of describing the dynamics by weighing the costs and benefits is a common

theme in many subsequent models developed. The basic Lotka-Volterra model considers the general cost-to-benefit value to be described as rate in minus rate out. In a more recent paper, [17], the authors approach the cost and benefit problem by assigning a single constant to represent the total effects of cost and benefits respectively. They devise a ratio-based method to measure the effect of cost compared to benefit.

Various extended forms of the basic Lotka-Volterra model exist which will be briefly discussed in this section. One of the more common modifications to the basic Lotka-Volterra model is to define some functions which describe the birth-rate and predator-prey interactions. Chapter 2.4 in [5] talks about this to some extent. The birth-rate function defined for N_1 has the notion of a carrying capacity. This puts an upper-bound on the number of entities that can be sustained in a hypothetical ecosystem. Here, the author proposes a Lotka-Volterra-type model with a logistic birth-rate function for N_1 . This ensures the growth of N_1 in the absence of predators is capped by the carrying capacity of the ecosystem.

Another modification that can be added here is a functional response term which models the rate at which N_2 can consume the resources provided by N_1 . The classic reference [10] devises the so-called Holling type-I, type-II and type-III functional responses. Holling derived these equations from biological data using the well-known time-budget argument. Other forms of functional response exist, most notably the Beddington-DeAngelis functional response. The dynamics of a classic predator-prey model with Beddington-DeAngelis functional response are examined in [6]. A more recent paper, [14], studies the dynamics of a predator-prey system with Beddington-DeAngelis functional response that incorporates a fear of predators. Alternatively, one may also derive a specific functional response to the problem on hand.

When a logistic-growth function is defined for N_1 and a Holling type-II functional response is added to a basic Lotka-Volterra model, the resulting equations are called the Rosenzweig-MacArthur model. These ideas can be generalized for an arbitrary number

of predators and prey, which leads into some of the literature on the generalized Lotka-Volterra-type equations. These are explored in [3]. It allows the construction of a food-web system and permits the modelling different types of interactions between species such as competition and predation, which will be useful for our model. The dynamics exhibited are extremely varied. Some other alternatives to the Lotka-Volterra model exist such as the Arditi-Ginzberg model given in [2]. This model examines the functional response as a function of the ratio of predators to prey.

Food chain modelling is essentially a combination of some of the techniques of predator-prey modelling and competition modelling. The basic idea is illustrated in Chapter 2.7 of [5]. One constructs a state diagram which shows all of the interactions between the various species, and the rates at which this happens. The most basic models assume constant rates of interaction, while the most advanced ones will use specific functions to describe them. This can be anything, such as competition, predation and even interactions with some sort of external influence. By considering the positive and negative interactions, one may write down a system of equations to model the specific scenario. It is possible to analyse such a system to determine the effects that each state variable has on the others. In the context of a food-chain, one may wish to determine if it is possible for a higher-level species to hunt a lower-level species to extinction, etc. In the literature, the types of food-chain models that combine predation and competition are referred to as intraguild predation models. The model presented in [11] was one of the first to provide a general framework for combining the effects of competition and predation. The more recent work [15] extends this model framework to include delay effects.

1.3 Competition Models

Just like predator-prey models, competition models are of a varied sort. The two main types of competition that can be modelled are intraspecies and interspecies competition.

The former refers to members of one species competing against themselves for common resources, e.g. shelter, food, etc. The latter refers to two distinct species competing against each other. This can manifest itself in different ways, but one example might be two distinct species at the same level on a food chain competing for shared resources. The simplest model for intraspecies competition would look something like the following:

$$\frac{dN}{dt} = aN - bN^2, \quad (1.3)$$

where N describes the population density of the species, a describes the growth rate of N , and b describes the intraspecies competition rate. The simplest model for interspecies competition would look something like the following:

$$\begin{aligned} \frac{dN_1}{dt} &= aN_1 - \beta_1 N_1 N_2, \\ \frac{dN_2}{dt} &= bN_2 - \beta_2 N_1 N_2, \end{aligned} \quad (1.4)$$

where N_1 describes the population of the first species, N_2 describes the population of the second species, a describes the growth rate of N_1 , β_1 describes the rate at which N_1 competes with N_2 , b describes the growth rate of N_2 and β_2 describes the competition rate of N_2 with N_1 . The papers [9] and [16] explain the dynamics of certain classes of more general Lotka-Volterra models.

In Chapter 2.5 of [5], some more advanced competition models are discussed. This class of model is referred to as a competitive Lotka-Volterra model. The idea is fairly straightforward and consists of starting with a basic Lotka-Volterra model and modifying the growth term to that of a logistic model. One makes the assumption that the interspecies competition works the same way as the intraspecies competition. Writing this in a slightly simplified

manner, one obtains:

$$\begin{aligned}\frac{dN_1}{dt} &= aN_1 - bN_1^2 - \beta_1 N_1 N_2, \\ \frac{dN_2}{dt} &= cN_2 - dN_2^2 - \beta_2 N_1 N_2,\end{aligned}\tag{1.5}$$

where a and b describe the growth rate of N_1 and N_2 respectively, b and d describe the intraspecies competition rates of N_1 and N_2 respectively, and β_1 and β_2 describe the competition rates between N_1 and N_2 . Two important ideas are the notion of strong and weak competition. Strong competition refers to when the effects of the interspecies competition are greater than that of the intraspecies competition. Similarly, weak competition refers to when the effects of intraspecies competition are greater than that of the interspecies competition. Strong and weak competition often influence the ability of one competitor's ability to invade the other and drive it to extinction. This approach assumes that competition is an effect which can be modelled by a constant. A more recent approach is to replace the competition constant with a function to model more advanced phenomenon such as the fear effect. This approach is used in [21], [22], [7], [19], [20].

1.4 Fear Effect

The fear effect is a fairly recent concept to have been studied within the framework mathematical models. A biological field study presented in [18] investigated the fear effect and its impact on food chains. Paraphrasing, the article describes the fear effect as a certain type of anxiety or stress which affects the lower members in a food chain, usually mid-level predators and herbivores brought about by the predatory actions of a top-level predator. The article goes on to describe that this fear can be brought about by either direct predation (predators eating their prey) or indirect predation (the large presence of a large carnivore, and resulting increased risk of lower-level members being eaten). A reaction to this fear is called a fear response. It usually manifests itself as reduced reproduction rates

in an afflicted species and a decrease in foraging for food. This is done as a means of self-preservation, but too much of a fear response can have a negative impact on the population of a species, especially if it reduces the ability of said species to reproduce and feed sufficiently to sustain its existence. In [18], a study was conducted which showed exactly that. A food-chain consisting of an implied top-level predator, a mid-level predator and some lower species was studied. Indirect effects of the large predator on the mid-level predator were studied. This was accomplished by leaving signatures of the large predator's presence for the mid-level predator to discover. The mid-level predator's fear response had a negative effect and reduced its population. For the lower-level species, this meant there was less of a predation risk from the mid-level predator, so a population boom soon followed. This exacerbated the effects of competition at this lower-level, and in a sense changed some of the arrangements of the food chain, which is referred to as a trophic cascade in the literature. As the fear effect can have a large effect on a food-chain, mathematicians decided to investigate the result using models. From the above discussion, the two key elements which the fear effect has an impact on are birth-rate and predation. Therefore, a modified growth-term and a functional response will be needed to sufficiently model this behaviour. [19] and [20] give an overview of the various forms of non-trivial functional responses and how they can be applied to study the fear effect through the birth-rate function. [22], [21] and [7] extend this work by using some of these ideas to modify the predation terms to give a more complete picture. In the next section, the motivation for this model will be discussed.

1.5 The Model

1.5.1 Motivation

The model presented in this section was inspired by [21], [22], [7] and [18]. In [18], a group of researchers studied some of the effects that the fear response can have in a

food chain out in the field. They considered an ecosystem comprised of large predators, mesopredators and prey of the mesopredator. The researchers played back sounds of large predators to the mesopredators to see how the large predator's perceived presence could affect the overall food chain. They observed that the fear of the large predators drove the mesopredators to forage for food less, i.e. eating few of their prey. This reduced the predation level of the mesopredators on the prey, leading to an increased number of prey. In some instances, this led to some of the prey's competitors facing increased competition from the prey. The authors described an instance where one species of prey invaded one of its competitors. In this case, the fear of large predators caused a shift in the structure of the food chain. Some more recent references have studied this effect mathematically.

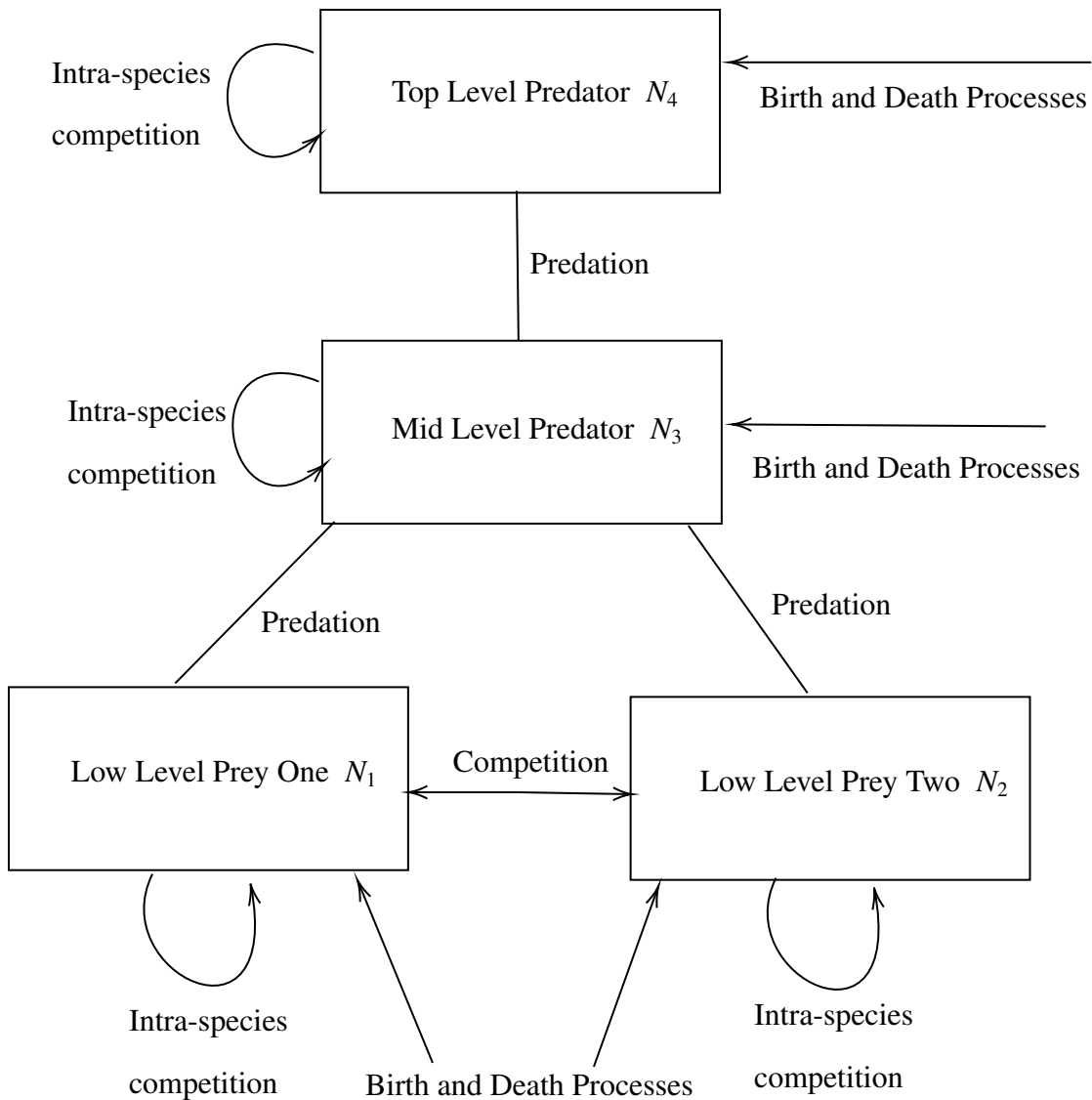
In [7], the authors considered a three-species food chain model with fear effect. The model consisted of a top-level predator, mesopredator and prey. Their results showed the fear effect can lead the system to a stable state in the long-term. In [22], the authors considered a model involving three species. One species is a predator, with two prey who are in competition. Both prey have differing anti-predation strategies. The authors studied how the differing anti-predation methods can affect the system. In [21], the authors directly considered some of the results of [18] in two different ways. The first three-component model studies the indirect effect of playing sounds of top-level predators on the mesopredator. The fear response level solely effects the birth-rate of the mesopredator. The other two species are the prey of the mesopredator, and the mesopredator's prey's prey. The four-component model adds in the direct effects of a top-level predator. In both cases, effects on the structure of the food chain can be noticed, but occur in differing ways.

For our model, we will study the effects of competition in such a three-tier food chain. [7] studies a three-tier food chain without competition, [22] studies a two-tier food chain with competition, and [21] considers a three and four-tier food chain with different effects of fear response. Our model will combine some of these ideas into a three-tier food chain

with competition at the lowest level. This type of food chain was discussed in some detail in [18], so it will be interesting to study it mathematically.

1.5.2 Flowchart

The following flowchart summarizes the food web structure and the relationships between each species.



1.5.3 Model Derivation and Explanation

Using the above flowchart and assumptions, we may derive the following model. We need not account for any fear effect in the top level predator's birth and death processes due to it being the top-level predator. The model reads as:

$$\left\{ \begin{array}{l} \frac{dN_1}{dt} = N_1 [B_1(\alpha_1, N_3) - D_1 - c_1 N_1 - \beta_1 N_2] - f_1(\alpha_1, N_1, N_3)N_3, \\ \frac{dN_2}{dt} = N_2 [B_2(\alpha_2, N_3) - D_2 - c_2 N_2 - \beta_2 N_1] - f_2(\alpha_2, N_2, N_3)N_3, \\ \frac{dN_3}{dt} = N_3 [B_3(\alpha_3, N_4) - D_3 - c_3 N_3] + \varepsilon_1 f_1(\alpha_1, N_1, N_3)N_3 \\ \quad + \varepsilon_2 f_2(\alpha_2, N_2, N_3)N_3 - f_3(\alpha_3, N_3, N_4)N_4, \\ \frac{dN_4}{dt} = N_4 [B - c_4 N_4] + \varepsilon_3 f_3(\alpha_3, N_3, N_4)N_4 \\ N_1(0) \geq 0, N_2(0) \geq 0, N_3(0) \geq 0, N_4 \geq 0. \end{array} \right. \quad (1.6)$$

It should be pointed out that some components of the predation terms for N_3 and N_4 were absorbed into the f_i functions. This point will be important later. The model components can be nicely summarized in the tables below:

Parameter	Explanation
α_1	Fear response of first low-level prey due to mid-level predator
α_2	Fear response of second low-level prey due to mid-level predator
α_3	Fear response of mid-level predator due to top-level predator
B	Reproduction rate of top-level predator
$\beta_i, i = 1, 2$	Competition rates between each i -th low-level prey
$c_i, i = 1, 2, 3, 4$	Intra-species competition level for i -th species
$D_i, i = 1, 2, 3$	Death rate for i -th species
$\varepsilon_i, i = 1, 2, 3$	Biomass transfer efficiency constants
N_1	First low-level prey density
N_2	Second low-level prey density
N_3	Mid-level predator density
N_4	Top-level predator density

Table 1.1: Description of model variables and parameters

Function	Description
$B_i(\cdot, \cdot), i = 1, 2, 3$	Per-capita birth rates of each N_i
$f_i(\cdot), i = 1, 2, 3$	Functional response function describing biomass transfer from N_i to N_{i+1}

Table 1.2: Description of model functions

1.5.4 Determining the Functional Response and Birthrate Functions

We will need to impose certain conditions on the functions $B_i(\cdot)$ and $f_i(\cdot)$ for $i = 1, 2, 3$ so that they maintain a certain biological context with respect to the fear effect. These may be derived from our assumptions regarding the fear effect, as well as consulting [22] for completeness. The following functions were chosen as they were some of the simplest ones which met the needed biological criterion. This both simplifies the analysis, but ensures our model still maintains the needed biological meanings.

We state the following assumptions regarding the birth rate functions:

- i) In the absence of a fear response or predators, the birth rate is a positive, fixed constant.
- ii) As fear response increases, birth rate decreases. Similarly, as predator population increases, birth rate decreases.

We may now state this mathematically for each birth rate function, where $i = 1, 2, 3, j = 3, 4$:

- i) $B_i(0, N_j) = B_i(\alpha_i, 0) = \gamma_i > 0$, where γ_i is the positive, fixed birthrate constant
- ii) $\lim_{\alpha_i \rightarrow \infty} B_i(\alpha_i, N_j) = \lim_{N_j \rightarrow \infty} B_i(\alpha_i, N_j) = 0$
- iii) $\frac{\partial B_i(\alpha_i, N_j)}{\partial \alpha_i} < 0, \frac{\partial B_i(\alpha_i, N_j)}{\partial N_j} < 0$

The function:

$$B_i(\alpha_i, N_j) = \frac{\gamma_i}{1 + \alpha_i N_j} \quad (1.7)$$

satisfies the above conditions. Those readers familiar with the literature will recognize this as a Holling Type II functional response. A direct calculation can easily verify that i) and ii) hold. The derivatives are given by:

$$\begin{aligned}\frac{\partial B_i(\alpha_i, N_j)}{\partial \alpha_i} &= -\frac{\gamma_i N_j}{(N_j \alpha_i + 1)^2}, \\ \frac{\partial B_i(\alpha_i, N_j)}{\partial N_j} &= -\frac{\gamma_i \alpha_i}{(N_j \alpha_i + 1)^2}.\end{aligned}\tag{1.8}$$

Using the fact that each parameter is positive, and that each N_j is positive under the conditions of Lemma 2.1, we also see that iii) holds.

Let us now consider the functional response functions. In the manner of [22], let us consider the special case:

$$f_i(\alpha_i, N_i, N_j) = f_i(\alpha_i, N_i) = \hat{f}_i(\alpha_i)N_i, \quad i = 1, 2, 3, \quad j = 3, 4.\tag{1.9}$$

In essence, we have a linear functional response with a scaling function \hat{f}_i which takes into account the fear response α_i . We impose the following conditions on $\hat{f}_i(\alpha_i)$, where $i = 1, 2, 3$:

- i) $\hat{f}_i(0) = p_i > 0$, where p_i is the positive, fixed predation constant
- ii) $\lim_{\alpha_i \rightarrow \infty} \hat{f}_i(\alpha_i) = 0$
- iii) $\frac{d\hat{f}_i(\alpha_i)}{d\alpha_i} < 0$

We then pick the suitable function:

$$\hat{f}_i(\alpha_i) = \frac{p_i}{1 + \alpha_i}\tag{1.10}$$

to describe the functional response, where p_i is the initial predation rate. A direct calcu-

lation can easily verify that i), ii) and iii) hold. For the rest of this paper, we will use the above functional response and birthrate functions.

The final model then reads:

$$\begin{cases} \frac{dN_1}{dt} = N_1 \left[\frac{\gamma_1}{1 + \alpha_1 N_3} - D_1 - c_1 N_1 - \beta_1 N_2 - \frac{p_1}{1 + \alpha_1} N_3 \right], \\ \frac{dN_2}{dt} = N_2 \left[\frac{\gamma_2}{1 + \alpha_2 N_3} - D_2 - c_2 N_2 - \beta_2 N_1 - \frac{p_2}{1 + \alpha_2} N_3 \right], \\ \frac{dN_3}{dt} = N_3 \left[\frac{\gamma_3}{1 + \alpha_3 N_4} - D_3 - c_3 N_3 + \varepsilon_1 \frac{p_1}{1 + \alpha_1} N_1 + \varepsilon_2 \frac{p_2}{1 + \alpha_2} N_2 - \frac{p_3}{1 + \alpha_3} N_4 \right], \\ \frac{dN_4}{dt} = N_4 \left[B - c_4 N_4 + \varepsilon_3 \frac{p_3}{1 + \alpha_3} N_3 \right] \\ N_1(0) \geq 0, N_2(0) \geq 0, N_3(0) \geq 0, N_4 \geq 0. \end{cases} \quad (1.11)$$

This model studies how the fear effect can cascade down the food chain, while also incorporating competition and predation effects. As discussed in the motivation, such a model had not yet been studied in the literature.

Chapter 2

Well-Posedness of the Model

In this section, we will show that the model admits a unique, positive solution in a positively invariant set and is bounded. We will start with the following lemma.

Lemma 2.1 \mathbb{R}_+^4 is a positively invariant set for (1.11). Furthermore, (1.11) admits positive solutions for positive initial conditions.

Proof The main goal here will be to rewrite (1.11) in a more convenient form, then derive an expression for a solution. We will then be able to find a positively invariant set based off of the information encoded in these solutions.

