

MATHEMATICAL BIOLOGY: ANALYSIS OF PREDATOR-PREY
SYSTEMS IN PATCHY ENVIRONMENT INFLUENCED BY THE FEAR
EFFECT

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Abstract

Mathematical Biology: Analysis of Predator-Prey Systems in
Patchy Environment Influenced by the Fear Effect

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This thesis is focused on studying the population dynamics of a predator-prey system in a patchy environment, taking anti-predation responses into consideration.

Firstly, we conduct mathematical analysis on the equilibrium solutions of the system. Using techniques from calculus we show that particular steady state solutions exist when the parameters of the system meet certain criteria. We then show that a further set of conditions leads to the local stability of these solutions.

The second step is to extend the existing mathematical analysis by way of numerical simulations. We use octave to confirm the previous results, as well as to show that more complicated dynamics can exist, such as stable oscillations. We consider more complex and meaningful functions for nonlinear dispersal between patches and nonlinear predation, and show that the proposed model exhibits behaviours we expect to see in a population model.

Keywords: Predator-prey, population dynamics, anti-predation response, patch model, dispersal, asymptotic stability

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Chapter 1

Introduction

The goal of this thesis is to extend previous research in the population dynamics of predator-prey patch models [20, 10, 11] to account for the fear effect [24, 19, 22, 28, 27]. The following is a literature review, establishing the relevant research that has been done in this field so far.

1.1 Single Species Population Dynamics

People have been interested in studying populations for quite some time. The natural place to begin is to start by considering a population in isolation. Clearly the real world is much more complicated, but it's good to start simple and understand the simple case before trying to match the complexity of a real biological system. It also seems simpler to begin with (although may be more complex to analyze in detail) a discrete time model.

Such a model can be thought of as an insect or fish population that have one breeding season per year, and thus have clear cut generations. In such a model we would expect the population in generation $n+1$ to increase from generation n by the amount of births that occurred, which we would expect to be determined by how many adults there are to give birth, thus for a population of size N we can say we might see an increase in the population by bN . We also expect there to be some deaths between time n and $n + 1$, so the population should decrease by dN . This gives us the Malthusian equation in discrete time [1, 18]: $N_{n+1} = (1 + b - d)N_n = \lambda N_n$. This is

simply a linear equation, and doesn't match very well with reality.

The discrete case can be useful, but for this paper, we really would like to consider continuous time. In this case, instead of considering the number of births and deaths b and d respectively between generations, we consider the birth rate and death rate over the next small interval of time δt . In this case we get the equation $N(t + \delta t) = N(t) + bN(t)\delta t - dN(t)\delta t$ which, when we consider $\delta t \rightarrow 0$ simplifies to the Malthusian equation in continuous time [1, 18]: $\frac{dN}{dt} = (b - d)N$. This is better, but still too simple. In either case of the Malthusian equation, if $b - d < 0$ then the population goes extinct, which may be reasonable, but if $b - d > 0$ then the population tends to infinity, which is clearly not realistic.

To account for this we assume that there is some limiting amount of resources in the species environment, which we call the carrying capacity. Mathematically, this looks like $\frac{dN}{dt} = (b - d)N(1 - \frac{N}{K}) = bN - dN - aN^2$ where K (or $a = \frac{b-d}{K}$) denotes the carrying capacity. For $N < K$ the new term $(1 - \frac{N}{K})$ is positive, so that the population still has room to grow, but if $N > K$ then the population size is too large and thus must decrease, as shown by this term being negative. This function, called the logistic equation [1, 18], isn't the only function that matches the s-shaped empirical data as well as it does, but it is mathematically the simplest.

1.2 Predator-Prey Systems

We now have a pretty acceptable equation describing the population of a single species, but there is a major element of real life that hasn't been incorporated yet. In the real world, species interact with each other and, more specifically, hunt each other. To model predation, we make a few assumptions regarding the way a predator interacts with its prey. These assumptions are as follows: the prey is limited only by the predator, the per capita rate at which predation occurs (the functional response) is linear, predators do not interfere with each other, the predator goes extinct in the absence of the prey, and every death of the prey contributes the same amount of growth to the predator. This collection of assumptions give us the Lotka-Volterra model

[1, 18, 14, 15, 25, 26].

$$\begin{aligned}\frac{du}{dt} &= \alpha u - \gamma uv \\ \frac{dv}{dt} &= e\gamma uv - mv\end{aligned}\tag{1.1}$$

This model does a decent job of describing the things that it was made to describe, but this system is structurally unstable. That is, if we make some small change the behaviour we see can change dramatically. This is the result of our previous assumptions not matching very well with reality. However, we already discussed the ways that we would make a population model more realistic in Section 1.1, so now we apply those principles to this model. These modifications, in addition to assuming the functional response is a non-linear function of u , gives us the Rosenzweig-MacArthur model [1, 18, 23].

$$\begin{aligned}\frac{du}{dt} &= bu - du - au^2 - \Phi(u)v \\ \frac{dv}{dt} &= e\Phi(u)v - mv\end{aligned}\tag{1.2}$$

Now things are starting to look quite good, but if it's not linear, then what sort of function should the functional response be? For this we have the Holling type II functional response [1, 18, 6, 7, 8], which often matches very well with empirical data. There are also, less commonly seen, Holling types I, III, and IV functional response equations for other possibilities we see in the real world.

The type II function is given by $N = su(T - hN)$. The motivation for this equation is an assumption that the number of prey caught is density dependent in addition to being proportional to the amount of time spent searching. The predator will also need to spend time handling the prey once caught, thus in our equation N is the number of prey caught per time period T , s is the effective search rate and h is the handling time. We want to include this function in our model as the average number of prey caught N per time period T , so we rearrange to find that $\Phi(u) = \frac{N}{T} = \frac{su}{1+shu}$. Using this function in the Rosenzweig-MacArthur model gives us the following model.

$$\begin{aligned}\frac{du}{dt} &= bu - du - au^2 - \frac{su}{1 + shu}v \\ \frac{dv}{dt} &= \frac{esu}{1 + shu}v - mv\end{aligned}\tag{1.3}$$

In this way we have an increasingly more realistic model, but there are still more elements that we must consider.

1.3 The Fear Effect

All of the models that we have considered so far have made the assumption that the only way that a predator can interact with and change the population of the prey is through the direct effect of predation. However, it is becoming increasingly popular to consider the possibility of an indirect interaction that the predator can impose on the prey.

The supposition is that if the prey sense predators nearby then the anti-predation response has significant drawbacks that reduce their growth rate. The existence of this so called fear effect was studied by Zanette et al. [28] on a population of song sparrows. In this study the song sparrows were protected from all predation so that only the fear effect would influence the population. Meanwhile, predator sounds were played for some groups, while only non-predator sounds were played for the other groups. Zanette et al. found that the populations that were subjected to predator sounds experienced a 40% reduction in offspring compared to the control group.

There were notable ways in which it was observed how the fear effect reduces the populations growth rate in the case of song sparrows, of course these details will likely be different in a different species, but we hypothesize that there is some manifestation of the fear effect in many more species than just the song sparrows. These behaviours were that fewer eggs were laid by the sparrows, fewer of those eggs proportionally hatched, and more hatched nestlings died before reaching adulthood. Since we now have a study that confirms the existence of this effect, mathematicians have begun incorporating it into their current models. The 2016 paper

by Wang et al. [27] applies the fear effect to a predator-prey model following logistic growth.

$$\begin{aligned}\frac{du}{dt} &= f(k, v)ru - du - au^2 - g(u)v \\ \frac{dv}{dt} &= cg(u)v - mv\end{aligned}\tag{1.4}$$

It can be seen clearly that this is the Rosenzweig-MacArthur model except for the inclusion of the function $f(k, v)$ modifying the growth rate r of the prey. This is a function of the predator population v ; and k , which is the term representing the intensity of the fear effect. The form for f proposed by Wang et al. is $f(k, v) = \frac{1}{1+kv}$. In this way, when $k = 0$ the denominator is equal to one, and the function representing the fear effect vanishes, but as long as $k > 0$ an increase in either of the population size of the predator or the intensity of the fear effect (the value of k) has the effect of scaling down the growth rate r of the prey. Other functions that have been considered for are $f(k, v) = e^{-kv}$, or $f(k_1, k_2, v) = \frac{1}{1+k_1v+k_2v^2}$, but in this paper we focus on the simpler function.

1.4 Metapopulations

There are some circumstances where the Rosenzweig-MacArthur model must be complicated in a different way than the fear effect. In all of the models we have so far discussed, we have implicitly assumed that the environment that the populations inhabit is spatially homogeneous. That is, there is no notable difference between different patches of habitat, and the populations can move freely and easily throughout the entirety of the patch.

However, there are some environments, such as archipelagos, where movement between patches, while still possible, is not as fluid. In this case a species can migrate between patches, and we can see extinction and recolonization happening among the patches, so that the species survives by constantly migrating between patches (islands in the archipelago example). To study this, it is generally easier to model the dynamics of colonized versus extinct patches, rather than the population size of the species [1, 18, 13, 16].

If we consider there to be K habitable patches, then we can assume that a proportion $p(t)$ of the patches are colonized at time t . Then the probability of a patch becoming extinct over some short time interval δt is $e\delta t$, and so the average proportion of sites that cease to be colonized over this time interval is $ep(t)\delta t$. Similarly, we can assume that the probability that a patch that is uncolonized at time t becomes colonized over a short time interval δt is $cp(t)\delta t$. Only uncolonized patches can become colonized, so the average number of patches that become colonized in the interval δt is $cp(t)(1 - p(t))\delta t$. Thus, if we consider smaller and smaller time intervals by taking the limit as $\delta t \rightarrow 0$, we get the ODE

$$\frac{dp}{dt} = cp(1 - p) - ep.$$

This model describes a single species inhabiting a patchy environment, but we are interested in models that include a predator and a prey. In a 1950s study, Huffaker [9] showed that a predator-prey system in a patchy environment can allow the persistence of the two species, when in a spatially homogeneous environment the system quickly tended towards extinction. In this study, Huffaker designed an environment of rubber balls and oranges and introduced an herbivorous mite species and a predatory mite species. When fewer oranges were included, and so the environment is more similar to spatially homogeneous, the herbivorous mites were hunted to extinction, immediately followed by the predatory mites. However, if more oranges were included, so that the environment is less spatially homogeneous, the species persisted.

To introduce a predator to our patch model, we first make some observations. If a predator exists in a patch, with no prey, then the predator must either go extinct or migrate away from that patch, so we can assume that there are no patches inhabited only by the predator. The reverse is not true, a prey species can inhabit a patch with no predator species. Therefore we have three possible states: extinct, inhabited only by prey, or inhabited by both prey and predator. We denote these three states as 0, 1, and 2 respectively. Denote the colonization rate of the prey species as c_1 , the colonization rate of the predator species as c_2 , the extinction rate of a patch in state 1 as e_1 , the extinction rate of a patch in state 2 as e_2 , the proportion of sites

in state 1 as p_1 , and the proportion of sites in state 2 as p_2 .

The only way for a patch that isn't in state 1 to become state 1 is for it to originally be extinct, and become colonized by a patch that has a prey species on it, (ie is in state 1 or 2). Thus the increase in the number of patches in state 1 is given by $c_1(1 - p_1 - p_2)(p_1 + p_2)$. A patch in state 1 can stop being in state 1 either by the prey going extinct so that it becomes state 0, or by being colonized by a predator so that it becomes state 2. Thus the decrease in the number of patches in state 1 is given by $c_2p_1p_2 + e_1p_1$. The only way for a patch to become state 2 is for it to already be in state 1 and be colonized by a predator, and the only way for it to stop being state 2 is for the species inhabiting it to go extinct. Thus the increase in the amount of patches in state 2 is given by $c_2p_1p_2$, and the decrease is given by e_2p_2 . This gives us the patch model with predation.

$$\begin{aligned}\frac{dp_1}{dt} &= c_1(1 - p_1 - p_2)(p_1 + p_2) - c_2p_1p_2 - e_1p_1 \\ \frac{dp_2}{dt} &= c_2p_1p_2 - e_2p_2\end{aligned}\tag{1.5}$$

These models are a convenient way to simplify the study of a patchy environment as opposed to working with a population model. Unfortunately, we are interested in studying the consequences of the fear effect in such an environment, which necessitates a population model, such as those in [12, 2, 3, 17]. In order to study a patchy environment while continuing to model the population of the species, Li et al. [12] consider a species u in patch i to be distinct from a species u in patch j . Therefore we define species u in patch i as u_i .

In this paper, a two patch system is considered, and migration between the two patches implies an additional two terms to each equation. Since we consider a species in patch 1 to be distinct from a species in patch 2, then the immigration from patch 2 to patch 1 results in a positive change in the population of the species in patch 1, whereas emigration from patch 1 to patch 2 produces a decrease in the population of patch 1. The reverse is true for patch 2. Therefore, Li et al. include the migration functions $m(\alpha, v_1)$, and $m(\alpha, v_2)$, where α represents the preys vigilance level, and v_i represents the population of the predator in patch i .

These authors also consider the growth rate function (which includes the fear effect) and the functional response function to be functions of α and v_i . This leads them to this model.

$$\begin{aligned}\frac{du_1}{dt} &= b_1(\alpha, v_1)u_1 - d_1 - au_1^2 - c(\alpha, v_1)u_1v_1 - m(\alpha, v_1)u_1 + m(\alpha, v_2)u_2 \\ \frac{du_2}{dt} &= b_2(\alpha, v_2)u_2 - d_2 - au_2^2 - c(\alpha, v_2)u_2v_2 + m(\alpha, v_1)u_1 - m(\alpha, v_2)u_2\end{aligned}\tag{1.6}$$

In this way, they study the population dynamics of the prey species in a patchy environment, while treating the predator population as a parameter, rather than a state variable as we see in the previous models.

