POPULATION DYNAMICS WITH ALLEE AND REFUGE EFFECTS

BURÇİN KÜLAHÇIOĞLU

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Approval of the Graduate School of Natural and Applied Sciences

Prof. Dr. Abbas Kenan Çiftçi
Director

I certify that this thesis satisfies all the requirements as a thesis for the degree of Doctor of Philosophy.

Prof. Dr. Gözde Yazgı Tütüncü
Head of Department

We have read the dissertation entitled **"Population Dynamics with Allee and Refuge Effects"** completed by **BURÇİN KÜLAHÇIOĞLU** under supervision of **Prof. Dr. Ünal Ufuktepe** and we certify that in our opinion it is fully adequate, in scope and in quality, as a dissertation for the degree of Doctor of Philosophy.

Prof. Dr. Ünal Ufuktepe
Supervisor

Examining Committee Members

Date: 25/12/2018

Prof. Dr. Ünal Ufuktepe
Dept. of Mathematics, AUM, KUWAIT

Prof. Dr. Emine Mısırlı
Dept. of Mathematics, Ege University

Prof. Dr. Gözde Yazgı Tütüncü
Dept. of Mathematics, İUE

Assoc. Prof. Dr. Fatma Serap Topal
Dept. of Mathematics, Ege University

Asst. Prof. Dr. Sevin Gümgüm
Dept. of Mathematics, İUE

ABSTRACT

POPULATION DYNAMICS WITH ALLEE AND REFUGE EFFECTS

BURÇİN KÜLAHÇIOĞLU
Ph.D. in Applied Mathematics and Statistics
Graduate School of Natural and Applied Sciences
Supervisor: Prof. Dr. Ünal Ufuktepe
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The Allee and the refuge effects are observable mechanisms in the nature. Incorporating these effects into the population models allows more biological processes to be taken into account and makes the model represent the nature better. The main purpose of this thesis is to formulate more realistic population models and to gather information about the future behavior of the populations by analyzing these models. In this thesis, we construct discrete-time population models by incorporating the refuge and Allee effects to previously used host-parasitoid and prey-predator models. We show the existence of positive fixed points and study the stability properties. We analyze the global behavior for some of the models. The numerical simulations and bifurcation diagrams verify the impact of refuge and the Allee mechanism on the system.

Keywords: population models, discrete dynamical systems, allee effect, refuge effect, stability analysis.

ÖZ

ALLEE VE SIĞINMA ETKİLERİ ALTINDA POPÜLASYON DİNAMİĞİ

BURÇİN KÜLAHÇIOĞLU
Uygulamalı Matematik ve İstatistik, Doktora
Fen Bilimleri Enstitüsü
Tez Danışmanı: Prof. Dr. Ünal Ufuktepe
Ocak 2019

Allee ve sığınak etkileri doğada gözlemlenebilen mekanizmalardır. Bu etkilerin popülasyon modellerine dahil edilmesi, daha fazla biyolojik sürecin hesaba katılmasına imkân verir ve modelin doğayı daha iyi temsil etmesini sağlar. Bu tezin temel amacı daha gerçekçi popülasyon modelleri oluşturmak ve bu modelleri analiz ederek popülasyonların gelecekteki davranışları hakkında bilgi edinmektir. Bu tezde, daha önceden çalışılmış konakçı-parazitoid ve av-avcı modellerine sığınak etkisi ve Allee etkisi eklenerek kesikli-zaman popülasyon modelleri oluşturulmuştur. Pozitif sabit noktaların varlığı gösterilmiş ve kararlılık analizleri yapılmıştır. Modellerin bazıları için global davranış incelenmiştir. Nümerik simülasyonlar ve dallanma diyagramları, sığınak ve Allee mekanizmalarının sistem üzerindeki etkisini doğrulamaktadır.

Anahtar Kelimeler: popülasyon modelleri, kesikli dinamik sistemler, allee etkisi, sığınak etkisi, kararlılık analizi.

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To my family, and in memory of my beloved father ...

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Chapter 1

Introduction

Discrete-time models are both more amenable to computerization and mathematically simpler. As a result, many researchers prefer to use discrete-time models in their study areas. In this thesis, we use discrete-time population models in order to gather information about the future behavior of the populations.

If there is co-evolution between two species, then two-dimensional models are used to describe the population dynamics and the interaction. The most well-known examples of two dimensional population models are prey-predator and host-parasitoid interactions.

Predator-prey interactions are an important study areas for ecologists and mathematicians. The dynamic interaction between these species is a dominant theme because of its universal applicability and importance. Traditionally, most common studies in this arena focus on the dynamics of the populations under varying effects and parameters [1, 6, 20, 24, 26, 27, 37, 47]. Allee effects and hiding behavior of prey represent an important portion of these studies. Numerous researchers, including Hassell and May ([12, 15]), have studied the hiding behavior of prey.

Host-parasitoid interactions is another important area attracting researchers' attention [5, 18, 22, 23, 34, 50]. Insect parasitoids are natural enemies of insects, and used as biological control agents. They effect some insect groups including Diptera (two-winged flies) and the Hymenoptera (bees, wasps, sawflies and ants) [13]. Some pests that are resistant to chemicals can be destroyed by parasitoids. This underlines the importance of studying host-parasitoid interaction, developing existing models, and investigating dynamic behaviors.

The first and the main aim of this thesis is to formulate "better" population models. Here, "better" refers to "more realistic". Technically, we add the Allee and the refuge effects; biologically, we add the concepts "cooperation", "cost of rarity", and "heterogeneity of the environment" to the existing models in order to achieve this aim. In all chapters, we develop models under various Allee and refuge settings. We refer to studies [6, 7, 37, 41] in order to incorporate these effects in the systems we study.

The second aim is to find an answer to the question "How will the populations behave in the long run?" . In order to achieve this goal, we analyze the dynamical properties of the formulated systems. For all the models we construct, we give the proof of existence of the positive fixed point under some conditions. We study the stability of the system for both hyperbolic and non-hyperbolic cases. We write some codes with Mathematica for the calculation of non-negative fixed points under some conditions of parameters, for simulations of phase diagrams, time series, and bifurcation diagrams in Numerical Simulations sections. We give numerical simulations for verification and illustration of the result. In addition, we study the global behavior of some of the models.

Finally, we aim to compare the models mathematically , and to highlight the biological relevance of the results.

We organize this thesis as follows:

In the next chapter, we give a short introduction to discrete dynamical systems and stability analysis. In addition, we mention about the Allee and the refuge effects, with reference to the literature.

In Chapter 3, we formulate and study a host-parasitoid model. In [22], the following model is given and analyzed:

$$\begin{aligned} H_{t+1} &= \frac{\lambda H_t}{1 + kH_t e^{-bP_t}} e^{-bP_t}, \\ P_{t+1} &= \beta H_t (1 - e^{-bP_t}), \end{aligned} \tag{1.1}$$

where H_t and P_t are the population sizes of host and parasitoid, respectively at time t. All parameters are positive. First we add a constant proportion refuge effect to the model, and study the resulting model. We then add both refuge effect and a mate limitation Allee effect on the host population, and compare the models.

In Chapter 4, we add predator saturation on prey and mate limitation on predator into the system given by [37]:

$$\begin{aligned} N_{t+1} &= N_t + rN_t(1 - N_t) - (1 - d)aN_tP_t, \\ P_{t+1} &= P_t + aP_t((1 - d)N_t - P_t), \end{aligned} \tag{1.2}$$

where the parameters are positive. In this model, N_t and P_t are the population sizes of prey and predator, respectively at time t. We study the resulting model.

In Chapter 5, we construct and study discrete-time Holling Type 2 models with the refuge and Allee effects, respectively. The prey-predator model given by [1] is as follows:

$$\begin{aligned} x_{n+1} &= ax_n(1 - x_n) - \frac{bx_ny_n}{1 + \varepsilon x_n}, \\ y_{n+1} &= \frac{dx_ny_n}{1 + \varepsilon x_n}, \end{aligned} \tag{1.3}$$

where x_t and y_t are the population sizes of prey and predator, respectively at time t. All parameters are positive. We add a constant number of refuge, and mate limitation Allee effects.

In Chapter 6, we draw conclusion.

Chapter 2

Preliminaries

Discrete time models investigate the dynamic behavior of the system by doing iterations. When the current situation of the system is known, one-step iterated value gives the value of the following period. These models consist of difference equations generated by the maps. The problem is that difference equations are unsolvable except linear case and some special cases. Thus, in order to discover the long-run behavior of the system, instead of solving it, some different approaches may be used, such as finding fixed points and making stability analysis of them.

In this chapter, firstly, we give some concepts, definitions and theorems which are essential in the analysis of discrete time systems. We refer to the book [10] for this part. Then we present some population models, and explain the derivation of models with Allee and the refuge effects. We refer various studies for this part most of which are based on the studies [2, 3, 7, 15].

2.1 One Dimensional Models

Let $f : \mathbb{R} \to \mathbb{R}$ be a map where $\mathbb{R}$ is the set of real numbers. If we take an initial point $x_0 \in \mathbb{R}$, and iterate this point with respect to the map f, then the set of values found by iterations give the orbit $O(x_0)$ of the point x_0. That is

$$O(x_0) = \{x_0, f(x_0), f^2(x_0), f^3(x_0), ...\},$$

where $f^n = \underbrace{fofofo...f}_{\text{n times}}$. If we let $x_n = f^n(x_0)$, then we obtain the first-order difference equation

$$x_{n+1} = f(x_n). \tag{2.1}$$

Definition (Fixed Point)**.** Consider the first order difference equation (2.1). A point x^* is said to be a fixed point of the map f if $f(x^*) = x^*$.

2.1.1 One Dimensional Stability Analysis

Definition. [10] Let $f : \mathbb{I} \to \mathbb{I}$ be a map and x^* be a fixed point of f, where $\mathbb{I}$ is an interval in the set of real numbers $\mathbb{R}$. Then x^* is said to be

- stable if for any $\varepsilon > 0$, there exists $\delta > 0$ such that for all $x_0 \,\epsilon\, \mathbb{I}$ with $|x_0\text{-}x^*| < \delta$ we have $|f^n(x_0)\text{-}x^*| < \varepsilon$ for all n $\epsilon\, \mathbb{Z}^+$.
- attracting if there exists $\eta > 0$, such that $|x_0 - x^*| < \eta$ implies $\lim_{n\to\infty} f^n(x_0) = x^*$; globally attracting if $\eta = \infty$.
- asymptotically stable if it is both stable and attracting, it is globally asymptotically stable if it is both stable and globally attracting.

Theorem 2.1 *[10] Let f be a map which is continuously differentiable at x^*. And let x^* be a hyperbolic fixed point of the map f that is $|f'(x^*)| \neq 1$. Then*

(i) If $|f'(x^*)| < 1$, then x^* is asymptotically stable.