We may rewrite (1.11) as:

$$\begin{aligned}
 \frac{dN_1}{dt} &= N_1 F_1(N_1, N_2, N_3), \\
 \frac{dN_2}{dt} &= N_2 F_2(N_1, N_2, N_3), \\
 \frac{dN_3}{dt} &= N_3 F_3(N_1, N_2, N_3, N_4) \\
 \frac{dN_4}{dt} &= N_4 F_4(N_3, N_4),
 \end{aligned}
 \tag{2.1}$$

recalling that some linear N_3 and N_4 terms were absorbed into the f_i functions, which allows

us to factor and rewrite the system as above. One may write:

$$\begin{aligned}
 N_1(t) &= N_1(0) \exp\left(\int_0^t F_1(N_1(\tau), N_2(\tau), N_3(\tau)) d\tau\right), \\
 N_2(t) &= N_2(0) \exp\left(\int_0^t F_2(N_1(\tau), N_2(\tau), N_3(\tau)) d\tau\right), \\
 N_3(t) &= N_3(0) \exp\left(\int_0^t F_3(N_1(\tau), N_2(\tau), N_3(\tau), N_4(\tau)) d\tau\right), \\
 N_4(t) &= N_4(0) \exp\left(\int_0^t F_4(N_3(\tau), N_4(\tau)) d\tau\right).
 \end{aligned} \tag{2.2}$$

From this, it follows that R_+^4 is a positively invariant set for (1.11) as claimed, thus, completing the proof. ■

It is possible to consider the quantity $R_i = \gamma_i - D_i, i = 1, 2, 3$. This can be thought of as the (intrinsic) growth rates of N_1, N_2 and N_3 in the absence of fear response. These values will be assumed to be positive. Using the previous result, we can consider the effect of the intrinsic growth rates R_1 and R_2 on N_1 and N_2 respectively in the absence of predation and interspecies competition.

Proposition 2.1 For $i = 1, 2$, when $R_i < 0$, $N_i(t) \rightarrow 0$.

Proof From (1.11), Lemma 2.1 and the comparison theorem, we can obtain the following comparison system for N_1 and N_2 :

$$\begin{aligned}
 \frac{dN_1}{dt} &\leq N_1(\gamma_1 - D_1 - c_1 N_1) \leq R_1 N_1, \\
 \frac{dN_2}{dt} &\leq N_2(\gamma_2 - D_2 - c_2 N_2) \leq R_2 N_2.
 \end{aligned} \tag{2.3}$$

Observe that the equations for N_1 and N_2 may be explicitly solved using standard methods.

Solving the equations for N_1 and N_2 , we obtain:

$$\begin{aligned} N_1(t) &\leq N_1(0) e^{R_1 t}, \\ N_2(t) &\leq N_2(0) e^{R_2 t}. \end{aligned} \tag{2.4}$$

If R_1 or R_2 is negative, it follows that:

$$\lim_{t \rightarrow \infty} N_1(t) = \lim_{t \rightarrow \infty} N_2(t) = 0. \tag{2.5}$$

The statement of the theorem follows. ■

Lemma 2.2 *The solutions admitted by (1.11) are bounded.*

Proof Using Lemma 2.1 and the fact that (1.11) is of the Gaussian type, there exists a unique solution to (1.11). The other piece to take care of is the boundedness aspect. Define:

$$P(t) = \varepsilon_1 \varepsilon_3 N_1 + \varepsilon_2 \varepsilon_3 N_2 + \varepsilon_3 N_3 + N_4. \tag{2.6}$$

From Lemma 2.1, we get that each $N_i(t)$, $i = 1, 2, 3, 4$ is positive $\forall t > 0$, and so if $P(t)$ is bounded, then it implies that each $N_i(t)$ is bounded. Therefore we need only show that $P(t)$ is bounded. There is not a readily usable, explicit form of $P(t)$ at the moment, so it will be

best to consider $\frac{dP}{dt}$. Calculating, one obtains:

$$\begin{aligned}
\frac{dP}{dt} &= \varepsilon_1 \varepsilon_3 \frac{dN_1}{dt} + \varepsilon_2 \varepsilon_3 \frac{dN_2}{dt} + \varepsilon_3 \frac{dN_3}{dt} + \frac{dN_4}{dt} \\
&\leq \varepsilon_1 \varepsilon_3 N_1 [\gamma_1 - D_1 - c_1 N_1] + \varepsilon_2 \varepsilon_3 N_2 [\gamma_2 - D_2 - c_2 N_2] + \varepsilon_3 N_3 [\gamma_3 - D_3 - c_3 N_3] \\
&\quad + N_4 [B - c_4 N_4] \\
&= \varepsilon_1 \varepsilon_3 N_1 [\gamma_1 - D_1 - c_1 N_1] + \varepsilon_2 \varepsilon_3 N_2 [\gamma_2 - D_2 - c_2 N_2] + \varepsilon_3 N_3 [\gamma_3 - D_3 - c_3 N_3] \\
&\quad + N_4 [2B - B - c_4 N_4] \\
&= -D_1 \varepsilon_1 \varepsilon_3 N_1 - D_2 \varepsilon_2 \varepsilon_3 N_2 - \varepsilon_3 D_3 N_3 - B N_4 + \varepsilon_1 \varepsilon_3 N_1 [\gamma_1 - c_1 N_1] + \varepsilon_2 \varepsilon_3 N_2 [\gamma_2 - c_2 N_2] \\
&\quad + \varepsilon_3 N_3 [\gamma_3 - c_3 N_3] + N_4 [2B - c_4 N_4] \\
&\leq \varepsilon_1 \varepsilon_3 N_1 [\gamma_1 - c_1 N_1] + \varepsilon_2 \varepsilon_3 N_2 [\gamma_2 - c_2 N_2] + \varepsilon_3 N_3 [\gamma_3 - c_3 N_3] + N_4 [2B - c_4 N_4] - mP,
\end{aligned} \tag{2.7}$$

where $m = \min\{D_1, D_2, D_3, B\}$. This expression follows from the positivity of $N_i(t)$ for each i , as well as the fact that each $B_i(\alpha_i, N_i) \leq \gamma_i$, $i = 1, 2, 3$ due to how it is defined. Each term is a downwards opening parabola, with one root at zero, and the other at a non-trivial positive value. The maximum of each term must occur at the midpoint. We may use this property to greatly simplify our expression for $\frac{dP}{dt}$. Calculating, we find that:

$$\begin{aligned}
\frac{dP}{dt} + mP &\leq \frac{\varepsilon_1 \varepsilon_3 \gamma_1^2}{4c_1} + \frac{\varepsilon_2 \varepsilon_3 \gamma_2^2}{4c_2} + \frac{\varepsilon_3 \gamma_3^2}{4c_3} + \frac{B^2}{c_4} \\
&= \frac{c_1((c_4 \varepsilon_3 \gamma_3^2 + 4B^2 c_3) + c_3 c_4 \varepsilon_2 \varepsilon_3 \gamma_2^2) + \varepsilon_1 \varepsilon_3 \gamma_1^2 c_2 c_3 c_4}{4c_1 c_2 c_3 c_4}.
\end{aligned} \tag{2.8}$$

For better readability, let:

$$C = \frac{c_1((c_4 \varepsilon_3 \gamma_3^2 + 4B^2 c_3) + c_3 c_4 \varepsilon_2 \varepsilon_3 \gamma_2^2) + \varepsilon_1 \varepsilon_3 \gamma_1^2 c_2 c_3 c_4}{4c_1 c_2 c_3 c_4}. \tag{2.9}$$

Solving (2.8), one obtains the solution:

$$P(t) \leq \frac{e^{-mt}(mP(0) + C(e^{mt} - 1))}{m} = \left(P(0) - \frac{C}{m}\right)e^{-mt} + \frac{C}{m} \quad (2.10)$$

where $P(0)$ is the initial value of $P(t)$ (which depends on each $N_i(0)$). Taking a limit, one obtains:

$$\limsup_{t \rightarrow \infty} P(t) \leq \frac{C}{m} = \frac{c_1((c_4\varepsilon_3\gamma_3^2 + 4B^2c_3) + c_3c_4\varepsilon_2\varepsilon_3\gamma_2^2) + \varepsilon_1\varepsilon_3\gamma_1^2c_2c_3c_4}{4c_1c_2c_3c_4m} \quad (2.11)$$

As the lim sup of $P(t)$ is finite, then $P(t)$ is clearly bounded above. Lemma 2.1 implies that each $N_i(t)$ is bounded below, and so $P(t)$ is bounded below. As $P(t)$ is bounded, it suffices to conclude that each $N_i(t)$ is bounded as well, thus completing the proof. ■

We conclude that the problem posed by (1.11) is a well-posed problem from the positivity and boundedness results.

Chapter 3

Dynamics of Two Subsystems

To better understand the dynamics of the full system, we will study the dynamics of two subsystems. We will study the relationship between N_1 and N_2 which is represented by a competition subsystem, and the relationship between N_3 and N_4 which is given by a predator-prey subsystem.

3.1 Dynamics of the $N_1 - N_2$ Competition Subsystem

In this section, we will summarize the equilibria and their stability with respect to the of competition in the absence of predators. In this case, the model becomes:

$$\begin{aligned}\frac{d\hat{N}_1}{dt} &= \hat{N}_1[\gamma_1 - D_1 - c_1\hat{N}_1 - \beta_1\hat{N}_2] = \hat{N}_1[R_1 - c_1\hat{N}_1 - \beta_1\hat{N}_2] = R_1\hat{N}_1 - c_1\hat{N}_1^2 - \beta_1\hat{N}_1\hat{N}_2, \\ \frac{d\hat{N}_2}{dt} &= \hat{N}_2[\gamma_2 - D_2 - c_2\hat{N}_2 - \beta_2\hat{N}_1] = \hat{N}_2[R_2 - c_2\hat{N}_2 - \beta_2\hat{N}_1] = R_2\hat{N}_2 - c_2\hat{N}_2^2 - \beta_2\hat{N}_1\hat{N}_2,\end{aligned}\tag{3.1}$$

where R_1 and R_2 are the intrinsic growth rates.

3.1.1 Equilibria and Stability

The equilibria of this system are given by:

$$\begin{aligned}
 \hat{E}_0(0, 0) &= (0, 0), \\
 \hat{E}_1(\hat{N}_1^*, 0) &= \left(\frac{R_1}{c_1}, 0 \right), \\
 \hat{E}_2(0, \hat{N}_2^*) &= \left(0, \frac{R_2}{c_2} \right), \\
 \hat{E}_3(\hat{N}_1^+, \hat{N}_2^+) &= \left(\frac{R_2\beta_1 - c_2R_1}{\beta_1\beta_2 - c_1c_2}, \frac{R_1\beta_2 - c_1R_2}{\beta_1\beta_2 - c_1c_2} \right).
 \end{aligned} \tag{3.2}$$

The first three equilibria always exist, given the assumption that R_1 and R_2 are positive. The existence criteria of the last equilibrium is slightly more involved.

Existence is conditional on both the numerator and denominator being simultaneously positive or negative. In the case where the denominator is positive, this corresponds to a condition of strong competition, i.e. the total inter-species competition is greater than the intra-species competition. Similarly, in the case where the denominator is negative, this corresponds to a condition of weak competition, i.e. the total intra-species competition is greater than that of the total inter-species competition. We also require that the denominator is not equal to zero, in other words, that $\beta_1\beta_1 \neq c_1c_2$.

For the case of strong competition, i.e. $\beta_1\beta_2 > c_1c_2$, we require that:

$$R_2\beta_1 > c_2R_1, \quad R_1\beta_2 > c_1R_2. \tag{3.3}$$

For the case of weak competition, i.e. $\beta_1\beta_2 < c_1c_2$, we require that:

$$R_2\beta_1 < c_2R_1, \quad R_1\beta_2 < c_1R_2. \tag{3.4}$$

Calculating the Jacobian of this system yields:

$$\mathbf{J}(N_1, N_2) = \begin{pmatrix} R_1 - 2c_1N_1 - \beta_1N_2 & -\beta_1N_1 \\ -\beta_2N_2 & R_2 - 2c_2N_2 - \beta_2N_1 \end{pmatrix}. \quad (3.5)$$

Evaluating the Jacobian at \hat{E}_0 yields:

$$\mathbf{J}(0, 0) = \begin{pmatrix} R_1 & 0 \\ 0 & R_2 \end{pmatrix}. \quad (3.6)$$

The eigenvalues are the product down the diagonal. As R_1, R_2 are assumed to be positive, this equilibrium is unstable. Evaluating the Jacobian at \hat{E}_1 yields:

$$\mathbf{J}\left(\frac{R_1}{c_1}, 0\right) = \begin{pmatrix} -R_1 & -\frac{R_1\beta_1}{c_1} \\ 0 & R_2 - \frac{\beta_2R_1}{c_1} \end{pmatrix}. \quad (3.7)$$

This admits eigenvalues:

$$\begin{aligned} \lambda_1 &= -R_1, \\ \lambda_2 &= \frac{R_2c_1 - \beta_2R_1}{c_1}. \end{aligned} \quad (3.8)$$

This equilibrium is stable when the condition:

$$R_2c_1 < \beta_2R_1 \quad (3.9)$$

holds. Evaluating the Jacobian at \hat{E}_2 yields:

$$\mathbf{J}\left(0, \frac{R_2}{c_2}\right) = \begin{pmatrix} R_1 - \frac{\beta_1R_2}{c_2} & 0 \\ -\frac{R_2\beta_2}{c_2} & -R_2 \end{pmatrix}. \quad (3.10)$$

This yields eigenvalues:

$$\begin{aligned}\lambda_1 &= \frac{R_1 c_2 - \beta_1 R_2}{c_2}, \\ \lambda_2 &= -R_2.\end{aligned}\tag{3.11}$$

This equilibrium is stable when the condition:

$$R_1 c_2 < \beta_1 R_2\tag{3.12}$$

holds. Evaluating the Jacobian at \hat{E}_3 yields:

$$\mathbf{J}(\hat{N}_1^+, \hat{N}_2^+) = \begin{pmatrix} \frac{c_1(R_1 c_2 - \beta_1 R_2)}{\beta_1 \beta_2 - c_1 c_2} & \frac{\beta_1(R_1 c_2 - \beta_1 R_2)}{\beta_1 \beta_2 - c_1 c_2} \\ \frac{\beta_2(R_1 \beta_2 - R_2 c_1)}{c_1 c_2 - \beta_1 \beta_2} & \frac{c_2(R_1 \beta_2 - R_2 c_1)}{c_1 c_2 - \beta_1 \beta_2} \end{pmatrix}.\tag{3.13}$$

This matrix has the characteristic equation:

$$\lambda^2 + \lambda \frac{c_2(R_1 \beta_2 - R_2 c_1) + c_1(R_2 \beta_1 - R_1 c_2)}{\beta_1 \beta_2 - c_1 c_2} + \frac{(R_1 \beta_2 - R_2 c_1)(R_1 c_2 - \beta_1 R_2)}{\beta_1 \beta_2 - c_1 c_2} = 0.\tag{3.14}$$

By the Routh-Hurwitz criteria, this equilibrium will be stable when the constant term and the coefficient of the λ term are both positive. Let us work on the λ term first. In the case of strong competition ($\beta_1 \beta_2 > c_1 c_2$), equation (3.3) is satisfied. This guarantees that the numerator will be positive in this term, and so the coefficient of the λ term is positive, satisfying the Routh-Hurwitz criteria. In the case of weak competition ($\beta_1 \beta_2 < c_1 c_2$), equation (3.4) is satisfied. This guarantees that the numerator of this term will be positive. As the denominator is negative, this means that the coefficient of the λ term is positive, satisfying the Routh-Hurwitz criteria again. This means that the coefficient of the λ term is always satisfied whenever \hat{N}_1^+ and \hat{N}_2^+ exist. Therefore, the constant term will govern stability in this case.

Referring once again to the case of strong competition, i.e. $\beta_1\beta_2 > c_1c_2$, we have that (3.3) holds. This then implies that the following conditions must hold on the constant term:

$$\begin{aligned} R_1\beta_2 > R_2c_1, \quad R_1c_2 > \beta_1R_2, \quad \text{or,} \\ R_1\beta_2 < R_2c_1, \quad R_1c_2 < \beta_1R_2, \end{aligned} \quad (3.15)$$

as per Routh-Hurwitz. Note that in both possibilities exactly one inequality is satisfied, as per (3.3), but one is not satisfied. This suggests that the strong competition case is unstable when it exists. In the case of weak competition, i.e. $\beta_1\beta_2 < c_1c_2$, we have that (3.4) holds. This then implies that the following conditions must hold on the constant term:

$$\begin{aligned} R_1\beta_2 < R_2c_1, \quad R_1c_2 > \beta_1R_2, \quad \text{or,} \\ R_1\beta_2 > R_2c_1, \quad R_1c_2 < \beta_1R_2, \end{aligned} \quad (3.16)$$

as per Routh-Hurwitz. The second condition in the above condition will fail to hold as per (3.4). However, the first condition will always hold as long as (3.4) is satisfied. Put another way, the weak competition case will always be stable when it exists. Due to the previous conditions failing to be satisfied for the strong competition case, this eliminates any possible bistable conditions.

The results may be summarized in the following table:

Equilibrium Point	Existence	Stability
$\hat{E}_0 = (0, 0)$	Always	Always Unstable
$\hat{E}_1 = \left(\frac{R_1}{c_1}, 0\right)$	Always	$R_2c_1 < \beta_2R_1$
$\hat{E}_2 = \left(0, \frac{R_2}{c_2}\right)$	Always	$R_1c_2 < \beta_1R_2$
$\hat{E}_3 = \left(\frac{R_2\beta_1 - c_2R_1}{\beta_1\beta_2 - c_1c_2}, \frac{R_1\beta_2 - c_1R_2}{\beta_1\beta_2 - c_1c_2}\right)$	Given by (3.3) or (3.4)	Strong Competition Case is Unstable when it Exists. Weak Competition Case is Stable when it Exists, Given by (3.4)

Table 3.1: Summary of equilibria and their stability for N_1 - N_2 subsystem

3.2 Dynamics of the $N_3 - N_4$ Predator-Prey Subsystem

In this section, we will study the equilibria and their stability with respect to the case in which there are no low-level members of the food chain. In this case, the model becomes:

$$\begin{aligned}\frac{d\bar{N}_3}{dt} &= \bar{N}_3 \left[\frac{\gamma_3}{1 + \alpha_3 \bar{N}_4} - D_3 - c_3 \bar{N}_3 - \frac{p_3}{1 + \alpha_3} \bar{N}_4 \right], \\ \frac{d\bar{N}_4}{dt} &= \bar{N}_4 \left[B - c_4 \bar{N}_4 + \frac{\varepsilon_3 p_3}{1 + \alpha_3} \bar{N}_3 \right].\end{aligned}\tag{3.17}$$

3.2.1 Equilibria and Stability

The equilibria of this system are given by:

$$\begin{aligned}\bar{E}_0(0, 0) &= (0, 0), \\ \bar{E}_1(\bar{N}_3^*, 0) &= \left(\frac{R_3}{c_3}, 0 \right), \\ \bar{E}_2(0, \bar{N}_4^*) &= \left(0, \frac{B}{c_4} \right), \\ \bar{E}_3(\bar{N}_3^+, \bar{N}_4^+) &= (C(c_4 \bar{N}_4^+ - B), \bar{N}_4^+)\end{aligned}\tag{3.18}$$

where:

$$A = \frac{p_3}{1 + \alpha_3}, \quad C = \frac{1 + \alpha_3}{p_3 \varepsilon_3},\tag{3.19}$$

$$s_1 = (BCc_3 - D_3)^2 \alpha_3^2 + 2(BCc_3 - D_3 + 2\gamma_3)(Cc_3c_4 + A)\alpha_3 + (Cc_3c_4 + A)^2.$$

The existence of \bar{E}_1 follows from the assumption that R_3 is always positive. The existence of \bar{E}_0 and \bar{E}_2 are trivial. However, the analysis of the existence of \bar{E}_3 is not so trivial. The analysis will parallel a similar case in the full model.