Chapter 2

Model Formulation

Our work is motivated by [12], where the authors studied a two-patch predator-prey model with the fear effect. In [12], the authors proposed a model where a single prey species inhabits two different patches and can move without obstacles between patches. The authors assume that a single predator species lives on two different patches as well but consider a simplified scenario where the predator population density stays as constant. The authors considered that the anti-predator behaviors of the prey reduce the offspring reproduction success in the prey and also reduce the prey dispersal between patches because for some species, the prey takes refuge when perceiving predation risks and avoids movement between patches.

In our work, we relax the assumption that the predator population density in both patches remains constant but consider that the predator population may change with time. This is reasonable in particular because we model a specialist predator in our two-patch model. Here a specialist predator is a predator whose diet focuses on certain prey species. As a consequence, the abundance of the food resource will largely impact the predator population density.

Moreover, we study a different scenario compared to the work in [12]. We consider a two-patch problem, where in particular one patch is a high-quality patch, where the living conditions are optimal and favor the population growth for both the prey and the predator. However, the other patch is a low-quality patch, where the living conditions are less-favorable

and provide only limited support for population growth. Without predation, prey in general would inhabit a high-quality patch as long as the resource on the patch is sufficient. However, prey may move from the high-quality patch to the low-quality patch when prey perceive predation risks. For example, birds, such as song sparrows, may relocate to areas with denser shrubs where there is less presence of the predator. More importantly, birds anti-predation measures do not involve staying still and hiding from the predators. Instead, the birds flee and so the anti-predator defense of the prey facilitates the movement of the prey between patches.

Based on the aforementioned considerations, we propose the following model

$$\begin{aligned}
\frac{du_1}{dt} &= \frac{r_1 u_1}{1 + k_1 v_1} - d_1 u_1 - a_1 u_1^2 - G_1(u_1) v_1 - C_{12}(k_1, v_1) u_1 + C_{21}(k_2, v_2) u_2, \\
\frac{du_2}{dt} &= \frac{r_2 u_2}{1 + k_2 v_2} - d_2 u_2 - a_2 u_2^2 - G_2(u_2) v_2 + C_{12}(k_1, v_1) u_1 - C_{21}(k_2, v_2) u_2, \\
\frac{dv_1}{dt} &= e_1 G_1(u_1) v_1 - m_1 v_1 - p_{12} v_1 + p_{21} v_2, \\
\frac{dv_2}{dt} &= e_2 G_2(u_2) v_2 - m_2 v_2 + p_{12} v_1 - p_{21} v_2.
\end{aligned} \tag{2.1}$$

In model (2.1), we consider two species: the prey species u and the predator species v . We also consider two patches, indicated by subscripts 1 and 2, so that u_1 represents the prey population density in patch 1, and u_2 represents the prey population density in patch 2. Similarly, in model (2.1), v_1 represents the predator population density in patch 1 and v_2 represents the predator population density in patch 2.

The parameter r_i represents the offspring production rate of the prey in patch i , d_i represents the death rate by natural causes of the prey in patch i , a_i represents the intraspecific competition for the prey on each individual patch, e_i represents the biomass conversion from the prey to the predator in patch i , and m_i represents the death rate by natural causes of the predator in patch i .

In model (2.1), the parameter k_i represents the fear effect. Here, the formulation of the fear effect term follows the same formulation in [27]. In [27], the formulation of the fear effect term is based on the biological evidence that the prey perceives predation risks nearby and

takes avoidance behaviors for their own survival. As a consequence, the reproduction success of the prey is significantly reduced. More precisely, k_i represents the level of anti-predator defense of the prey. If k_i is larger, the prey in patch i is more likely to take avoidance behaviors when perceiving predation risks. The predation risks are then largely related to the population density of the predator. If there are more predators in patch i , then the prey in the same patch is more likely to perceive the presence of the predator nearby.

In model (2.1), G_i represents the functional response of the predator in patch i . Widely accepted functional responses including the Holling-type functional responses are prey-dependent ones. For example, if we choose the linear/Holling type I functional response, then we have

$$G_i(u_i) = g_i u_i,$$

where g_i represents the successful attack of the prey by the predator in patch i [1, 18]. The well-known Holling type II functional response reads

$$G_i(u_i) = \frac{g_i u_i}{1 + g_i h_i u_i},$$

where g_i represents the successful attacking rate of the predator on the prey in patch i and h_i represents the handling of the prey by the predator [6, 7]. In the analysis of Chapter 4, to have mathematically tractable results, we choose the linear functional response $G_i(u_i) = g_i u_i$. In Chapter 5, we also explore other possible dynamics induced by the Holling type II functional response by using numerical simulations.

Finally, in (2.1), C_{ij} represents the dispersal of the prey in patch i to patch j . In general, the dispersal rate depends on how strong the anti-predator defense of the prey is on patch i and also on the predator's population density on patch i . For simplicity, for the analysis below, we adopt the constant dispersal rate instead, i.e. $C_{12}(k_1, v_1) = c_{12}$ and $C_{21}(k_2, v_2) = c_{21}$. Here, the dispersal rates of the prey between patches may be different. Similarly, p_{ij} represents the dispersal of the predator in patch i to patch j and are constants.

Chapter 3

Preliminary Analysis

Before we proceed with a more in-depth analysis, we prove that the proposed model (2.1) is valid. To this end, we will show the positivity and the boundedness for the model.

3.1 Positivity

First let us consider u_1 . The rate of change in prey's population density in patch 1 is given by

$$\frac{du_1}{dt} = \frac{r_1 u_1}{1 + k_1 v_1} - d_1 u_1 - a_1 u_1^2 - G_1(u_1) v_1 - C_{12} u_1 + C_{21} u_2$$

We can then manipulate the equation as following

$$\begin{aligned} \frac{du_1}{u_1} &= \left(\frac{r_1}{1 + k_1 v_1} - d_1 - a_1 u_1 - \frac{G_1(u_1) v_1}{u_1} - \frac{C_{12} u_1}{u_1} + \frac{C_{21} u_2}{u_1} \right) dt, \\ \int \frac{du_1}{u_1} &= \int \left(\frac{r_1}{1 + k_1 v_1} - d_1 - a_1 u_1 - \frac{G_1(u_1) v_1}{u_1} - \frac{C_{12} u_1}{u_1} + \frac{C_{21} u_2}{u_1} \right) dt, \\ \ln |u_1(t)| &= \int \left(\frac{r_1}{1 + k_1 v_1} - d_1 - a_1 u_1 - \frac{G_1(u_1) v_1}{u_1} - \frac{C_{12} u_1}{u_1} + \frac{C_{21} u_2}{u_1} \right) dt + C, \\ |u_1(t)| &= \exp \left(\int \left(\frac{r_1}{1 + k_1 v_1} - d_1 - a_1 u_1 - \frac{G_1(u_1) v_1}{u_1} - \frac{C_{12} u_1}{u_1} + \frac{C_{21} u_2}{u_1} \right) dt + C \right), \end{aligned}$$

$$u_1(t) = \exp \int \left(\frac{r_1}{1 + k_1 v_1} - d_1 - a_1 u_1 - \frac{G_1(u_1) v_1}{u_1} - \frac{C_{12} u_1}{u_1} + \frac{C_{21} u_2}{u_1} \right) dt \cdot (\pm e^C),$$

where C is an arbitrary constant.

Because C is an arbitrary constant, for notational convenience, we denote $\pm e^C = \beta$, where β is an arbitrary constant. Next, we show that the constant β can be determined by the initial population density. Followed by the analysis above, we have

$$u_1(t) = \beta \exp \int \left(\frac{r_1}{1 + k_1 v_1} - d_1 - a_1 u_1 - \frac{G_1(u_1) v_1}{u_1} - \frac{C_{12} u_1}{u_1} + \frac{C_{21} u_2}{u_1} \right) dt \quad (3.1)$$

Let $u_1(0)$ be the initial population density. For biologically reasonable assumptions, one must have $u_1(0) \geq 0$. Fix $t = 0$ in (3.1) and we then obtain $u_1(0) = \beta$. This altogether leads to

$$u_1(t) = u_1(0) \exp \int \left(\frac{r_1}{1 + k_1 v_1} - d_1 - a_1 u_1 - \frac{G_1(u_1) v_1}{u_1} - \frac{C_{12} u_1}{u_1} + \frac{C_{21} u_2}{u_1} \right) dt.$$

Because the exponential function is always positive and the initial population density $u_1(0)$ is always non-negative, the population density $u_1(t)$ stays non-negative for all time. Moreover, $u_1(t) = 0$ only if the initial population density $u_1(0) = 0$. Hence, the positivity of u_1 holds.

The same approach can be used to prove the positivity for each of the state variables u_2 , v_1 , v_2 . Because the proofs are similar, we omit the proofs here. Also, note that the proof of the positivity is valid for general functional response G_i and general dispersal function C_{ij} .

3.2 Boundedness

Since we have already proven that each state variable is nonnegative for all time, then if we show that the sum of all state variables is bounded above, it must follow that each state variable is bounded above. Firstly, we define $\bar{e} = \max\{e_1, e_2\}$ and $\bar{m} = \min\{m_1, m_2\}$. This allows us to

define a new variable $G = \bar{e}(u_1 + u_2) + v_1 + v_2$.

Then we can take the derivative of the new variable G with respect to time, and we obtain

$$\begin{aligned} \frac{dG}{dt} &= \bar{e}\left(\frac{du_1}{dt} + \frac{du_2}{dt}\right) + \frac{dv_1}{dt} + \frac{dv_2}{dt} \\ &= \bar{e}\left[\frac{r_1u_1}{1+k_1v_1} - d_1u_1 - a_1u_1^2 - G_1(u_1)v_1 - C_{12}(k_1, v_1)u_1 + C_{21}(k_2, v_2)u_2\right. \\ &\quad \left. + \frac{r_2u_2}{1+k_2v_2} - d_2u_2 - a_2u_2^2 - G_2(u_2)v_2 + C_{12}(k_1, v_1)u_1 - C_{21}(k_2, v_2)u_2\right] \\ &\quad + e_1G_1(u_1)v_1 - m_1v_1 - p_{12}v_1 + p_{21}v_2 + e_2G_2(u_2)v_2 - m_2v_2 + p_{12}v_1 - p_{21}v_2. \end{aligned}$$

The dispersal terms for both the prey and the predator are cancelled out. Therefore, we obtain

$$\begin{aligned} \frac{dG}{dt} &= \bar{e}\left[\frac{r_1u_1}{1+k_1v_1} - d_1u_1 - a_1u_1^2 - G_1(u_1)v_1\right. \\ &\quad \left. + \frac{r_2u_2}{1+k_2v_2} - d_2u_2 - a_2u_2^2 - G_2(u_2)v_2\right] \\ &\quad + e_1G_1(u_1)v_1 - m_1v_1 + e_2G_2(u_2)v_2 - m_2v_2. \end{aligned}$$

Since $\bar{e} = \max\{e_1, e_2\}$, we can substitute e_1 and e_2 with \bar{e} to get an upper bound of dG/dt where

$$\begin{aligned} \frac{dG}{dt} &\leq \bar{e}\left[\frac{r_1u_1}{1+k_1v_1} - d_1u_1 - a_1u_1^2 - G_1(u_1)v_1\right. \\ &\quad \left. + \frac{r_2u_2}{1+k_2v_2} - d_2u_2 - a_2u_2^2 - G_2(u_2)v_2\right] \\ &\quad + \bar{e}[G_1(u_1)v_1 + G_2(u_2)v_2] - m_1v_1 - m_2v_2. \end{aligned}$$

This allows us to cancel out the predation terms so that

$$\frac{dG}{dt} \leq \bar{e}\left[\frac{r_1u_1}{1+k_1v_1} - d_1u_1 - a_1u_1^2 + \frac{r_2u_2}{1+k_2v_2} - d_2u_2 - a_2u_2^2\right] - m_1v_1 - m_2v_2.$$

Because we have proved the positivity of the state variables v_1, v_2 and the parameters k_1, k_2

are positive as well, each of the denominators in the preceding fractions are greater than or equal to one. Therefore, since $\frac{dG}{dt}$ is lesser than the current version, it must also be lesser than the same equation in the absence of these denominators. Also, by replacing m_1, m_2 with $\bar{m} = \min\{m_1, m_2\}$, we obtain

$$\frac{dG}{dt} \leq \bar{e} \left[r_1 u_1 - d_1 u_1 - a_1 u_1^2 + r_2 u_2 - d_2 u_2 - a_2 u_2^2 \right] - \bar{m} v_1 - \bar{m} v_2.$$

The above inequality is equivalent to

$$\frac{dG}{dt} \leq \bar{e} \left[(r_1 + \bar{m})u_1 - d_1 u_1 - a_1 u_1^2 + (r_2 + \bar{m})u_2 - d_2 u_2 - a_2 u_2^2 \right] - \bar{m} G(t)$$

Let

$$F_1(u_1) = (r_1 + \bar{m})u_1 - d_1 u_1 - a_1 u_1^2 \quad \text{and} \quad F_2(u_2) = (r_2 + \bar{m})u_2 - d_2 u_2 - a_2 u_2^2.$$