(ii) If $|f'(x^*)| > 1$*, then* x^* *is unstable.*

Theorem 2.2 *[10] Let* x^* *be a fixed point of the map* f *such that* $f'(x)$, $f''(x)$, *and* $f'''(x)$ *are continuous at* x^**. There are two types of non-hyperbolic fixed points:*

(I) $f'(x^*) = 1$

- *(i) If* $f''(x^*) \neq 0$ *then* x^* *is unstable (semistable).*
- *(ii) If* $f''(x^*) = 0$ *and* $f'''(x^*) > 0$*, then* x^* *is unstable.*
- *(iii) If* $f''(x^*) = 0$ *and* $f'''(x^*) < 0$*, then* x^* *is asymptotically stable.*

(II) $f'(x^*) = -1$

- *(i) If* $Sf(x^*) < 0$*, then* x^* *is asymptotically stable,*
- *(ii) If* $Sf(x^*) > 0$*, then* x^* *is unstable, where* $Sf(x)$ *is Schwarzian derivative of* f *such that:*

$$Sf(x) = \frac{f'''(x)}{f'(x)} - \frac{3}{2}\left(\frac{f''(x)}{f'(x)}\right)^2.$$

2.1.2 One Dimensional Bifurcation

Parameters are used in modelling to represent growth rate, capacity constraint, interaction strength etc. Bifurcation refers to the change of dynamic structure of the system as the parameter changes. This requires finding values of parameters at which the behavior is changing, and also the interval of parameters for which the system exhibits the same behavior.

Remark. [10]: Let $H_\mu(x) = H(\mu, x)$ is a $\mathbb{C}^2$ one-parameter family of one-dimensional maps (i.e both $\frac{\partial^2 H}{\partial x^2}$ and $\frac{\partial^2 H}{\partial \mu^2}$ exist and are continuous), and x^* is a fixed point of H_{μ^*}, with $H'_{\mu^*}(x^*) = 1$.

- Transcritical bifurcation appears if

$$\frac{\partial H}{\partial x}(\mu^*, x^*) = 1, \quad \frac{\partial H}{\partial \mu}(\mu^*, x^*) = 0, \text{and} \quad \frac{\partial^2 H}{\partial x^2}(\mu^*, x^*) \neq 0.$$

- Pitchfork bifurcation appears if

$$\frac{\partial H}{\partial x}(\mu^*, x^*) = 1, \quad \frac{\partial H}{\partial \mu}(\mu^*, x^*) = 0, \text{and} \quad \frac{\partial^2 H}{\partial x^2}(\mu^*, x^*) = 0.$$

Theorem 2.3 *[Period-doubling Bifurcation] : Suppose that*

1. $H_\mu(x^*) = x$ *for all* μ *in an interval around* μ^*
2. $H'_\mu(x^*) = -1$
3. $\frac{\partial^2 H}{\partial \mu \partial x}(\mu^*, x^*) \neq 0$

Then there is an interval I *about* x^* *and a function* $p : I \to \mathbb{R}$ *such that* $H_{p(x)}(x) \neq x$ *but* $H^2_{p(x)}(x) = x$.

2.2 Two Dimensional Models

Two dimensional discrete time linear systems have the form

$$X_{n+1} = AX_n, \tag{2.2}$$

where $A=\begin{pmatrix} a_1 & a_2 \\ a_3 & a_4 \end{pmatrix}$ and $X_n = \begin{pmatrix} x_n \\ y_n \end{pmatrix}$.

The only fixed point of (2.2) is $X^* = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$.

2.2.1 Two Dimensional Stability Analysis

Theorem 2.4 *(The Trace-Determinant Plane)[10]: Let* $A = (a_{ij})$ *be a* 2×2 *matrix. The spectral radius* $\rho(A) < 1$ *if and only if*

$$|trA| - 1 < detA < 1$$

Corollary 2.5 *: The origin in (2.2) is asymptotically stable if and only if*

$$|trA| - 1 < detA < 1$$

Linear models are generally unrealistic for real world applications, as interactions do not allow the system to be linear. Ignoring these relations makes the model simpler, but less reliable. Hence, for a dynamical system, being linear with no interactions is a strong condition, and generally does not hold.

For the stability analysis of non-linear models, linearization methods should be used. It is common to use the eigenvalues of the Jacobian matrix evaluated at the fixed point to determine the nature of that fixed point. Here, Jacobian matrix can be thought as coefficient matrix in linear case. This linearization can be done for the neighborhood of a point.

Theorem 2.6 *(Stability via Linearization)[10]: Let* $f : \mathbb{G} \subset \mathbb{R}^2 \to \mathbb{R}^2$ *be a* $\mathbb{C}^1$ *map, where* $\mathbb{G}$ *is an open subset of* $\mathbb{R}^2$*,* X^* *is a fixed point of f, and A is the Jacobian matrix such that* $A = Df(X^*)$*. Then the following statements hold true:*

(i) If $\rho(A) < 1$*, then* X^* *is asymptotically stable.*

(ii) If $\rho(A) > 1$*, then* X^* *is unstable.*

(iii) If $\rho(A) = 1$*, then* X^* *may or may not be stable.*

By using Theorem 2.6 and Corollary 2.5, we can determine if X^* is stable or unstable. In addition, the stability type of it can be analyzed according to eigenvalues after linearization. Let A be the Jacobian matrix such that $A = Df(X^*)$, and λ_1 and λ_2 are corresponding eigenvalues. The followings hold true for X^*:

$$X^* \quad is \begin{cases} \text{saddle,} & \text{if} \quad 0 < \lambda_1 < 1 < \lambda_2 \\ \text{oscillatory saddle,} & \text{if} \quad -1 < \lambda_1 < 0, \quad \lambda_2 < -1 \\ \text{sink,} & \text{if} \quad 0 < \lambda_2 < \lambda_1 < 1 \\ \text{oscillatory sink,} & \text{if} \quad 0 < \lambda_1 < 1, \quad -1 < \lambda_2 < 0 \\ \text{source,} & \text{if} \quad \lambda_2 > \lambda_1 > 1 \\ \text{oscillatory source,} & \text{if} \quad \lambda_1 > 1, \quad \lambda_2 < -1 \\ \text{spiral sink,} & \text{if} \quad \lambda = a \pm ib, \quad |\lambda| < 1, \quad b \neq 0 \\ \text{spiral source,} & \text{if} \quad \lambda = a \pm ib, \quad |\lambda| > 1, \quad b \neq 0 \\ \text{center,} & \text{if} \quad \lambda = a \pm ib, \quad |\lambda| = 1, \quad b \neq 0. \end{cases}$$

2.2.2 Center Manifolds

Stability of the fixed points of a map can be analyzed according to eigenvalues after linearization. In some cases, the orbits around the fixed point can be restrained by neither the attraction of the stable manifold nor the repulsion of the unstable manifold. These kinds of orbits refer to the center manifold of a fixed point.

The following theorem has analogues for stable and unstable manifolds, but we focus on the center manifold.

Theorem 2.7 *[25, 29, 33] Consider a map $F : \mathbb{R}^k \to \mathbb{R}^k$ such that $F \in \mathbb{C}^2$ and $F(0) = 0$. Let DF_0 be the linear part of the map, and the center subspace E^c is the space spanned by the eigenvectors of DF_0 corresponding to the eigenvalues satisfying $|\lambda|$=1. Then there exist center manifold M_c tangent to E^c and it is invariant.*

The theorem is applicable for more dimensions, but we only consider it for the two-dimensional case. If $|\lambda_i| \neq 1$ $i = 1, 2$, then it is simple. But the non-hyperbolic case with $|\lambda_1| = 1$ and $|\lambda_2| < 1$ is a more complicated case, because it can be either stable or unstable. If a non-hyperbolic map is defined on $\mathbb{R}^2$, then the dynamics may be analyzed by studying the dynamics on an associated one-dimensional center manifold M_c.. We focus on the extinction fixed point $(0, 0)$ to use the theorem. Then the two-dimensional discrete system can be written as follows:

$$\begin{aligned} x_{n+1} &= Ax_n + f(x_n, y_n) \\ y_{n+1} &= By_n + g(x_n, y_n), \end{aligned} \tag{2.3}$$

or

$$\begin{aligned} x &\longrightarrow Ax + f(x, y) \\ y &\longrightarrow By + g(x, y), \end{aligned} \tag{2.4}$$

where A lies on the unit circle, B lies in the unit circle, and the functions f and g satisfies the following conditions:

$$\begin{aligned} f(0, 0) = 0, &\quad g(0, 0) = 0 \\ Df(0, 0) = 0, &\quad Dg(0, 0) = 0. \end{aligned} \tag{2.5}$$

Theorem 2.8 *[10] There is a C^r center manifold for the system (2.4) that can be represented locally as*
$M_c = \{(x, y) \in \mathbb{R} \times \mathbb{R} : y = h(x),\ |x| < \delta,\ h(0) = 0,\ Dh(0) = 0,$ for sufficiently small $\delta\}$.
Furthermore, the dynamics restricted to M_c are given locally by the map

$$x \longrightarrow Ax + f(x, h(x)), \qquad x \in \mathbb{R}. \tag{2.6}$$

Theorem 2.9 *[10] If the fixed point 0 of the equation (2.6) is stable, asymptotically stable, or unstable then the fixed point $(0, 0)$ of the system (2.4) is also stable, asymptotically stable, or unstable, respectively.*

By substituting $y_n = h(x_n)$ into the second equation of the system (2.3), we obtain

$$y_{n+1} = h(x_{n+1}) = h(Ax_n + f(x_n, h(x_n)) = Bh(x_n) + g(x_n, h(x_n))$$

Finally, we obtain the following functional equation:

$$h[Ax + f(x, h(x))] - Bh(x) - g(x, h(x)) = 0$$

Center Manifold Theorem is applicable for only the fixed point $(0, 0)$. Hence the other fixed points must be transformed $(0, 0)$ to use this theorem.

2.2.3 Two Dimensional Bifurcation

If the Jacobian matrix of a two-dimensional system has an eigenvalue 1 or -1 at the point $(0, 0)$, Center Manifold Theorem may be used to find one dimensional map $f_\mu(u)$ defined on the center manifold M_c. Bifurcation types can be determined just as in one-dimensional case. If the system has Jacobian matrix has eigenvalues $\lambda_{1,2}$ with $|\lambda| = 1$, then we have Neimark-Sacker bifurcation, which can not be observed in one-dimensional case.

2.3 Some Population Models

For discrete time one dimensional population modelling, there are two types: linear and non-linear. First is linear model in which growth rate can be about birth, death, immigration, emigration rate, and is independent from density. These models are in the form: $x_{n+1}=rx_n$, where r is growth rate and it is constant. The second is non-linear model, in which growth depends on density. A population model is said to be density-dependent if the per-capita growth rate of the population changes according to the density. The general form is $x_{n+1}=f(x_n)x_n$. The classical approach suggests that f, namely fitness function (per-capita growth rate), should be chosen as a decreasing function because of intraspecific competition and capacity constraint [28].

Two-dimensional models represent the interaction between two species. Depending on the model chosen, the interaction can be mutualistic, commensalistic, prey-predator, competitive, etc. An absolute isolation is almost impossible for any organism, and interactions are essential for survival. In nature, every single organism may be affected by others in some way. However, if the interaction between two species has a great importance for both population, then two dimensional systems may be used to model the population dynamics. Other factors, which affect the growth of the population, are covered by the growth parameter in these models.