The equations read:

$$\begin{aligned} \frac{\gamma_3}{1 + \alpha_3 \bar{N}_4} - D_3 - c_3 \bar{N}_3 - A \bar{N}_4 &= 0, \\ B - c_4 \bar{N}_4 + \frac{\bar{N}_3}{C} &= 0. \end{aligned} \quad (3.20)$$

Solving the second equation, one obtains:

$$\bar{N}_3 = C(c_4 \bar{N}_4 - B). \quad (3.21)$$

For $\bar{N}_3 > 0$, we require that:

$$\bar{N}_4 > \frac{B}{c_4}. \quad (3.22)$$

One may obtain a quadratic equation in \bar{N}_4 by plugging the solution for \bar{N}_3 into the first equation. This reads:

$$a_2 \bar{N}_4^2 + a_1 \bar{N}_4 + a_0, \quad (3.23)$$

where the coefficients are given by:

$$\begin{aligned} a_2 &= \alpha_3(Cc_3c_4 + A), \\ a_1 &= A + Cc_3c_4 + \alpha_3(D_3 - BCc_3), \\ a_0 &= D_3 - BCc_3 - \gamma_3. \end{aligned} \quad (3.24)$$

Computing the discriminant, one obtains:

$$\Delta = a_1^2 - 4a_2a_0 = (A + Cc_3c_4 + (D_3 - BCc_3)\alpha_3)^2 + 4\alpha_3(Cc_3c_4 + A)(BCc_3 + R_3) > 0, \quad (3.25)$$

per the assumption that $R_3 > 0$. A positive discriminant implies two real solutions. It can be shown that there is only one positive, and therefore, biologically meaningful solution. Consider the case when $a_0 < 0$. For $a_0 = 0$, we have that $\gamma_3 > D_3 - BCc_3 \iff R_3 > -BCc_3$, this implies the quadratic always has one positive solution. This will always hold

per the assumption $R_3 > 0$. For $a_0 \geq 0$, this implies that $0 < \gamma_3 \geq D_3 - BCc_3 \iff 0 < R_3 \geq -BCc_3$, which fails to hold per the assumption $R_3 > 0$. Furthermore, when $D_3 - BCc_3 > 0$, we have $a_1 > 0$, which implies there can be no positive solutions for $a_0 \geq 0$. Solving the quadratic, we find that the system admits a distinct positive solution:

$$\bar{N}_4^+ = \frac{C(B\alpha_3 - c_4)c_3 - D_3\alpha_3 - A + \sqrt{s_1}}{2\alpha_3(Cc_3c_4 + A)}, \quad \gamma_3 > \max\{0, D_3 - BCc_3\}, \quad (3.26)$$

where the condition comes from solving $a_0 < 0$. Going further with this, we verify the condition $\bar{N}_4^+ > \frac{B}{c_4}$. Calculating, we obtain:

$$\begin{aligned} \bar{N}_4^+ > \frac{B}{c_4} &\iff \frac{C(B\alpha_3 - c_4)c_3 - D_3\alpha_3 - A + \sqrt{s_1}}{2\alpha_3(Cc_3c_4 + A)} > \frac{B}{c_4} \\ &\iff c_4 \sqrt{s_1} > c_4(BCc_3\alpha_3 + Cc_3c_4 + D_3\alpha_3 + A) + 2AB\alpha_3 \\ &\iff 4\alpha_3(Cc_3c_4 + A)[c_4^2\gamma_3 - (AB^2\alpha_3 + c_4(D_3c_4 + BD_3\alpha_3 + AB))] > 0 \end{aligned} \quad (3.27)$$

Solving the last line for γ_3 , one obtains the inequality:

$$\gamma_3 > D_3 + \frac{B[AB\alpha_3 + c_4(D_3\alpha_3 + A)]}{c_4^2} > D_3 - BCc_3, \quad (3.28)$$

which always ensures that the condition $\gamma_3 > \max\{0, D_3 - BCc_3\}$ holds. Therefore, when (3.28) holds, we get that this equilibrium exists.

The Jacobian matrix corresponding to (3.17) is given by:

$$\mathbf{J}(N_3, N_4) = \begin{pmatrix} \frac{\gamma_3}{1+\alpha_3 N_4} - D_3 - 2c_3 N_3 - \frac{p_3 N_4}{1+\alpha_3} & -N_3 \left(\frac{\gamma_3 \alpha_3}{(1+\alpha_3 N_4)^2} + \frac{p_3}{1+\alpha_3} \right) \\ \frac{N_4 \varepsilon_3 p_3}{1+\alpha_3} & B - 2c_4 N_4 + \frac{\varepsilon_3 p_3 N_3}{1+\alpha_3} \end{pmatrix}. \quad (3.29)$$

Let us consider the extinction case. Evaluating at the trivial equilibrium yields:

$$\mathbf{J}(0, 0) = \begin{pmatrix} \gamma_3 - D_3 & 0 \\ 0 & B \end{pmatrix} = \begin{pmatrix} R_3 & 0 \\ 0 & B \end{pmatrix}. \quad (3.30)$$

The eigenvalues are trivially R_3 and B , which are both positive constants. Therefore, the trivial equilibrium is always unstable.

Let us consider the case where N_3 excludes N_4 . Evaluating the Jacobian at \bar{E}_1 yields:

$$\mathbf{J}(\bar{N}_3^*, 0) = \begin{pmatrix} -R_3 & -\frac{R_3(\gamma_3\alpha_3^2 + \gamma_3\alpha_3 + p_3)}{(1+\alpha_3)c_3} \\ 0 & \frac{B(1+\alpha_3)c_3 + \varepsilon_3 p_3 R_3}{(1+\alpha_3)c_3} \end{pmatrix}. \quad (3.31)$$

The eigenvalues are given by the characteristic equation:

$$\begin{aligned} (-R_3 - \lambda) \left(\frac{B(1 + \alpha_3)c_3 + \varepsilon_3 p_3 R_3}{(1 + \alpha_3)c_3} - \lambda \right) &= 0 \\ \iff \lambda_1 = -R_3, \quad \lambda_2 = \frac{B(1 + \alpha_3)c_3 + \varepsilon_3 p_3 R_3}{(1 + \alpha_3)c_3}. \end{aligned} \quad (3.32)$$

As we assumed R_3 to be positive, λ_1 is always negative. On the other hand, λ_2 is always positive. Therefore, this equilibrium is unstable.

Let us consider the case where N_4 excludes N_3 . Evaluating the Jacobian at \bar{E}_2 yields:

$$\mathbf{J}(0, \bar{N}_4^*) = \begin{pmatrix} \frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} - D_3 - \frac{p_3 B}{(1 + \alpha_3)c_4} & 0 \\ \frac{B\varepsilon_3 p_3}{c_4(1 + \alpha_3)} & -B \end{pmatrix}. \quad (3.33)$$

The eigenvalues are given by the characteristic equation:

$$\begin{aligned} (-B - \lambda) \left(\frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} - D_3 - \frac{p_3 B}{(1 + \alpha_3)c_4} - \lambda \right) &= 0 \\ \lambda_1 = -B, \quad \lambda_2 = \frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} - D_3 - \frac{p_3 B}{(1 + \alpha_3)c_4}. \end{aligned} \quad (3.34)$$

It's assumed that B is a positive constant, so λ_1 will always be negative. In order for this equilibrium to be stable, we require that $\lambda_2 < 0$. Therefore, this equilibrium is locally

asymptotically stable if and only if:

$$\frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} < D_3 + \frac{p_3 B}{(1 + \alpha_3)c_4} \quad (3.35)$$

Note that when (3.35) holds, it will drive N_3 to extinction.

Let us consider the coexistence case. The explicit values of \bar{N}_3^+ and \bar{N}_4^+ will be omitted for now to simplify the analysis. Evaluating the Jacobian at \bar{E}_3 and making some simplifications via (3.17) yields:

$$\begin{aligned} \mathbf{J}(\bar{N}_3^+, \bar{N}_4^+) &= \begin{pmatrix} \frac{\gamma_3}{1 + \alpha_3 \bar{N}_4^+} - D_3 - 2c_3 \bar{N}_3^+ - \frac{p_3 \bar{N}_4^+}{1 + \alpha_3} & -\bar{N}_3^+ \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 \bar{N}_4^+)^2} + \frac{p_3}{1 + \alpha_3} \right) \\ \frac{\bar{N}_4^+ \varepsilon_3 p_3}{1 + \alpha_3} & B - 2c_4 \bar{N}_4^+ + \frac{\varepsilon_3 p_3 \bar{N}_3^+}{1 + \alpha_3} \end{pmatrix} \\ &= \begin{pmatrix} -c_3 \bar{N}_3^+ & -\bar{N}_3^+ \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 \bar{N}_4^+)^2} + \frac{p_3}{1 + \alpha_3} \right) \\ \frac{\bar{N}_4^+ \varepsilon_3 p_3}{1 + \alpha_3} & -c_4 \bar{N}_4^+ \end{pmatrix} \\ &= \begin{pmatrix} \mathbf{J}_{11} & \mathbf{J}_{12} \\ \mathbf{J}_{21} & \mathbf{J}_{22} \end{pmatrix}. \end{aligned} \quad (3.36)$$

The eigenvalues are given by the characteristic equation:

$$\lambda^2 + a_1 \lambda + a_2 = 0, \quad (3.37)$$

where:

$$a_1 = -(\mathbf{J}_{11} + \mathbf{J}_{22}), \quad (3.38)$$

and:

$$a_2 = \mathbf{J}_{11} \mathbf{J}_{22} - \mathbf{J}_{12} \mathbf{J}_{21}. \quad (3.39)$$

Writing this another way, we have the characteristic equation as:

$$\lambda^2 - \lambda \operatorname{tr} \mathbf{J}(\bar{N}_3^+, \bar{N}_4^+) + \det \mathbf{J}(\bar{N}_3^+, \bar{N}_4^+) = 0. \quad (3.40)$$

Expanding the trace yields:

$$\operatorname{tr} \mathbf{J}(\bar{N}_3^+, \bar{N}_4^+) = -(c_3 \bar{N}_3^+ + c_4 \bar{N}_4^+) < 0. \quad (3.41)$$

Similarly, for the determinant, this yields:

$$\begin{aligned} \det \mathbf{J}(\bar{N}_3^+, \bar{N}_4^+) &= \mathbf{J}_{11} \mathbf{J}_{22} - \mathbf{J}_{12} \mathbf{J}_{21} \\ &= (-c_3 \bar{N}_3^+) (-c_4 \bar{N}_4^+) - \left[-\bar{N}_3^+ \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 \bar{N}_4^+)^2} + \frac{p_3}{1 + \alpha_3} \right) \right] \frac{\bar{N}_4^+ \varepsilon_3 p_3}{1 + \alpha_3} \\ &= c_3 c_4 \bar{N}_3^+ \bar{N}_4^+ + \left[\bar{N}_3^+ \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 \bar{N}_4^+)^2} + \frac{p_3}{1 + \alpha_3} \right) \right] \frac{\bar{N}_4^+ \varepsilon_3 p_3}{1 + \alpha_3} > 0. \end{aligned} \quad (3.42)$$

By Theorem B.2 in [5], this equilibrium will be unconditionally stable. This analysis implies N_3 may only exist in conjunction with N_4 . Otherwise, it will be invaded by N_4 . The results may be summarized in the following table:

Equilibrium Point	Existence	Stability
$\bar{E}_0 = (0, 0)$	Always	Always Unstable
$\bar{E}_1 = \left(\frac{R_3}{c_3}, 0 \right)$	Always	Always Unstable
$\bar{E}_2 = \left(0, \frac{B}{c_4} \right)$	Always	Given by (3.35)
$\bar{E}_3 = (\bar{N}_3^+, \bar{N}_4^+)$	Given by (3.28)	Stable, when \bar{E}_3 exists

Table 3.2: Summary of equilibria and their stability for N_3 - N_4 subsystem

One may also prove the following results.

Theorem 3.1 (3.17) *admits no periodic solutions in the region*

$$R = \{(\bar{N}_3, \bar{N}_4) \mid \bar{N}_3, \bar{N}_4 > 0\}. \quad (3.43)$$

Proof This result can be proven with the Dulac criterion, given as Theorem B.6 in [5]. Let:

$$B(\bar{N}_3, \bar{N}_4) = \frac{1}{\bar{N}_3 \bar{N}_4}, \quad (3.44)$$

such that B is defined on the region:

$$R = \{(\bar{N}_3, \bar{N}_4) \mid \bar{N}_3, \bar{N}_4 > 0\} \quad (3.45)$$

B is continuously differentiable on R , as required by the criterion. Referring to (3.17), define:

$$\begin{aligned} \frac{d\bar{N}_3}{dt} &= \tilde{f}(\bar{N}_3, \bar{N}_4) = \bar{N}_3 \left[\frac{\gamma_3}{1 + \alpha_3 \bar{N}_4} - D_3 - c_3 \bar{N}_3 - \frac{p_3}{1 + \alpha_3} \bar{N}_4 \right], \\ \frac{d\bar{N}_4}{dt} &= \tilde{g}(\bar{N}_3, \bar{N}_4) = \bar{N}_4 \left[B - c_4 \bar{N}_4 + \frac{\varepsilon_3 p_3}{1 + \alpha_3} \bar{N}_3 \right]. \end{aligned} \quad (3.46)$$

Calculating, one obtains:

$$\begin{aligned} \frac{\partial(B\tilde{f})}{\partial\bar{N}_3} + \frac{\partial(B\tilde{g})}{\partial\bar{N}_4} &= \frac{\partial}{\partial\bar{N}_3} \left[\frac{1}{\bar{N}_3 \bar{N}_4} \tilde{f}(\bar{N}_3, \bar{N}_4) \right] + \frac{\partial}{\partial\bar{N}_4} \left[\frac{1}{\bar{N}_3 \bar{N}_4} \tilde{g}(\bar{N}_3, \bar{N}_4) \right] \\ &= \frac{\partial}{\partial\bar{N}_3} \left[\frac{1}{\bar{N}_4} \left[\frac{\gamma_3}{1 + \alpha_3 \bar{N}_4} - D_3 - c_3 \bar{N}_3 - \frac{p_3}{1 + \alpha_3} \bar{N}_4 \right] \right] \\ &\quad + \frac{\partial}{\partial\bar{N}_4} \left[\frac{1}{\bar{N}_3} \left[B - c_4 \bar{N}_4 + \frac{\varepsilon_3 p_3}{1 + \alpha_3} \bar{N}_3 \right] \right] \\ &= -\frac{c_3}{\bar{N}_4} - \frac{c_4}{\bar{N}_3} \\ &= -\left[\frac{c_3}{\bar{N}_4} + \frac{c_4}{\bar{N}_3} \right] < 0, \end{aligned} \quad (3.47)$$

as c_3 and c_4 are positive parameters. Comparing this result to the Dulac criterion, it is clearly not identically zero and does not change sign in R . Therefore, we may conclude there exist no periodic solutions of (3.17) in R , by the Dulac criterion. ■

Theorem 3.2 *The coexistence equilibrium, \bar{E}_3 , is globally asymptotically stable when it exists.*

Proof By the Poincare-Bendixson Theorem, (Theorem B.5 in [5]), (3.17) will either admit a periodic solution, or approach a fixed point. In the previous result, we showed that (3.17) admits no periodic solutions. Therefore, Poincare-Bendixson tells us that the solutions of (3.17) will either be/approach a fixed point for arbitrary initial conditions. This fixed point must be the equilibrium point \bar{E}_3 . Therefore, the solutions of (3.17) will tend towards \bar{E}_3 , when it exists, for arbitrary initial conditions. This implies \bar{E}_3 is globally asymptotically stable when it exists, completing the proof. ■

Dynamical systems theory implies that \bar{E}_3 will become stable as \bar{E}_2 loses stability, provided that \bar{E}_3 exists.

3.2.2 Impact of the Fear Effect on the Stability of \bar{E}_2 and \bar{E}_3

Let us examine how the fear effect, α_3 can change the sign of (3.35). Rewriting the above equation as a function of α_3 , one obtains:

$$q(\alpha_3) = \frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} - D_3 - \frac{p_3 B}{(1 + \alpha_3)c_4}. \quad (3.48)$$

Referring to (3.35) and multiplying through by both terms involving α_3 , the stability condition reads:

$$\begin{aligned} q(\alpha_3) &< 0 \\ \iff \frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} - D_3 - \frac{p_3 B}{(1 + \alpha_3)c_4} &< 0 \\ \iff -a\alpha_3^2 + b\alpha_3 + c &< 0, \end{aligned} \quad (3.49)$$

where:

$$a = \frac{BD_3}{c_4} > 0, \quad b = R_3 - \frac{BD_3}{c_4} - \frac{B^2 p_3}{c_4^2} = R_3 - \frac{B}{c_4} \left(D_3 + \frac{B p_3}{c_4} \right), \quad c = R_3 - \frac{B p_3}{c_4}. \quad (3.50)$$

Let us consider the roots of the above quadratic to help us find the ranges of α_3 such that (3.35) holds. Applying the quadratic formula, one obtains the solutions to the equation:

$$q(\alpha_3) = 0 \quad (3.51)$$

as:

$$\alpha_3 = \frac{b \pm \sqrt{b^2 + 4ac}}{2a}. \quad (3.52)$$

As $a > 0$, it follows that $-a < 0$. Therefore, this parabola will always open downwards. Recall that when:

$$q(\alpha_3) < 0, \quad (3.53)$$

it is equivalent to saying that (3.35) holds, and that \bar{E}_2 is stable. If:

$$q(\alpha_3) > 0 \quad (3.54)$$

it is equivalent to saying that (3.35) fails to hold, and that this equilibrium is unstable. The characteristics of a are known, but the signs of b and c may vary. This leads to several possible cases. We will also have to take into account that $\alpha_3 > 0$ as per our model in this analysis.

$$\text{Case i: } b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) > 0 \text{ and } c = R_3 - \frac{Bp_3}{c_4} > 0$$

Using the multiplicative and additive properties of the roots of a quadratic equation, one may deduce that there exist two distinct real roots, one positive and one negative. As $\alpha_3 > 0$, the positive root is the only one we care about. In this case, the positive root is given by:

$$\alpha_3^+ = \frac{b + \sqrt{b^2 + 4ac}}{2a}. \quad (3.55)$$

As q opens downwards, it follows that $q(\alpha_3) < 0$ for values of $\alpha_3 > \alpha_3^+$. Therefore, (3.35) holds (and \bar{E}_2 is stable) when $\alpha_3 > \alpha_3^+$.

Case ii: $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) < 0$ and $c = R_3 - \frac{Bp_3}{c_4} > 0$

Using the multiplicative and additive properties of the roots of a quadratic equation, one may deduce that there exist two distinct real roots, one positive and one negative. As $\alpha_3 > 0$, the positive root is the only one we care about. In this case, the positive root is given by:

$$\alpha_3^+ = \frac{b + \sqrt{b^2 + 4ac}}{2a}. \quad (3.56)$$

As q opens downwards, it follows that $q(\alpha_3) < 0$ for values of $\alpha_3 > \alpha_3^+$. Therefore, (3.35) holds (and \bar{E}_2 is stable) when $\alpha_3 > \alpha_3^+$.

Case iii: $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) > 0$ and $c = R_3 - \frac{Bp_3}{c_4} < 0$

In this case, there are two possible sub-cases which follow from the additive and multiplicative properties of the roots of a quadratic equation. If the discriminant is positive, i.e. the condition:

$$\begin{aligned} b^2 + 4ac &> 0 \\ \iff \left(R_3 + \frac{BD_3}{c_4} - \frac{B^2 p_3}{c_4^2} \right)^2 + \frac{4BD_3}{c_4} \left(R_3 - \frac{Bp_3}{c_4} \right) &> 0 \end{aligned} \quad (3.57)$$

holds, then there exist two real positive roots. The roots are given by the equations:

$$\alpha_3^- = \frac{b - \sqrt{b^2 + 4ac}}{2a}, \quad \alpha_3^+ = \frac{b + \sqrt{b^2 + 4ac}}{2a}. \quad (3.58)$$

In our case, $\alpha_3 > 0$ and q opens downwards. This suggests that $q(\alpha_3) < 0$ for values of α_3 outside the roots. Therefore, (3.35) holds (and \bar{E}_2 is stable) when $\alpha_3 \notin [\alpha_3^-, \alpha_3^+]$.

In the case when the discriminant is negative, i.e. when the condition:

$$b^2 + 4ac < 0$$

$$\iff \left(R_3 + \frac{BD_3}{c_4} - \frac{B^2 p_3}{c_4^2} \right)^2 + \frac{4BD_3}{c_4} \left(R_3 - \frac{Bp_3}{c_4} \right) < 0 \quad (3.59)$$

holds, then the roots are complex. Due to the geometry of q , and that $\alpha_3 > 0$ as per our model, then (3.35) holds (and \bar{E}_2 is stable) when $\alpha_3 > 0$.

$$\text{Case iv: } b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) < 0 \text{ and } c = R_3 - \frac{Bp_3}{c_4} < 0$$

In this case, there are two possible sub-cases which follow from the additive and multiplicative properties of the roots of a quadratic equation. If the discriminant is positive, i.e. (3.57) holds, then there exist two real negative roots. The roots are given by the equations:

$$\alpha_3^- = \frac{b - \sqrt{b^2 + 4ac}}{2a}, \quad \alpha_3^+ = \frac{b + \sqrt{b^2 + 4ac}}{2a}. \quad (3.60)$$

As q opens downwards, then $q(\alpha_3) < 0, \forall \alpha_3 > \alpha_3^+$. For us, this means that (3.35) holds (and \bar{E}_2 is stable) when $\alpha_3 > 0$.

If the discriminant is negative, i.e. (3.59) holds, then both roots will be complex, and $q(\alpha_3) < 0, \forall \alpha_3$. In our case, (3.35) holds (and \bar{E}_2 is stable) when $\alpha_3 > 0$.

$$\text{Case v: } b = 0 \iff R_3 = \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) \text{ and } c = 0 \iff R_3 = \frac{Bp_3}{c_4}$$

This case occurs only for certain combinations of parameters, namely when:

$$R_3 = \gamma_3 - D_3 = \frac{Bp_3}{c_4}, \quad D_3 = \frac{-p_3(B - c_4)}{c_4}, \quad c_4 > B. \quad (3.61)$$

In this case one obtains:

$$q(\alpha_3) = -\frac{BD_3\alpha_3^2}{c_4}. \quad (3.62)$$

This equation has a single root at $\alpha_3 = 0$. As $\alpha_3 > 0$ and using the fact that q opens downwards, one has that $q(\alpha_3) < 0$ for $\alpha_3 > 0$. Therefore, (3.35) holds (and \bar{E}_2 is stable) when $\alpha_3 > 0$.