Each function $F_i(u_i)$ is a quadratic function of a single variable. Moreover, the leading coefficient of the quadratic function is negative, which leads to the parabola to be facing downward. Each function $F_i(u_i)$ has two zeros $u_i = 0$ and $u_i = (r_i + \bar{m} - d_i)/a_i$. Therefore, we can find the maximum of each function $F_i(u_i)$ where

$$F_1(u_1) \leq \frac{(r_1 + \bar{m} - d_1)^2}{4a_1} \quad \text{and} \quad F_2(u_2) \leq \frac{(r_2 + \bar{m} - d_2)^2}{4a_2}.$$

Let

$$\eta = \bar{e} \left[\frac{(r_1 + \bar{m} - d_1)^2}{4a_1} + \frac{(r_2 + \bar{m} - d_2)^2}{4a_2} \right].$$

Then we obtain

$$\frac{dG}{dt} \leq \eta - \bar{m} G$$

Let's consider the extreme case where

$$\begin{aligned}\frac{dG}{dt} &= \eta - \bar{m}G, \\ \frac{dG}{\eta - \bar{m}G} &= dt, \\ \int \frac{dG}{\eta - \bar{m}G} &= \int dt, \\ \frac{-\ln|\eta - \bar{m}G|}{\bar{m}} &= t + C_1, \\ \ln|\eta - \bar{m}G| &= -\bar{m}t - \bar{m}C_1,\end{aligned}$$

where C_1 is an arbitrary constant. Let $-\bar{m}C_1 = C_2$, where C_2 is also an arbitrary constant. This gives

$$\begin{aligned}\ln|\eta - \bar{m}G| &= -\bar{m}t + C_2, \\ |\eta - \bar{m}G| &= e^{-\bar{m}t + C_2}, \\ |\eta - \bar{m}G| &= e^{-\bar{m}t} \cdot e^{C_2}, \\ \eta - \bar{m}G &= (\pm e^{C_2}) \cdot e^{-\bar{m}t}.\end{aligned}$$

Now we let $\pm e^{C_2} = C$, where C is an arbitrary constant to obtain

$$\begin{aligned}\eta - \bar{m}G &= Ce^{-\bar{m}t} \\ G &= \frac{\eta - Ce^{-\bar{m}t}}{\bar{m}} \\ G &= \frac{\eta}{\bar{m}} - \frac{Ce^{-\bar{m}t}}{\bar{m}}\end{aligned}\tag{3.2}$$

It is easy to see that $\lim_{t \rightarrow \infty} \frac{Ce^{-\bar{m}t}}{\bar{m}} = 0$. It follows that $\limsup_{t \rightarrow \infty} G(t) \leq \frac{\eta}{\bar{m}}$ by the comparison principle. Since G is the sum of all populations, up to a constant stretch factor, and G is clearly bounded above by the comparison principle, together with the positivity of all state variables, it must be true that each population is also bounded above.

Chapter 4

Equilibrium Analysis

In this chapter, we calculate the equilibrium solutions. Because we consider a specialist predator, i.e. the predator consumes the prey only and no other resources, there are only three possible equilibrium solutions: 1) both the predator and the prey are extinct, 2) the predator is extinct but the prey exists, 3) both the prey and the predator survive and coexist.

For this chapter, we will assume that the following functions G_i (biomass conversion from the prey in patch i to the predator in the same patch), and C_{ij} (dispersal of the prey in patch i to patch j) are linear functions in terms of the prey's population densities for simplicity. We calculate the extinction equilibrium and the conditions which lead to a predator-free equilibrium. For the coexistence equilibrium solution, we refer to the numerical simulations in Chapter 5.

4.1 Nondimensionalization of the Model

To simplify the calculation and reduce the number of parameters, we begin the analysis by non-dimensionalizing the model. We will adopt the following re-scalings

$$u_1 = \alpha \bar{u}_1, \quad u_2 = \beta \bar{u}_2, \quad v_1 = \eta \bar{v}_1, \quad v_2 = \theta \bar{v}_2, \quad t = \tau \bar{t},$$

where $\alpha, \beta, \eta, \theta, \tau$ are undetermined coefficients.

We can then obtain the following results

$$\begin{aligned}
\frac{d\bar{u}_1}{d\bar{t}} &= \frac{\tau}{\alpha} \cdot \frac{du_1}{dt} \\
&= \frac{\tau}{\alpha} \left(\frac{r_1 u_1}{1 + k_1 v_1} - d_1 u_1 - a_1 u_1^2 - g_1 u_1 v_1 - c_{12} u_1 + c_{21} u_2 \right) \\
&= \frac{\tau}{\alpha} \left(\frac{r_1 \alpha \bar{u}_1}{1 + k_1 \eta \bar{v}_1} - d_1 \alpha \bar{u}_1 - a_1 \alpha^2 \bar{u}_1^2 - g_1 \alpha \bar{u}_1 \eta \bar{v}_1 - c_{12} \alpha \bar{u}_1 + c_{21} \beta \bar{u}_2 \right) \\
&= \frac{\tau r_1 \bar{u}_1}{1 + \eta k_1 \bar{v}_1} - \tau d_1 \bar{u}_1 - \alpha \tau a_1 \bar{u}_1^2 - \eta \tau g_1 \bar{u}_1 \bar{v}_1 - \tau c_{12} \bar{u}_1 + \frac{\beta \tau c_{21} \bar{u}_2}{\alpha}.
\end{aligned}$$

Similarly, direct calculations lead to

$$\begin{aligned}
\frac{d\bar{u}_2}{d\bar{t}} &= \frac{\tau}{\beta} \cdot \frac{du_2}{dt} \\
&= \frac{\tau}{\beta} \left(\frac{r_2 u_2}{1 + k_2 v_2} - d_2 u_2 - a_2 u_2^2 - g_2 u_2 v_2 + c_{12} u_1 - c_{21} u_2 \right) \\
&= \frac{\tau}{\beta} \left(\frac{r_2 \beta \bar{u}_2}{1 + k_2 \theta \bar{v}_2} - d_2 \beta \bar{u}_2 - a_2 \beta^2 \bar{u}_2^2 - g_2 \beta \bar{u}_2 \theta \bar{v}_2 + c_{12} \alpha \bar{u}_1 - c_{21} \beta \bar{u}_2 \right) \\
&= \frac{\tau r_2 \bar{u}_2}{1 + \theta k_2 \bar{v}_2} - \tau d_2 \bar{u}_2 - \beta \tau a_2 \bar{u}_2^2 - \theta \tau g_2 \bar{u}_2 \bar{v}_2 + \frac{\alpha \tau c_{12} \bar{u}_1}{\beta} - \tau c_{21} \bar{u}_2, \\
\frac{d\bar{v}_1}{d\bar{t}} &= \frac{\tau}{\eta} \cdot \frac{dv_1}{dt} \\
&= \frac{\tau}{\eta} (e_1 g_1 u_1 v_1 - m_1 v_1 - p_{12} v_1 + p_{21} v_2) \\
&= \frac{\tau}{\eta} (e_1 g_1 \alpha \bar{u}_1 \eta \bar{v}_1 - m_1 \eta \bar{v}_1 - p_{12} \eta \bar{v}_1 + p_{21} \theta \bar{v}_2) \\
&= \alpha \tau e_1 g_1 \bar{u}_1 \bar{v}_1 - \tau m_1 \bar{v}_1 - \tau p_{12} \bar{v}_1 + \frac{\theta \tau p_{21} \bar{v}_2}{\eta}, \\
\frac{d\bar{v}_2}{d\bar{t}} &= \frac{\tau}{\theta} \cdot \frac{dv_2}{dt} \\
&= \frac{\tau}{\theta} (e_2 g_2 u_2 v_2 - m_2 v_2 + p_{12} v_1 - p_{21} v_2) \\
&= \frac{\tau}{\theta} (e_2 g_2 \beta \bar{u}_2 \theta \bar{v}_2 - m_2 \theta \bar{v}_2 + p_{12} \eta \bar{v}_1 - p_{21} \theta \bar{v}_2) \\
&= \beta \tau e_2 g_2 \bar{u}_2 \bar{v}_2 - \tau m_2 \bar{v}_2 + \frac{\eta \tau p_{12} \bar{v}_1}{\theta} - \tau p_{21} \bar{v}_2.
\end{aligned}$$

In order to reduce the number of parameters, we choose

$$\alpha = \frac{r_1}{a_1}, \quad \beta = \frac{r_1}{a_2}, \quad \eta = \frac{1}{k_1}, \quad \theta = \frac{1}{k_2}, \quad \tau = \frac{1}{r_1}.$$

Moreover, we redefine the parameters where

$$\begin{aligned} \bar{d}_1 &= \frac{d_1}{r_1}, & \bar{g}_1 &= \frac{g_1}{k_1 r_1}, & \bar{c}_{12} &= \frac{c_{12}}{r_1}, & \bar{c}_{21} &= \frac{a_1 c_{21}}{a_2 r_1}, & \bar{r} &= \frac{r_2}{r_1}, \\ \bar{d}_2 &= \frac{d_2}{r_1}, & \bar{g}_2 &= \frac{g_2}{k_2 r_1}, & \varepsilon &= \frac{a_2}{a_1}, & \bar{e}_1 &= \frac{e_1 g_1}{a_1}, & \bar{m}_1 &= \frac{m_1}{r_1}, \\ \bar{p}_{12} &= \frac{p_{12}}{r_1}, & \bar{p}_{21} &= \frac{k_1 p_{21}}{k_2 r_1}, & \bar{e}_2 &= \frac{e_2 g_2}{a_2}, & \bar{m}_2 &= \frac{m_2}{r_1}, & \mu &= \frac{k_2}{k_1}. \end{aligned}$$

Making these substitutions and dropping the bars for notional convenience gives us our nondimensional model

$$\begin{aligned} \frac{du_1}{dt} &= \frac{u_1}{1+v_1} - d_1 u_1 - u_1^2 - g_1 u_1 v_1 - c_{12} u_1 + c_{21} u_2, \\ \frac{du_2}{dt} &= \frac{r u_2}{1+v_2} - d_2 u_2 - u_2^2 - g_2 u_2 v_2 + \varepsilon c_{12} u_1 - \varepsilon c_{21} u_2, \\ \frac{dv_1}{dt} &= e_1 u_1 v_1 - m_1 v_1 - p_{12} v_1 + p_{21} v_2, \\ \frac{dv_2}{dt} &= e_2 u_2 v_2 - m_2 v_2 + \mu p_{12} v_1 - \mu p_{21} v_2. \end{aligned} \tag{4.1}$$

4.2 Equilibrium Solutions

Now that we have derived the non-dimensionalized model (4.1), next we determine what the equilibrium solutions of the system are. This is done by letting $du_1/dt = du_2/dt = dv_1/dt = dv_2/dt = 0$, and solving for the state variables. Clearly, one such equilibrium solution is the trivial equilibrium $E_0(u_1^*, u_2^*, v_1^*, v_2^*) = (0, 0, 0, 0)$.

We analyze the existence of a semi-trivial equilibrium $E_1(u_1^*, u_2^*, 0, 0)$. We begin by considering the simpler case of a subsystem of (4.1)

$$\begin{aligned}\frac{du_1}{dt} &= u_1 - d_1u_1 - (u_1)^2 - c_{12}u_1 + c_{21}u_2, \\ \frac{du_2}{dt} &= ru_2 - d_2u_2 - (u_2)^2 + \varepsilon c_{12}u_1 - \varepsilon c_{21}u_2.\end{aligned}\tag{4.2}$$

We take $(du_1/dt) = (du_2/dt) = 0$ in (4.2) and rearrange to find that

$$f_1(u_1) := \frac{(u_1)^2 - (1 - d_1 - c_{12})u_1}{c_{21}} = u_2$$

In a similar way, we can rearrange $(du_2)/(dt) = 0$ to view it as $-(u_2)^2 + (r - d_2 - \varepsilon c_{21})u_2 + \varepsilon c_{12}u_1 = 0$. This is a quadratic in u_2 , and so we solve for u_2 using the quadratic formula to get the functions

$$\begin{aligned}f_{21}(u_1) &:= \frac{1}{2}[(r - d_2 - \varepsilon c_{21}) + \sqrt{(r - d_2 - \varepsilon c_{21})^2 + 4\varepsilon c_{12}u_1}] = u_2, \\ f_{22}(u_1) &:= \frac{1}{2}[(r - d_2 - \varepsilon c_{21}) - \sqrt{(r - d_2 - \varepsilon c_{21})^2 + 4\varepsilon c_{12}u_1}] = u_2.\end{aligned}$$

Since we know that the function $u_2 = f_1(u_1)$ is derived from $du_1/dt = 0$; and the functions $u_2 = f_{21}(u_1)$, and $u_2 = f_{22}(u_1)$ are derived from $du_2/dt = 0$; then it must be that the intersection points of f_1 with either f_{21} or f_{22} is a steady state solution to the system (4.2). Furthermore, we only are interested in positive solutions, so any intersections that happen outside of the first quadrant are biologically unrealistic.

Note now that f_1 is a concave up quadratic intersecting the origin. Thus in the first quadrant, our region of interest, f_1 is eventually an increasing function. In both f_{21} and f_{22} we find the only state variable in the term $\sqrt{(r - d_2 - \varepsilon c_{21})^2 + 4\varepsilon c_{12}u_1}$, where it is multiplied only by positive parameters. In f_{21} the radical is positive, so in the first quadrant this is an increasing function. Conversely, in f_{22} the radical is negative, and so it is a decreasing function. Moreover, we can clearly see that $f_{22}(0) = 0$, and therefore $f_{22} < 0$ for all $u_1 \geq 0$. Therefore it is impossible

for there to be an intersection between f_1 and f_{22} in the first quadrant.