Almost all organisms in nature live as preys, predators, parasites or parasitoids in some way. Generally, host-parasitoid models are thought as a special case of prey-predator interaction. However, unlike the parasites and parasitoids, predators are generally bigger than their prey. Parasites harm to their hosts but generally do not kill unlike parasitoids. So, technically the biologists use these three words in specific ways.

The co-evolution of prey-predator and host-parasite are similar with one important difference- the host should not be killed. Similar to prey-predator interaction, the host is eventually killed by parasitoid. However, the evolutionary strategy of the parasitoid is different from that of a parasite or predator. The parasitized host can no longer be considered as a member of the host species, but must be viewed as a container for the parasitoid [48].

2.3.1 Derivation of Models with Allee Effect

The Allee Effect is a biological concept characterized by positive causal relationship between the number of individuals in a population and their overall individual fitness [3]. Here just a simple idea works: “The more the merrier”

[7]. The classical approach focuses on the intra specific competition. Because of limited capacity and resources, if the population is small, then each individual can access a greater amount of resources. However, the classical idea lacks the terms “cooperation” and “the cost of rarity”.

If the population is too small, then foraging, hunting, finding mates for reproduction, or protection becomes more difficult for individuals. These difficulties are caused by lack of cooperation, and can be thought as the cost of rarity [40]. As a result, when the population is small, a positive relationship between the population size and the growth should be expected. On the other hand, at high densities, competition is more dominant than cooperation, so the Allee effect begins to lose its impact. As a result, the relationship reverses itself at high densities. Considering the Allee effect is important in understanding why some populations get smaller and even face extinction.

Allee Effect was identified by Warder Clyde Allee, who is best known for his research on animal behavior and proto-cooperation. As a zoologist he generally gave examples of Allee effect on animals, not on plants. In the early studies, Allee effect could be observed in experiments, but no mechanism could be proposed. For example, during efforts to combat with the tsetse flies, it was observed that below a minimum density, they disappeared suddenly and spontaneously. A laboratory experiment showed that higher densities of fertilized urchin and frog eggs led to these species accelerated development. Group rotifers were observed to be more resistant to chemical toxins than individuals [7].

The Allee effect can be categorized in two main types: strong and weak. If there exist a critical size or density below which the population becomes extinct, then the population has a strong Allee effect; If there is no critical density, but the population growth rate rises with increasing densities, then it has a weak Allee effect [30, 43].

In [31] the following mathematical definition is given and used:

Definition (Strong Allee Effect)**.** Model x_{n+1}=$g(x_n)x_n$ is said to have a strong Allee effect if the following conditions hold true.

(i) $g'(x) > 0$ for $x \in (0, \epsilon)$ for some $\epsilon > 0$

(ii) $g(0) < 1$

(iii) There exists a unique $k > 0$ such that $g(k) = 1$ and $g'(k) < 0$

Allee Effect changes the fitness function of the model. If $f(x)$ is the fitness function of the model without Allee effect, then the new fitness is $g(x) = A(x)f(x)$, where $A(x)$ is the Allee effect function representing the positive density factor. If there is no Allee effect, then $A(x) = 1$ and the fitness will be equal to the negative density factor $f(x)$.

Although there are many mechanisms of the Allee effect, they can be categorised into two main types:

(i) mechanisms related to survival

(ii) mechanisms related to reproduction

Allee effect caused by predator saturation is a mechanism related to survival whereas Allee effect caused by mate limitation is a mechanism related to reproduction. Many authors focused on these two mechanisms [8, 37, 41].

Predator saturation causes an increase in individual prey vulnerability, as prey population gets sparser. This mechanism is observed in many species, including colonial seabirds, synchronously emerging insects, island fox, and American toad [7]. For the Allee effect due to predator saturation, generally $A(x) = exp(-m/(1 + sx))$, where m represents predation intensity and s is the proportional to the handling time, is used [41]. Here, handling time can be considered as a function of the time spent in pursuing, hunting, eating, and digesting prey. On the other hand, the predation intensity β depends on the distance between species, their speeds, and the proportion of successful attacks [14].

Mate limitation is probably the most observable mechanism of the Allee effect. Cod, gypsy moth, alpine marmot, Glanville fritillary butterfly are some species facing mate limitation effect [7]. The formula $A(x) = x/(m + x)$ is used for the probability of finding a mate, where $1/m$ is an individual's searching efficiency.

In [45], more information about the model derivation can be found.

"Allee principle" was introduced in the 1950s, but there were few studies about this effect until 90s. Between these years, the field of ecology was heavily focused on the role of competition (the classical approach). However, when the bio-diversity crisis emerged, it became important to focus on the causes. As a result, the Allee effect became a popular area. Depending on the models used, the Allee effect may have a stabilizing [40] or destabilizing influence [49] on the models.

2.3.2 Derivation of Models with Refuge Effect

Although Refuge Effect is not used as frequently as Allee Effect in recent studies, it is important for developing the models. There is no complex mechanism for it, it simply assumes that some prey may be completely free from predation within a temporal or spatial refuge. Refuge effect depends on the heterogeneity of the environment. Researchers recognize that the physical setting is never perfectly uniform, so part of the host population may be less exposed, and thus less vulnerable to attack. It has become common to refer to patchy environments, which are spatially as well as temporally heterogeneous. Part of the argument is that refuges serve as sites for maintaining vulnerable species that might otherwise become extinct. Such sites also indirectly benefit the exploiting species, since a constant spillover of victims into the unprotected areas guarantees a constant food source [9].

The prey refuge effect is a mechanism caused by heterogeneity in the environment. It refers to the fact that some of the prey can be sheltered from danger or can be inaccessible to predators. The refuge effect has been studied widely by Jana [21], McNair [35]. This effect contributes positive feedback to the growth of prey while having a negative impact on predators. The studies indicate that the effect of refuge used by prey has a substantial effect on the coexistence of prey and predator, in that it increases the equilibrium density of prey population, and stabilizes the positive fixed point of the system.

Some studies on the prey refuge effect show that this effect either decreases with increasing prey density, or increases with both predator and prey density, and the addition of prey refuge substantially reduces the risk of prey extinction [32, 44]. However, it also plays a destabilizing role under a very restricted set of conditions [32].

The refuge effect is commonly considered to act on a fixed proportion or fixed number of the prey population [16, 20, 24, 35, 39, 42].

Chapter 3

A Host-Parasitoid Model

In this chapter, firstly, we give the model construction. Then we develop new models by incorporating the refuge effect and the Allee effect. We investigate the resulting models.

3.1 Model Construction

The general framework for discrete-type host-parasitoid model is as follows:

$$\begin{aligned} H_{t+1} &= rH_t f(H_t, P_t), \\ P_{t+1} &= \beta H_t \left(1 - f(H_t, P_t)\right), \end{aligned} \tag{3.1}$$

where H_t and P_t are population sizes of host and parasitoids, respectively in the generation t. In the host population, r is reproduction rate of hosts, and the function $f(H_t, P_t)$ is the fraction of host escaping parasitism. In the parasitoid equation, β is the average number of eggs (larvae) released by parasitoid on a single host. Model (3.1) remains the basis for most recent studies.

Nicholson-Bailey Model is one of classical models, used in many texts. This model adds further assumptions to the general model. The total number of encounters with hosts by parasitoids is in direct proportion to host density and the encounter number is distributed randomly among the available hosts. Using Poisson distribution, the following system is found:

$$\begin{aligned} H_{t+1} &= rH_t e^{-aP_t} \\ P_{t+1} &= \beta H_t \left(1 - e^{-aP_t}\right) \end{aligned} \tag{3.2}$$

where e^{-aP_t} stands for probability of not to be infested by parasitoid and $1-e^{-aP_t}$ is the probability of being infested by parasitoid at time t. Equation (3.2) is known as Nicholsan-Bailey host-parasitoid model which is commonly used in ecology. The first studies depend on this model [36]. The other host-parasitoid models are thought to be developed versions of Nicholsan-Bailey, which although not realistic itself enough, is a good base for the developments.

If the reproduction of host is constant, then the model is unrealistic due to the fact that, in the absence of the parasitoid, the host grows exponentially with no limit. In order to make the model realistic, a density dependent model may be used. Unlike the predator in the general prey-predator models, the parasitoid in the host-parasitoid models has a production rate closely defined by interactions between host and parasitoid. Hence, generally it is sufficient to use a density dependent population model for the host, which is also thought to stabilize the system [4].

In 1980, Wang [50] asked a key question: 'Does the ordering of parasitism and density dependence in the host life cycle have a significant effect on the dynamics of the model?' May et al. addressed this question by giving some different models in [34]. They proposed 3 different model types [34]:

- Model 1: In the following type of models, parasitism acts first, and then the density dependence takes place at a level determined by the density of parasitized and unparasitized hosts (i.e. $g(H_t)$):

$$\begin{aligned} H_{t+1} &= \lambda H_t g(H_t) f(P_t), \\ P_{t+1} &= H_t \left(1 - f(P_t)\right). \end{aligned} \tag{3.3}$$

- Model 2: Density dependence acts first followed by parasitism in the following type:

$$\begin{aligned} H_{t+1} &= \lambda H_t g(H_t) f(P_t), \\ P_{t+1} &= H_t g(H_t) \left(1 - f(P_t)\right). \end{aligned} \tag{3.4}$$

- Model 3: Parasitism acts first and then the density dependence takes places but now only on the survivors from parasitism (i.e. $H_t f(P_t)$) and the model type is:

$$\begin{aligned} H_{t+1} &= H_t g(H_t, f(P_t)) f(P_t), \\ P_{t+1} &= H_t \left(1 - f(P_t)\right). \end{aligned} \tag{3.5}$$

In [34], it is concluded that the sequence of host parasitoid interaction and density dependence has a marked effect on the population dynamics by examining three different host-parasitoid models. Of the three models discussed, the most frequent choice will be between Models 2 and 3.

After three frameworks for host-parasitoid interaction was proposed in [34], some different models have been created accordingly. In model (3.5), if we substitute $f(P_t) = exp(-bP_t)$ and $g(H_t, f(P_t)) = \lambda/(1 + kH_t exp(-bP_t))$, and add β multiplier to the second equation, the resulting model is as follows:

$$\begin{aligned} &H_{t+1} = \frac{\lambda H_t}{1 + kH_t e^{-bP_t}} e^{-bP_t}, \\ &P_{t+1} = \beta H_t (1 - e^{-bP_t}). \end{aligned} \tag{3.6}$$

In [22], the model (3.6) was formulated and studied. In (3.6), the host population in the absence of the parasitoid is modeled by Beverton-Holt equation $\lambda H/(1 + kH)$, which is obtained if a decreasing rational function is used as fitness (density function). The parameter β denotes average number of egg (larvae) released by parasitoid on a single host. All parameters are positive. In [28], the Allee and the refuge effects are added to the model (3.6), separately.