Case vi: $b = 0 \iff R_3 = \frac{B}{c_4}\left(D_3 + \frac{Bp_3}{c_4}\right)$ and $c \neq 0 \iff R_3 \neq \frac{Bp_3}{c_4}$

In this case, one obtains:

$$q(\alpha_3) = -a\alpha_3^2 + c = -\frac{BD_3\alpha_3^2}{c_4} + R_3 - \frac{Bp_3}{c_4}. \quad (3.63)$$

This equation has roots given by:

$$\alpha_3 = \pm \frac{\sqrt{ac}}{a}. \quad (3.64)$$

If $c = R_3 - \frac{Bp_3}{c_4} > 0$, there are two real roots, one positive and negative. As $\alpha_3 > 0$ and q opens downwards, one has $q(\alpha_3) < 0$ for $\alpha_3 > \alpha_3^+ = \frac{\sqrt{ac}}{a}$. Therefore, (3.35) holds (and \bar{E}_2 is stable) when $\alpha_3 > \alpha_3^+$. If $c = R_3 - \frac{Bp_3}{c_4} < 0$, both roots are complex, and so $q(\alpha_3) < 0, \forall \alpha_3$. In our situation, (3.35) holds (and \bar{E}_2 is stable) when $\alpha_3 > 0$.

Case vii: $b \neq 0 \iff R_3 \neq \frac{B}{c_4}\left(D_3 + \frac{Bp_3}{c_4}\right)$ and $c = 0 \iff R_3 = \frac{Bp_3}{c_4}$

In this case, one obtains:

$$q(\alpha_3) = -a\alpha_3^2 + b\alpha_3 = \alpha_3(b - a\alpha_3) = -\frac{\alpha_3(B^2p_3 + BD_3c_4(1 + \alpha_3) - R_3c_4^2)}{c_4^2}. \quad (3.65)$$

This equation has roots given by:

$$\alpha_3^0 = 0, \quad \alpha_3^+ = \frac{b}{a}. \quad (3.66)$$

If $b = R_3 - \frac{B}{c_4}\left(D_3 + \frac{Bp_3}{c_4}\right) > 0$, there will be two non-negative roots. As α_3 and q opens downwards, one will find that $q(\alpha_3) < 0$ for $\alpha_3 > \alpha_3^+$. In our situation, (3.35) holds (and \bar{E}_2 is stable) when $\alpha_3 > \alpha_3^+$. If $b = R_3 - \frac{B}{c_4}\left(D_3 + \frac{Bp_3}{c_4}\right) < 0$, $\alpha_3^0 < 0$. As $\alpha_3 > 0$ and q opens

downward, one will find that $q(\alpha_3) < 0$ for $\alpha_3 > 0$. In our situation, (3.35) holds (and \bar{E}_2 is stable) when $\alpha_3 > \alpha_3^0$.

3.2.3 Discussion and Biological Implications

In this section we will discuss the biological meaning of each of the previously discussed cases. We will endeavour to explain what they represent in the model and how each case affects N_3 and N_4 differently. Recall the definitions of b and c :

$$b = R_3 - \frac{BD_3}{c_4} - \frac{B^2p_3}{c_4^2} = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right), \quad c = R_3 - \frac{Bp_3}{c_4}. \quad (3.67)$$

Each case in the previous section can be better understood once some meaning is given to each term of b and c . The $\frac{Bp_3}{c_4}$ term in c can be thought of as the "total cost-to-benefit ratio" for N_4 . Recall that R_3 is just the intrinsic growth rate for N_3 . Therefore, c may be thought of as a means to compare the growth of N_3 to the growth of N_4 expressed as a ratio cost and benefit. If $c < 0$, this implies that the intrinsic growth rate of N_3 is less than the cost-to-benefit measure for N_4 . Similarly, if $c > 0$, this implies that the growth rate of N_3 is greater than the cost-to-benefit measure for N_4 .

Let us consider the second term in b , i.e.:

$$\frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right). \quad (3.68)$$

The $\frac{B}{c_4}$ component can be thought of as the ratio of the growth of N_4 to its competition. The $D_3 + \frac{Bp_3}{c_4}$ component is just the sum of "total cost-to-benefit ratio" for N_4 and the natural death rate of N_3 . This can be thought of as a way to measure the total cost-to-benefit of N_4 coupled with loss of N_3 through death. Therefore, (3.68) can be thought of as the ratio of growth of N_4 to its competition weighted with respect to the death losses of N_3 and total cost-to-benefit ratio of N_4 . If $b < 0$, this implies that the intrinsic growth rate of N_3 is

less than the weighted cost-to-benefit measure for N_4 . Similarly, if $b > 0$, this implies the growth rate of N_3 is greater than this weighted measure.

Now that we have given some meaning to b and c , this will allow us to explain each case in the previous section in more detail, and relate it to a specific biological scenario.

Case i: $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) > 0$ and $c = R_3 - \frac{Bp_3}{c_4} > 0$

When $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) > 0$ and $c = R_3 - \frac{Bp_3}{c_4} > 0$, this implies that the effect of R_3 (intrinsic growth rate of N_3) outweighs the combined cost and benefit measures of N_4 . This can occur if p_3 (predation) is weaker, or if intra-species competition, c_4 is larger. The following simulations were conducted with model parameters given by:

$$\varepsilon_3 = c_3 = 1, \gamma_3 = 5, D_3 = 1, p_3 = 1, B = 1, c_4 = 1, N_3(0) = N_4(0) = 5. \quad (3.69)$$

Referring to $q(\alpha_3)$, this gives values:

$$b = 3, c = 3, \alpha_3^+ = 3, \quad (3.70)$$

where α_3^+ is the threshold value, i.e. for $\alpha_3 > \alpha_3^+$, \bar{E}_2 becomes stable (N_4 drives N_3 to extinction).

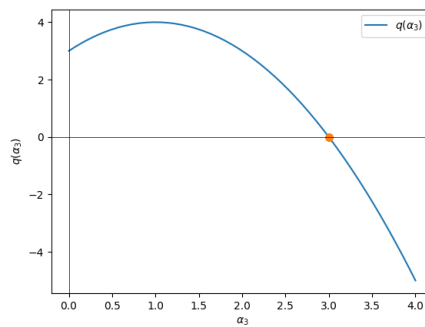
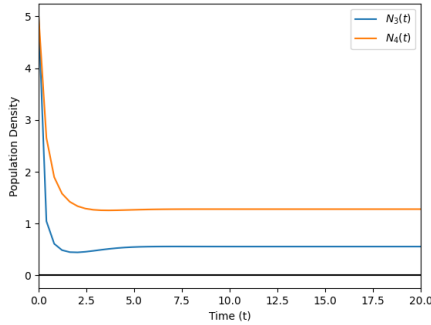
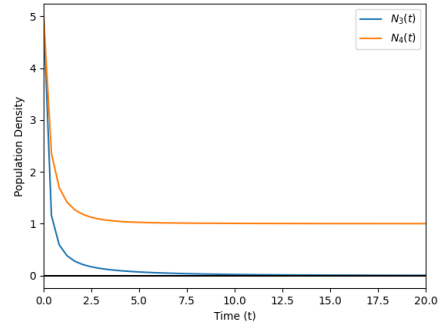


Figure 3.1: Graph of $q(\alpha_3)$ for Case i

From the shape of the graph of $q(\alpha_3)$, we see that there is a threshold in which the fear response of N_3 to N_4 , α_3 , fails to be beneficial, and causes \bar{E}_2 to become stable. In this case, a relatively smaller fear response level is beneficial for coexistence, while a higher level is harmful for N_3 .



(a) Taking $\alpha_3 = 1$ results in coexistence



(b) Taking $\alpha_3 = 4$ (outside of threshold) results in N_4 excluding N_3

Figure 3.2: Simulations of N_3 - N_4 with parameters given by (3.69)

Case ii: $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) < 0$ and $c = R_3 - \frac{Bp_3}{c_4} > 0$

When $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) < 0$ and $c = R_3 - \frac{Bp_3}{c_4} > 0$, this implies that the weighted measure of cost-to-benefit of N_4 has a greater effect than the intrinsic growth-rate of N_3 , R_3 . However, since $c = R_3 - \frac{Bp_3}{c_4} > 0$, this implies that the basic cost-to-benefit measure is smaller than R_3 . Overall, we still find ourselves in a similar scenario to Case i, but at a reduced level. The following simulations were conducted with model parameters given by:

$$\varepsilon_3 = c_3 = 1, \gamma_3 = 5, D_3 = 1, p_3 = 1, B = 2, c_4 = 1, N_3(0) = N_4(0) = 5. \quad (3.71)$$

Referring to $q(\alpha_3)$, this gives values:

$$b = -2, c = 2, \alpha_3^+ = \frac{\sqrt{5} - 1}{2} \approx 0.62. \quad (3.72)$$

where α_3^+ is the threshold value, i.e. for $\alpha_3 > \alpha_3^+$, \bar{E}_2 becomes stable (N_4 drives N_3 to extinction).

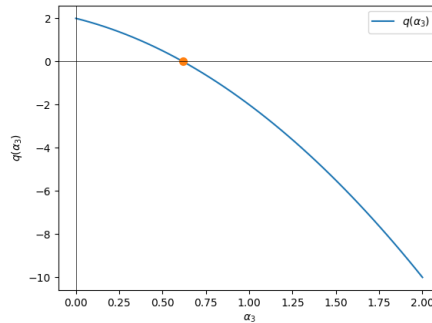
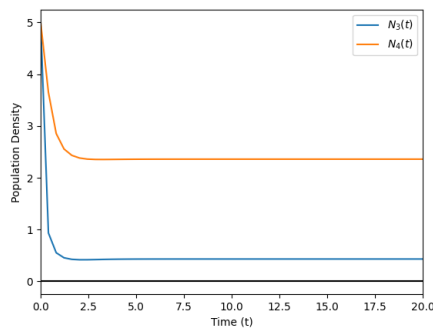
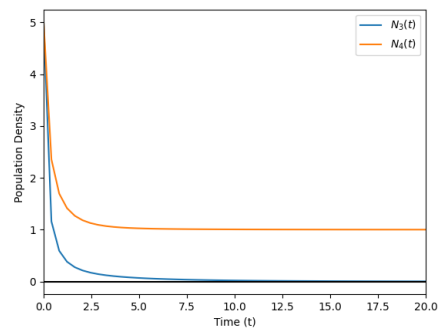


Figure 3.3: Graph of $q(\alpha_3)$ for Case ii

From the shape of the graph of $q(\alpha_3)$, we see that there is a threshold in which the fear response of N_3 to N_4 , α_3 , fails to be beneficial, and causes \bar{E}_2 to become stable. In this case, a relatively smaller fear response level is beneficial for coexistence, while a higher level is harmful for N_3 . Comparing this to Case i, note that the threshold value is smaller. This suggests that there are increased adverse effects to N_3 from N_4 reducing the efficacy of the fear response.



(a) Taking $\alpha_3 = 0.2$ results in coexistence



(b) Taking $\alpha_3 = 1$ (outside of threshold) results in N_4 excluding N_3

Figure 3.4: Simulations of N_3 - N_4 with parameters given by (3.71)

Case iii: $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) > 0$ and $c = R_3 - \frac{Bp_3}{c_4} < 0$

When $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) > 0$ and $c = R_3 - \frac{Bp_3}{c_4} < 0$, this implies that the cost-

to-benefit measure of N_4 outweighs the effect of R_3 . However, since $b = R_3 - \frac{B}{c_4}(D_3 + \frac{Bp_3}{c_4}) > 0$, this implies that the weighted measure is adversely affected by either B or c_4 . In this case, the predation rate of N_4 must have a greater effect. The following simulations were conducted with differing model parameters corresponding to the discriminant being positive or negative. For the choice of parameters:

$$\varepsilon_3 = c_3 = 1, \gamma_3 = 10, D_3 = 1, p_3 = 22, B = 1, c_4 = 2, N_3(0) = N_4(0) = 1, \quad (3.73)$$

the discriminant is positive. Referring to $q(\alpha_3)$, this gives values:

$$b = 3, c = -2, \alpha_3 \in [0.76, 5.24], \quad (3.74)$$

where the interval denotes the range of α_3 in which \bar{E}_2 is unstable, i.e. coexistence occurs.

For the choice of parameters:

$$\varepsilon_3 = c_3 = 1, \gamma_3 = 9, D_3 = 1, p_3 = 22, B = 1, c_4 = 2, N_3(0) = N_4(0) = 1, \quad (3.75)$$

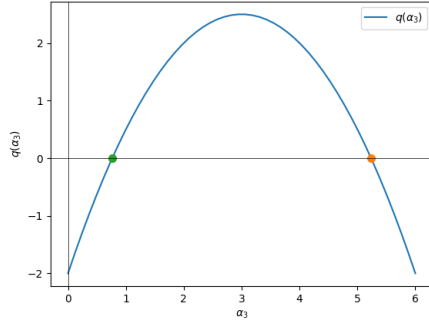
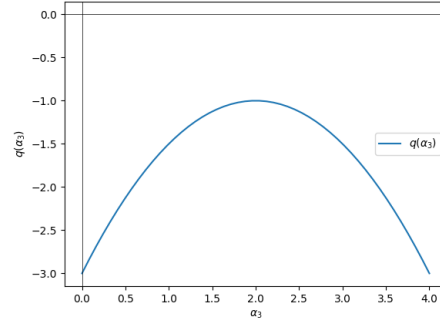
the discriminant is negative. Referring to $q(\alpha_3)$, this gives values:

$$b = 2, c = -3. \quad (3.76)$$

As the roots are complex, \bar{E}_2 is stable for all α_3 .

When the discriminant of $q(\alpha_3)$ is positive, there is a range of values in which the fear response of N_3 on N_4 , α_3 is beneficial, and causes \bar{E}_2 to become stable. This case is most realistic, as one expects too little fear response to have no effect, and too much to have a harmful effect. From the parameter values, this suggests that cost and benefits are more in-balance compared to some of the other cases.

When the discriminant of $q(\alpha_3)$ is negative, the roots are purely complex. This means that

(a) Graph of $q(\alpha_3)$ for Case iii with positive discriminant(b) Graph of $q(\alpha_3)$ for Case iii with negative discriminantFigure 3.5: Graphs of $q(\alpha_3)$ for Case iii

the fear response level, α_3 has no effect on the system stability. In this case, the negative effects from N_4 on N_3 are too great, that the fear response is rendered useless.

$$\text{Case iv: } b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) < 0 \text{ and } c = R_3 - \frac{Bp_3}{c_4} < 0$$

When $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) < 0$ and $c = R_3 - \frac{Bp_3}{c_4} < 0$, this implies that the cost-to-benefit measures of N_4 outweigh the effect of R_3 . This could mean that N_3 has a low intrinsic growth rate, relative to the growth and predation rates of N_4 . The following simulations were conducted with differing model parameters corresponding to the discriminant being positive or negative. For the choice of parameters:

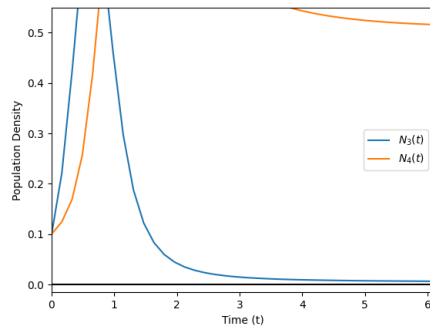
$$\varepsilon_3 = c_3 = 1, \gamma_3 = 5, D_3 = 1, p_3 = 2, B = 2, c_4 = 0.9, N_3(0) = N_4(0) = 5, \quad (3.77)$$

the discriminant is positive. Referring to $q(\alpha_3)$, this gives values:

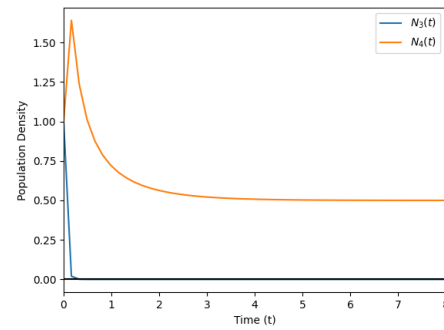
$$b \approx -8.1, c \approx -0.44. \quad (3.78)$$

For the choice of parameters:

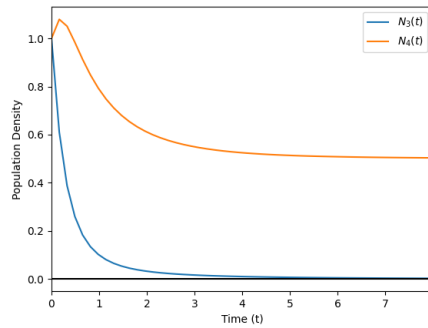
$$\varepsilon = c_3 = 1, \gamma_3 = 1, D_3 = 0.5, p_3 = 2, B = 0.5, c_4 = 1, N_3(0) = N_4(0) = 5, \quad (3.79)$$



(a) Taking $\alpha_3 = 5$ results in coexistence. The line for N_3 is non-zero and approaches a positive constant. $N_3(0) = N_4(0) = 0.1$



(b) Taking $\alpha_3 = 0.2$ (before interval) results in N_4 excluding N_3



(c) Taking $\alpha_3 = 10$ (after interval) results in N_4 excluding N_3

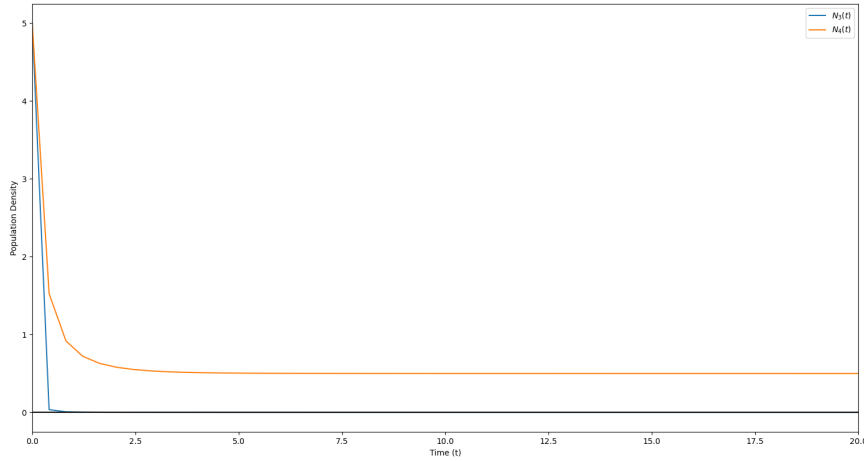
Figure 3.6: Simulations of N_3 - N_4 with parameters given by (3.73)

the discriminant is negative. Referring to $q(\alpha_3)$, this gives values:

$$b = -0.25, c = -0.5. \quad (3.80)$$

Recall that in Case iv, \bar{E}_2 is always stable for all α_3 .

When the discriminant is positive, this causes there to be two negative roots of $q(\alpha_3)$. Biologically speaking, this means that a negative fear response from N_3 is needed in order for \bar{E}_2 to be stable. As per the model, this would equate to a substantial increase in the birth-rate of N_3 along with the predation term changing signs. This suggests N_3 would essentially begin preying on N_4 , reversing the structure of the food chain. When the discriminant is

(a) Taking $\alpha_3 = 5$ results in N_4 excluding N_3 Figure 3.7: Simulations of $N_3 - N_4$ with parameters given by (3.75)

negative, the fear response has no effect on the persistence of N_3 . This is caused by the sign of b and c , discussed earlier.

$$\text{Case v: } b = 0 \iff R_3 = \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) \text{ and } c = 0 \iff R_3 = \frac{Bp_3}{c_4}$$

When $b, c = 0 \iff R_3 = \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) R_3 = \frac{Bp_3}{c_4}$, this implies the cost-to-benefit measures are equal to R_3 . This occurs as per (3.61). The following simulations were conducted with model parameters given by:

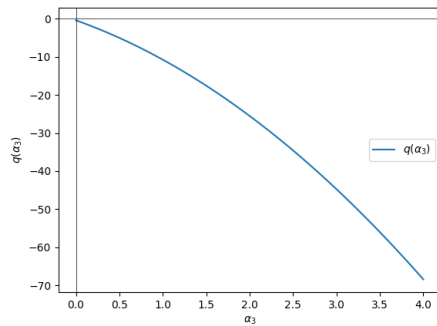
$$\varepsilon_3 = c_3 = 1, \gamma_3 = 1, D_3 = 0.5, p_3 = 1, B = 0.5, c_4 = 1, N_3(0) = N_4(0) = 5. \quad (3.81)$$

Referring to $q(\alpha_3)$, this gives values:

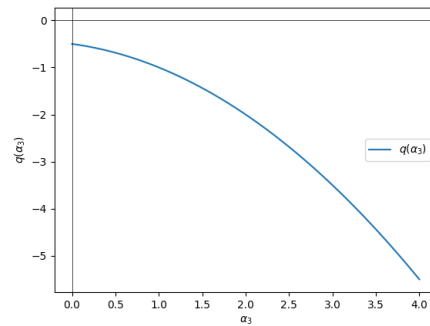
$$b = 0, c = 0, \alpha_3^+ = 0, \quad (3.82)$$

where α_3^+ is the threshold value. In this case, as $\alpha_3 > 0$ as per our model, it follows that \bar{E}_2 is always stable, i.e. N_4 excludes N_3 .