This means that we only need to analyze intersections between f_1 and f_{21} . A possible intersection between these functions is shown in Figure 4.1. In order to find the intersection of f_1 and f_{21} it is equivalent to consider the existence of the positive roots of

$$F(u_1) := f_{21}(u_1) - f_1(u_1).$$

We also note that clearly

$$\begin{aligned} \frac{df_1}{du_1} &= \frac{2u_1 - (1 - d_1 - c_{12})}{c_{21}}, \\ \frac{df_{21}}{du_1} &= \frac{\varepsilon c_{12}}{\sqrt{(r - d_2 - \varepsilon c_{21})^2 + 4\varepsilon c_{12}u_1}}. \end{aligned} \quad (4.3)$$

In each of these equations there are only two terms that may change sign from positive to negative: $(1 - d_1 - c_{12})$ and $(r - d_2 - \varepsilon c_{21})$. So we break this problem into cases based on whether these terms are positive, negative, or zero.

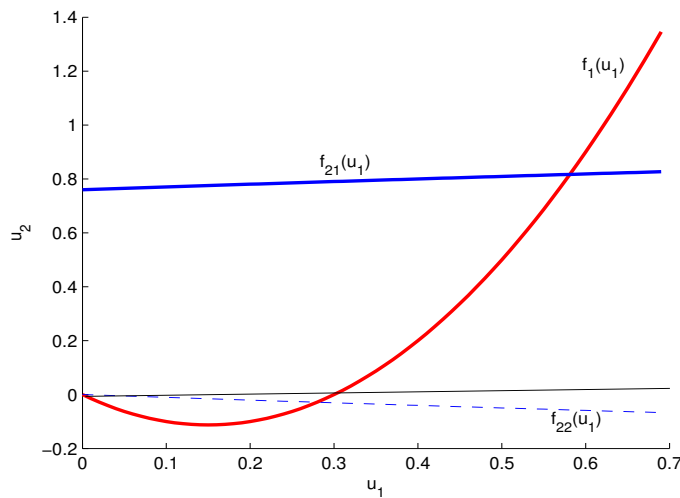


Figure 4.1: Illustration of existence of predator-free equilibrium.

Case I: $(1 - d_1 - c_{12}) \geq 0$ and $(r - d_2 - \varepsilon c_{21}) > 0$.

In this case it can be seen that $(df_1)/(du_1) < 0$ for $u_1 < (1 - d_1 - c_{12})/2$. Since we also have that $f_1(0) = 0$, we therefore know that $f_1(u_1) < 0$ for $0 < u_1 < (1 - d_1 - c_{12})/2$. Thus the range

in which it is possible to find an intersection in the first quadrant is for $u_1 \geq (1 - d_1 - c_{12})/2$.

Since finding an intersection between these two functions is equivalent to finding a zero of the function $F(u_1)$, we now consider this function for $u_1 \geq (1 - d_1 - c_{12})/2$. Firstly, we find that $F(0) = (r - d_2 - \varepsilon c_{21}) > 0$. We also find that $F'(0) = (\varepsilon c_{12})(r - d_2 - \varepsilon c_{21}) + (1 - d_1 - c_{12})/c_{21} > 0$. So as we enter the first quadrant of the (u_1, t) plane, this function is above zero in the (u_1, u_2) plane, and is increasing. We already established that there is no solution prior to the point $u_1 = (1 - d_1 - c_{12})/2$. Note that $F'((1 - d_1 - c_{12})/2) = \varepsilon c_{12}/(\sqrt{(r - d_2 - \varepsilon c_{21})^2 + 2\varepsilon c_{12}(1 - d_1 - c_{12})}) > 0$, so at this point F is still increasing. However, consider the limits

$$\lim_{u_1 \rightarrow \infty} \frac{df_{21}}{du_1} = \lim_{u_1 \rightarrow \infty} \frac{\varepsilon c_{12}}{\sqrt{(r - d_2 - \varepsilon c_{21})^2 + 4\varepsilon c_{12}u_1}} = \lim_{u_1 \rightarrow \infty} \frac{1}{\sqrt{u_1}} = 0,$$

and

$$\lim_{u_1 \rightarrow \infty} -\frac{df_1}{du_1} = \lim_{u_1^* \rightarrow \infty} -u_1 = -\infty.$$

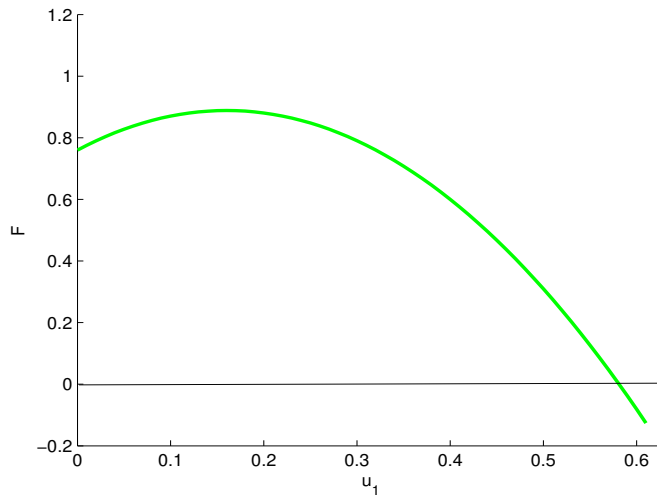
Therefore we can see that $F'(\infty) < 0$, that is, $F(u_1)$ is eventually decreasing for all time. This is confirmed by noting that:

$$F''(u_1) = -2\varepsilon^2 c_{12}^2 [(r - d_2 - \varepsilon c_{21})^2 + 4\varepsilon c_{12}u_1]^{-\frac{3}{2}} - 2/c_{21} < 0$$

This implies that the function is concave down for all possible values of u_1 , and therefore there is a point \bar{u}_1 such that $F'(u_1) > 0$ for $u_1 < \bar{u}_1$ and $F'(u_1) < 0$ for $u_1 > \bar{u}_1$. All of this suggests that there is a unique point, $u_1^* > \bar{u}_1 > (1 - d_1 - c_{12})/2$ such that $F(u_1^*) = 0$. One such possible root of the function $F(u_1) = 0$ is shown in Figure 4.2. Thus in this case the predator-free subsystem admits a unique equilibrium $(u_1^*, f_1(u_1^*))$.

Case II: $(1 - d_1 - c_{12}) < 0$ and $(r - d_2 - \varepsilon c_{21}) > 0$.

Just as in case I, we have that

Figure 4.2: Illustration of function F .

$$F(0) = (r - d_2 - \epsilon c_{21}) > 0,$$

$$F'(0) = \frac{\epsilon c_{12}}{r - d_2 - \epsilon c_{21}} + \frac{1 - d_1 - c_{12}}{c_{21}},$$

$$F''(u_1) < 0.$$

In this case, however, we aren't guaranteed that $F'(0) > 0$. In the scenario that we do have $F'(0) > 0$, then the same reasoning as in case I applies. Then there must be some unique $u_1^* > \bar{u}_1$ such that $F(u_1^*) = 0$. If, instead, we have that $F'(0) \leq 0$, the conclusion still remains, since $F(0)$ is greater than zero and $F''(u_1) < 0$ guarantees that $F'(u_1)$ remains negative from this point forward. This indicates that the function F will cross the u_1 axis exactly once. As before, we denote the positive root of $F(u_1) = 0$ as u_1^* . Thus, in this case, the predator-free subsystem admits a unique equilibrium $(u_1^*, f_1(u_1^*))$.

Case III: $(1 - d_1 - c_{12}) \geq 0$ and $(r - d_2 - \epsilon c_{21}) \leq 0$.

By similar discussions to those in Case I, we conclude that the predator-free subsystem admits a unique equilibrium $(u_1^*, f_1(u_1^*))$ in this case.

Case IV: $(1 - d_1 - c_{12}) < 0$ and $(r - d_2 - \varepsilon c_{21}) < 0$.

In this case, since the term $(r - d_2 - \varepsilon c_{21}) < 0$, the function $F'(u_1)$ takes on a slightly different form. Here we have

$$\begin{aligned} F(0) &= 0, \\ F'(0) &= -\frac{\varepsilon c_{12}}{r - d_2 - \varepsilon c_{21}} + \frac{1 - d_1 - c_{12}}{c_{21}}, \\ F''(u_1) &< 0. \end{aligned}$$

The negative sign in front of the term $\varepsilon c_{12}/(r - d_2 - \varepsilon c_{21})$ together with the assumption $r - d_2 - \varepsilon c_{21} < 0$ leads to $\varepsilon c_{12}/(r - d_2 - \varepsilon c_{21}) > 0$. This comes from simplifying $\varepsilon c_{12}/(\sqrt{(r - d_2 - \varepsilon c_{21})^2})$, where the result must be the positive root, since this is a result of f_{21} . The negative root was ruled out when we considered f_{22} previously. The term $(1 - d_1 - c_{12})/c_{21}$ must always be negative by assumption, and so we have that $F'(0) > 0$ if and only if

$$\left| \frac{\varepsilon c_{12}}{r - d_2 - \varepsilon c_{21}} \right| > \left| \frac{1 - d_1 - c_{12}}{c_{21}} \right|. \quad (4.4)$$

The consequence of this is that $F(u_1) > F(0) = 0$ for $0 < u_1 \ll 1$. Then, by the same reasoning as in Case I, there exists a unique $u_1^* > 0$ such that $F(u_1^*) = 0$, which is shown on the left in Figure 4.3.

Alternatively, it is possible that

$$\left| \frac{\varepsilon c_{12}}{r - d_2 - \varepsilon c_{21}} \right| < \left| \frac{1 - d_1 - c_{12}}{c_{21}} \right|. \quad (4.5)$$

In this case $F'(0) < 0$, and so $F(u_1) < F(0) = 0$ for $u_1 > 0$. We therefore conclude that in this case there is no positive equilibrium for the subsystem (4.2), as shown on the right in

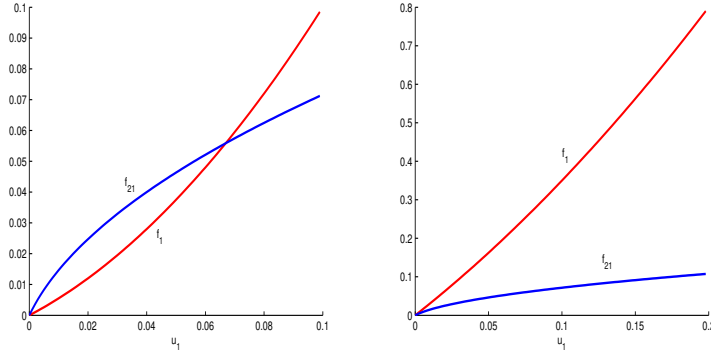


Figure 4.3: Illustration of intersection of function f_1 with function f_{21} .

Figure 4.3.

Case V: $(1 - d_1 - c_{12}) < 0$ and $(r - d_2 - \varepsilon c_{21}) = 0$.

In this case $f_{21}(u_1) = \sqrt{\varepsilon c_{12} u_1}$, and so we have

$$\begin{aligned}
 F(0) &= 0, \\
 F'(u_1) &= \frac{\varepsilon c_{12}}{2\sqrt{\varepsilon c_{12} u_1}} + \frac{(1 - d_1 - c_{12}) - 2u_1}{c_{21}}, \\
 F''(u_1) &< 0.
 \end{aligned}$$

Since we are assuming that $(1 - d_1 - c_{12}) < 0$, it is clear that $F'(u_1) > 0$ if and only if

$$\begin{aligned}
 \frac{\varepsilon c_{12}}{2\sqrt{\varepsilon c_{12} u_1}} &> -\frac{(1 - d_1 - c_{12}) - 2u_1}{c_{21}} \\
 \implies \varepsilon c_{12} c_{21} &> -[(1 - d_1 - c_{12}) - 2u_1] \cdot 2\sqrt{\varepsilon c_{12} u_1} \\
 \implies \varepsilon c_{12} c_{21} &> 4u_1 \sqrt{\varepsilon c_{12} u_1} - 2(1 - d_1 - c_{12}) \sqrt{\varepsilon c_{12} u_1}
 \end{aligned}$$

Now both terms on the left-hand side and right-hand side are positive. However, the term on the left is a constant, but each term on the right contains the variable u_1 . Nevertheless, we can see that for small enough u_1 , we must have that the left-hand side is greater than the right-

hand side, which leads to $F'(u_1) > 0$. Again, by similar discussions as in Case I, there must be a unique $u_1^* > 0$ such that $F(u_1^*) = 0$. And so, in this case the predator-free subsystem admits a unique equilibrium $(u_1^*, f_1(u_1^*))$.

Since the four dimensional system (4.1) is equivalent to the subsystem (4.2) when $v_1 = v_2 = 0$, it must be that the semi-trivial equilibrium $E(u_1^*, u_2^*, 0, 0)$ exists exactly when (4.2) admits the equilibrium $E(u_1^*, u_2^*)$. Therefore we have the following lemma.

Lemma 4.2.1 *The predator-free subsystem (4.2) admits a unique equilibrium (u_1^*, u_2^*) and the system (4.1) admits a unique equilibrium $(u_1^*, u_2^*, 0, 0)$ if the conditions stated in one of cases I-III or V are satisfied; or if (4.4) holds in case IV. The subsystem does not have a positive equilibrium if (4.5) holds in case IV.*

4.3 Stability of Equilibrium Solutions

Now we would like to perform analysis to determine when these equilibrium solutions are stable and when they are unstable, given that they exist. We start by considering the subsystem, before going on to analyze the trivial equilibrium of the entire system, and finally the semi-trivial equilibrium of the entire system.