The system of equations (3.6) has four parameters, namely, λ, b, k and β. Due to the abundance of the parameters, the results seem to be complicated. Model (3.6) can be simplified by substituting $N_t = \beta H_t$ and $y_t = bP_t$.

$$\begin{aligned} N_{t+1} &= \frac{\lambda N_t}{1+\frac{k}{\beta}N_t e^{-y_t}} e^{-y_t}, \\ y_{t+1} &= bN_t\left(1-e^{-y_t}\right). \end{aligned} \tag{3.7}$$

Let $x_t = bN_t$ and $c = k/(\beta b)$, then the model (3.7) can be written as follows:

$$\begin{aligned} x_{t+1} &= \frac{\lambda x_t e^{-y_t}}{1+cx_t e^{-y_t}}, \\ y_{t+1} &= x_t\left(1-e^{-y_t}\right), \end{aligned} \tag{3.8}$$

where x_t and y_t denotes the population sizes of host and parasitoid, respectively at time t.

3.2 The Model with the Refuge Effect on Host

We incorporate a constant proportion refuge effect to the model (3.8), and obtain

$$\begin{aligned} x_{t+1} &= \frac{(1-\Psi)\lambda x_t}{1+cx_t} + \frac{\Psi\lambda x_t e^{-y_t}}{1+cx_t e^{-y_t}}, \\ y_{t+1} &= \Psi x_t\left(1-e^{-y_t}\right), \end{aligned} \tag{3.9}$$

where Ψ is the proportion of host available to parasitoid, $(1-\Psi)$ is proportion of protective refuge, and $0 < \Psi \leq 1$. If $\Psi = 1$, we obtain the model (3.8). In this section, we present the existence and the stability of the positive fixed points of the model (3.9), respectively.

To determine the fixed points, we need to solve the non-linear system given by:

$$\begin{aligned} x &= \frac{(1-\Psi)\lambda x}{1+cx} + \frac{\Psi\lambda x e^{-y}}{1+cxe^{-y}}, \\ y &= \Psi x\left(1-e^{-y}\right). \end{aligned} \tag{3.10}$$

By computation of above system

(i) The extinction fixed point $E_0 = (0,0)$ exists for all values of parameters.

(ii) The axial fixed point is $E_1 = (\frac{\lambda-1}{c}, 0)$ when the absence of the parasitoid for $\lambda > 1$.

(iii) The positive fixed point is $E_2 = (x^*, y^*)$, where $x^* = \frac{y^*}{\Psi(1-e^{-y^*})}$ by the second equation of (3.10). In order to show the existence of the positive fixed point, we substitute $x = y/(\Psi(1-e^{-y}))$ into the first equation of (3.10), and obtain

$$\frac{1}{\lambda} = \frac{(1-\Psi)\Psi(e^{y}-1)}{e^{y}(\Psi+cy)-\Psi} + \frac{\Psi^2 e^{-y}(e^{y}-1)}{\Psi(e^{y}-1)+cy}. \tag{3.11}$$

If (3.11) is hold, then the positive fixed point exists. Let

$$F = \frac{(1-\Psi)\Psi(e^{y}-1)}{e^{y}(\Psi+cy)-\Psi} \qquad \textit{and} \qquad G = \frac{\Psi^2 e^{-y}(e^{y}-1)}{\Psi(e^{y}-1)+cy}.$$

We investigate the properties of these functions.

$$F'(y) = -\frac{c\Psi(1-\Psi)e^{y}(e^{y}-y-1)}{(\Psi-e^{y}(\Psi+cy))^2} < 0, \tag{3.12}$$

and

$$G'(y) = -\frac{\Psi^2 e^{y}\left(\Psi(e^{y}-1)^2 + c(e^{y}-y-1)\right)}{(\Psi(e^{y}-1)+cy)^2} < 0, \tag{3.13}$$

which implies that F and G are both decreasing functions of y.

In addition, we have

$$\lim_{y\to 0} F(y) = \frac{(1-\Psi)\Psi}{c+\Psi} \qquad \textit{and} \qquad \lim_{y\to 0} G(y) = \frac{\Psi^2}{c+\Psi}. \tag{3.14}$$

As a result, if $H(y) = F(y) + G(y)$, then $H(y)$ is decreasing function with

$$\lim_{y\to 0} H(y) = \frac{(1-\Psi)\Psi}{c+\Psi} + \frac{\Psi^2}{c+\Psi} = \frac{\Psi}{c+\Psi}. \tag{3.15}$$

The positive fixed point exists if $\lambda = 1/H(y)$, $H(y) \neq 0$. $1/H(y)$ is increasing function, and

$$\lim_{y\to 0} \frac{1}{H(y)} = 1 + \frac{c}{\Psi}. \tag{3.16}$$

Consequently, the positive fixed points exists if $\lambda > 1 + (c/\Psi)$. Since a constant function $(1/\lambda)$ and a decreasing function $H(y)$ can intersect at most once, the positive fixed point is unique (See Figure 3.1).

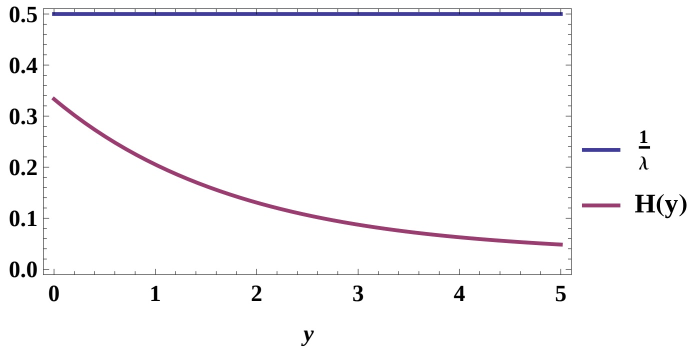
3.2.1 Local Asymptotic Stability of the Fixed Points of the Model (3.9)

The Jacobian matrix of system (3.9) is

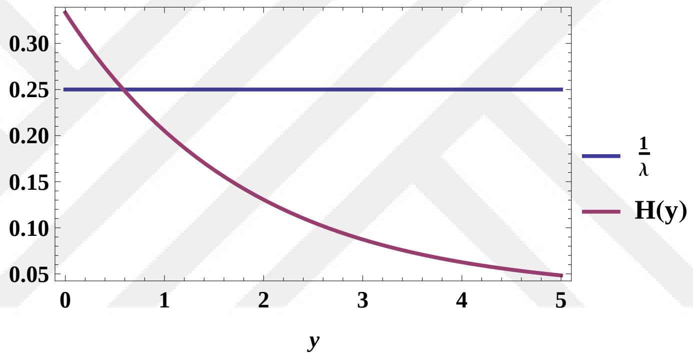
$$\begin{pmatrix} \lambda\left(\frac{1}{(1+cx)^2} - \frac{\Psi}{(1+cx)^2} + \frac{\Psi e^y}{(e^y+cx)^2}\right) & -\frac{\lambda\Psi e^y x}{(e^y+cx)^2} \\ \\ \Psi\left(1-e^{-y}\right) & \Psi e^{-y} x \end{pmatrix}$$

(i)By substituting E_0 into the Jacobian matrix, we obtain

$$J(E_0) = \begin{pmatrix} \lambda & 0 \\ 0 & 0 \end{pmatrix}.$$



(a) The case $\lambda < 1 + \frac{c}{\Psi}$ for $\lambda = 2$, $c = 1$ and $\Psi = 0.5$



(b) The case $\lambda > 1 + \frac{c}{\Psi}$ for $\lambda = 4$, $c = 1$ and $\Psi = 0.5$

Figure 3.1: The positive fixed point of the model (3.9) exists if the two functions intersect. (a) If $\lambda < 1 + \frac{c}{\Psi}$, there is no intersection (no positive fixed point). (b) If $\lambda > 1 + \frac{c}{\Psi}$, they intersect once (unique positive fixed point).

E_0 is stable if $\lambda < 1$ and saddle if $\lambda > 1$.

(ii) The Jacobian matrix for E_1 is

$$J(E_1) = \begin{pmatrix} \dfrac{1}{\lambda} & \dfrac{\Psi(1-\lambda)}{\lambda c} \\ \\ 0 & \dfrac{\Psi(\lambda-1)}{c} \end{pmatrix}.$$

The eigenvalues of $J(E_1)$ are $\lambda_1 = \frac{1}{\lambda}$ and $\lambda_2 = \frac{\Psi(\lambda-1)}{c}$. Then E_1 is stable if $1 < \lambda < 1 + \frac{c}{\Psi}$.

If $\lambda = 1$ or $\lambda = 1 + \frac{c}{\Psi}$, then E_1 is non-hyperbolic. The system goes through transcritical bifurcations for these values of λ. The fixed points are semistable in both cases by Center Manifold Theorem.

Under the condition $\lambda = 1$, the fixed points are $E_0 = E_1 = (0,0)$. The corresponding Jacobian matrix is as follows:

$$J_{\lambda=1}(0,0) = \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix}.$$

The eigenvalues are $\lambda_1 = 1$ and $\lambda_2 = 0$. This is the non-hyperbolic case. Then we use the Center Manifold Theorem. Now we write the system as follows:

$$\begin{aligned} x_{n+1} &= Ax_n + f(x_n, y_n) \\ y_{n+1} &= By_n + g(x_n, y_n), \end{aligned} \tag{3.17}$$

where,

$$A = 1,$$

$$B = 0,$$

$$f(x,y) = \frac{(1-\Psi)}{1+cx} + \frac{\Psi \lambda x e^{-y}}{1+cxe^{-y}} - x, \quad \textit{and}$$

$$g(x,y) = \Psi x \left(1 - e^{-y}\right).$$

By taking the derivatives we obtain

$$f_x = \frac{1-\Psi}{cx+1} - \frac{cx(1-\Psi)}{(cx+1)^2} + \frac{\Psi e^{-y}}{cxe^{-y}+1} - \frac{cx\Psi e^{-2y}}{\left(cxe^{-y}+1\right)^2} - 1,$$

$$f_y = \frac{cx^2\Psi e^{-2y}}{\left(cxe^{-y}+1\right)^2} - \frac{x\Psi e^{-y}}{cxe^{-y}+1},$$

and

$$g_x = \Psi\left(1 - e^{-y}\right),$$

$$g_y = \Psi x e^{-y}.$$

As a result $f(0,0) = 0$, $g(0,0) = 0$, $Df(0,0) = 0$, and $Dg(0,0) = 0$.

Since the eigenvectors are unit vectors, h function can be in the form

$$h(x) = c_1x^2 + c_2x^3 + O(x^4).$$

The following functional equation must be solved in order to find c_1 and c_2:

$$h(Ax + f(x, h(x))) - Bh(x) - g(x, h(x)) = 0$$

We use the power series expansion for the exponential function around $x = 0$ to solve this functional equation. We get

$$f(x,y) \approx \frac{(1-\Psi)\lambda x}{1+cx} + \frac{\Psi\lambda x(1-y+\frac{y^2}{2})}{1+cx(1-y+\frac{y^2}{2})} - x, \quad .$$

$$g(x,y) \approx \Psi x\left(1-(1-y+\tfrac{y^2}{2})\right).$$

The solution of the functional equation is $c_1 = 0$ and $c_2 = 0$. By using the first equation of (3.17), now we are interested in the new one-dimensional equation :

$$P(x) = x - cx^2 + c^2x^3 - c^3x^4 + O(x^5)$$

$P'(0) = 1$ and $P''(0) = -2c \neq 0$. Hence by Theorem 2.2, we can say that E_0 is semistable in case $\lambda = 1$.