In this case, the only root occurs at $\alpha_3 = 0$, which tells us nothing about the stability of the

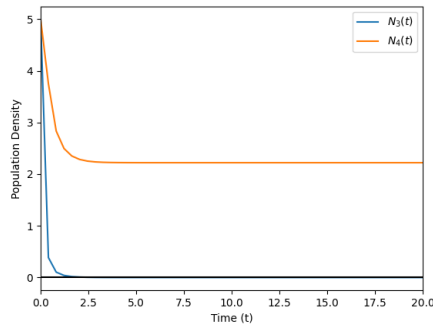


(a) Graph of $q(\alpha_3)$ for Case iv with positive discriminant

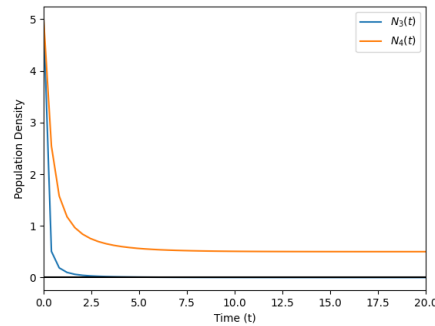


(b) Graph of $q(\alpha_3)$ for Case iv with negative discriminant

Figure 3.8: Graphs of $q(\alpha_3)$ for Case iv



(a) In the positive discriminant case, taking $\alpha_3 = 1$ results in N_4 excluding N_3 . Parameters given by (3.77)



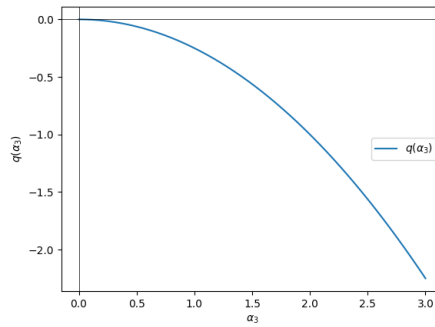
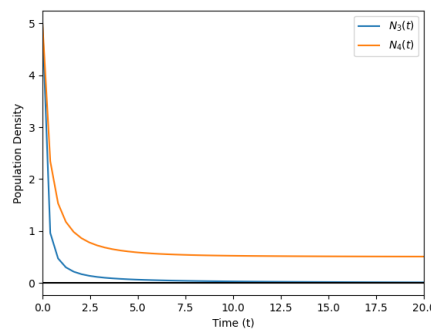
(b) Taking $\alpha_3 = 1$ results in N_4 excluding N_3 . Parameters given by (3.79)

Figure 3.9: Simulations of N_3 - N_4 for Case iv

system. As in Case iv, the fear response, α_3 , has no effect on helping N_3 persist, meaning \bar{E}_2 is always stable. It appears that R_3 is too small to counteract the predation from N_4 .

$$\text{Case vi: } b = 0 \iff R_3 = \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) \text{ and } c \neq 0 \iff R_3 \neq \frac{Bp_3}{c_4}$$

When $b = 0 \iff R_3 = \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right)$ and $c = R_3 - \frac{Bp_3}{c_4} > 0$, this implies that R_3 is in-balance with the weighted cost-to-benefit measure of N_4 , but that R_3 is greater than the standard cost-to-benefit ratio. This represents a situation in which the predation rate of N_4 is weaker. If $c = R_3 - \frac{Bp_3}{c_4} < 0$, this implies that R_3 is weaker than both cost-to-benefit

Figure 3.10: Graph of $q(\alpha_3)$ for Case v(a) Taking $\alpha_3 = 1$ results in N_4 excluding N_3 Figure 3.11: Simulations of N_3 - N_4 for Case v with parameters given by (3.81)

measures. This is caused by a stronger predation rate. The following simulations were conducted with differing model parameters depending on if c was positive or negative. For the choice of parameters:

$$\varepsilon_1 = c_3 = 1, \gamma_3 = 3, D_3 = 1, p_3 = 1, B = 1, c_4 = 1, N_3(0) = N_4(0) = 5, \quad (3.83)$$

c is positive. Referring to $q(\alpha_3)$, this gives values:

$$b = 0, c = 1, \alpha_3^+ = 1, \quad (3.84)$$

where α_3^+ is the threshold at which \bar{E}_2 becomes stable for $\alpha_3 > \alpha_3^+$. For the choice of

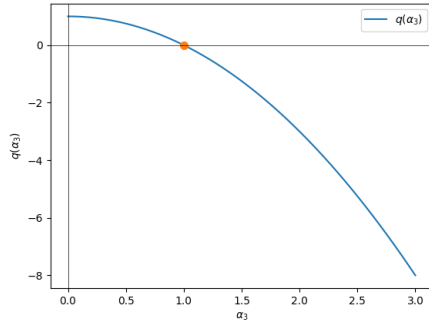
parameters:

$$\varepsilon_3 = c_3 = 1, \gamma_3 = 7, D_3 = 1, p_3 = 22, B = 1, c_4 = 2, N_3(0) = N_4(0) = 5, \quad (3.85)$$

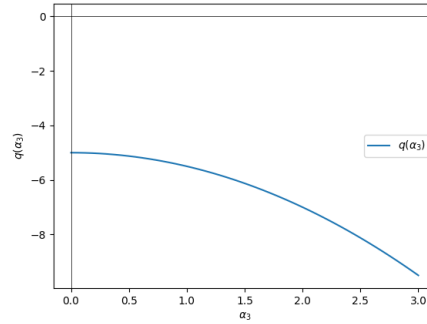
c is negative. Referring to $q(\alpha_3)$, this gives values:

$$b = 0, c = -5. \quad (3.86)$$

When $c = R_3 - \frac{Bp_3}{c_4} < 0$, the roots are complex, meaning that \bar{E}_2 is stable for all α_3 .



(a) Graph of $q(\alpha_3)$ for Case vi with $c > 0$



(b) Graph of $q(\alpha_3)$ for Case vi with $c < 0$

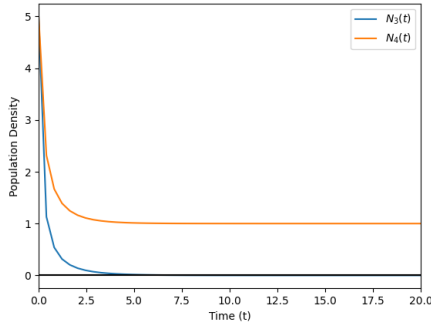
Figure 3.12: Graphs of $q(\alpha_3)$ for Case vi

When $c = R_3 - \frac{Bp_3}{c_4} < 0$, we note that there is a threshold at which the fear response, α_3 becomes harmful to the persistence of N_3 , meaning \bar{E}_2 becomes stable. This corresponds to the weaker predation, similar to Case i.

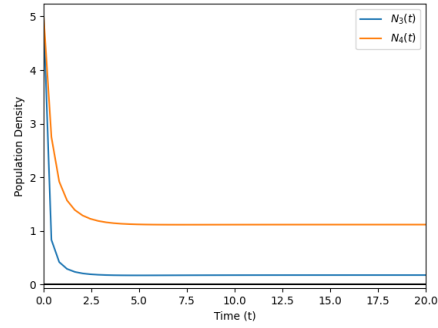
When $c \leq R_3 - \frac{Bp_3}{c_4} < 0$, we note that both roots are complex. This corresponds to a stronger predation rate that cannot be countered by the fear response rate, α_3 .

$$\text{Case vii: } b \neq 0 \iff R_3 \neq \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) \text{ and } c = 0 \iff R_3 = \frac{Bp_3}{c_4}$$

When $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) > 0$ and $c = 0 \iff R_3 = \frac{Bp_3}{c_4}$, this implies that R_3 is in-balance with the cost-benefit ratio of N_4 through c . As $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) > 0$, this suggests that the intra-species competition, c_4 is larger than the growth-rate of N_4 , B , suggesting the

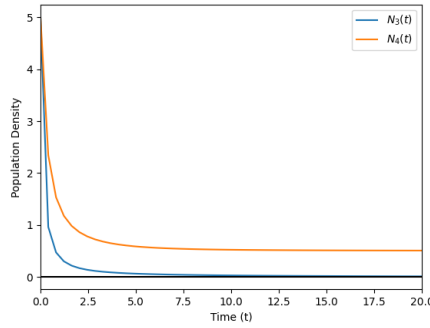


(a) Taking $\alpha_3 = 5$ results in N_4 excluding N_3



(b) Taking $\alpha_3 = 0.5$ results in coexistence

Figure 3.13: Simulations of N_3 - N_4 for Case vi with parameters given by (3.83)



(a) Taking $\alpha_3 = 1$ results in N_4 excluding N_3

Figure 3.14: Simulations of N_3 - N_4 for Case vi with parameters given by (3.85)

predation rate, p_3 provides more of a benefit to N_4 than B . This could help strengthen the effect of the fear response. If $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) < 0$, this implies the benefits of N_4 are stronger, whether through predation or growth-rate, which could weaken the effect of the fear response. The following simulations were conducted with differing model parameters depending on if b was positive or negative. For the choice of parameters:

$$\varepsilon_3 = c_3 = 1, \gamma_3 = 12, D_3 = 1, p_3 = 22, B = 1, c_4 = 2, N_3(0) = N_4(0) = 5., \quad (3.87)$$

b is positive. Referring to $q(\alpha_3)$, this gives values:

$$b = 5, c = 0, \alpha_3^+ = 10, \quad (3.88)$$

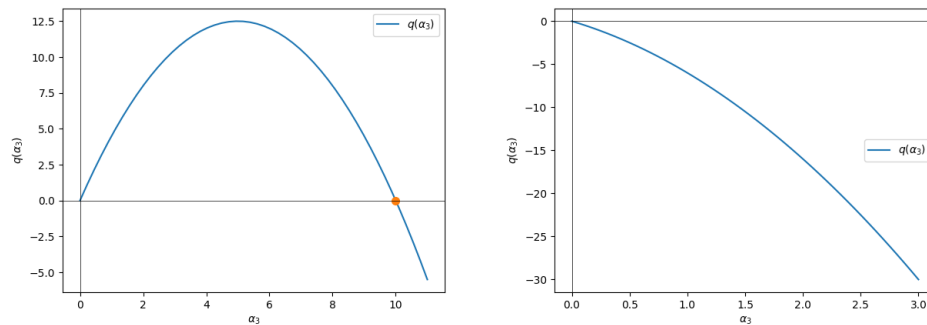
where α_3^+ is the threshold at which \bar{E}_2 becomes stable for $\alpha_3 > \alpha_3^+$. For the choice of parameters:

$$\varepsilon_3 = c_3 = 1, \gamma_3 = 3, D_3 = 1, p_3 = 1, B = 2, c_4 = 1, N_3(0) = N_4(0) = 5, \quad (3.89)$$

b is negative. Referring to $q(\alpha_3)$, this gives values:

$$b = -4, c = 0. \quad (3.90)$$

Recall that when $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) < 0$, that both roots are negative, meaning that \bar{E}_2 is stable for all $\alpha_3 > 0$.

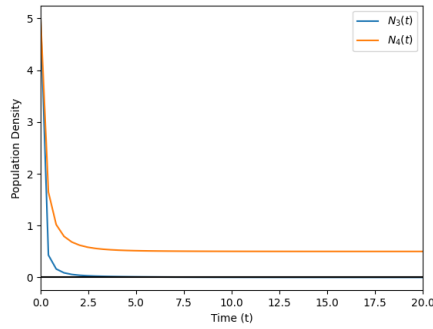


(a) Graph of $q(\alpha_3)$ for Case vii with $b > 0$ (b) Graph of $q(\alpha_3)$ for Case vii with $b < 0$

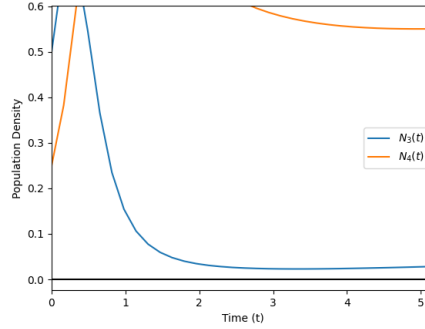
Figure 3.15: Graphs of $q(\alpha_3)$ for Case vii

When $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) > 0$, note the threshold at which the fear response harms the persistence of N_3 . This is in line with what we saw in some of the other cases, and from the previous discussion.

When $b = R_3 - \frac{B}{c_4} \left(D_3 + \frac{Bp_3}{c_4} \right) < 0$, a positive fear response has no effect on the persistence of N_3 . This is similar to Case iv when the discriminant is positive due to the increased benefits to N_4 .

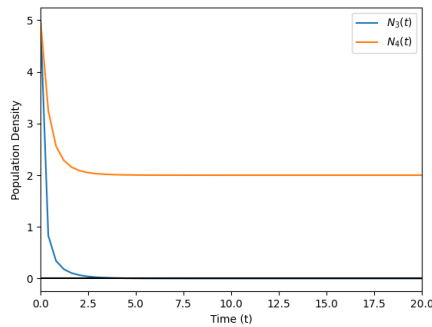


(a) Taking $\alpha_3 = 15$ results in N_4 excluding N_3



(b) Taking $\alpha_3 = 5$ results in coexistence. The value of N_3 increases slightly above the horizontal axis and approached a constant positive value. $N_3(0) = 0.5, N_4(0) = 0.25$

Figure 3.16: Simulations of N_3 - N_4 for Case vii with parameters given by (3.87)



(a) Taking $\alpha_3 = 1$ results in N_4 excluding N_3

Figure 3.17: Simulations of N_3 - N_4 for Case vii with parameters given by (3.89)

Chapter 4

Analysis of the Full Model

4.1 Equilibrium Point Analysis

We proved in Section 3 that (1.11) admits a positive, unique and bounded solution for positive initial conditions. Therefore, an analysis of the system at its equilibria is justified. Recalling the definition of an equilibrium point, we get that the equilibrium points of (1.11) are given by the solutions of the equations:

$$\begin{cases}
 N_1 \left[\frac{\gamma_1}{1 + \alpha_1 N_3} - D_1 - c_1 N_1 - \beta_1 N_2 - \frac{p_1}{1 + \alpha_1} N_3 \right] = 0, \\
 N_2 \left[\frac{\gamma_2}{1 + \alpha_2 N_3} - D_2 - c_2 N_2 - \beta_2 N_1 - \frac{p_2}{1 + \alpha_2} N_3 \right] = 0, \\
 N_3 \left[\frac{\gamma_3}{1 + \alpha_3 N_4} - D_3 - c_3 N_3 + \varepsilon_1 \frac{p_1}{1 + \alpha_1} N_1 + \varepsilon_2 \frac{p_2}{1 + \alpha_2} N_2 - \frac{p_3}{1 + \alpha_3} N_4 \right] = 0, \\
 N_4 \left[B - c_4 N_4 + \varepsilon_3 \frac{p_3}{1 + \alpha_3} N_3 \right] = 0.
 \end{cases} \tag{4.1}$$

In order for the equilibria to maintain a biological meaning, we wish to only consider the solutions of (4.1) which are positive. The equilibria and their existence criteria will be studied and derived in this section.

For $E_0(0, 0, 0, 0)$

From (4.1), we obtain:

$$E_0(0, 0, 0, 0) = (0, 0, 0, 0) \quad (4.2)$$

Existence is trivially unconditional.

For $E_1(N_{11}^*, 0, 0, 0)$

From (4.1), we obtain:

$$E_1(N_{11}^*, 0, 0, 0) = \left(\frac{\gamma_1 - D_1}{c_1}, 0, 0, 0 \right) = \left(\frac{R_1}{c_1}, 0, 0, 0 \right). \quad (4.3)$$

Existence is unconditional due to our assumption that (??) holds.

For $E_2(0, N_{22}^*, 0, 0)$

From (4.1), we obtain:

$$E_2(0, N_{22}^*, 0, 0) = \left(0, \frac{\gamma_2 - D_2}{c_2}, 0, 0 \right) = \left(0, \frac{R_2}{c_2}, 0, 0 \right). \quad (4.4)$$

Existence is unconditional due to our assumption that (??) holds.

For $E_3(N_{31}^*, N_{32}^*, 0, 0)$

From (4.1), we obtain:

$$\begin{aligned}
E_3(N_{31}^*, N_{32}^*, 0, 0) &= \left(\frac{(D_2 - \gamma_2)\beta_1 - c_2(D_1 - \gamma_1)}{c_1c_2 - \beta_1\beta_2}, \frac{(D_1 - \gamma_1)\beta_2 - c_1(D_2 - \gamma_2)}{c_1c_2 - \beta_1\beta_2}, 0, 0 \right) \\
&= \left(\frac{R_2\beta_1 - c_2R_1}{\beta_1\beta_2 - c_1c_2}, \frac{R_1\beta_2 - c_1R_2}{\beta_1\beta_2 - c_1c_2}, 0, 0 \right)
\end{aligned} \tag{4.5}$$

Existence is conditional on both the numerator and denominator being simultaneously positive or negative. This follows the analysis of \hat{E}_3 in Chapter 3. Please refer to equations (3.3) and (3.4).

For $E_4(0, 0, N_{43}^*, 0)$

From (4.1), we obtain:

$$E_4(0, 0, N_{43}^*, 0) = \left(0, 0, \frac{\gamma_3 - D_3}{c_3}, 0 \right) = \left(0, 0, \frac{R_3}{c_3}, 0 \right). \tag{4.6}$$

Existence is unconditional due to our assumption that (??) holds.

For $E_5(0, 0, 0, N_{54}^*)$

From (4.1), we obtain:

$$E_5(0, 0, 0, N_{54}^*) = \left(0, 0, 0, \frac{B}{c_4} \right). \tag{4.7}$$

Existence is trivially unconditional.

For $E_6(0, 0, N_{63}^*, N_{64}^*)$

The analysis here is parallel to a case in Chapter 3. Define:

$$A = \frac{p_3}{1 + \alpha_3}, \quad C = \frac{1 + \alpha_3}{p_3 \varepsilon_3}, \quad (4.8)$$

$$s_1 = (BCc_3 - D_3)^2 \alpha_3^2 + 2(BCc_3 - D_3 + 2\gamma_3)(Cc_3c_4 + A)\alpha_3 + (Cc_3c_4 + A)^2.$$

We then have:

$$N_{63}^* = C(c_4 N_{64}^* - B), \quad N_{64}^* = \frac{C(B\alpha_3 - c_4)c_3 - D_3\alpha_3 - A + \sqrt{s_1}}{2\alpha_3(Cc_3c_4 + A)}. \quad (4.9)$$

The equilibrium exists when the condition:

$$\gamma_3 > D_3 + \frac{B[AB\alpha_3 + c_4(D_3\alpha_3 + A)]}{c_4^2} \quad (4.10)$$

holds.

For $E_7(0, N_{72}^*, N_{73}^*, 0)$

The analysis of this equilibrium parallels that of the work done in Chapter 3. Define:

$$J = \frac{p_2}{1 + \alpha_2}, \quad K = \frac{1 + \alpha_2}{\varepsilon_2 p_2}, \quad (4.11)$$

$$s_2 = (R_3 K c_2 - D_2)^2 \alpha_2^2 + 2(R_3 K c_2 - D_2 + 2\gamma_2)(K c_2 c_3 + J)\alpha_2 + (K c_2 c_3 + J)^2.$$

We obtain:

$$N_{72}^* = K(c_3 N_{73}^* - R_3), \quad (4.12)$$

$$N_{73}^* = \frac{K(R_3 \alpha_2 - c_3)c_2 - D_2 \alpha_2 - J + \sqrt{s_2}}{2\alpha_2(K c_2 c_3 + J)}.$$

The existence condition is given by:

$$\gamma_2 > D_2 + \frac{R_3[JR_3\alpha_2 + c_3(D_2\alpha_2 + J)]}{c_3^2}. \quad (4.13)$$

For $E_8(0, N_{82}^*, 0, N_{84}^*)$

From (4.1), we obtain:

$$E_8(0, N_{82}^*, 0, N_{84}^*) = \left(0, \frac{\gamma_2 - D_2}{c_2}, 0, \frac{B}{c_4}\right) = \left(0, \frac{R_2}{c_2}, 0, \frac{B}{c_4}\right). \quad (4.14)$$

Existence is unconditional due to our assumption that (??) holds.

For $E_9(N_{91}^*, 0, 0, N_{94}^*)$

From (4.1), we obtain:

$$E_9(N_{91}^*, 0, 0, N_{94}^*) = \left(\frac{\gamma_1 - D_1}{c_1}, 0, 0, \frac{B}{c_4}\right) = \left(\frac{R_1}{c_1}, 0, 0, \frac{B}{c_4}\right) \quad (4.15)$$

Existence is unconditional due to our assumption that (??) holds.