4.3.1 Stability of the Subsystem Steady States

From the analysis for the existence of the predator-free equilibrium, we see that when the predator population density is at extinction, the full model (4.1) simplifies to the 2-dimensional system (4.2). The existence of a predator-free equilibrium of the full model (4.1) is equivalent to the existence of a positive equilibrium for the subsystem (4.2).

We analyze the subsystem (4.2) first and then extend the analysis to the full model (4.1) in later sections. To do this we first find the Jacobian matrix evaluated at the trivial equilibrium $(0, 0)$

$$J_0 = \begin{bmatrix} 1 - d_1 - c_{12} & c_{21} \\ \epsilon c_{12} & r - \epsilon c_{21} - d_2 \end{bmatrix}.$$

According to the Routh-Hurwitz criteria for second-order systems [4, 5], (4.1) has a stable trivial equilibrium if and only if $\text{Tr}(J_0) < 0$ and $\text{Det}(J_0) > 0$. Thus, $(0, 0)$ is asymptotically stable if

$$\begin{aligned} 1 - d_1 - c_{12} + r - \epsilon c_{21} - d_2 &< 0, \\ (1 - d_1 - c_{12})(r - \epsilon c_{21} - d_2) - \epsilon c_{12} c_{21} &> 0. \end{aligned} \tag{4.6}$$

Conversely, the equilibrium is unstable if either

$$1 - d_1 - c_{12} + r - \epsilon c_{21} - d_2 > 0, \tag{4.7}$$

or

$$(1 - d_1 - c_{12})(r - \epsilon c_{21} - d_2) - \epsilon c_{12} c_{21} < 0. \tag{4.8}$$

We consider the consequences of the instability of the trivial equilibrium in terms of the conditions outlined in Lemma 4.2.1. Let us first consider that (4.7) holds. The possibilities for this to be true are if both terms $(1 - d_2 - c_{12})$ and $(r - d_2 - \epsilon c_{21})$ are positive, which places us within Case I; or if $(1 - d_1 - c_{12})$ is positive, $(r - d_2 - \epsilon c_{21})$ is less than or equal to zero, and $|1 - d_1 - c_{12}| > |r - d_2 - \epsilon c_{21}|$ which places us in Case III; or if $(1 - d_1 - c_{12})$ is less than or equal to zero, $(r - d_2 - \epsilon c_{21})$ is positive, and $|1 - d_1 - c_{12}| < |r - d_2 - \epsilon c_{21}|$ which places us in either Case I or Case II. Therefore if this stability condition fails, then we must be within the boundaries of either Case I, Case II, or Case III, and so by 4.2.1 there is a unique positive equilibrium.

Now we consider when (4.8) holds. Each of the parameters ϵ , c_{12} , and c_{21} are positive. Therefore this equation holds if either of the terms $(1 - d_1 - c_{12})$ or $(r - d_2 - \epsilon c_{21})$ are equal to 0, which will place us in either of Case I, Case III, or Case V. It can also be that (4.8) holds

if $(1 - d_1 - c_{12})$ is positive and $(r - d_2 - \epsilon c_{21})$ is negative, which places us in Case III; or if $(1 - d_1 - c_{12})$ is negative and $(r - d_2 - \epsilon c_{21})$ is positive, which places us in Case II. Finally we can meet this condition if these terms share a sign and $|(1 - d_1 - c_{12}) * (r - d_2 - \epsilon c_{21})| < |\epsilon c_{12} c_{21}|$. This places us in either Case I or in Case IV. In the instance that we are in Case IV we are further in the scenario that equation (4.4) holds. Therefore, in order for the assumption (4.8) to be true, it must also be the case that there is a unique positive equilibrium by Lemma 4.2.1. We therefore propose the following lemma.

Lemma 4.3.1 *Assume that $(0, 0)$ is unstable. Then (4.2) has a unique positive equilibrium (u_1^*, u_2^*) , which is asymptotically stable.*

Proof The existence of the positive equilibrium (u_1^*, u_2^*) has already been shown, it remains to be shown that it is asymptotically stable. We consider the Jacobian matrix of (4.2) at (u_1^*, u_2^*) :

$$J_1 = \begin{bmatrix} 1 - d_1 - c_{12} - 2u_1^* & c_{21} \\ \epsilon c_{12} & r - \epsilon c_{21} - d_2 - 2u_2^* \end{bmatrix}.$$

In order to prove asymptotic stability, we check the Routh-Hurwitz criteria for second order systems. If the following conditions are satisfied, the positive equilibrium (u_1^*, u_2^*) is locally asymptotically stable

$$\begin{aligned} \text{Tr}(J_1) &= (1 - d_1 - c_{12} - 2u_1^*) + (r - \epsilon c_{21} - d_2 - 2u_2^*) < 0, \\ \text{Det}(J_1) &= (1 - d_1 - c_{12} - 2u_1^*)(r - \epsilon c_{21} - d_2 - 2u_2^*) - \epsilon c_{12} c_{21} > 0. \end{aligned} \tag{4.9}$$

We first consider $\text{Tr}(J_1)$

$$\begin{aligned} &(1 - d_1 - c_{12} - 2u_1^*) + (r - \epsilon c_{21} - d_2 - 2u_2^*) \\ &= \left(\frac{u_1^* - d_1 u_1^* - c_{12} u_1^* - (u_1^*)^2}{u_1^*} - u_1^* \right) + \left(\frac{r u_2^* - d_2 u_2^* - \epsilon c_{21} u_2^* - (u_2^*)^2}{u_2^*} - u_2^* \right). \end{aligned}$$

Using the facts that

$$\begin{aligned} u_1^* - d_1 u_1^* - (u_1^*)^2 - c_{12} u_1^* + c_{21} u_2^* &= 0, \\ r u_2^* - d_2 u_2^* - (u_2^*)^2 + \epsilon c_{12} u_1^* - \epsilon c_{21} u_2^* &= 0 \end{aligned}$$

we can conclude that

$$\text{Tr}(J_1) = \left(-\frac{c_{21} u_2^*}{u_1^*} - u_1^* \right) + \left(-\frac{\epsilon c_{12} u_1^*}{u_2^*} - u_2^* \right) < 0. \quad (4.10)$$

Upon consideration of the determinant, we again refer back to the original system (4.2). The determinant is given by $(1 - d_1 - c_{12} - 2u_1^*)(r - \epsilon c_{21} - d_2 - 2u_2^*) - \epsilon c_{12} c_{21}$, and by definition of the Jacobian each of the terms found here are derived by the partial derivative of the original system. We take advantage of this fact, note that

$$(1 - d_1 - c_{12} - 2u_1^*) = -c_{21} \left. \frac{df_1}{du_1} \right|_{(u_1^*, u_2^*)}, \quad (4.11)$$

and

$$(r - \epsilon c_{21} - d_2 - 2u_2^*) = -\epsilon c_{12} / \left(\left. \frac{df_{21}}{du_1} \right|_{(u_1^*, u_2^*)} \right), \quad (4.12)$$

which follow from f_1 and f_{21} respectively. It is also clear from (4.3) that

$$\left. \frac{df_{21}}{du_1} \right|_{(u_1^*, u_2^*)} > 0.$$

Substitution of (4.11) and (4.12) into (4.9) gives

$$\begin{aligned}
\text{Det}(J_1) &= (1 - d_1 - c_{12} - 2u_1^*)(r - \epsilon c_{21} - d_2 - 2u_2^*) - \epsilon c_{12}c_{21} \\
&= \left(-c_{21} \frac{df_1}{du_1} \Big|_{(u_1^*, u_2^*)}\right) \left(-\epsilon c_{12} / \left[\frac{df_{21}}{du_1} \Big|_{(u_1^*, u_2^*)}\right]\right) - \epsilon c_{12}c_{21} \\
&= \epsilon c_{12}c_{21} \left(\frac{df_1}{du_1} \Big|_{(u_1^*, u_2^*)} / \left[\frac{df_{21}}{du_1} \Big|_{(u_1^*, u_2^*)}\right]\right) - \epsilon c_{12}c_{21} \\
&= \epsilon c_{12}c_{21} \left[\left(\frac{df_1}{du_1} \Big|_{(u_1^*, u_2^*)} / \left[\frac{df_{21}}{du_1} \Big|_{(u_1^*, u_2^*)}\right]\right) - 1\right].
\end{aligned}$$

Thus, it must be that

$$\begin{aligned}
&\text{Det}(J_1) > 0 \\
&\Leftrightarrow \left(\frac{df_1}{du_1} \Big|_{(u_1^*, u_2^*)} / \left[\frac{df_{21}}{du_1} \Big|_{(u_1^*, u_2^*)}\right]\right) - 1 > 0 \\
&\Leftrightarrow \left(\frac{df_1}{du_1} \Big|_{(u_1^*, u_2^*)} / \left[\frac{df_{21}}{du_1} \Big|_{(u_1^*, u_2^*)}\right]\right) > 1 \\
&\Leftrightarrow \frac{df_1}{du_1} \Big|_{(u_1^*, u_2^*)} > \frac{df_{21}}{du_1} \Big|_{(u_1^*, u_2^*)}.
\end{aligned}$$

This is, of course, exactly the scenario in which $F'(u_1) < 0$. In each of the cases referred to in Lemma 4.2.1, the positive equilibrium (u_1^*, u_2^*) exists only within the range of $F'(u_1) < 0$, and therefore it is proven that $\text{Det}(J_1) > 0$.

□

4.3.2 Stability of the Trivial Equilibrium

First of all, we linearize the nonlinear system 4.1 about the equilibrium by calculating the Jacobian matrix. We denote the Jacobian matrix by

$$J = \begin{bmatrix} J_{11} & c_{21} & J_{13} & 0 \\ \varepsilon c_{12} & J_{22} & 0 & J_{24} \\ e_1 v_1 & 0 & J_{33} & p_{21} \\ 0 & e_2 v_2 & \mu p_{12} & J_{44} \end{bmatrix},$$

where:

$$\begin{aligned} J_{11} &= \frac{1}{1 + v_1} - d_1 - 2u_1 - g_1 v_1 - c_{12}, & J_{13} &= -\frac{u_1}{(1 + v_1)^2} - g_1 u_1, \\ J_{22} &= \frac{r}{1 + v_2} - d_2 - 2u_2 - g_2 v_2 - \varepsilon c_{21}, & J_{24} &= -\frac{r u_2}{(1 + v_2)^2} - g_2 u_2, \\ J_{33} &= e_1 u_1 - m_1 - p_{12}, & J_{44} &= e_2 u_2 - m_2 - p_{21} \mu. \end{aligned}$$

Since the trivial equilibrium $E_0(0, 0, 0, 0)$ has all compartments 0, by substituting E_0 into the Jacobian matrix, we get

$$J_0 = \begin{bmatrix} 1 - d_1 - c_{12} & c_{21} & 0 & 0 \\ \varepsilon c_{12} & r - d_2 - \varepsilon c_{21} & 0 & 0 \\ 0 & 0 & -m_1 - p_{12} & p_{21} \\ 0 & 0 & \mu p_{12} & -m_2 - \mu p_{21} \end{bmatrix}.$$

To determine the stability we would like to find the eigenvalues of this matrix by calculating the determinant of $\lambda I - J_0$ and solving the characteristic equation. To find the determinant we conduct determinant expansion by minors in the matrix $\lambda I - J_0$. Direct calculations show that

$$\begin{aligned}
\det(\lambda I - J_0) &= (\lambda - 1 + d_1 + c_{12}) \cdot \begin{vmatrix} \lambda - r + d_2 + \varepsilon c_{21} & 0 & 0 \\ 0 & \lambda + m_1 + p_{12} & -p_{21} \\ 0 & -\mu p_{12} & \lambda + m_2 + \mu p_{21} \end{vmatrix} \\
&+ c_{21} \cdot \begin{vmatrix} -\varepsilon c_{12} & 0 & 0 \\ 0 & \lambda + m_1 + p_{12} & -p_{21} \\ 0 & -\mu p_{12} & \lambda + m_2 + \mu p_{21} \end{vmatrix} \\
&= (\lambda - 1 + d_1 + c_{12}) \cdot (\lambda - r + d_2 + \varepsilon c_{21}) \cdot \begin{vmatrix} \lambda + m_1 + p_{12} & -p_{21} \\ -\mu p_{12} & \lambda + m_2 + \mu p_{21} \end{vmatrix} \\
&+ c_{21} \cdot (-\varepsilon c_{12}) \cdot \begin{vmatrix} \lambda + m_1 + p_{12} & -p_{21} \\ -\mu p_{12} & \lambda + m_2 + \mu p_{21} \end{vmatrix} \\
&= \left[\lambda^2 + (m_1 + p_{12} + m_2 + p_{21}\mu) \lambda + (m_1 + p_{12})(m_2 + \mu p_{21}) - \mu p_{12} p_{21} \right] \\
&\left[\lambda^2 + (-1 + d_1 + c_{12} - r + d_2 + \varepsilon c_{21}) \lambda + (1 - d_1 - c_{12})(r - d_2 - \varepsilon c_{21}) - \varepsilon c_{12} c_{21} \right].
\end{aligned}$$

By $\det(\lambda I - J_0) = 0$, this gives us the two quadratic equations

$$\lambda^2 + (-1 + d_1 + c_{12} - r + d_2 + \varepsilon c_{21}) \lambda + (1 - d_1 - c_{12})(r - d_2 - \varepsilon c_{21}) - \varepsilon c_{12} c_{21} = 0,$$

and

$$\lambda^2 + (m_1 + m_2 + p_{12} + \mu p_{21}) \lambda + (m_1 m_2 + \mu m_1 p_{21} + m_2 p_{21}) = 0.$$

Since the eigenvalues are determined by the two quadratic equations respectively, we can apply the Routh-Hurwitz criteria for quadratic equations instead. The Routh-Hurwitz criteria show that the solutions for the quadratic $\lambda^2 + a_1 \lambda + a_2 = 0$ have negative real parts if and only if $a_1 > 0$, and $a_2 > 0$. We want to apply this criteria to both quadratics, which gives us the conditions

$$\begin{aligned}
-1 + d_1 + c_{12} - r + d_2 + \varepsilon c_{21} &> 0, \\
(1 - d_1 - c_{12})(r - d_2 - \varepsilon c_{21}) - \varepsilon c_{12} c_{21} &> 0,
\end{aligned} \tag{4.13}$$

and

$$\begin{aligned}
m_1 + m_2 + p_{12} + \mu p_{21} &> 0, \\
m_1 m_2 + \mu m_1 p_{21} + m_2 p_{21} &> 0.
\end{aligned} \tag{4.14}$$

All of these parameters are greater than or equal to zero, so clearly conditions (4.14) are always true. This leaves us only with the conditions (4.13).