(iii) The positive fixed point E_2 cannot be found explicitly. However, if we assign $z = e^{-y^*}$, $E_2 = (x^*, y^*) = (\frac{A+\sqrt{A^2+4c^2z(-1+\lambda-\lambda\Psi+\lambda\Psi z)}}{2c^2z}, -\log z)$ where $A = \lambda cz - cz - c$. By substituting these values into J we obtain matrix $J^* = J(x^*, y^*)$. If $|\mathrm{tr}J^*| - 1 < \det J^* < 1$, then E_2 is stable. We try to analyze the stability of E_2 deeper in the Numerical Simulations section.

3.3 The Model with Host-Refuge and Allee Effect

If we add the mate limitation Allee effect to the model (3.9), we obtain

$$\begin{aligned} x_{t+1} &= \frac{(1-\Psi)\lambda x_t}{1+cx_t}\frac{x_t}{s+x_t} + \frac{\Psi\lambda x_t e^{-y_t}}{1+cx_t e^{-y_t}}\frac{x_t}{s+x_t}, \\ y_{t+1} &= \Psi x_t\left(1-e^{-y_t}\right), \end{aligned} \tag{3.18}$$

where $s > 0$ is the Allee effect constant.

The solutions of the following system of equations are the fixed points.

$$\begin{aligned} x &= \frac{(1-\Psi)\lambda x}{1+cx}\frac{x}{s+x} + \frac{\Psi\lambda x e^{-y}}{1+cxe^{-y}}\frac{x}{s+x}, \\ y &= \Psi x\left(1-e^{-y}\right). \end{aligned} \tag{3.19}$$

(i) $F_0 = (0,0)$ is extinction fixed point for all values of parameters.

(ii) $F_1 = (\frac{A+\sqrt{A^2-4cs}}{2c}, 0)$ and $F_2 = (\frac{A-\sqrt{A^2-4cs}}{2c}, 0)$ are axial fixed points where $A = \lambda - cs - 1$ for $(1+\sqrt{cs})^2 \leq \lambda$.

(iii) $F_3 = (x^*, y^*)$ is the positive fixed point, where $x^* = \frac{y^*}{\Psi(1-e^{-y^*})}$ by the second equation of (3.19). First we show the existence of the positive fixed point. If we substitute $x = y/(\Psi(1-e^{-y}))$ in the first equation of (3.19), we obtain

$$\frac{1}{\lambda} = f(y) + g(y), \tag{3.20}$$

where

$$f(y) = \frac{(1-\Psi)\Psi e^y\left(e^y-1\right)y}{\left(\Psi\left(e^y-1\right)s + e^y y\right)\left(e^y(\Psi+cy)-\Psi\right)}, \tag{3.21}$$

and

$$g(y) = \frac{\Psi^2\left(e^y-1\right)y}{\left(\Psi\left(e^y-1\right)+cy\right)\left(\Psi\left(e^y-1\right)s+e^y y\right)}. \tag{3.22}$$

Since

$$g'(y) = -\frac{\Psi^2 e^y y\left(e^y - y - 1\right)}{\left(\Psi\left(e^y-1\right)+cy\right)\left(\Psi\left(e^y-1\right)s+e^y y\right)^2} - \frac{\Psi^3\left(e^y-1\right)\left(1+e^y(y-1)\right)}{\left(\Psi\left(e^y-1\right)+cy\right)^2\left(\Psi\left(e^y-1\right)s+e^y y\right)} < 0, \quad (3.23)$$

the function $g(y)$ is a decreasing function of y.

And we have

$$\lim_{y\to 0} g(y) = \frac{\Psi^2}{(c+\Psi)(1+\Psi s)} \quad (3.24)$$

Now, we continue with the graphical properties of $f(y)$.

$$f'(y) = \frac{(1-\Psi)\Psi e^y\left(e^y-y-1\right)\left(\Psi^2\left(e^y-1\right)^2 s - ce^{2y}y^2\right)}{\left(\Psi\left(e^y-1\right)s+e^y y\right)^2\left(\Psi - e^y(\Psi+cy)\right)^2}. \quad (3.25)$$

If $s < \frac{c}{\Psi^2}$, then $f'(y) < 0$, which means $f(y)$ is decreasing function. And also

$$\lim_{y\to 0} f(y) = \frac{(1-\Psi)\Psi}{(c+\Psi)(1+\Psi s)}. \quad (3.26)$$

Let $h(y) = f(y) + g(y)$, $h(y)$ is a decreasing function of y if $s < \frac{c}{\Psi^2}$. And

$$\lim_{y\to 0} h(y) = \frac{(1-\Psi)\Psi}{(c+\Psi)(1+\Psi s)} + \frac{\Psi^2}{(c+\Psi)(1+\Psi s)} = \frac{\Psi}{(c+\Psi)(1+\Psi s)} \quad (3.27)$$

The positive fixed point exists if $\lambda = \frac{1}{h(y)}$ where $h(y) \neq 0$. $\frac{1}{h(y)}$ is an increasing function of y and

$$\lim_{y\to 0} \frac{1}{h(y)} = \frac{(c+\Psi)(1+\Psi s)}{\Psi}. \quad (3.28)$$

As a result the positive fixed point exists and it is unique if $s < \frac{c}{\Psi^2}$ and $\lambda > \frac{(c+\Psi)(1+\Psi s)}{\Psi}$ (See Figure 3.2).

Otherwise, neither the existence nor the uniqueness is guaranteed (See Figure 3.3).

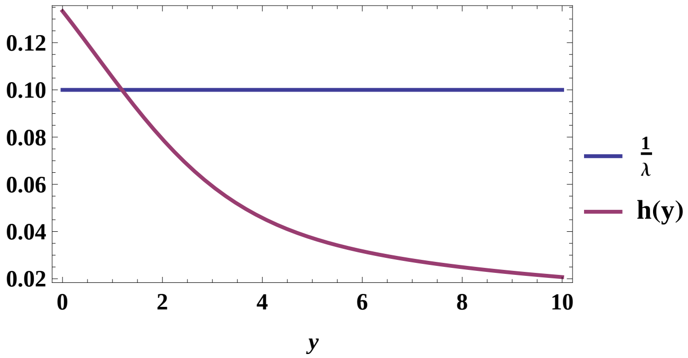


Figure 3.2: The positive fixed point of the model (3.18) exists if the two functions intersect. If $s < \frac{c}{\Psi^2}$ and $\lambda > \frac{(c+\Psi)(1+\Psi s)}{\Psi}$, they intersect once (unique positive fixed point). The figure depicts this case for $\lambda = 10$, $c = 1$, $s = 3$, and $\Psi = 0.5$.

3.3.1 Local Asymptotic Stability of the Fixed Points of the Model (3.18)

The corresponding Jacobian matrix is as follows:

$$J_A = \begin{pmatrix} \frac{\lambda x\left((e^y+cx)^2(x+s(2+cx)) - \Psi(-1+e^y)\left(e^y(2s+x+csx)+cx\left(s-cx^2\right)\right)\right)}{(s+x)^2(1+cx)^2(e^y+cx)^2} & -\frac{\lambda \Psi e^y x^2}{(s+x)(e^y+cx)^2} \\ \Psi\left(1-e^{-y}\right) & \Psi e^{-y} x \end{pmatrix}.$$

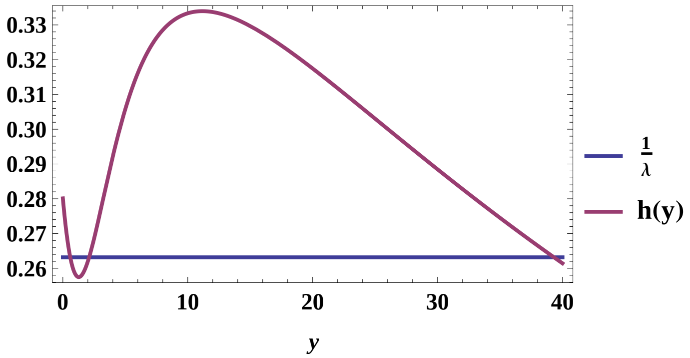
(i) $J_A(F_0)$ is 0 matrix, so F_0 is stable for all parameter values by Trace-determinant Theorem.

(ii) The Jacobian matrix evaluated at F_1 is

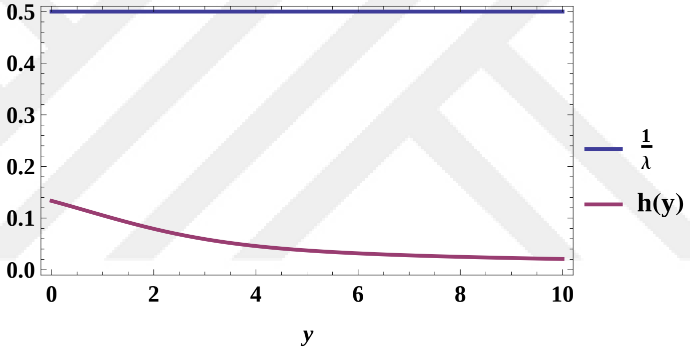
$$J_A(F_1) = \begin{pmatrix} 1 - \frac{\sqrt{A^2-4cs}}{\lambda} & \frac{\Psi\left(1-\lambda-cs-\sqrt{A^2-4cs}\right)}{2\lambda c} \\ 0 & \frac{\Psi\left(A+\sqrt{A^2-4cs}\right)}{2c} \end{pmatrix}.$$

We have $\lambda_1 = 1 - \frac{\sqrt{A^2-4cs}}{\lambda}$ and $\lambda_2 = \frac{\Psi\left(A+\sqrt{A^2-4cs}\right)}{2c}$. Hence, $|\lambda_{1,2}| < 1$ if $s < \frac{c}{\Psi^2}$ and $\left(1+\sqrt{cs}\right)^2 < \lambda < \frac{(c+\Psi)(1+\Psi s)}{\Psi}$.

(iii) The Jacobian matrix at F_2 is



(a) The case $s > \frac{c}{\Psi^2}$ for $\lambda = 3.8$, $c = 0.01$, $s = 5$, and $\Psi = 0.5$



(b) The case $\lambda < \frac{(c+\Psi)(1+\Psi s)}{\Psi}$ for $\lambda = 2$, $c = 1$, $s = 3$, and $\Psi = 0.5$

Figure 3.3: The positive fixed point of the model (3.18) exists if the two functions intersect. (a)Multiple intersections, multiple positive fixed points (b)No intersection, no positive fixed point

$$J_A(F_2) = \begin{pmatrix} 1 + \frac{\sqrt{A^2-4cs}}{\lambda} & \frac{\Psi\left(1-\lambda-cs+\sqrt{A^2-4cs}\right)}{2\lambda c} \\ 0 & \frac{\Psi\left(A-\sqrt{A^2-4cs}\right)}{2c} \end{pmatrix}.$$

We have $\lambda_1 = 1 + \frac{\sqrt{A^2-4cs}}{\lambda}$ and $\lambda_2 = \frac{\Psi\left(A-\sqrt{A^2-4cs}\right)}{2c}$. Since $\lambda_1 > 1$, F_2 is unstable.