For $E_{10}(N_{101}^*, 0, N_{103}^*, 0)$

The analysis of this equilibrium parallels the work done in Chapter 3. Define:

$$\begin{aligned} H &= \frac{p_1}{1 + \alpha_1}, & I &= \frac{\varepsilon_1 p_1}{1 + \alpha_1}, \\ s_3 &= (R_3 I c_1 - D_1)^2 \alpha_1^2 + 2(R_3 I c_1 - D_1 + 2\gamma_1)(I c_1 c_3 + H) \alpha_1 + (I c_1 c_3 + H)^2. \end{aligned} \quad (4.16)$$

We obtain:

$$\begin{aligned} N_{101}^* &= I(c_3 N_{103}^* - R_3), \\ N_{103}^* &= \frac{I(R_3 \alpha_1 - c_3)c_1 - D_1 \alpha_1 - H + \sqrt{s_3}}{2\alpha_1(Ic_1c_3 + H)}. \end{aligned} \quad (4.17)$$

The existence condition is given by:

$$\gamma_1 > D_1 + \frac{R_3[HR_3\alpha_1 + c_3(D_1\alpha_1 + H)]}{c_3^2}. \quad (4.18)$$

For $E_{11}(N_{111}^*, N_{112}^*, N_{113}^*, 0)$

As E_{11} is always unstable when it exists, we may omit its existence criterion since it will never be stable to begin with.

For $E_{12}(0, N_{122}^*, N_{123}^*, N_{124}^*)$

From (4.1), we obtain:

$$\begin{aligned} \frac{\gamma_2}{1 + \alpha_2 N_{123}} - D_2 - c_2 N_{122} - \frac{p_2}{1 + \alpha_2} N_{123} &= 0, \\ \frac{\gamma_3}{1 + \alpha_3 N_{124}} - D_3 - c_3 N_{123} + \frac{\varepsilon_2 p_2}{1 + \alpha_2} N_{122} - \frac{p_3}{1 + \alpha_3} N_{124} &= 0, \\ B - c_4 N_{124} + \frac{\varepsilon_3 p_3}{1 + \alpha_3} N_{123} &= 0. \end{aligned} \quad (4.19)$$

Rearranging the second and third equation in terms of N_{123}^* yields:

$$\begin{aligned} N_{123}^* &= \frac{1 + \alpha_3}{\varepsilon_3 p_3} (c_4 N_{124}^* - B), \\ N_{123}^* &= \frac{1}{c_3} \left[\frac{\gamma_3}{1 + \alpha_3 N_{124}^*} - D_3 + \frac{\varepsilon_2 p_2 N_{122}^*}{1 + \alpha_2} - \frac{p_3 N_{124}^*}{1 + \alpha_3} \right]. \end{aligned} \quad (4.20)$$

In order for these to be positive, the following inequalities must hold:

$$\begin{aligned} N_{124}^* &> \frac{B}{c_4}, \\ \frac{\gamma_3}{1 + \alpha_3 N_{124}^*} + \frac{\varepsilon_2 p_2 N_{122}^*}{1 + \alpha_2} &> D_3 + \frac{p_3}{1 + \alpha_3} N_{124}^*. \end{aligned} \quad (4.21)$$

Setting the two equations equal yields:

$$G_1(N_{124}^*) = \frac{1 + \alpha_3}{\varepsilon_3 p_3} (c_4 N_{124}^* - B) - \frac{1}{c_3} \left(\frac{\gamma_3}{1 + \alpha_3 N_{124}^*} - D_3 - \frac{p_3 N_{124}^*}{1 + \alpha_3} \right) = \frac{\varepsilon_2 p_2 N_{122}^*}{c_3 (1 + \alpha_2)}. \quad (4.22)$$

Plugging the first equation for N_{123}^* into the first equation of the original system yields:

$$G_2(N_{124}^*) = \frac{1}{c_2} \left[\frac{\gamma_2}{1 + \frac{\alpha_2 (1 + \alpha_3) (c_4 N_{124}^* - B)}{\varepsilon_3 p_3}} - D_2 - \frac{p_2 (1 + \alpha_3) (c_4 N_{124}^* - B)}{\varepsilon_3 p_3 (1 + \alpha_2)} \right] = N_{122}^*. \quad (4.23)$$

Let us treat N_{122}^* as a function of N_{124}^* . E_{12} is given by the intersections of G_1 and G_2 , ensuring that the constraints in (4.21) hold true.

For $E_{13}(N_{131}^*, 0, N_{133}^*, N_{134}^*)$

From (4.1), we obtain the system of equations:

$$\begin{aligned} \frac{\gamma_1}{1 + \alpha_1 N_{133}} - D_1 - c_1 N_{131} - \frac{p_1}{1 + \alpha_1} N_{133} &= 0, \\ \frac{\gamma_3}{1 + \alpha_3 N_{134}} - D_3 - c_3 N_{133} + \frac{\varepsilon_1 p_1}{1 + \alpha_1} N_{131} - \frac{p_3}{1 + \alpha_3} N_{134} &= 0, \\ B - c_4 N_{134} + \frac{\varepsilon_3 p_3}{1 + \alpha_3} N_{133} &= 0. \end{aligned} \quad (4.24)$$

Rearranging the second and third equation in terms of N_{133}^* yields:

$$\begin{aligned} N_{133}^* &= \frac{1 + \alpha_3}{\varepsilon_3 p_3} (c_4 N_{134}^* - B), \\ N_{133}^* &= \frac{1}{c_3} \left[\frac{\gamma_3}{1 + \alpha_3 N_{134}^*} - D_3 + \frac{\varepsilon_1 p_1 N_{131}^*}{1 + \alpha_1} - \frac{p_3 N_{134}^*}{1 + \alpha_3} \right]. \end{aligned} \quad (4.25)$$

In order for these to be positive, the following inequalities must hold:

$$\begin{aligned} N_{134}^* &> \frac{B}{c_4}, \\ \frac{\gamma_3}{1 + \alpha_3 N_{134}^*} + \frac{\varepsilon_1 p_1 N_{131}^*}{1 + \alpha_1} &> D_3 + \frac{p_3}{1 + \alpha_3} N_{134}^*. \end{aligned} \quad (4.26)$$

Setting the two equations equal yields:

$$G_1(N_{134}^*) = \frac{1 + \alpha_3}{\varepsilon_3 p_3} (c_4 N_{134}^* - B) - \frac{1}{c_3} \left(\frac{\gamma_3}{1 + \alpha_3 N_{134}^*} - D_3 - \frac{p_3 N_{134}^*}{1 + \alpha_3} \right) = \frac{\varepsilon_1 p_1 N_{131}^*}{c_3 (1 + \alpha_1)}. \quad (4.27)$$

Plugging the first equation for N_{133}^* into the first equation of the original system yields:

$$G_2(N_{134}^*) = \frac{1}{c_1} \left[\frac{\gamma_1}{1 + \frac{\alpha_1 (1 + \alpha_3) (c_4 N_{134}^* - B)}{\varepsilon_3 p_3}} - D_1 - \frac{p_1 (1 + \alpha_3) (c_4 N_{134}^* - B)}{\varepsilon_3 p_3 (1 + \alpha_1)} \right] = N_{131}^*. \quad (4.28)$$

Let us treat N_{131}^* as a function of N_{134}^* . E_{13} is given by the intersections of G_1 and G_2 , ensuring that the constraints in (4.26) hold true.

For $E_{14}(N_{141}^*, N_{142}^*, 0, N_{144}^*)$

This case is nice combination of E_3 and E_8 . Combining the results, we obtain:

$$E_{14}(N_{141}^*, N_{142}^*, 0, N_{144}^*) = \left(\frac{R_2 \beta_1 - c_2 R_1}{\beta_1 \beta_2 - c_1 c_2}, \frac{R_1 \beta_2 - c_1 R_2}{\beta_1 \beta_2 - c_1 c_2}, 0, \frac{B}{c_4} \right). \quad (4.29)$$

The $\frac{B}{c_4}$ term always exists, so existence is then dependent on a case of strong or weak

competition. The existence criteria for this equilibrium is identical to the criteria for $E_3(N_{31}^*, N_{32}^*, 0, 0)$, given by (3.3) and (3.4).

For $E_{15}(N_1^+, N_2^+, N_3^+, N_4^+)$

The study of E_{15} through analytic means will be omitted in this thesis.

Theorem 4.1 *The equilibria E_0, E_1, E_2, E_5, E_8 and E_9 always exist. The equilibria $E_3, E_4, E_6, E_7, E_{10}, E_{11}, E_{12}, E_{13}$ and E_{14} exist conditionally.*

Proof These results follow from the above analysis. ■

The results may be succinctly summarized in the following table:

Equilibrium Point	Existence	Stability
$E_0(0, 0, 0, 0)$	Always	Always Unstable
$E_1(N_{11}^*, 0, 0, 0)$	Always	Always Unstable
$E_2(0, N_{22}^*, 0, 0)$	Always	Always Unstable
$E_3(N_{31}^*, N_{32}^*, 0, 0)$	Given by (3.3) or (3.4)	Unstable when Exists
$E_4(0, 0, N_{43}^*, 0)$	Always	Always Unstable
$E_5(0, 0, 0, N_{54}^*)$	Always	Always Unstable
$E_6(0, 0, N_{63}^*, N_{64}^*)$	Given by (4.10)	Conditions Given by (4.50)
$E_7(0, N_{72}^*, N_{73}^*, 0)$	Given by (4.13)	Unstable when Exists
$E_8(0, N_{82}^*, 0, N_{84}^*)$	Always	Conditions Given by (4.55)
$E_9(N_{91}^*, 0, 0, N_{94}^*)$	Always	Conditions Given by (4.58)
$E_{10}(N_{101}^*, 0, N_{103}^*, 0)$	Given by (4.18)	Unstable when Exists
$E_{11}(N_{111}^*, N_{112}^*, N_{113}^*, 0)$	Conditional	Unstable when Exists
$E_{12}(0, N_{122}^*, N_{123}^*, N_{124}^*)$	Conditional	Conditions Given by (4.70)
$E_{13}(N_{131}^*, 0, N_{133}^*, N_{134}^*)$	Conditional	Conditions Given by (4.76)
$E_{14}(N_{141}^*, N_{142}^*, 0, N_{144}^*)$	Given by (3.3) or (3.4)	Conditions Given by (4.83)
$E_{15}(N_1^+, N_2^+, N_3^+, N_4^+)$	Omitted	Omitted

Table 4.1: Summary of equilibria and their stability

4.2 Stability of the Equilibria

In this section, we will study some of the equilibrium points derived in Section 4.2. The Jacobian matrix corresponding to (1.11) is given by:

$$\mathbf{J}(N_1, N_2, N_3, N_4) = \begin{pmatrix} \mathbf{J}_{11} & \mathbf{J}_{12} & \mathbf{J}_{13} & \mathbf{J}_{14} \\ \mathbf{J}_{21} & \mathbf{J}_{22} & \mathbf{J}_{23} & \mathbf{J}_{24} \\ \mathbf{J}_{31} & \mathbf{J}_{32} & \mathbf{J}_{33} & \mathbf{J}_{34} \\ \mathbf{J}_{41} & \mathbf{J}_{42} & \mathbf{J}_{43} & \mathbf{J}_{44} \end{pmatrix}, \quad (4.30)$$

where:

$$\begin{aligned}
\mathbf{J}_{11} &= \frac{\gamma_1}{1 + \alpha_1 N_3} - D_1 - 2c_1 N_1^* - \beta_1 N_2 - \frac{p_1 N_3}{1 + \alpha_1}, \\
\mathbf{J}_{12} &= -\beta_1 N_1, \\
\mathbf{J}_{13} &= -N_1 \left(\frac{\gamma_1 \alpha_1}{(1 + \alpha_1 N_3)^2} + \frac{p_1}{1 + \alpha_1} \right), \\
\mathbf{J}_{14} &= 0, \\
\mathbf{J}_{21} &= -\beta_2 N_2, \\
\mathbf{J}_{22} &= \frac{\gamma_2}{1 + \alpha_2 N_3} - D_2 - 2c_2 N_2 - \beta_2 N_1 - \frac{p_2 N_3}{1 + \alpha_2}, \\
\mathbf{J}_{23} &= -N_2 \left(\frac{\gamma_2 \alpha_2}{(1 + \alpha_2 N_3)^2} + \frac{p_2}{1 + \alpha_2} \right), \\
\mathbf{J}_{24} &= 0, \\
\mathbf{J}_{31} &= \frac{\varepsilon_1 p_1 N_3}{1 + \alpha_1}, \\
\mathbf{J}_{32} &= \frac{\varepsilon_2 p_2 N_3}{1 + \alpha_2}, \\
\mathbf{J}_{33} &= \frac{\gamma_3}{1 + \alpha_3 N_4} - D_3 - 2c_3 N_3 + \frac{\varepsilon_1 p_1 N_1}{1 + \alpha_1} + \frac{\varepsilon_2 p_2 N_2}{1 + \alpha_2} - \frac{p_3 N_4}{1 + \alpha_3}, \\
\mathbf{J}_{34} &= -N_3 \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 N_4)^2} + \frac{p_3}{1 + \alpha_3} \right), \\
\mathbf{J}_{41} &= 0, \\
\mathbf{J}_{42} &= 0, \\
\mathbf{J}_{43} &= \frac{\varepsilon_3 p_3 N_4}{1 + \alpha_3}, \\
\mathbf{J}_{44} &= B - 2c_4 N_4 + \frac{\varepsilon_3 p_3 N_3}{1 + \alpha_3}.
\end{aligned} \tag{4.31}$$

Let us now consider the stability of the various equilibrium points. Some were previously studied in the context of various subsystems, but now we will factor in the coupling that

occurs in the four component model. Evaluating the Jacobian at E_0 yields:

$$\mathbf{J}(0, 0, 0, 0) = \begin{pmatrix} \gamma_1 - D_1 & 0 & 0 & 0 \\ 0 & \gamma_2 - D_2 & 0 & 0 \\ 0 & 0 & \gamma_3 - D_3 & 0 \\ 0 & 0 & 0 & B \end{pmatrix} = \begin{pmatrix} R_1 & 0 & 0 & 0 \\ 0 & R_2 & 0 & 0 \\ 0 & 0 & R_3 & 0 \\ 0 & 0 & 0 & B \end{pmatrix}. \quad (4.32)$$

The eigenvalues are given by the characteristic equation:

$$\begin{aligned} (R_1 - \lambda)(R_2 - \lambda)(R_3 - \lambda)(B - \lambda) &= 0 \\ \iff \lambda_1 = R_1, \quad \lambda_2 = R_2, \lambda_3 = R_3, \lambda_4 = B. \end{aligned} \quad (4.33)$$

As we assumed R_1 , R_2 and R_3 to be positive, λ_1 , λ_2 and λ_3 are always positive. Furthermore, B is a positive constant. Therefore, the trivial equilibrium is always unstable.

Evaluating the Jacobian at E_1 yields:

$$\mathbf{J}\left(\frac{R_1}{c_1}, 0, 0, 0\right) = \begin{pmatrix} -R_1 & -\frac{R_1\beta_1}{c_1} & -\frac{R_1(\gamma_1\alpha_1^2 + \gamma_1\alpha_1 + p_1)}{c_1(1+\alpha_1)} & 0 \\ 0 & R_2 - \frac{\beta_2 R_1}{c_1} & 0 & 0 \\ 0 & 0 & R_3 + \frac{\varepsilon_1 p_1 R_1}{c_1(1+\alpha_1)} & 0 \\ 0 & 0 & 0 & B \end{pmatrix}. \quad (4.34)$$

The eigenvalues are given by:

$$\begin{aligned} \lambda_1 &= -R_1, \\ \lambda_2 &= \frac{R_2 c_1 - \beta_2 R_1}{c_1}, \\ \lambda_3 &= \frac{c_1 R_3 (1 + \alpha_1) + \varepsilon_1 p_1 R_1}{c_1 (1 + \alpha_1)}, \\ \lambda_4 &= B. \end{aligned} \quad (4.35)$$

B is always a positive constant, so λ_4 is always positive. Therefore, this equilibrium is unstable.

Evaluating the Jacobian at E_2 yields:

$$\mathbf{J}\left(0, \frac{R_2}{c_2}, 0, 0\right) = \begin{pmatrix} R_1 - \frac{\beta_1 R_2}{c_2} & 0 & 0 & 0 \\ -\frac{R_2 \beta_2}{c_2} & -R_2 & -\frac{R_2(\gamma_2 \alpha_2^2 + \gamma_2 \alpha_2 + p_2)}{c_2(1 + \alpha_2)} & 0 \\ 0 & 0 & R_3 + \frac{\varepsilon_2 p_2 R_2}{c_2(1 + \alpha_2)} & 0 \\ 0 & 0 & 0 & B \end{pmatrix}. \quad (4.36)$$

The eigenvalues are given by:

$$\begin{aligned} \lambda_1 &= \frac{R_1 c_2 - \beta_1 R_2}{c_2}, \\ \lambda_2 &= -R_2, \\ \lambda_3 &= \frac{R_3(1 + \alpha_2)c_2 + \varepsilon_2 p_2 R_2}{c_2(1 + \alpha_2)}, \\ \lambda_4 &= B. \end{aligned} \quad (4.37)$$

B is a positive constant, so λ_4 is always positive. Therefore, this equilibrium is unstable.

Evaluating the Jacobian at E_3 yields and making simplifications using (4.1) yields:

$$\mathbf{J}(N_{31}^*, N_{32}^*, 0, 0) = \begin{pmatrix} -c_1 N_{31}^* & -N_{31}^* \beta_1 & N_{31}^* \left(-\alpha_1 \gamma_1 - \frac{p_1}{1 + \alpha_1}\right) & 0 \\ -N_{32}^* \beta_2 & -c_2 N_{32}^* & N_{32}^* \left(-\alpha_2 \gamma_2 - \frac{p_2}{1 + \alpha_2}\right) & 0 \\ 0 & 0 & R_3 + \frac{\varepsilon_1 p_1 N_{31}^*}{1 + \alpha_1} + \frac{\varepsilon_2 p_2 N_{32}^*}{1 + \alpha_2} & 0 \\ 0 & 0 & 0 & B \end{pmatrix}. \quad (4.38)$$

The eigenvalues are given by:

$$\begin{aligned}
\lambda_1 &= \frac{-c_1 N_{31}^* - c_2 N_{32}^* + \sqrt{(N_{31}^*)^2 c_1^2 - 2N_{32}^* (c_2 c_1 - 2\beta_1 \beta_2) N_{31}^* + (N_{32}^*)^2 c_2^2}}{2}, \\
\lambda_2 &= \frac{-c_1 N_{31}^* - c_2 N_{32}^* - \sqrt{(N_{31}^*)^2 c_1^2 - 2N_{32}^* (c_2 c_1 - 2\beta_1 \beta_2) N_{31}^* + (N_{32}^*)^2 c_2^2}}{2}, \\
\lambda_3 &= \frac{\alpha_1 (R_3 \alpha_2 + \varepsilon_2 p_2 N_{32}^* + R_3) + \alpha_2 (\varepsilon_1 p_1 N_{31}^* + R_3) + \varepsilon_2 p_2 N_{32}^* + \varepsilon_1 p_1 N_{31}^* + R_3}{(1 + \alpha_1)(1 + \alpha_2)}, \\
\lambda_4 &= B.
\end{aligned} \tag{4.39}$$

λ_3 is always positive when N_{31}^* and N_{32}^* exist, and B is a positive constant, so λ_4 is always positive. Therefore, this equilibrium is unstable.

Evaluating the Jacobian at E_4 yields:

$$\mathbf{J}\left(0, 0, \frac{R_3}{c_3}, 0\right) = \begin{pmatrix} \frac{\gamma_1}{1 + \frac{\alpha_1 R_3}{c_3}} - D_1 - \frac{p_1 R_3}{c_3(1 + \alpha_1)} & 0 & 0 & 0 \\ 0 & \frac{\gamma_2}{1 + \frac{\alpha_2 R_3}{c_3}} - D_2 - \frac{p_2 R_3}{c_3(1 + \alpha_2)} & 0 & 0 \\ \frac{R_3 \varepsilon_1 p_1}{c_3(1 + \alpha_1)} & \frac{R_3 \varepsilon_2 p_2}{c_3(1 + \alpha_2)} & -R_3 & -\frac{R_3}{c_3} \left(\gamma_3 \alpha_3 + \frac{p_3}{1 + \alpha_3} \right) \\ 0 & 0 & 0 & B + \frac{\varepsilon_3 p_3 R_3}{c_3(1 + \alpha_3)} \end{pmatrix}. \tag{4.40}$$

The eigenvalues are given by:

$$\begin{aligned}
\lambda_1 &= -\frac{c_3 \alpha_2^2 R_3 D_2 + c_3 \alpha_2 R_3 D_2 + c_3^2 \alpha_2 D_2 + R_3^2 \alpha_2 p_2 - \gamma_2 c_3^2 \alpha_2 + c_3^2 D_2 + R - 3c_3 p_2 - \gamma_2 c_3^2}{c_3(\alpha_2^2 R_3 + \alpha_2 R_3 + \alpha_2 c_3 + c_3)}, \\
\lambda_2 &= -\frac{D_1 R_3 \alpha_1^2 + D_1 R_3 \alpha_1 c_3 + D_1 \alpha_1 c_3^2 + R_3^2 \alpha_1 p_1 - \alpha_1 c_3^2 \gamma_1 + D_1 c_3^2 + R_3 c_3 p_1 - c_3^2 \gamma_1}{c_3(R_3 \alpha_1^2 + R_3 \alpha_1 + \alpha_1 c_3 + c_3)}, \\
\lambda_3 &= -R_3, \\
\lambda_4 &= \frac{B \alpha_3 c_3 + R_3 p_3 \varepsilon_3 + B c_3}{c_3(1 + \alpha_3)}.
\end{aligned} \tag{4.41}$$

As we assumed R_3 to be positive, λ_4 is always positive. Therefore E_4 is always unstable.