Thus we have the following lemma.

Lemma 4.3.2 *The trivial equilibrium solution $(u_1, u_2, v_1, v_2) = (0, 0, 0, 0)$ to the non-dimensionalized system (4.1) is locally asymptotically stable if and only if*

$$\begin{aligned}
-1 + d_1 + c_{12} - r + d_2 + \varepsilon c_{21} &> 0, \\
(1 - d_1 - c_{12})(r - d_2 - \varepsilon c_{21}) - \varepsilon c_{12} c_{21} &> 0
\end{aligned}$$

are satisfied.

4.3.3 Stability of Semi-Trivial Equilibrium

Just as in the case of the trivial equilibrium, we analyze the local stability of the predator-free equilibrium via the linearization of system (4.1) about the steady state. We substitute the predator-free equilibrium $E_1(u_1^*, u_2^*, 0, 0)$ into the matrix J to get the relevant Jacobian matrix J_1

$$J_1 = \begin{bmatrix} 1 - d_1 - 2u_1^* - c_{12} & c_{21} & -u_1^* - g_1 u_1^* & 0 \\ \varepsilon c_{12} & r - d_2 - 2u_2^* - \varepsilon c_{21} & 0 & -ru_2^* - g_2 u_2^* \\ 0 & 0 & e_1 u_1^* - m_1 - p_{12} & p_{21} \\ 0 & 0 & \mu p_{12} & e_2 u_2^* - m_2 - \mu p_{21} \end{bmatrix}.$$

As in the trivial case, we determine the stability by finding the eigenvalues. To that end we consider $\det(\lambda I - J_1) = 0$.

$$\det(\lambda I - J_1)$$

$$\begin{aligned} &= (\lambda - 1 + d_1 + 2u_1^* + c_{12}) \cdot \begin{vmatrix} \lambda - r + d_2 + 2u_2^* + \varepsilon c_{21} & 0 & ru_2^* + g_2 u_2^* \\ 0 & \lambda - e_1 u_1^* + m_1 + p_{12} & -p_{21} \\ 0 & -\mu p_{12} & \lambda - e_2 u_2^* + m_2 + \mu p_{21} \end{vmatrix} \\ &- (-c_{21}) \cdot \begin{vmatrix} -c_{21} & u_1^* + g_1 u_1^* & 0 \\ 0 & \lambda - e_1 u_1^* + m_1 + p_{12} & -p_{21} \\ 0 & -\mu p_{12} & \lambda - e_2 u_2^* + m_2 + \mu p_{21} \end{vmatrix} \\ &= (\lambda - 1 + d_1 + 2u_1^* + c_{12}) \cdot (\lambda - r + d_2 + 2u_2^* + \varepsilon c_{21}) \cdot \begin{vmatrix} \lambda - e_1 u_1^* + m_1 + p_{12} & -p_{21} \\ -\mu p_{12} & \lambda - e_2 u_2^* + m_2 + \mu p_{21} \end{vmatrix} \\ &+ \varepsilon c_{12} \cdot (-c_{21}) \cdot \begin{vmatrix} \lambda - e_1 u_1^* + m_1 + p_{12} & -p_{21} \\ -\mu p_{12} & \lambda - e_2 u_2^* + m_2 + \mu p_{21} \end{vmatrix} \\ &= \left[\lambda^2 + (-e_1 u_1^* + m_1 + p_{12} - e_2 u_2^* + m_2 + p_{21} \mu) \lambda + (-e_1 u_1^* + m_1 + p_{12})(-e_2 u_2^* + m_2 + \mu p_{21}) - \mu p_{12} p_{21} \right] \\ &\left[\lambda^2 + (-1 + d_1 + 2u_1^* + c_{12} - r + d_2 + 2u_2^* + \varepsilon c_{21}) \lambda + (1 - d_1 - 2u_1^* - c_{12})(r - d_2 - 2u_2^* - \varepsilon c_{21}) - \varepsilon c_{12} c_{21} \right]. \end{aligned}$$

This gives us the two quadratic equations:

$$\lambda^2 + (-1 + d_1 + 2u_1^* + c_{12} - r + d_2 + 2u_2^* + \varepsilon c_{21}) \lambda + (1 - d_1 - 2u_1^* - c_{12})(r - d_2 - 2u_2^* - \varepsilon c_{21}) - \varepsilon c_{12} c_{21} = 0,$$

and

$$\lambda^2 + (-e_1 u_1^* + m_1 + p_{12} - e_2 u_2^* + m_2 + p_{21} \mu) \lambda + (-e_1 u_1^* + m_1 + p_{12})(-e_2 u_2^* + m_2 + \mu p_{21}) - \mu p_{12} p_{21} = 0.$$

Just as before, we can apply the Routh-Hurwitz criteria to each quadratic to determine a set of conditions for stability. The conditions we get are

$$\begin{aligned} c_{12} + \varepsilon c_{21} + d_1 + d_2 + 2u_1^* + 2u_2^* - r - 1 &> 0, \\ (1 - d_1 - 2u_1^* - c_{12})(r - d_2 - 2u_2^* - \varepsilon c_{21}) - \varepsilon c_{12} c_{21} &> 0 \\ m_1 + m_2 + p_{12} + \mu p_{21} - e_1 u_1^* - e_2 u_2^* &> 0, \\ (-e_1 u_1^* + m_1 + p_{12})(-e_2 u_2^* + m_2 + \mu p_{21}) - \mu p_{12} p_{21} &> 0. \end{aligned} \tag{4.15}$$

Therefore we can conclude the following Lemma.

Lemma 4.3.3 *The semi-trivial equilibrium solution $E(u_1^*, u_2^*, 0, 0)$ of the system (4.1) is stable if and only if the conditions (4.15) are met.*

Chapter 5

Numerical Simulations

5.1 Verifying Analyses

In this chapter we use numerical simulations to confirm the previous mathematical analysis. We also use numerical simulations to make estimations of the behaviour in more complicated circumstances for which the mathematical analysis is beyond the scope of this thesis (ie non-linear functional response and/or nonlinear migration functions). To begin with, we consider the trivial equilibrium. We would like to select parameter values that will, according to our previous analysis, give us a stable trivial equilibrium. Intuitively, we know that if the prey goes extinct then the predator will follow. We also have that for many of the parameters x , $0 < x < 1$. Therefore, we try setting each parameter to an approximate average value of 0.5 but increase the death rates of the prey d_1 and d_2 to 0.9. Then we can apply Lemma 4.3.2 to check if this choice for the set of parameters gives a stable equilibrium.

Recall that this theorem is written in terms of the non-dimensionalized model but we have chosen values for the parameters from the original model. Converting the parameters relevant to this theorem gives

i) $c_{12} = c_{21} = r = \varepsilon = 1$,

ii) $d_1 = d_2 = 1.8$.

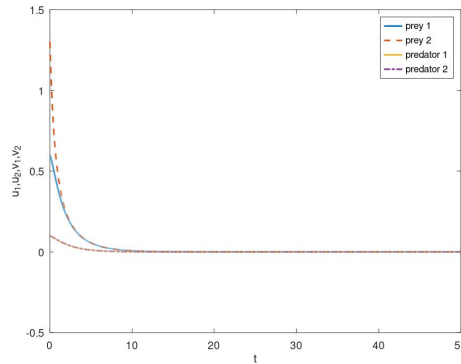


Figure 5.1: Stable Trivial Equilibrium

Then

$$\begin{aligned}
 & 1 - d_1 - c_{12} + r - d_2 - \varepsilon c_{21} \\
 &= 1 - 1.8 - 1 + 1 - 1.8 - 1 \\
 &= -3.6 < 0,
 \end{aligned} \tag{5.1}$$

and

$$\begin{aligned}
 & (1 - d_1 - c_{12})(r - d_2 - \varepsilon c_{21}) - \varepsilon c_{12} c_{21} \\
 &= (1 - 1.8 - 1)(1 - 1.8 - 1) - 1 \\
 &= 2.24 > 0.
 \end{aligned} \tag{5.2}$$

Clearly both of these statements are true, and so the conditions of Lemma 4.3.2 are met. Therefore we should expect all trajectories to tend to zero. This is exactly what we see happen in the numerical simulation as shown in Figure 5.1.

For the case of the semi-trivial equilibrium, we are able to apply the Lemmas 4.2.1 and 4.3.3. We must choose parameters that meet the conditions of the former to ensure that such an equilibrium exists, and conditions which meet the latter in order for it to be stable. Through some trial and error we choose the parameter values $a_2 = 0.8$, $d_2 = 0.25$, and $c_{12} = 0.75$; while we keep each other parameter at the average value of 0.5. We use these values to calculate the value of the relevant non-dimensional counterparts.

$$\text{i) } d_1 = m_1 = m_2 = p_{12} = p_{21} = r = \mu = 1$$

$$\text{ii) } c_{12} = \frac{3}{2}$$

$$\text{iii) } d_2 = e_1 = \frac{1}{2}$$

$$\text{iv) } \varepsilon = c_{21} = \frac{8}{5}$$

$$\text{v) } e_2 = \frac{5}{16}$$

Using these values we start by applying Lemma 4.2.1 to show that we expect the semi-trivial equilibrium to exist.

$$1 - d_1 - c_{12} = 1 - 1 - \frac{3}{2} = -\frac{3}{2} < 0$$

$$r - d_2 - \varepsilon c_{21} = 1 - \frac{1}{2} - \left(\frac{8}{5}\right)\left(\frac{8}{5}\right) = -\frac{103}{50} < 0$$

According to this calculation these parameter values place us within Case IV of Lemma 4.2.1, and so we have one more calculation to determine if the equilibrium should exist.

$$\begin{aligned} \left| \frac{\varepsilon c_{12}}{r - d_2 - \varepsilon c_{21}} \right| &= \left| \frac{(1.6)(1.5)}{1 - 0.5 - (1.6)(1.6)} \right| \\ &= \left| \frac{2.4}{-2.06} \right| \\ &\approx 1.165 > 0.9375 \\ &= \left| \frac{-1.5}{1.6} \right| \\ &= \left| \frac{1 - d_1 - c_{12}}{c_{21}} \right| \end{aligned}$$

Therefore it is the case that (4.4) holds in Case IV of Lemma 4.2.1, and so the semi-trivial equilibrium should exist.