3.4 Global Behaviors

Theorem 3.1 *For the model (3.9)*

(i) $E_0 = (0,0)$ *is globally asymptotically stable if* $\lambda < 1$

(ii) $E_1 = \left(\frac{\lambda-1}{c}, 0\right)$ *is globally asymptotically stable if* $1 < \lambda < 1 + \frac{c}{\Psi}$.

Proof.

(i) We have

$$\begin{aligned} x_{t+1} = \frac{(1-\Psi)\lambda x_t}{1+cx_t} + \frac{\Psi\lambda x_t e^{-y_t}}{1+cx_t e^{-y_t}} &= \frac{(1-\Psi)\lambda x_t}{1+cx_t} + \frac{\Psi\lambda x_t}{e^{y_t}+cx_t} \\ &\leq \frac{(1-\Psi)\lambda x_t}{1+cx_t} + \frac{\Psi\lambda x_t}{1+cx_t} = \frac{\lambda x_t}{1+cx_t} < \lambda x_t. \end{aligned}$$

Hence, if $\lambda < 1$,

$$\lim_{t\to\infty} x_t = 0.$$

Since $y_{t+1} = \Psi x_t \left(1 - e^{-y_t}\right)$,

$$\lim_{t\to\infty} y_t = 0,$$

which means that $(0,0)$ is globally attracting. Thus, E_0 is globally asymptotically stable if $\lambda < 1$.

(ii) Let $u = x - (\lambda - 1)/c$ and $v = y$. By rewriting the model (3.9)

$$\begin{aligned} u_{t+1} &= \frac{(1-\Psi)\lambda\left(u_t + \left(\frac{\lambda-1}{c}\right)\right)}{1 + c\left(u_t + \left(\frac{\lambda-1}{c}\right)\right)} + \frac{\Psi\lambda\left(u_t + \left(\frac{\lambda-1}{c}\right)\right)}{e^{v_t} + c\left(u_t + \left(\frac{\lambda-1}{c}\right)\right)} - \left(\frac{\lambda-1}{c}\right) \\ v_{t+1} &= \Psi x_t \left(1 - e^{-v_t}\right). \end{aligned} \tag{3.29}$$

Now, system (3.29) has fixed point $(0,0)$ which corresponds to point E_1 of the model (3.9). By some simplifications we obtain

$$u_{t+1} \leq \frac{\lambda\left(u_t + \left(\frac{\lambda-1}{c}\right)\right)}{1 + c\left(u_t - \left(\frac{\lambda-1}{c}\right)\right)} - \left(\frac{\lambda-1}{c}\right) = \frac{u_t}{cu_t + \lambda} < \frac{u_t}{\lambda}$$

If $\lambda > 1$,

$$\lim_{t\to\infty} u_t = 0,$$

which implies that

$$\lim_{t\to\infty} x_t = \frac{\lambda - 1}{c}.$$

And also,

$$v_{t+1} = \Psi x_t \left(1 - e^{-v_t}\right) = \Psi \left(u_t + \left(\frac{\lambda-1}{c}\right)\right)\left(1 - e^{-v_t}\right) \le \Psi \left(u_t + \left(\frac{\lambda-1}{c}\right)\right) v_t$$

Since $\lim_{t\to\infty} u_t = 0$,

$$\lim_{t\to\infty} y_t = \lim_{t\to\infty} v_t = 0$$

if $\lambda < 1 + \frac{c}{\Psi}$. □

Theorem 3.2 *For the model (3.18),* $(0,0)$ *is globally asymptotically stable if* $\lambda < 1$.

Proof. We have

$$x_{t+1} = \frac{(1-\Psi)\lambda x_t}{1 + c x_t}\frac{x_t}{s + x_t} + \frac{\Psi \lambda x_t}{e^{y_t} + c x_t}\frac{x_t}{s + x_t}$$

By comparison we obtain

$$x_{t+1} \le \frac{\lambda x_t}{1 + c x_t}\frac{x_t}{s + x_t} < \frac{\lambda x_t}{1 + c x_t} < \lambda x_t < x_t$$

if $\lambda < 1$. Then

$$\lim_{t\to\infty} x_t = 0,$$

which also implies

$$\lim_{t\to\infty} y_t = 0.$$

Hence, the fixed point $(0,0)$ is globally attracting if $\lambda < 1$, and it is locally asymptotically stable for all values of parameters. □

For the model (3.18), the global behavior of the other fixed points is omitted, since local stability of $(0,0)$ does not allow any other fixed points to behave stable, globally. Since F_0 is locally asymptotically stable for all values of parameters, at least with a very small initial value, the system goes to extinction even with a large growth parameter λ. As a result, the other points cannot be globally attractive.

The global behavior of the coexistence case is also omitted for model (3.9) in this part. On the other hand, in the next part, we give some numerical simulations to show that the systems may begin to exhibit chaotic behavior as growth parameter λ increases.

3.5 Numerical Simulations

In this section, we give some numerical simulations of the models (3.9) and (3.18), respectively.

3.5.1 Numerical simulations of the model (3.9)

We analyze the model without the refuge effect ($\Psi = 1$), under intermediate value of refuge ($\Psi = 0.5$), and a high proportion refuge ($\Psi = 0.1$). Without loss of generality, we fix the parameter $c = 1$. We consider the following cases satisfying $\lambda > 1 + \frac{c}{\Psi}$:

(i) Let $\Psi = 1$

If we assign $\lambda = 4$, then the positive fixed point is $E_2 = (1.52154, 0.907636)$ and the eigenvalues of $J(E_2)$ are $0.616761 \pm 0.749917i$. Hence, E_2 is a spiral sink (Figure 3.4).

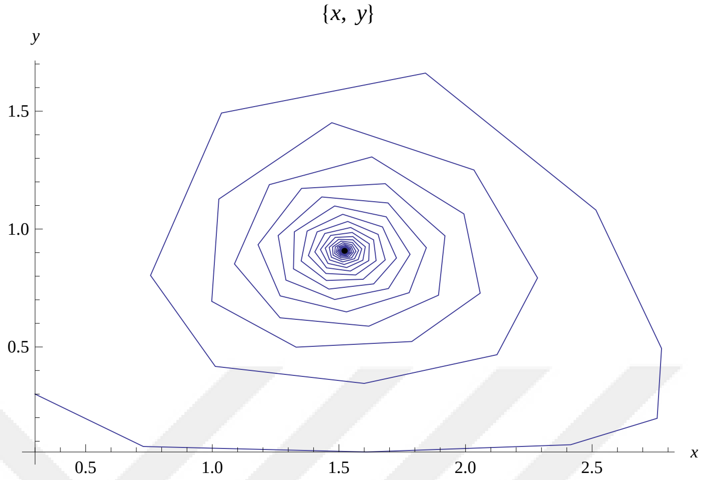


Figure 3.4: Phase portrait for the model (3.9) for $\Psi = 1$, $c = 1$, and $\lambda = 4$

If λ is increased, the fixed point is unstable, and the system has a Neimark-Sacker bifurcation. Let $\lambda = 4.4$, then $E_2 = (1.60132, 1.02915)$ and the eigenvalues of $J(E_2)$ are $0.604116 \pm 0.808446i$. Hence, $E_2 = (1.60132, 1.02915)$ is not stable (Figure 3.5).

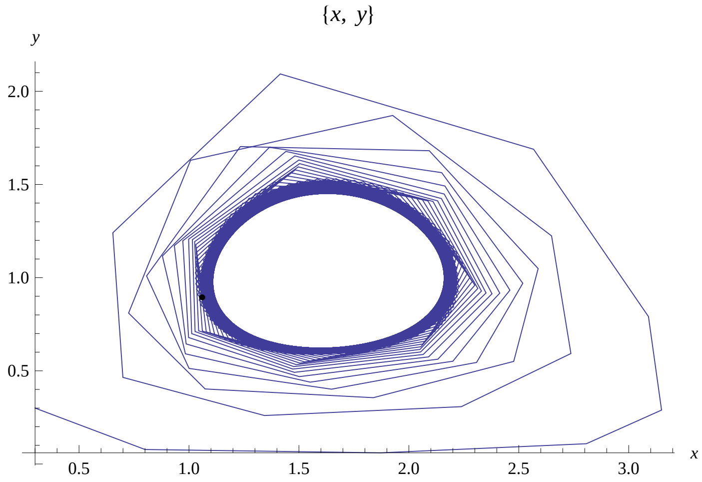


Figure 3.5: Phase portrait for the model (3.9) for $\Psi = 1$, $c = 1$, and $\lambda = 4.4$

(ii) Let $\Psi = 0.5$

If we assign $\lambda = 4$, then the fixed point is $E_2 = (2.64166, 0.584952)$ and the eigenvalues of $J(E_2)$ are $0.534534 \pm 0.257186i$. E_2 is spiral sink.

If $\lambda = 4.4$, $E_2 = (2.88453, 0.783299)$ and the eigenvalues of $J(E_2)$ are $0.495923 \pm 0.346354i$. E_2 is spiral sink (Figure 3.6).

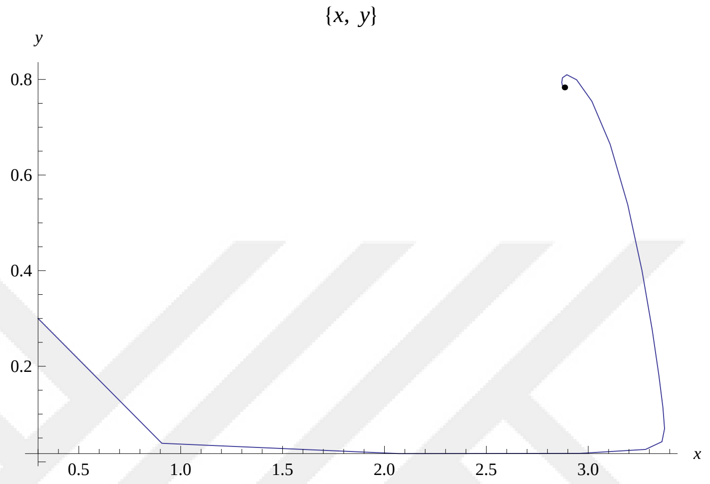


Figure 3.6: Phase portrait for the model (3.9) for $\Psi = 0.5$, $c = 1$, and $\lambda = 4.4$

Even with an extremely large growth parameter λ, the positive fixed point is stable. For example if $\lambda = 50$, the fixed point $E_2 = (24.0038, 12.0018)$, and the corresponding eigenvalues are $0.0201073 \pm 0.0379244i$.

(ii) Let $\Psi = 0.1$

The positive fixed point does not exist if $\lambda < 11$. Let $\lambda = 12$, then $E_2 = (10.9794, 0.189877)$ with corresponding eigenvalues (0.905805, 0.087284). As a result the positive fixed point is a sink (Figure 3.7).

The bifurcation diagrams are given in Figure 3.8.

We observe that, the refuge effect increases the interval of parameter λ, which makes the positive fixed point stable. As Ψ decreases, if the growth rate is not sufficiently large, the positive point does not exist as we expected.