Evaluating the Jacobian at E_5 yields:

$$\mathbf{J}\left(0, 0, 0, \frac{B}{c_4}\right) = \begin{pmatrix} R_1 & 0 & 0 & 0 \\ 0 & R_2 & 0 & 0 \\ 0 & 0 & \frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} - D_3 - \frac{p_3 B}{c_4(1 + \alpha_3)} & 0 \\ 0 & 0 & \frac{B \varepsilon_3 p_3}{c_4(1 + \alpha_3)} & -B \end{pmatrix}. \quad (4.42)$$

The eigenvalues are given by:

$$\lambda_2 = R_1,$$

$$\lambda_3 = R_2,$$

$$\lambda_4 = -\frac{BD_3\alpha_3^2c_4 + B^2\alpha_3p_3 + BD_3\alpha_3c_4 + D_3\alpha_3c_4^2 - \gamma_3c_4^2\alpha_3 + Bc_4p_3 + D_3c_4^2 - \gamma_3c_4^2}{c_4(B\alpha_3^2 + \alpha_3B + \alpha_3c_4 + c_4)}, \quad (4.43)$$

$$\lambda_4 = -B.$$

As we assumed R_1 and R_2 to be positive, it follows that λ_1 and λ_2 are positive as well.

Therefore, E_5 is always unstable.

Evaluating the Jacobian at E_6 yields:

$$\mathbf{J}(0, 0, N_{63}^*, N_{64}^*) = \begin{pmatrix} \frac{\gamma_1}{1 + \alpha_1 N_{63}^*} - D_1 - \frac{p_1 N_{63}^*}{1 + \alpha_1} & 0 & 0 & 0 \\ 0 & \frac{\gamma_2}{1 + \alpha_2 N_{63}^*} - D_2 - \frac{p_2 N_{63}^*}{1 + \alpha_2} & 0 & 0 \\ \frac{N_{63}^* \varepsilon_1 p_1}{1 + \alpha_1} & \frac{N_{63}^* \varepsilon_2 p_2}{1 + \alpha_2} & -c_3 N_{63}^* & -N_{63}^* \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 N_{64}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) \\ 0 & 0 & \frac{N_{64}^* \varepsilon_3 p_3}{1 + \alpha_3} & -c_4 N_{64}^* \end{pmatrix}. \quad (4.44)$$

Expanding along the first row, the first eigenvalue is given by:

$$\lambda_1 = \frac{\gamma_1}{1 + \alpha_1 N_{63}^*} - D_1 - \frac{p_1 N_{63}^*}{1 + \alpha_1}. \quad (4.45)$$

The remaining eigenvalues are determined by the minor:

$$\begin{pmatrix} \frac{\gamma_2}{1 + \alpha_2 N_{63}^*} - D_2 - \frac{p_2 N_{63}^*}{1 + \alpha_2} & 0 & 0 \\ \frac{N_{63}^* \varepsilon_2 p_2}{1 + \alpha_2} & -c_3 N_{63}^* & -N_{63}^* \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 N_{64}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) \\ 0 & \frac{N_{64}^* \varepsilon_3 p_3}{1 + \alpha_3} & -c_4 N_{64}^* \end{pmatrix}. \quad (4.46)$$

Expanding along the first row once again gives the second eigenvalue as:

$$\lambda_2 = \frac{\gamma_2}{1 + \alpha_2 N_{63}^*} - D_2 - \frac{p_2 N_{63}^*}{1 + \alpha_2}. \quad (4.47)$$

The remaining eigenvalues may be characterized by the matrix:

$$\begin{pmatrix} -c_3 N_{63}^* & -N_{63}^* \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 N_{64}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) \\ \frac{N_{64}^* \varepsilon_3 p_3}{1 + \alpha_3} & -c_4 N_{64}^* \end{pmatrix}. \quad (4.48)$$

This matrix has the characteristic equation:

$$\lambda^2 + \lambda(c_3 N_{63}^* + c_4 N_{64}^*) + \frac{c_3 c_4 \varepsilon_3 p_3 (N_{63}^* N_{64}^*)^2}{1 + \alpha_3} \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 N_{64}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) = 0. \quad (4.49)$$

The Routh-Hurwitz criterion for a second degree polynomial says that the constant term and the constant on the λ term must both be positive in order to have eigenvalues with negative real part. Note that both of these constants are always positive when N_{63}^* and N_{64}^* exist. Therefore, λ_1 and λ_2 determine the stability of this equilibrium point, and so need to

be negative to guarantee stability. This gives the following:

$$\begin{aligned} \frac{\gamma_1}{1 + \alpha_1 N_{63}^*} &< D_1 + \frac{p_1 N_{63}^*}{1 + \alpha_1}, \\ \frac{\gamma_2}{1 + \alpha_2 N_{63}^*} &< D_2 + \frac{p_2 N_{63}^*}{1 + \alpha_2}. \end{aligned} \quad (4.50)$$

Therefore, E_6 is stable when the above conditions hold.

Evaluating the Jacobian at E_7 yields:

$$\mathbf{J}(0, N_{72}^*, N_{73}^*, 0) = \begin{pmatrix} \frac{\gamma_1}{1 + \alpha_1 N_{73}^*} - D_1 - \beta_1 N_{72}^* - \frac{p_1 N_{73}^*}{1 + \alpha_1} & 0 & 0 & 0 \\ -\beta_2 N_{72}^* & -c_2 N_{72}^* & -N_{72}^* \left(\frac{\gamma_2 \alpha_2}{(1 + \alpha_2 N_{73}^*)^2} + \frac{p_2}{1 + \alpha_2} \right) & 0 \\ \frac{N_{73}^* \varepsilon_1 p_1}{1 + \alpha_1} & \frac{N_{73}^* \varepsilon_2 p_2}{1 + \alpha_2} & -c_3 N_{73}^* & -N_{73}^* \left(\gamma_3 \alpha_3 + \frac{p_3}{1 + \alpha_3} \right) \\ 0 & 0 & 0 & B + \frac{\varepsilon_3 p_3 N_{73}^*}{1 + \alpha_3} \end{pmatrix}. \quad (4.51)$$

Expanding along the bottom row, one of the eigenvalues is apparently obvious. This is given by:

$$\lambda_4 = B + \frac{N_{73}^* p_3 \varepsilon_3}{1 + \alpha_3}, \quad (4.52)$$

which is always positive when N_{73}^* exists. Therefore, E_7 is unstable.

Evaluating the Jacobian at E_8 yields:

$$\mathbf{J}\left(0, \frac{R_2}{c_2}, 0, \frac{B}{c_4}\right) = \begin{pmatrix} R_1 - \frac{\beta_1 R_2}{c_2} & 0 & 0 & 0 \\ -\frac{R_2 \beta_2}{c_2} & -R_2 & -\frac{R_2}{c_2} \left(\gamma_2 \alpha_2 + \frac{p_2}{1 + \alpha_2} \right) & 0 \\ 0 & 0 & \frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} - D_3 + \frac{\varepsilon_2 p_2 R_2}{c_2 (1 + \alpha_2)} - \frac{p_3 B}{c_4 (1 + \alpha_3)} & 0 \\ 0 & 0 & \frac{B \varepsilon_3 p_3}{c_4 (1 + \alpha_3)} & -B \end{pmatrix}. \quad (4.53)$$

The eigenvalues are given by:

$$\begin{aligned}
 \lambda_1 &= \frac{R_1 c_2 - \beta_1 R_2}{c_2}, \\
 \lambda_2 &= -R_2, \\
 \lambda_3 &= \frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} - D_3 + \frac{\varepsilon_2 p_2 R_2}{c_2(1 + \alpha_2)} - \frac{p_3 B}{c_4(1 + \alpha_3)}, \\
 \lambda_4 &= -B.
 \end{aligned} \tag{4.54}$$

Note that λ_1 and λ_3 are always negative. When λ_1 and λ_3 are negative, the equilibrium is stable. This occurs when:

$$\begin{aligned}
 R_1 c_2 &< \beta_1 R_2, \\
 \frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} + \frac{\varepsilon_2 p_2 R_2}{c_2(1 + \alpha_2)} &< D_3 + \frac{p_3 B}{c_4(1 + \alpha_3)}.
 \end{aligned} \tag{4.55}$$

Therefore, when the above conditions hold, E_8 is stable.

Evaluating the Jacobian at E_9 yields:

$$\mathbf{J}\left(\frac{R_1}{c_1}, 0, 0, \frac{B}{c_4}\right) = \begin{pmatrix} -R_1 & -\frac{R_1 \beta_1}{c_1} & -\frac{R_1}{c_1} \left(\alpha_1 \gamma_1 + \frac{p_1}{1 + \alpha_1} \right) & 0 \\ 0 & R_2 - \frac{\beta_2 R_1}{c_1} & 0 & 0 \\ 0 & 0 & \frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} - D_3 + \frac{\varepsilon_1 p_1 R_1}{c_1(1 + \alpha_1)} - \frac{p_3 B}{c_4(1 + \alpha_3)} & 0 \\ 0 & 0 & \frac{B \varepsilon_3 p_3}{c_4(1 + \alpha_3)} & -B \end{pmatrix}. \tag{4.56}$$

The eigenvalues are given by:

$$\begin{aligned}
 \lambda_1 &= -R_1, \\
 \lambda_2 &= \frac{R_2 c_1 - \beta_2 R_1}{c_1}, \\
 \lambda_3 &= \frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} - D_3 + \frac{\varepsilon_1 p_1 R_1}{c_1(1 + \alpha_1)} - \frac{p_3 B}{c_4(1 + \alpha_3)}, \\
 \lambda_4 &= -B.
 \end{aligned} \tag{4.57}$$

Note that λ_1 and λ_4 are always negative. When λ_2 and λ_3 are negative, the equilibrium is stable. This occurs when:

$$\begin{aligned}
 R_2 c_1 &< \beta_2 R_1, \\
 \frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} + \frac{\varepsilon_1 p_1 R_1}{c_1(1 + \alpha_1)} &< D_3 + \frac{p_3 B}{c_4(1 + \alpha_3)}
 \end{aligned} \tag{4.58}$$

Therefore, when the above conditions hold, E_9 is stable.

Evaluating the Jacobian at E_{10} and making simplifications using (4.1) yields:

$$\mathbf{J}(N_{101}^*, 0, N_{103}^*, 0) = \begin{pmatrix} -c_1 N_{101}^* & -\beta_1 N_{101}^* & -N_{101}^* \left(\frac{\gamma_1}{(1 + \alpha_1 N_{103}^*)^2} + \frac{p_1}{1 + \alpha_1} \right) & 0 \\ 0 & \frac{\gamma_2}{1 + \alpha_2 N_{103}^*} - D_2 - \beta_2 N_{101}^* - \frac{p_2 N_{103}^*}{1 + \alpha_2} & 0 & 0 \\ \frac{N_{101}^* \varepsilon_1 p_1}{1 + \alpha_1} & \frac{N_{103}^* \varepsilon_2 p_2}{1 + \alpha_2} & -c_3 N_{103}^* & -N_{103}^* \left(\gamma_3 \alpha_3 + \frac{p_3}{1 + \alpha_3} \right) \\ 0 & 0 & 0 & B + \frac{\varepsilon_3 p_3 N_{103}^*}{1 + \alpha_3} \end{pmatrix}. \tag{4.59}$$

Expanding along the bottom row, one of the eigenvalues is apparently obvious. This is given by:

$$\lambda_4 = B + \frac{N_{103}^* p_3 \varepsilon_3}{1 + \alpha_3}, \tag{4.60}$$

which is always positive when N_3^* exists. Therefore, E_{10} is unstable.

Evaluating the Jacobian at E_{11} and making simplifications using (4.1) yields:

$$\mathbf{J}(N_{111}^*, N_{112}^*, N_{113}^*, 0) = \begin{pmatrix} -c_1 N_{111}^* & -\beta_1 N_{111}^* & -N_{111}^* \left(\frac{\gamma_1 \alpha_1}{(1 + \alpha_1 N_{113}^*)^2} + \frac{p_1}{1 + \alpha_1} \right) & 0 \\ -\beta_2 N_{112}^* & -c_2 N_{112}^* & -N_{112}^* \left(\frac{\gamma_2 \alpha_2}{(1 + \alpha_2 N_{113}^*)^2} + \frac{p_2}{1 + \alpha_2} \right) & 0 \\ \frac{N_{113}^* \varepsilon_1 p_1}{1 + \alpha_1} & \frac{N_{113}^* \varepsilon_2 p_2}{1 + \alpha_2} & -c_3 N_{113}^* & -N_{113}^* \left(\gamma_3 \alpha_3 + \frac{p_3}{1 + \alpha_3} \right) \\ 0 & 0 & 0 & B + \frac{\varepsilon_3 p_3 N_{113}^*}{1 + \alpha_3} \end{pmatrix}. \quad (4.61)$$

Expanding along the bottom row, one of the eigenvalues is apparently obvious. This is given by:

$$\lambda_4 = B + \frac{\varepsilon_3 p_3 N_{113}^*}{1 + \alpha_3}, \quad (4.62)$$

which is always positive when N_{113}^* exists. Therefore, E_{11} is unstable. This implies that competition and the fear response to N_3^* makes it impossible for N_3^* and the lowest members to coexist. We showed in the first subsystem that N_{111} and N_{112} may coexist in certain conditions. However, the coupled system prevents this from happening.

Evaluating the Jacobian at E_{12} and making some simplifications using (4.1) yields:

$$\mathbf{J}(0, N_{122}^*, N_{123}^*, N_{124}^*) = \begin{pmatrix} \frac{\gamma_1}{1 + \alpha_1 N_{123}^*} - D_1 - \beta_1 N_{122}^* - \frac{p_1 N_{123}^*}{1 + \alpha_1} & 0 & 0 & 0 \\ -\beta_2 N_{122}^* & -c_2 N_{122}^* & -N_{122}^* \left(\frac{\gamma_2 \alpha_2}{(1 + \alpha_3 N_{124}^*)^2} + \frac{p_2}{1 + \alpha_2} \right) & 0 \\ \frac{\varepsilon_1 p_1 N_{123}^*}{1 + \alpha_1} & \frac{\varepsilon_2 p_2 N_{123}^*}{1 + \alpha_2} & -c_3 N_{123}^* & A_{34} \\ 0 & 0 & \frac{\varepsilon_3 p_3 N_{124}^*}{1 + \alpha_3} & -c_4 N_{124}^* \end{pmatrix}, \quad (4.63)$$

where:

$$A_{34} = -N_{123}^* \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 N_{124}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) \quad (4.64)$$

Expanding along the top row, one may obtain the first eigenvalue as:

$$\lambda_1 = \frac{\gamma_1}{1 + \alpha_1 N_{123}^*} - D_1 - \beta_1 N_{122}^* - \frac{p_1 N_{123}^*}{1 + \alpha_1}. \quad (4.65)$$

The remaining eigenvalues are characterized by the minor:

$$\begin{pmatrix} -c_2 N_{122}^* & -N_{122}^* \left(\frac{\gamma_2 \alpha_2}{(1 + \alpha_3 N_{124}^*)^2} + \frac{p_2}{1 + \alpha_2} \right) & 0 \\ \frac{\varepsilon_2 p_2 N_{123}^*}{1 + \alpha_2} & -c_3 N_{123}^* & -N_{123}^* \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 N_{124}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) \\ 0 & \frac{\varepsilon_3 p_3 N_{124}^*}{1 + \alpha_3} & -c_4 N_{124}^* \end{pmatrix} \quad (4.66)$$

We may apply the Routh-Hurwitz Criterion to the characteristic equation of this matrix.

The characteristic equation is given by:

$$\lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0, \quad (4.67)$$

where:

$$\begin{aligned} a_1 &= c_2 N_{122}^* + c_3 N_{123}^* + c_4 N_{124}^* > 0, \\ a_2 &= c_2 N_{122}^* (c_3 N_{123}^* + c_4 N_{124}^*) + \frac{\varepsilon_2 p_2 N_{122}^* N_{123}^*}{1 + \alpha_2} \left(\frac{\gamma_2 \alpha_2}{(1 + \alpha_2 N_{123}^*)^2} + \frac{p_2}{1 + \alpha_2} \right) + c_3 c_4 N_{123}^* N_{124}^* + \\ &\frac{\varepsilon_3 p_3 N_{123}^* N_{124}^*}{1 + \alpha_3} \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 N_{124}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) > 0, \\ a_3 &= c_2 c_3 c_4 N_{122}^* N_{123}^* N_{124}^* + \frac{c_2 \varepsilon_3 p_3 N_{122}^* N_{123}^* N_{124}^*}{1 + \alpha_3} \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 N_{124}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) \\ &+ \frac{c_4 \varepsilon_2 p_2 N_{122}^* N_{123}^* N_{124}^*}{1 + \alpha_2} \left(\frac{\gamma_2 \alpha_2}{(1 + \alpha_2 N_{123}^*)^2} + \frac{p_2}{1 + \alpha_2} \right) > 0. \end{aligned} \quad (4.68)$$

The Routh-Hurwitz criterion for third degree polynomials as given in [5] states that if the conditions:

$$a_1, a_3 > 0, a_1 a_2 > a_3, \quad (4.69)$$

hold, then the eigenvalues will have negative real part. From (4.68), we see that $a_1, a_3 > 0$ when N_{122}^*, N_{123}^* and N_{124}^* exist. Therefore, when:

$$a_1 a_2 > a_3, \quad \frac{\gamma_1}{1 + \alpha_1 N_{123}^*} < D_1 + \beta_1 N_{122}^* + \frac{p_1 N_{123}^*}{1 + \alpha_1} \quad (4.70)$$

holds, then E_{12} will be stable.

Evaluating the Jacobian at E_{13} and making some simplifications using (4.1) yields:

$$\mathbf{J}(N_{131}^*, 0, N_{133}^*, N_{134}^*) = \begin{pmatrix} -c_1 N_{131}^* & -\beta_1 N_{131}^* & -N_{131}^* \left(\frac{\gamma_1 \alpha_1}{(1 + \alpha_3 N_{133}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) & 0 \\ 0 & \frac{\gamma_2}{1 + \alpha_2 N_{133}^*} - D_2 - \beta_2 N_{131}^* - \frac{p_2 N_{133}^*}{1 + \alpha_2} & 0 & 0 \\ \frac{N_{133}^* \varepsilon_1 p_1}{1 + \alpha_1} & \frac{N_{133}^* \varepsilon_2 p_2}{1 + \alpha_2} & -c_3 N_{133}^* & B_{34} \\ 0 & 0 & \frac{N_{134}^* \varepsilon_3 p_3}{1 + \alpha_3} & -c_4 N_{134}^* \end{pmatrix}, \quad (4.71)$$

where:

$$B_{34} = -N_{133}^* \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 N_{134}^*)^2} + \frac{p_3}{1 + \alpha_3} \right). \quad (4.72)$$

Expanding along the second row, one may obtain the second eigenvalue as:

$$\lambda_2 = \frac{\gamma_2}{1 + \alpha_2 N_{133}^*} - D_2 - \beta_2 N_{131}^* - \frac{p_2 N_{133}^*}{1 + \alpha_2}. \quad (4.73)$$

The remaining eigenvalues are characterized by the minor:

$$\begin{pmatrix} -c_1 N_{131}^* & -N_{131}^* \left(\frac{\gamma_1 \alpha_1}{(1 + \alpha_3 N_{133}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) & 0 \\ \frac{N_{133}^* \varepsilon_1 p_1}{1 + \alpha_1} & -c_3 N_{133}^* & -N_{133}^* \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 N_{134}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) \\ 0 & \frac{N_{134}^* \varepsilon_3 p_3}{1 + \alpha_3} & -c_4 N_{134}^* \end{pmatrix}. \quad (4.74)$$

This matrix is almost identical to the one for E_{12} , save for some subscripts. Utilizing this previous work, we have:

$$\begin{aligned}
b_1 &= c_1 N_{131}^* + c_3 N_{133}^* + c_4 N_{134}^* > 0, \\
b_2 &= c_1 N_{131}^* (c_3 N_{133}^* + c_4 N_{134}^*) + \frac{\varepsilon_1 p_1 N_{131}^* N_{133}^*}{1 + \alpha_1} \left(\frac{\gamma_1 \alpha_1}{(1 + \alpha_3 N_{133}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) + c_3 c_4 N_{133}^* N_{134}^* + \\
&\frac{\varepsilon_3 p_3 N_{133}^* N_{134}^*}{1 + \alpha_3} \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 N_{134}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) > 0, \\
b_3 &= c_1 c_3 c_4 N_{131}^* N_{133}^* N_{134}^* + \frac{c_1 \varepsilon_3 p_3 N_{131}^* N_{133}^* N_{134}^*}{1 + \alpha_3} \left(\frac{\gamma_3 \alpha_3}{(1 + \alpha_3 N_{134}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) \\
&+ \frac{c_4 \varepsilon_1 p_1 N_{131}^* N_{133}^* N_{134}^*}{1 + \alpha_1} \left(\frac{\gamma_1 \alpha_1}{(1 + \alpha_3 N_{133}^*)^2} + \frac{p_3}{1 + \alpha_3} \right) > 0.
\end{aligned} \tag{4.75}$$

Using our previous analysis, it follows that E_{13} is stable when the conditions:

$$b_1 b_2 > b_3, \quad \frac{\gamma_2}{1 + \alpha_2 N_{133}^*} < D_2 + \beta_2 N_{131}^* + \frac{p_2 N_{133}^*}{1 + \alpha_2} \tag{4.76}$$

hold.