Now we can use the chosen parameter values in the system 4.2 to determine the equilibrium values (u_1^*, u_2^*) .

$$\begin{aligned}
& \begin{cases} 0 = u_1^* - d_1 u_1^* - (u_1^*)^2 - c_{12} u_1^* + c_{21} u_2^* \\ 0 = r u_2^* - d_2 u_2^* - (u_2^*)^2 + \varepsilon c_{12} u_1^* - \varepsilon c_{21} u_2^* \end{cases} \\
\Rightarrow & \begin{cases} 0 = u_1^* - (1)u_1^* - (u_1^*)^2 - \left(\frac{3}{2}\right)u_1^* + \left(\frac{8}{5}\right)u_2^* \\ 0 = (1)u_2^* - \left(\frac{1}{2}\right)u_2^* - (u_2^*)^2 + \left(\frac{8}{5}\right)\left(\frac{3}{2}\right)u_1^* - \left(\frac{8}{5}\right)\left(\frac{8}{5}\right)u_2^* \end{cases} \\
\Rightarrow & \begin{cases} 0 = \frac{8}{5}u_2^* - (u_1^*)^2 - \frac{3}{2}u_1^* \\ 0 = \frac{12}{5}u_1^* - (u_2^*)^2 - \frac{103}{50}u_2^* \end{cases} \\
\Rightarrow & \begin{cases} \frac{5}{8}(u_1^*)^2 + \frac{15}{16}u_1^* = u_2^* \\ 0 = \frac{12}{5}u_1^* - (u_2^*)^2 - \frac{103}{50}u_2^* \end{cases}
\end{aligned}$$

Now we substitute the value of u_2^* from the first equation into the second equation and solve for the roots of the quartic that arises.

$$\begin{aligned}
& \frac{12}{5}u_1^* - \left(\frac{5}{8}(u_1^*)^2 + \frac{15}{16}u_1^*\right)^2 - \frac{103}{50}\left(\frac{5}{8}(u_1^*)^2 + \frac{15}{16}u_1^*\right) = 0 \\
\Rightarrow & \frac{12}{5}u_1^* - \left(\frac{25}{64}(u_1^*)^4 + \frac{75}{64}(u_1^*)^3 + \frac{225}{256}(u_1^*)^2\right) - \frac{103}{80}(u_1^*)^2 + \frac{309}{160}u_1^* = 0 \\
& \Rightarrow -\frac{25}{64}(u_1^*)^4 - \frac{75}{64}(u_1^*)^3 - \frac{2773}{1280}(u_1^*)^2 + \frac{693}{160}u_1^* = 0
\end{aligned}$$

Using sage math to solve for the roots of the resulting function yields two imaginary solutions, the trivial equilibrium, and $u_1^* \approx 1.1017$. We now return this value into the expression we found previously for u_2^* .

$$\begin{aligned}
u_2^* &= \frac{5}{8}(u_1^*)^2 + \frac{15}{16}u_1^* \\
&\approx 0.625(1.1017)^2 + (0.9375)(1.1017) \\
&\approx 1.7914
\end{aligned}$$

Now we have all the values necessary to apply Lemma 4.3.3 and determine stability. We have

$$\begin{aligned}
&c_{12} + \varepsilon c_{21} + d_1 + d_2 + 2u_1^* + 2u_2^* - r - 1 \\
&= 1.5 + (1.6)(1.6) + 1 + 0.5 + 2(1.1017) + 2(1.7914) - 1 - 1 \\
&= 9.3462 > 0,
\end{aligned}$$

and

$$\begin{aligned}
&(1 - d_1 - 2u_1^* - c_{12})(r - d_2 - 2u_2^* - \varepsilon c_{21}) - \varepsilon c_{12}c_{21} \\
&= (1 - 1 - 2(1.1017) - 1.5)(1 - 0.5 - 2(1.7914) - (1.6)(1.6)) - (1.6)(1.5)(1.6) \\
&= (-3.7034)(-5.6428) - 3.84 \\
&\approx 17.0575 > 0,
\end{aligned}$$

and

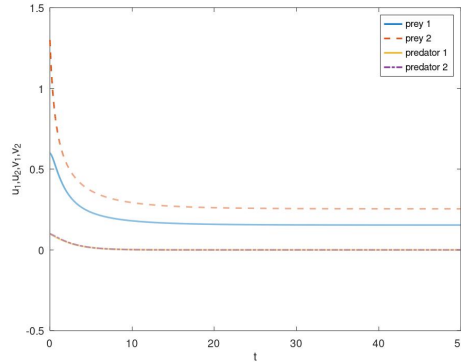


Figure 5.2: Stable Semi-Trivial Equilibrium

$$\begin{aligned}
 & m_1 + m_2 + p_{12} + \mu p_{21} - e_1 u_1^* - e_2 u_2^* \\
 &= 1 + 1 + 1 + (1)(1) - (0.5)(1.1017) - (0.3125)(1.7914) \\
 &\approx 2.8893 > 0,
 \end{aligned}$$

and finally

$$\begin{aligned}
 & (-e_1 u_1^* + m_1 + p_{12})(-e_2 u_2^* + m_2 + \mu p_{21}) - \mu p_{12} p_{21} \\
 &= (-0.5(1.1017) + 1 + 1)(-0.3125(1.7914) + 1 + (1)(1)) - (1)(1)(1) \\
 &= (1.44915)(1.4401875) - 1 \\
 &\approx 1.087 > 0.
 \end{aligned}$$

All of the conditions for Lemma 4.3.3 are met, and therefore we expect that the equilibrium not only exists, but is stable. This is exactly what we see in the numerical simulations shown in Figure 5.2.

It is interesting to note that numerical simulations suggest that if we keep all else the same but let $c_{21} = 0$, then the same set of parameters that give us a stable semi-trivial equilibrium

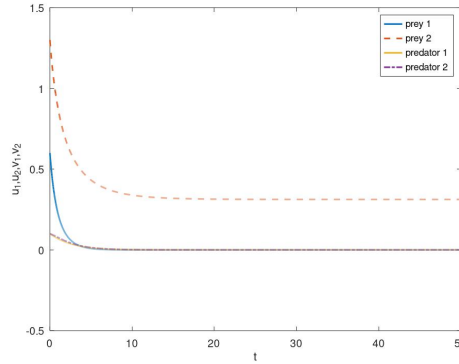


Figure 5.3: Prey Survives in Only Patch 2

where the prey survives in both patches will give us a stable semi-trivial equilibrium where only the prey in patch two survives. This makes intuitive sense, as there is no boost to the population through immigration, so a decline to extinction should be expected. This is confirmed in the simulation shown in Figure 5.3. We clearly could also choose a set of parameters that give us the prey surviving only in patch one, as the equations are symmetric.

5.2 Extending the Mathematical Analysis

The global stability analysis of the system is beyond the scope of this thesis, and no mathematical proof for the uniform persistence of the species in this system is given. That is, proof, that there is a globally asymptotically stable equilibrium $E(u_1^*, u_2^*, v_1^*, v_2^*)$ of the system (4.1). However, we can see in Figure 5.4 that we expect at least some stable positive equilibrium solution to exist. The parameters chosen to produce this result were

- | | |
|------------------------|---|
| i) $k_1 = k_2 = 1$ | v) $c_{12} = b_1 = 0.4$ |
| ii) $r_2 = 0.8$ | vi) $a_2 = g_1 = g_2 = c_{21} = p_{21} = 0.3$ |
| iii) $r_1 = b_2 = 0.6$ | vii) $d_2 = m_1 = p_{12} = 0.2$ |
| iv) $a_1 = 0.5$ | viii) $d_1 = m_2 = 0.1.$ |

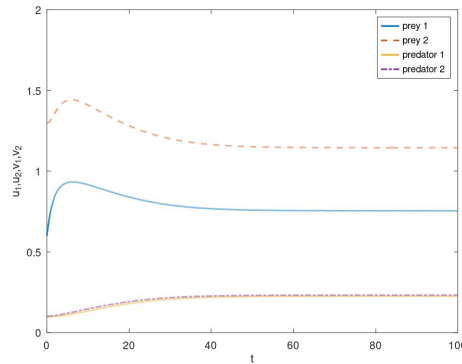


Figure 5.4: Stable Positive Equilibrium

All of the analysis covered in this paper assumes linear function in place of the functional response as well as the migration functions. However, a linear functional response is not the most likely. The most common is a Holling Type II functional response, so we include numerical simulations to cover this subject. As can be seen in Figure 5.5, we expect that a stable positive equilibrium is possible under these circumstances as well. In comparing Figures 5.4 and 5.5, the attraction of the equilibrium point seems stronger in the case of Holling Type II functional response. Where in the case of a linear functional response the prey populations initially overshoot their equilibrium values and then settle, the trajectories instead tend sharply towards the equilibrium and snap into place in the case of the Holling Type II functional response. This is of course, possibly an artifact of the particular choices of parameter values in each case, and it may be possible that a different choice would tend more sharply towards the equilibrium in the linear case; or less sharply in the Holling Type II case. The parameters chosen to produce Figure 5.5 are as follows, where $G(u_i) = (q_i u_i)/(1 + h_i u_i)$.

i) $k_1 = 1.5$

vi) $c_{12} = b_1 = 0.4$

ii) $r_2 = 0.8$

vii) $a_2 = h_1 = h_2 = q_1 = q_2 = c_{21} = p_{21} = 0.3$

iii) $k_2 = 0.7$

viii) $d_2 = m_1 = p_{12} = 0.2$

iv) $r_1 = b_2 = 0.6$

ix) $d_1 = m_2 = 0.1$

v) $a_1 = 0.5$

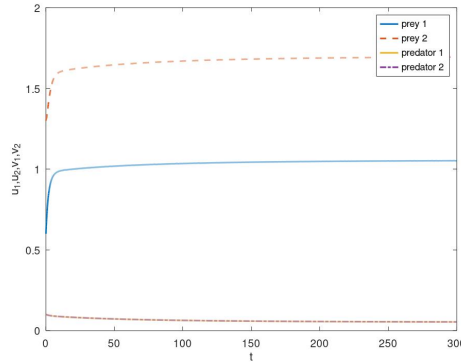


Figure 5.5: Stable Positive Equilibrium with Type II Functional Response

The original model 2.1 proposed in Chapter 2 includes the migration functions $C_{12}(k_1, v_1)$ and $C_{21}(k_2, v_2)$. We also assumed that these functions were linear for the sake of simplicity in the mathematical analysis, but now we use numerical simulations to consider otherwise, similarly to the functional response. Study of the fear effect is still relatively new, so unlike the functional response, there is no preferred migration function to turn to. Therefore we propose the function $C_{ij}(k_i, v_i) = (c_{ij}k_iv_i)/(1 + o_ik_iv_i)$, for $i, j \in \{1, 2\}$.

The assumption in this formulation is that the prey is migrating between patches based on the perceived danger, which will directly relate to how strong the fear effect is, included here as the term k_i ; and will also directly relate to how many predators there are within the patch, hence the inclusion of the state variable v_i . The constant term c_{ij} is included to scale the effect that these factors have on the migration of the prey and the parameter o_i determines how low or high the level of migration is able to be. This takes the same form as the Holling Type II functional response, for the same reasons. Just as we can't expect the level of predation to be boundless, and so must use a function that tapers off at some upper bound; we cannot expect the level of migration to be boundless, so we choose the same sort of function.

Numerical simulations suggest that this form of the migration terms has little effect on the qualitative behaviour of the system, but can have significant effects on the quantitative behaviour. We can see in Figure 5.6 that the general shapes of the trajectories are similar to those as in 5.4, but the points at which the populations reach equilibrium are different. We

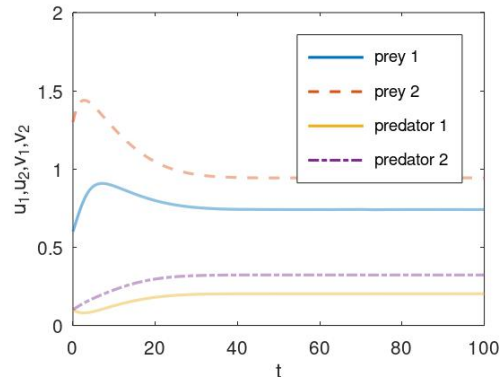


Figure 5.6: Stable Positive Equilibrium with Nonlinear Migration

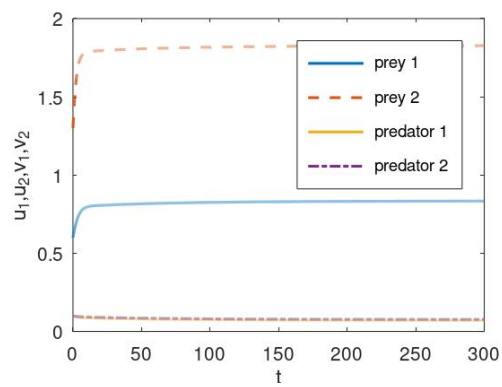


Figure 5.7: Type II Functional Response and Nonlinear Migration

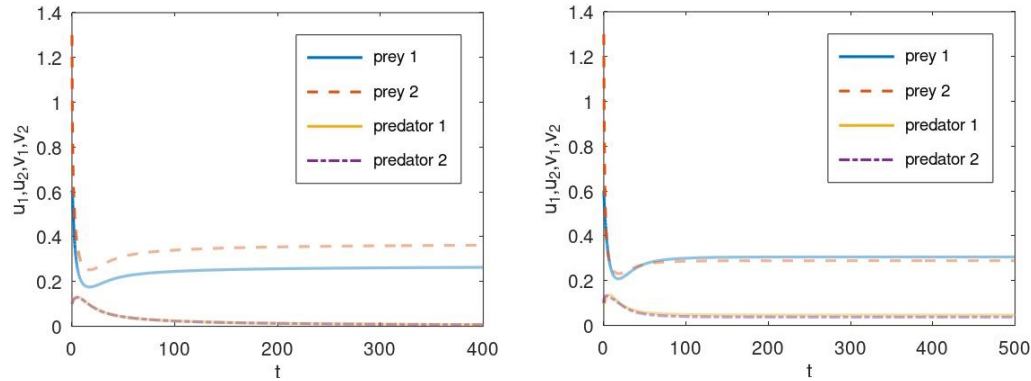


Figure 5.8: Migration Preventing Extinction

use the same choice of parameters as we did to achieve a positive equilibrium in the case of linear migration and linear functional response with respect to the prey's population, and this quantitative change is managed entirely by varying parameters within the functions C_{ij} .

These extra parameters which have the capacity to adjust the quantitative behaviour of the system gives an added flexibility to the system. A consequence of this flexibility is that a set of parameters which would lead to the extinction of a some or all of the species in a simpler system may not necessarily lead to extinction depending on the parameter values chosen in the migration function. This is something which we expect to see, based on Huffakers experiments with mites [1], and this is shown in Figure 5.8. On the left-hand side we see a set of parameters applied to the system 2.1, which lead to the extinction of the predator. On the right-hand side we use those same parameters but use a nonlinear migration, and variation in the parameters σ_i lead to the survival of all species.