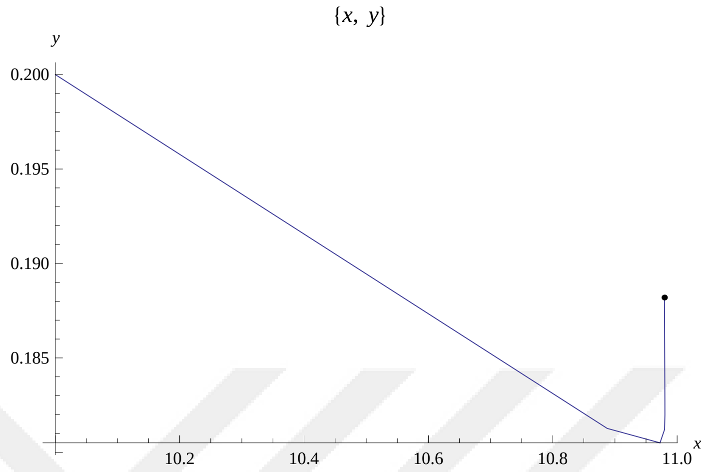


Figure 3.7: Phase portrait for the model (3.9) for $\Psi = 0.1$, $c = 1$, and $\lambda = 12$

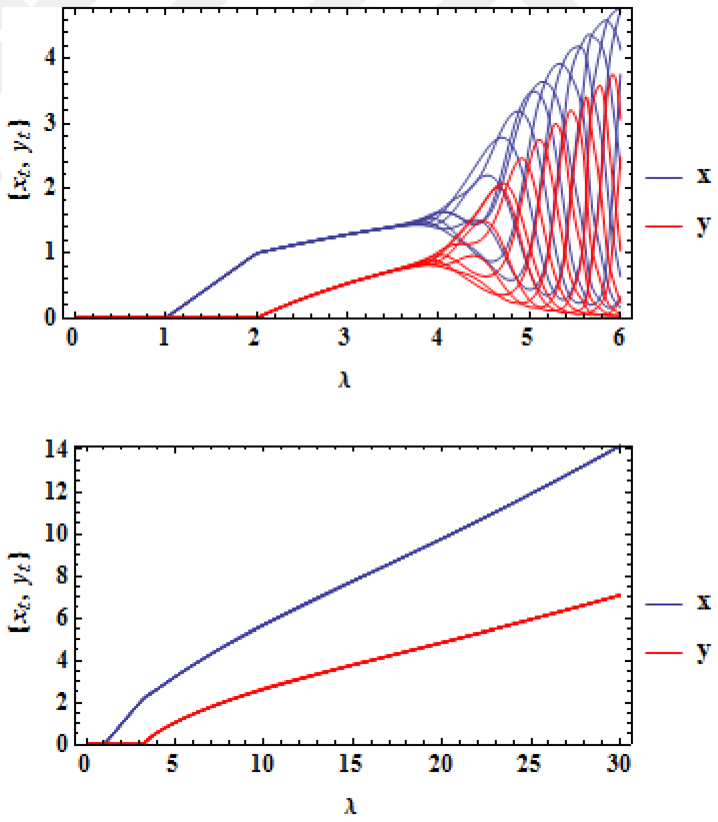


Figure 3.8: The bifurcation diagrams of the model (3.9) for $\Psi = 1$ and $\Psi = 0.5$, respectively.

3.5.2 Numerical simulations of the model (3.18)

We fix $c = 1$, $\Psi = 0.5$, and $s = 0.5$ in order to investigate how the interval of λ changes when an Allee effect is added to the model. We consider cases, which satisfies the conditions $s < \frac{c}{\Psi^2}$ and $\lambda > \frac{(c+\Psi)(1+\Psi s)}{\Psi}$.

First, we assume that $\lambda = 4$. Then the positive fixed point is $F_3 = (2.16476, 0.160471)$ with corresponding eigenvalues $(0.834265, 0.608611)$. As a result, F_3 is a sink. We give phase portrait in Figure 3.9, times series diagrams in Figures 3.10 and 3.11.

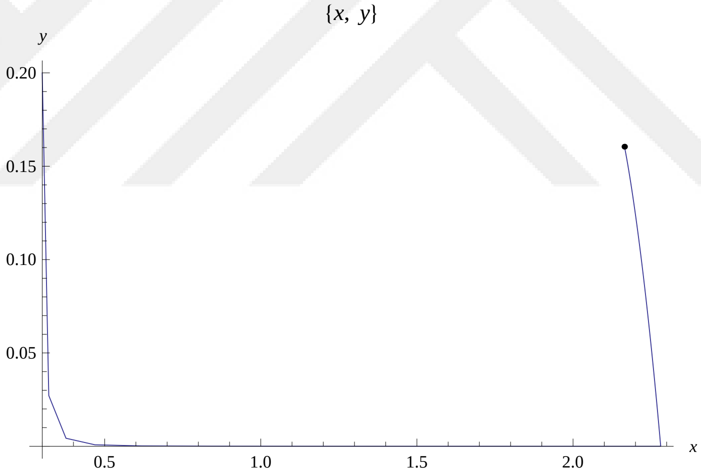


Figure 3.9: Phase portrait for the model (3.18) for $\Psi = 0.5$, $c = 1$, $s = 0.5$ and $\lambda = 4$

If we assign a large growth rate $\lambda = 10$, then the fixed point $F_3 = (5.31214, 2.41985)$ and eigenvalues are $0.312199 \pm 0.669214i$. F_3 is a spiral sink.

We observe that the positive fixed point remains stable for a large interval of growth parameter λ. In Figure 3.12, we give the bifurcation diagram.

Finally, we give the basin of attraction for the models (3.18) and (3.9) in Figure 3.13. In the analytical results, we show that the fixed point $F_0 = (0, 0)$ is stable for all values of parameters. In the numerical simulations, we show that the positive fixed point F_3 is stable for $\Psi = 0.5$, $c = 1$, $s = 0.5$ and $\lambda = 4$. We present the basin of attraction to show the set of points which are eventually iterated to

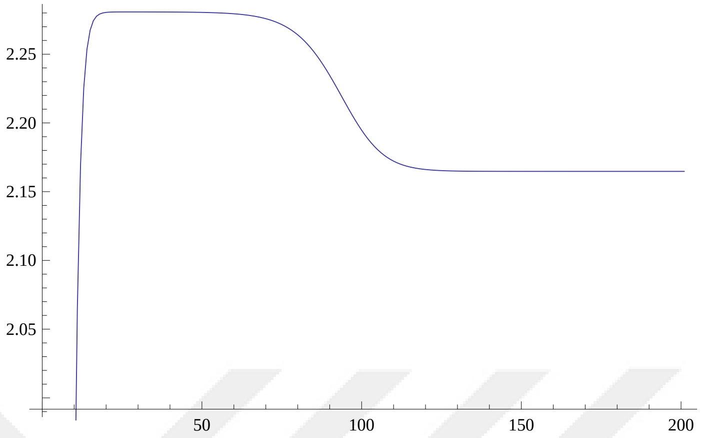


Figure 3.10: Time series of x for the model (3.18) for $\Psi = 0.5$, $c = 1$, $s = 0.5$ and $\lambda = 4$

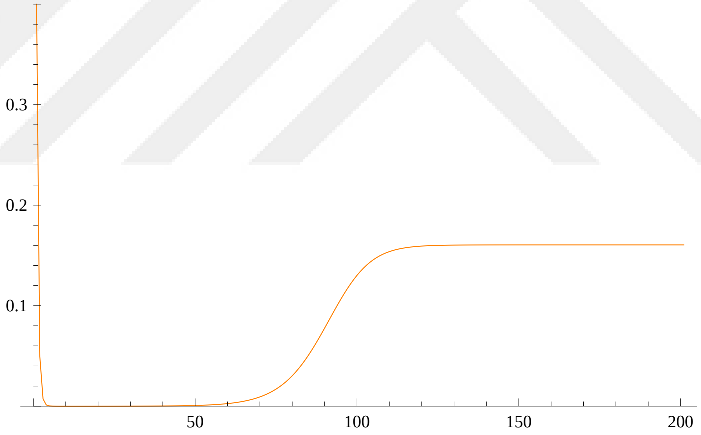


Figure 3.11: Time series of y for the model (3.18) for $\Psi = 0.5$, $c = 1$, $s = 0.5$ and $\lambda = 4$

either F_0 or F_3 under this set of parameters. For the basin of attraction of the model (3.9), let $s = 0$ (no Allee effect) and keep the other parameters the same, then only the positive fixed point is stable. For the basin of attraction code, we refer to [46].

3.6 Results

In [22], the model (3.6) was formulated, and the local and global stability of the fixed points are studied. They concluded that both populations become extinct if

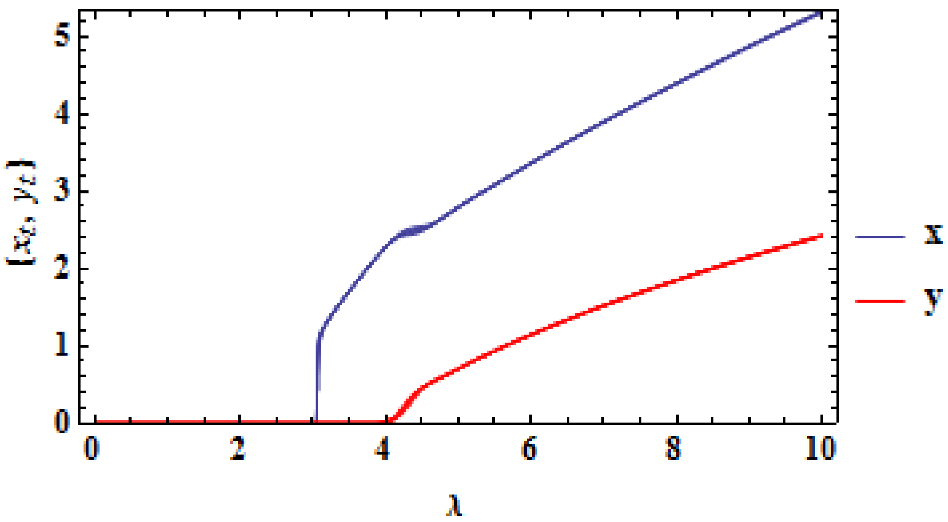
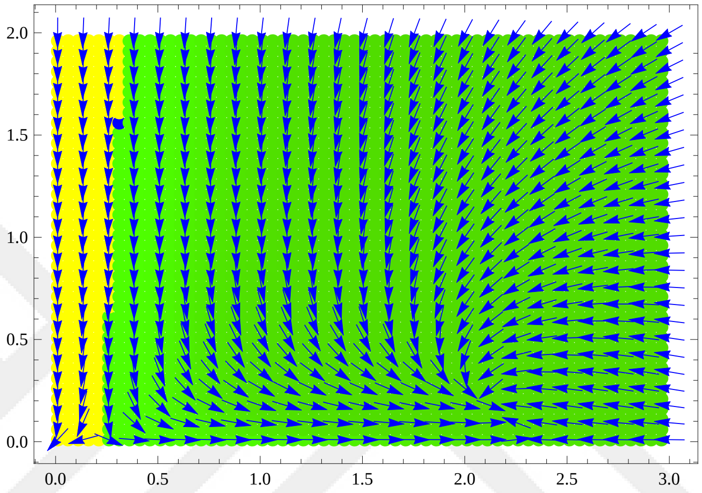
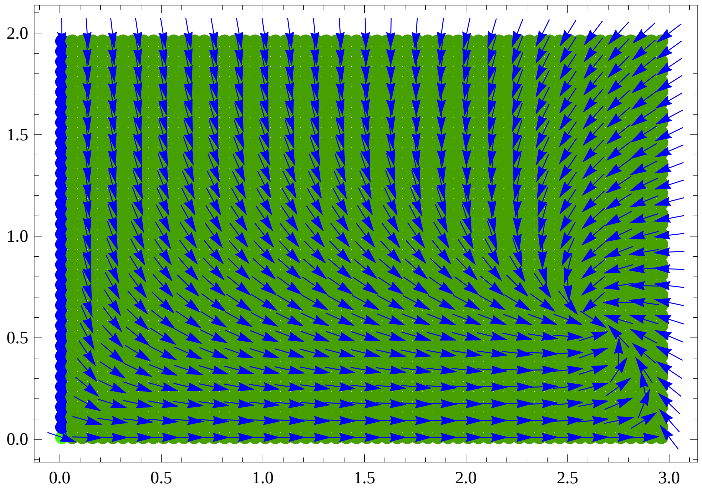