Evaluating the Jacobian at E_{14} and making some simplifications using (4.1) yields:

$$\mathbf{J}(N_{141}^*, N_{142}^*, 0, N_{144}^*) = \begin{pmatrix} -c_1 N_{141}^* & -\beta_1 N_{141}^* & -N_{141}^* \left(\gamma_1 \alpha_1 + \frac{p_1}{1 + \alpha_1} \right) & 0 \\ -\beta_2 N_{142}^* & -c_2 N_{142}^* & -N_{142}^* \left(\gamma_2 \alpha_2 + \frac{p_2}{1 + \alpha_2} \right) & 0 \\ 0 & 0 & \frac{\gamma_3}{1 + \frac{B\alpha_3}{c_4}} - D_3 + \frac{\varepsilon_1 p_1 N_{141}^*}{1 + \alpha_1} + \frac{\varepsilon_2 p_2 N_{142}^*}{1 + \alpha_2} - \frac{p_3 B}{c_4 (1 + \alpha_3)} & 0 \\ 0 & 0 & \frac{B\varepsilon_3 p_3}{c_4 (1 + \alpha_3)} & -B \end{pmatrix}. \tag{4.77}$$

Expanding along the bottom row, one may obtain the final eigenvalue as

$$\lambda_4 = -B. \tag{4.78}$$

The remaining eigenvalues are characterized by the minor:

$$\begin{pmatrix} -c_1 N_{141}^* & -\beta_1 N_{141}^* & -N_{141}^* \left(\gamma_1 \alpha_1 + \frac{p_1}{1+\alpha_1} \right) \\ -\beta_2 N_{142}^* & -c_2 N_{142}^* & -N_{142}^* \left(\gamma_2 \alpha_2 + \frac{p_2}{1+\alpha_2} \right) \\ 0 & 0 & \frac{\gamma_3}{1 + \frac{B\alpha_3}{c_4}} - D_3 + \frac{\varepsilon_1 p_1 N_{141}^*}{1+\alpha_1} + \frac{\varepsilon_2 p_2 N_{142}^*}{1+\alpha_2} - \frac{p_3 B}{c_4(1+\alpha_3)} \end{pmatrix} \quad (4.79)$$

Expanding along the fourth column gives the third eigenvalue as:

$$\lambda_3 = \frac{\gamma_3}{1 + \frac{B\alpha_3}{c_4}} - D_3 + \frac{\varepsilon_1 p_1 N_{141}^*}{1 + \alpha_1} + \frac{\varepsilon_2 p_2 N_{142}^*}{1 + \alpha_2} - \frac{p_3 B}{c_4(1 + \alpha_3)}. \quad (4.80)$$

The remaining to eigenvalues are characterized by the minor:

$$\begin{pmatrix} -c_1 N_{141}^* & -\beta_1 N_{141}^* \\ -\beta_2 N_{142}^* & -c_2 N_{142}^* \end{pmatrix} \quad (4.81)$$

This matrix has the characteristic equation:

$$\lambda^2 + \lambda(c_1 N_{141}^* + c_2 N_{142}^*) + N_{141}^* N_{142}^* (c_1 c_2 - \beta_1 \beta_2) = 0. \quad (4.82)$$

The Routh-Hurwitz criterion states that both of the constant terms on the above equation need to be positive to guarantee eigenvalues with negative real parts. The constant attached to the λ term is always positive when N_{141}^* and N_{142}^* exist. Therefore, all that matters is the constant term. λ_4 is always negative, but λ_3 can vary sign depending on the parameters. This gives the following conditions for stability after substituting the values of N_{141}^* and N_{142}^* :

$$c_1 c_2 > \beta_1 \beta_2, \quad \frac{\gamma_3}{1 + \frac{B\alpha_3}{c_4}} + \frac{\varepsilon_1 p_1}{1 + \alpha_1} \cdot \frac{R_2 \beta_1 - c_2 R_1}{\beta_1 \beta_2 - c_1 c_2} + \frac{\varepsilon_2 p_2}{1 + \alpha_2} \cdot \frac{R_1 \beta_2 - c_1 R_2}{\beta_1 \beta_2 - c_1 c_2} < D_3 + \frac{p_3 B}{c_4(1 + \alpha_3)}. \quad (4.83)$$

Note that the first condition describes the weak competition case. Therefore, if E_{14} corresponds to a case of strong competition, it must be unstable. This then implies that a case of weak competition is the only possible case of stability, provided that the second condition holds as well.

Chapter 5

Summary and Discussion

5.1 Results Involving Full Model and $N_1 - N_2$ Competition Subsystem

Our analysis showed that in this decoupled system the extinction case is unstable, and the strong competition coexistence case is unstable. The weak competition coexistence case is stable as well as the exclusion cases. In the full model, we see that all of these analogous cases are unstable. This suggests that N_3 and N_4 have a top-down effect on the persistence of N_1 and N_2 . Another relationship worth considering is the effect of N_4 on the persistence of N_1 and N_2 in the full model. This corresponds to the equilibria E_8 and E_9 of the full model. $\hat{N}_1^* = \frac{R_1}{c_1}$ will persist in the competition subsystem when the condition:

$$R_2 c_1 < \beta_2 R_1 \tag{5.1}$$

holds. Similarly, $\hat{N}_2^* = \frac{R_2}{c_2}$ will persist in the competition system when the condition:

$$R_1 c_2 < \beta_1 R_2 \tag{5.2}$$

holds. Comparing the stability conditions of E_9 given in (4.58) with (5.1), these two conditions are shared. If N_4 gets involved, it will allow $N_{91}^* = \frac{R_1}{c_1}$ to persist. Similarly, comparing the stability conditions of E_8 given in (4.55) with (5.2), these two conditions are shared. If N_4 gets involved, it will allow $N_{82}^* = \frac{R_2}{c_2}$ to persist. This suggests N_4 may have a beneficial effect on one of N_1 and N_2 , but have a negative effect on N_3 in the full model.

5.2 Results Involving Full Model and N_3 - N_4 Predator-Prey Subsystem

Let us now consider the predator-prey subsystem. This system has two equilibria of interest, namely $\bar{E}_2(0, \bar{N}_4^*)$ and $\bar{E}_3(\bar{N}_3^+, \bar{N}_4^+)$. \bar{E}_2 always exists and the stability is given by (3.35). This stability condition reads:

$$\frac{\gamma_3}{1 + \alpha_3 \bar{N}_4^*} < D_3 + \frac{p_3 \bar{N}_4^*}{1 + \alpha_3}. \quad (5.3)$$

This means that the fear response of N_3 and \bar{N}_4^* play a role in its ability to exclude N_3 . \bar{E}_3 is stable when it exists, which are given by (3.28) In the full model, we have the equilibrium point $E_6(0, 0, N_{63}^*, N_{64}^*)$. This is a combination of both of the previously mentioned equilibrium points in the predator-prey system, as this equilibrium covers the coexistence of N_3 and N_4 as well as the exclusion of the next lowest members of the food chain. E_6 is stable when it exists and (4.50) holds. The existence conditions are still given by (4.10), and the stability conditions read:

$$\begin{aligned} \frac{\gamma_1}{1 + \alpha_1 N_{63}^*} &< D_1 + \frac{p_1 N_{63}^*}{1 + \alpha_1}, \\ \frac{\gamma_2}{1 + \alpha_2 N_{63}^*} &< D_2 + \frac{p_2 N_{63}^*}{1 + \alpha_2}. \end{aligned} \quad (5.4)$$

Note the similarities of these conditions with the ones corresponding to \bar{E}_2 . The fear response of N_1 and N_2 both play a role in the stability. This suggests that the fear response of the lowest member(s) and equilibrium point of the next highest member will play a part in order for the next highest member(s) to exclude the next lowest member(s). Since we're also combining the coexistence of N_3 and N_4 this also invokes the existence criteria given by (3.28)

Another relationship worth considering is the effect of \bar{E}_2 on E_{14} . \bar{E}_2 is stable when the condition given in (3.35):

$$\frac{\gamma_3}{1 + \frac{B\alpha_3}{c_4}} < D_3 + \frac{p_3 B}{c_4(1 + \alpha_3)} \quad (5.5)$$

holds. E_{14} is stable when weak competition occurs and the second condition in (4.83):

$$\frac{\gamma_3}{1 + \frac{B\alpha_3}{c_4}} + \frac{\varepsilon_1 p_1}{1 + \alpha_1} \cdot \frac{R_2 \beta_1 - c_2 R_1}{\beta_1 \beta_2 - c_1 c_2} + \frac{\varepsilon_2 p_2}{1 + \alpha_2} \cdot \frac{R_1 \beta_2 - c_1 R_2}{\beta_1 \beta_2 - c_1 c_2} < D_3 + \frac{p_3 B}{c_4(1 + \alpha_3)} \quad (5.6)$$

holds. If (3.35) holds, then the second condition in (4.83) holds if:

$$0 \leq \frac{\varepsilon_1 p_1}{1 + \alpha_1} \cdot \frac{R_2 \beta_1 - c_2 R_1}{\beta_1 \beta_2 - c_1 c_2} + \frac{\varepsilon_2 p_2}{1 + \alpha_2} \cdot \frac{R_1 \beta_2 - c_1 R_2}{\beta_1 \beta_2 - c_1 c_2} < D_3 + \frac{p_3 B}{c_4(1 + \alpha_3)} - \frac{\gamma_3}{1 + \frac{B\alpha_3}{c_4}} \quad (5.7)$$

is true. If not, E_{14} is unstable. If the second part of (4.83) holds, then (3.35) holds since:

$$\frac{\gamma_3}{1 + \frac{B\alpha_3}{c_4}} \leq \frac{\gamma_3}{1 + \frac{B\alpha_3}{c_4}} + \frac{\varepsilon_1 p_1}{1 + \alpha_1} \cdot \frac{R_2 \beta_1 - c_2 R_1}{\beta_1 \beta_2 - c_1 c_2} + \frac{\varepsilon_2 p_2}{1 + \alpha_2} \cdot \frac{R_1 \beta_2 - c_1 R_2}{\beta_1 \beta_2 - c_1 c_2} \quad (5.8)$$

This means N_4 will determine if E_{14} is stable, which implies that N_4 has a top-down, helpful effect on N_1 and N_2 , and a negative effect on N_3 . N_1 and N_2 coexist in the competition subsystem with weak competition, but N_4 is required in order for N_1 and N_2 to coexist in the full model. If (3.35) is violated, one should expect N_3 to persist, which was discussed in Chapter 3.

Another relationship worth considering is the effect of \bar{E}_2 on E_8 . \bar{E}_2 is stable when the

condition given in (3.35):

$$\frac{\gamma_3}{1 + \frac{B\alpha_3}{c_4}} < D_3 + \frac{p_3B}{c_4(1 + \alpha_3)} \quad (5.9)$$

holds. E_8 is stable when \hat{E}_2 is stable in the competition model, and when the second condition in (4.55):

$$\frac{\gamma_3}{1 + \frac{\alpha_3B}{c_4}} + \frac{\varepsilon_2 p_2 R_2}{c_2(1 + \alpha_2)} < D_3 + \frac{p_3B}{c_4(1 + \alpha_3)} \quad (5.10)$$

holds. If (3.35) holds, then the second condition in (4.55) holds if:

$$0 \leq \frac{\varepsilon_2 p_2 R_2}{c_2(1 + \alpha_2)} < D_3 + \frac{p_3B}{c_4(1 + \alpha_3)} - \frac{\gamma_3}{1 + \frac{\alpha_3B}{c_4}} \quad (5.11)$$

is true. If not, E_8 is unstable. If the second part of (4.55) holds, then (3.35) since:

$$\frac{\gamma_3}{1 + \frac{\alpha_3B}{c_4}} \leq \frac{\gamma_3}{1 + \frac{\alpha_3B}{c_4}} + \frac{\varepsilon_2 p_2 R_2}{c_2(1 + \alpha_2)}. \quad (5.12)$$

This means that N_4 will determine if N_2 is stable in E_8 . This suggests that N_4 has a top-down helpful effect on N_2 and a negative effect on N_3 .

Another relationship worth considering is the effect of \bar{E}_2 on E_9 . \bar{E}_2 is stable when the condition given in (3.35):

$$\frac{\gamma_3}{1 + \frac{B\alpha_3}{c_4}} < D_3 + \frac{p_3B}{c_4(1 + \alpha_3)} \quad (5.13)$$

holds. E_9 is stable when \hat{E}_1 is stable in the competition subsystem, and when the second condition in (4.58):

$$\frac{\gamma_3}{1 + \frac{\alpha_3B}{c_4}} + \frac{\varepsilon_1 p_1 R_1}{c_1(1 + \alpha_1)} < D_3 + \frac{p_3B}{c_4(1 + \alpha_3)} \quad (5.14)$$

holds. If (3.35) holds, then the second condition in (4.58) holds if:

$$0 \leq \frac{\varepsilon_1 p_1 R_1}{c_1(1 + \alpha_1)} < D_3 + \frac{p_3B}{c_4(1 + \alpha_3)} - \frac{\gamma_3}{1 + \frac{\alpha_3B}{c_4}} \quad (5.15)$$

is true. If not, E_9 is unstable. If the second part of (4.58) holds, then (3.35) since:

$$\frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} \leq \frac{\gamma_3}{1 + \frac{\alpha_3 B}{c_4}} + \frac{\varepsilon_1 p_1 R_1}{c_1(1 + \alpha_1)}. \quad (5.16)$$

This means that N_4 will determine if N_1 is stable in E_9 . This suggests that N_4 has a top-down helpful effect on N_1 and a negative effect on N_3 .

5.3 Conclusion

In this work, we studied the dynamics of (1.11). We considered how competition and the fear effect could affect the long-term dynamics of a food chain model. In Chapter 3, we looked at the dynamics of the competition subsystem and the predator-prey subsystem.

We showed that in the competition subsystem that N_1 and N_2 could invade each other successfully under certain conditions. The coexistence of N_1 and N_2 required weak competition to come into play. In the predator-prey subsystem, we showed that N_4 could successfully invade N_3 under certain conditions, but N_3 was unable to invade N_4 . We showed that the coexistence equilibrium must be globally asymptotically stable and must become stable if the invasion equilibrium loses stability, provided the coexistence equilibrium exists. We investigated impact of the fear effect on making the coexistence equilibrium becoming stable.

For the full model, we considered the stability and existence of the equilibrium points. We showed there existed some relationships between some of the results covered in Chapter 3 and the full model. These were discussed in Chapter 5. We showed that it is impossible for N_1 and N_2 to invade N_3 , N_4 and coexist. This implies that the competition component can have a detrimental effect. We also showed that the presence of N_4 helped N_1 and N_2 to coexist which led to the invasion of N_3 . The presence of N_4 was also needed if N_1 or N_2

wanted to invade the other in the full model, at the expense of N_3 . The fear response played a role in this as seen in many of the discussed results in the stability criteria.

Some further work might consider looking at potential bifurcations that may occur, as well as considering E_{15} in-depth.

References

- [1] Abakuks, A. (1982), *The Mathematical Theory of the Dynamics of Biological Populations II*. Journal of the Royal Statistical Society: Series A (General), 145: 512-512. <https://doi.org/10.2307/2982110>
- [2] Roger Arditi and Lev R. Ginzburg. Coupling in predator-prey dynamics: Ratio-dependence. *Journal of Theoretical Biology*, 139(3):311–326, 1989.
- [3] Eric L. Berlow, Anje-Margiet Neutel, Joel E. Cohen, Peter C. De Ruiter, Bo Ebenman, Mark Emmerson, Jeremy W. Fox, Vincent A. A. Jansen, J. Iwan Jones, Giorgos D. Kokkoris, Dmitrii O. Logofet, Alan J. McKane, Jose M. Montoya, and Owen Petchey. Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology*, 73(3):585–598, 2004.
- [4] Brauer, F. and Castillo-Chavez, C. (2012) *Mathematical Models in Population Biology and Epidemiology, Volume 2*. Springer, Berlin. <https://doi.org/10.1007/978-1-4614-1686-9>
- [5] N.F. Britton. *Essential Mathematical Biology*. Springer Undergraduate Mathematics Series. Springer London, 2012.
- [6] Robert Stephen Cantrell, Chris Cosner, On the Dynamics of Predator–Prey Models with the Beddington–DeAngelis Functional Response, *Journal of Mathematical Anal-*

- ysis and Applications*, Volume 257, Issue 1, 2001, pp. 206-222, ISSN 0022-247X, <https://doi.org/10.1006/jmaa.2000.7343>.
- [7] Pingping Cong, Meng Fan, and Xingfu Zou. Dynamics of a three-species food chain model with fear effect. *Communications in Nonlinear Science and Numerical Simulation*, 99:105809, 2021.
- [8] (1982), *Deterministic mathematical models in population ecology*. By H.I.Freedman, The University of Alberta. Pure and Applied Mathematics: A series of monographs and textbooks, volume 57. Marcel Dekker, Inc., New York, 1980. *Can J Statistics*, 10: 315-315. <https://doi.org/10.2307/3556198>
- [9] Morris W Hirsch, Systems of differential equations that are competitive or cooperative. V. Convergence in 3-dimensional systems, *Journal of Differential Equations*, Volume 80, Issue 1, 1989, Pages 94-106, ISSN 0022-0396, [https://doi.org/10.1016/0022-0396\(89\)90097-1](https://doi.org/10.1016/0022-0396(89)90097-1).
- [10] Holling CS. Some Characteristics of Simple Types of Predation and Parasitism. *The Canadian Entomologist*. 1959;91(7):385-398. doi:10.4039/Ent91385-7
- [11] Holt, R. D., & Polis, G. A. (1997). A Theoretical Framework for Intraguild Predation. *The American Naturalist*, 149(4), 745–764. <http://www.jstor.org/stable/2463547>
- [12] Sharon Kingsland. Alfred j. lotka and the origins of theoretical population ecology. *Proceedings of the National Academy of Sciences of the United States of America*, 112(31):9493–9495, 2015.
- [13] Alfred J. Lotka. Analytical note on certain rhythmic relations in organic systems. *Proceedings of the National Academy of Sciences of the United States of America*, 6(7):410–415, 1920.

- [14] Shao, Y.; Kong, W. A Predator–Prey Model with Beddington–DeAngelis Functional Response and Multiple Delays in Deterministic and Stochastic Environments. *Mathematics* 2022, 10, 3378. <https://doi.org/10.3390/math1018337>
- [15] Shu, H., Hu, X., Wang, L. et al. Delay induced stability switch, multitype bistability and chaos in an intraguild predation model. *J. Math. Biol.* 71, 1269–1298 (2015). <https://doi.org/10.1007/s00285-015-0857-4>
- [16] Smale, S. On the differential equations of species in competition. *J. Math. Biology* 3, 5–7 (1976). <https://doi.org/10.1007/BF00307854>
- [17] Sommers P, Chesson P. Effects of Predator Avoidance Behavior on the Coexistence of Competing Prey. *Am Nat.* 2019 May;193(5):E132-E148. doi: 10.1086/701780. Epub 2019 Mar 7. PMID: 31002576.
- [18] Justin P. Suraci, Michael Clinchy, Lawrence M. Dill, Devin Roberts, and Liana Y. Zanette. Fear of large carnivores causes a trophic cascade. *Nature Communications*, 7(1):10698, Feb 2016.
- [19] Wang, Xiaoying, "Studying Both Direct and Indirect Effects in Predator-Prey Interaction" (2016). *Electronic Thesis and Dissertation Repository*. 3957. <https://ir.lib.uwo.ca/etd/3957>
- [20] Wang, X., Zanette, L. & Zou, X. Modelling the fear effect in predator–prey interactions. *J. Math. Biol.* 73, 1179–1204 (2016). <https://doi.org/10.1007/s00285-016-0989-1>
- [21] Yang Wang Xingfu Zou. Evolution of anti-predation response of prey in 1 predator-prey interactions.
- [22] Yang Wang Xingfu Zou. On mechanisms of trophic cascade caused by anti-predation response in food chain systems. *Mathematics in Applied Sciences and Engineering*, 1:pp. 181–206, 2021.

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