We see a similar situation when we consider the system with a Holling Type II functional response as well as a nonlinear migration term. We use the same choice of parameters as in the case of Holling Type II functional with linear migration in order to achieve the stable positive equilibrium in the simulations shown in Figure 5.7. Just as we saw in comparing Figure 5.4 with Figure 5.6, we can see that the migration term has little impact qualitatively in this circumstance as well when we compare Figure 5.5 with Figure 5.7, but again does influence the quantitative behaviour. Importantly, the model continues to exhibit the stable

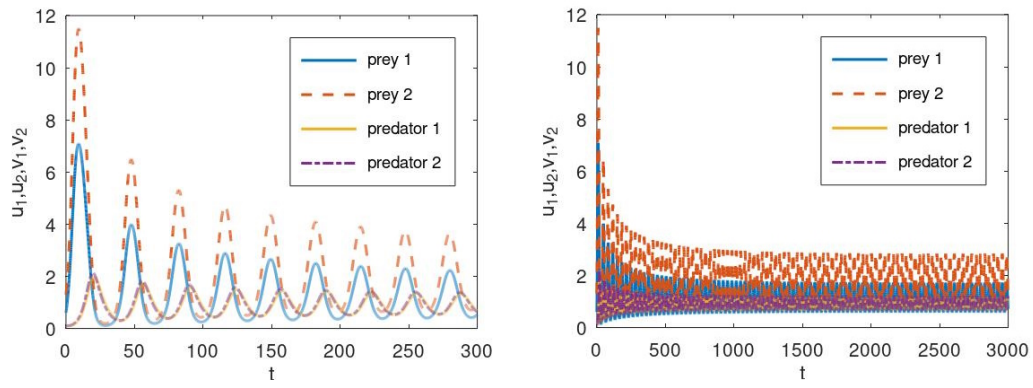


Figure 5.9: Oscillatory Holling Type II Functional Response

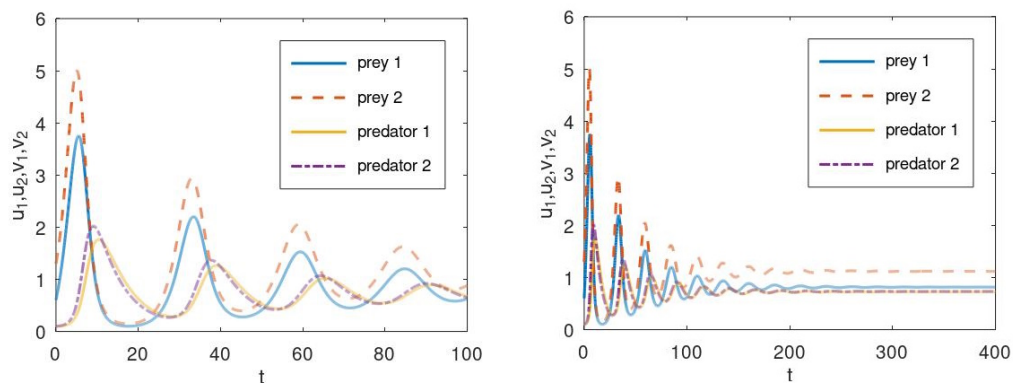


Figure 5.10: Oscillatory Behaviour With all Linear Functions

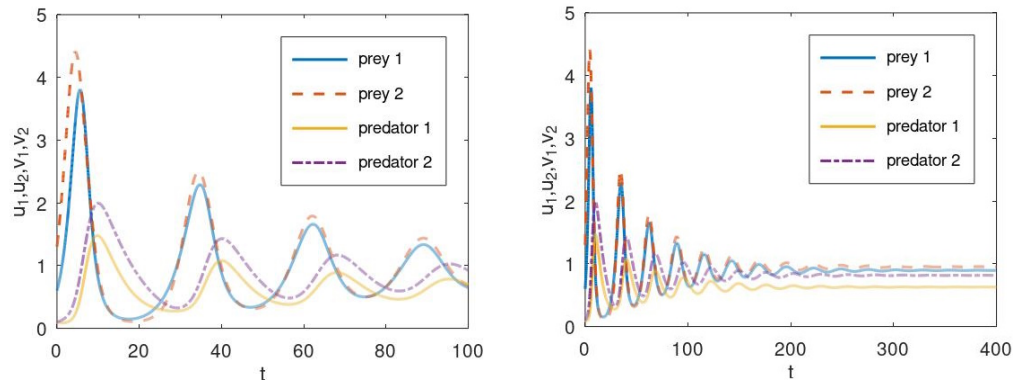


Figure 5.11: Oscillatory Nonlinear Migration

positive equilibrium when the simplifying assumptions we made in Chapter 4 are stripped away, and so when the model is made to be more biologically realistic it is still mathematically reasonable.

The simulations we have seen so far have confirmed our theorems and have also shown that a stable positive equilibrium is possible within this model; however we do not see an oscillatory pattern in those simulations which we would expect in a predator-prey system. Further simulations show that a different parameter choice does yield the expected oscillatory behaviours. We see oscillatory behaviour and a positive equilibrium with the Holling Type II functional response in Figure 5.9. The parameters chosen are the same as we used for Figure 5.5, with the exception of $a_1 = 0.05$, and $a_2 = 0.03$. The graph on the left-hand side shows a close up of the trajectories near time $t = 0$, while the graph on the right-hand side shows the asymptotic behaviour of this system, in that the oscillations do not damp out completely. Instead the system settles to a stable periodic equilibrium.

Using simulations we also see that this transient oscillatory behaviour is possible in any of the cases we considered previously. Figure 5.10 shows the oscillatory behaviour in the case where all functions in the model are linear with respect to the prey's population density, as we analyzed in Chapter 4. Again we see a close up on the left-hand side, while the right-hand side shows that in the long run these oscillations completely damp out and the trajectories reach a constant equilibrium value.

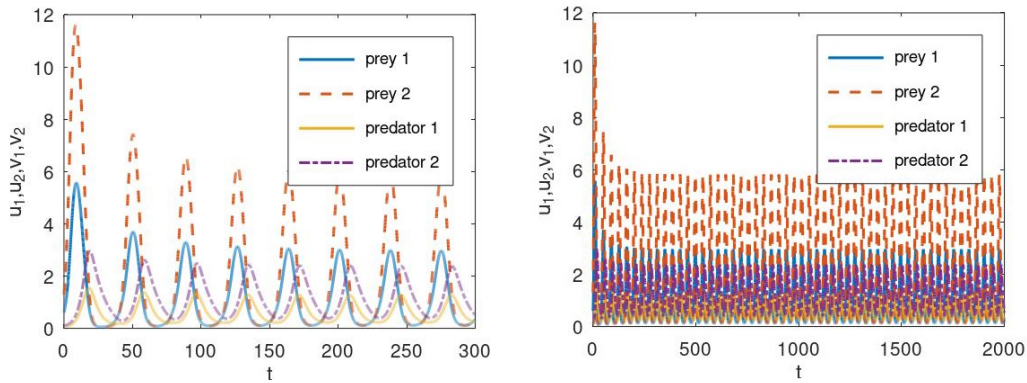


Figure 5.12: Oscillatory Behaviour With all Nonlinear Functions

Similarly, Figure 5.11 shows oscillatory behaviour when only the migration term is permitted to have a more complicated function, and Figure 5.12 shows that in the case where all the functions are permitted to be more complex we still see oscillatory behaviour. In all of these cases, the same parameters are used as in the simulations that didn't exhibit oscillatory behaviour, with the same exception; that $a_1 = 0.05$ and $a_2 = 0.03$. We see in the Figures that these different cases lead to the oscillations dampening out entirely in the long run, and the oscillations remaining for all time respectively.

Just as in the non-oscillatory case, we see again that the migration term has little effect on the overall behaviour of the system, but does impact the quantitative behaviour. We also see that using a Holling Type II functional response rather than a functional response that is linear with regards to the prey's population density, the population peaks are substantially greater, and it takes much longer for the system to settle towards the equilibrium value.

Chapter 6

Conclusion and Discussions

In this paper we extended current spatially non-homogeneous population dynamics models in order to account for the recently discovered fear effect. To that end we proposed the model (2.1). We expect that this model should be a plausible suggestion as it follows from previous research done by Li et al. [12] and Wang et al. [27]. The mathematical analysis in Chapter 3 and Chapter 4, as well as the numerical simulations done in Chapter 5 show that this hypothesis was correct, and the behaviour exhibited by this model matches what we would expect in these circumstances. That is; extinction of all species, persistence of the prey combined with extinction of the predator, and uniform persistence are all possible and stable within the constraints of this model. Additionally, we see the out of sync oscillatory behaviour that is typical of a predator-prey system.

Firstly, it is important to prove that this model is a valid proposition. Therefore we spent Chapter 3 using typical techniques from calculus to prove that the model meets the necessary conditions of being positive and bounded. Having shown that the model exhibits these important properties, we moved forward with equilibrium analysis in Chapter 4. The model (2.1) has a large amount of parameters, which is likely to overcomplicate our analysis. Thus in section 4.1 we reduce the number of parameters by nondimensionalizing the model, resulting in the simpler model (4.1).

It was our goal to determine the conditions necessary for the existence of a trivial equilibrium, and semi-trivial equilibrium, as well as a positive equilibrium. We successfully determined these conditions for the trivial equilibrium as well as the semi-trivial equilibrium, the latter of which is summarized in Lemma 4.2.1. For this 4-dimensional model, showing the conditions in which the positive equilibrium exists was beyond the scope of this thesis.

Having determined when the simpler equilibria exist, it was important to determine what further conditions lead to these steady state solutions being stable. Despite being a fourth order system, the simpler nature of these equilibria allowed us to make use of the Routh-Hurwitz criteria for second order systems to solve this problem. This is because the fourth order system simplifies, in these cases, to a pair of disjoint second order systems. These results are summarized in Lemma 4.3.2 and Lemma 4.3.3.

To extend the existing mathematical analysis we conducted numerical simulations in Chapter 5. Firstly, in section 5.1, we used simulations to test the conditions that we determined in Chapter 4. Using values we determined through use of the Lemmas 4.2.1, 4.3.2, and 4.15, we produced the graphs shown in Figures 5.1, and 5.2.

Afterwards we extend the analysis in section 5.2 by using simulations to determine whether a stable positive equilibrium may exist or not. We see that it does, and this simulation is shown in Figure 5.4. Additionally, when we relax the simplifying assumptions made in Chapter 4 to make the math more manageable, simulations suggest that the system will still exhibit a stable positive equilibrium solution. This is shown in Figures 5.5, 5.6, and 5.7.

These results were found using a set of parameter values that resulted in a relatively small carrying capacity, and do not exhibit the expected oscillatory behaviour. The lack of oscillations makes observing the equilibrium more clear, but we run several more simulations to show that oscillatory behaviour is also possible. To achieve this we adjust the parameter values to increase the carrying capacity, and this gives us the Figures 5.9, 5.10, 5.11, and 5.12. In the cases where we used a Holling Type II functional response, we see that after a long transient behavior, the solutions of the system eventually converge to an oscillation of consistent ampli-

tude and continues to oscillate for all time. In the simulations which instead used a functional response which is linear with regard to the prey's population density, the transient behaviour is that the oscillations entirely damp out and in the long term, the trajectories settle on a single equilibrium value, where they remain for all time.

In both the oscillatory and non-oscillatory simulations, it appears that the migration function has very little impact on the qualitative behaviour of the system, but impacts the quantitative behaviour, and adds important flexibility to the system. We see in Figure 5.8, as an example, that choosing the same set of parameters that leads to some species going extinct in a simpler system, a nonlinear migration leads to the possibility of those species persisting under the same set of parameters. This, of course, is the same thing that Huffaker noted in [9] and is the motivation for the patchiness of our model.

The form of the functional response, on the other hand, affects the qualitative behaviour the system much more significantly. In the non-oscillatory simulations, choosing a Holling Type II functional response increases the equilibrium population levels of the prey, and reduces the equilibrium population levels of the predator. Additionally, the trajectories become much more strongly attracted to this equilibrium value. In the case of the oscillatory simulations, the population peaks are larger for every species, but the rate of the oscillations is less. Where in the case of a functional response that is linear with regards to the prey population density, we see 4 oscillations between time $t = 0$ and $t = 100$, in the nonlinear case we see only 3 oscillations over the same time interval.

There is certainly more work to be done on this model than what has been done in this thesis. Obviously it would be important to use mathematical analysis to prove the uniform persistence of the species, and under which conditions this would be expected; such as Li et al. did in Theorem 4.2 of [12], and Wang et al. did in Theorem 4.4 of [27]. Since our model is essentially a combination of these it seems reasonable to expect a similar theorem could be found, especially in combination with the data from the numerical simulations. Additionally it remains to be seen what the conditions are for the existence and stability of the semi-trivial

equilibrium in the case of non-linear functions where linearity was assumed in Chapter 4. One may assume a number of different forms for the functions G_i , and C_{ij} , as well as considering a different possible form for the function describing the fear effect than the one considered by Wang et al. in their analysis in chapter 4 of [27]. We could consider the other possible functions mentioned in chapter 1 of this thesis, as Wang et al. did in Chapter 5.

It is also interesting to note that according to Theorem 4.5 of [27], there is a limit cycle under certain conditions of the simpler model, and consequently, a Hopf Bifurcation. Due to the similarity of the models it would be interesting to determine if that remains true in our patchy version of this model.

Finally, we may also take inspiration from Li et al. and extend their evolution analysis of section 4.2 in [12]. However, this looks to be quite an undertaking as it would turn our 4-dimensional model into a 6-dimensional model. Nevertheless, numerical simulations on the subject may be very interesting.

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