Figure 3.12: The bifurcation diagram of the model (3.18) for $s = 0.5$

$\lambda < 1$, the host survives but the parasitoid becomes extinct if $\lambda > 1$ and $\beta b\bar{N} < 1$, and the coexistence is possible if $\lambda > 1$ and $\beta b\bar{N} > 1$, where $\bar{N} = (\lambda - 1)/k$. In this chapter, we first reduce the number of parameters by substitution. Then we incorporate the refuge effect. Although the existence conditions of the fixed points are similar with the results of [22], the bifurcations diagrams depict that the refuge effect can have a stabilizing effect. Specifically, we observe that the interval of λ, which makes the positive fixed point stable, expands when the refuge effect is incorporated. Moreover, we investigate the non-hyperbolic case $\lambda = 1$ and show that the extinction fixed point is semistable under this condition. Next, we study the behavior of the model with both Allee and the refuge effects. We give the global asymptotic stability conditions of the extinction and exclusion fixed points analytically. We conclude that for the model without Allee effect, the extinction and exclusion fixed points are globally asymptotically stable under certain conditions. On the other hand, when Allee effect is added to the model, both populations become extinct if initial values are sufficiently small. This biologically means that if the density of the population is under the threshold level, then this population becomes extinct eventually, even if growth parameter is large. This may be observed as a direct consequence of the strong Allee effect.



(a) for the model (3.18) for $s = 0.5$



(b) for the model (3.9)

Figure 3.13: The basin of the attraction for the models (3.18) and (3.9), respectively, for $\Psi = 0.5$, $c = 1$, and $\lambda = 4$ (a)with Allee effect for $s = 0.5$, (b)without Allee effect

Chapter 4

A Predator-Prey Model

In this chapter, we consider the prey refuge and Allee effects on predator-prey interaction by using both analytic and numerical approaches. We construct a model that contains a predator saturation term. The refuge effect is commonly considered to act on a fixed proportion or fixed number of the prey population; our approach provides an extended model to study the dynamics of the predator-prey interaction under various different refuge settings.

4.1 The Model

The model previously considered in [6] and [47], which includes neither the Allee effect nor the prey refuge effect, is given by:

$$\begin{aligned} N_{t+1} &= N_t + rN_t(1 - N_t) - aN_tP_t \\ P_{t+1} &= P_t + aP_t(N_t - P_t), \end{aligned} \tag{4.1}$$

where N_t and P_t are the densities of the prey and predator population at time t respectively. The growth parameter r and the predation parameter a are both positive. Adding prey refuge to (4.1) results in the following model [37]:

$$\begin{aligned} N_{t+1} &= N_t + rN_t(1 - N_t) - (1-d)aN_tP_t \\ P_{t+1} &= P_t + aP_t((1-d)N_t - P_t), \end{aligned} \tag{4.2}$$

where $d \in [0, 1)$ is the proportion of prey that is not available to the predator because of the refuge effect. It is important to note that system (4.2) allows for prey reproduction while in refuge. For certain types of animals, this may not be the case.

In this study, we add the predator saturation to the model as follows. We consider the probability of escaping from the predator with a saturating functional response: $A(N) = exp(-\beta/(1 + sN))$, where β is predation intensity and s is proportional to the handling time.

The formula $Q(N) = N/(m + N)$ is used for the probability of finding a mate, where $1/m$ is an individual's searching efficiency. We add this effect to the predator, so we use $Q(P) = P/(m + P)$. We now extend the model given in (4.2) by adding a new predator saturation term to the prey population, as well as mate limitation of the predator. This results in the following system:

$$\begin{aligned} N_{t+1} &= N_t + rN_t(1 - N_t)e^{-\frac{\beta}{1+sN_t}} - (1-d)aN_tP_t \\ P_{t+1} &= P_t + aP_t((1-d)N_t - P_t)(\tfrac{P_t}{m+P_t}), \end{aligned} \tag{4.3}$$

where all parameters are positive.

4.2 The Existence and Stability of Fixed Points

The fixed points of the model (4.3) are $E_0 = (0, 0)$, $E_1 = (1, 0)$, and the positive fixed point $E_2 = (N^*, (1-d)N^*)$, for $0 \le d < 1$ and $0 < N^* < 1$.

Theorem 4.1 *The coexistence fixed point,* (N^*, P^*)*, exists and is unique if* $s < 1/\beta$ *for the model (4.3). Otherwise, there are either one or at most two positive fixed points.*

Proof. The solution of the following system gives the positive fixed point:

$$\begin{aligned} 0 &= r(1-N^*)e^{-\frac{\beta}{1+sN^*}} - a(1-d)P^* \\ 0 &= aP^*((1-d)N^* - P^*)(\tfrac{P^*}{m+P^*}). \end{aligned} \tag{4.4}$$

The second equation of the system is solvable if $(1-d)N^* = P^*$. Substitute this value into the first equation;

$$0 = r(1-N^*)e^{-\frac{\beta}{1+sN^*}} - a(1-d)^2N^*. \tag{4.5}$$

Let $f(N) = r(1-N)e^{-\frac{\beta}{1+sN}}$ and $g(N) = a(1-d)^2N$ on $N \in [0,1]$. By the Extreme Value Theorem, $f(N)$ must attain its maximum and minimum values on $[0,1]$. Now, there are two roots that make $f'(N) = 0$, which are $\dot{N}_1 = \dfrac{-2s-\beta s-\sqrt{\beta}s\sqrt{4+\beta+4s}}{2s^2}$ and $\dot{N}_2 = \dfrac{-2s-\beta s+\sqrt{\beta}s\sqrt{4+\beta+4s}}{2s^2}$. It is obvious that $\dot{N}_1 < 0$ for all $\beta > 0$ and $s > 0$, so $\dot{N}_1$ is not in the domain $[0,1]$. For $\dot{N}_2$, we have

$$\begin{cases} \dot{N}_2 = 0 & s = \frac{1}{\beta} \\ \dot{N}_2 < 0 & s < \frac{1}{\beta} \\ 0 < \dot{N}_2 < 1 & s > \frac{1}{\beta}. \end{cases}$$

Hence, for $s \leq 1/\beta$, there is no interior critical point. The boundary values are $f(0) = e^{-\beta}r$ and $f(1) = 0$. If $s \leq 1/\beta$, then $f'(N) < 0$, $f''(N) < 0$. Thus, f is a decreasing concave down function that takes its maximum value at 0 and minimum value at 1. Furthermore, because $g(0) = 0 < f(0)$, f cannot be below the linear function g, which implies that they should intersect. The function $g(N)$ is linear with positive slope $a(1-d)^2$. Then $f(N)$ and $g(N)$ intersect exactly once if $s < 1/\beta$. If $s > 1/\beta$, then $\dot{N}_2$ is a critical point. We have $f''(\dot{N}_2) < 0$, so f attains its max value at $\dot{N}$.

Under the condition $s > 1/\beta$, the following hold:

$$\begin{aligned} f'(N) > 0 &\quad \text{if } 0 < N < \dot{N}_2 \\ f'(N) = 0 &\quad \text{if } N = \dot{N}_2 \\ f'(N) < 0 &\quad \text{if } \dot{N}_2 < N < 1. \end{aligned}$$

As a result $f(N)$ can intersect with the linear function more than once. □

The numerical simulations for this theorem are given in Figure 4.1 and 4.2.

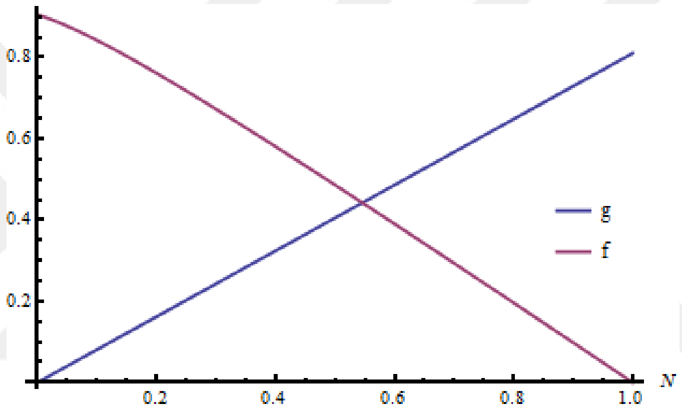


Figure 4.1: The positive fixed point of the model (4.3) for the case $s < \frac{1}{\beta}$ if $\beta = 0.1$, $a = 1$, $r = 1$, $s = 5$, and $d = 0.1$.

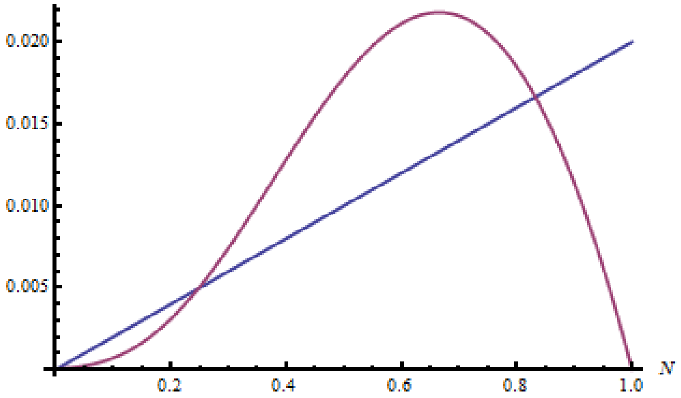
The Jacobian matrix of the system (4.3) is

$$\text{J=} \begin{pmatrix} Q(N,P) & a(-1+d)N \\ -\frac{a(-1+d)P^2}{m+P} & \Phi(N,P) \end{pmatrix},$$

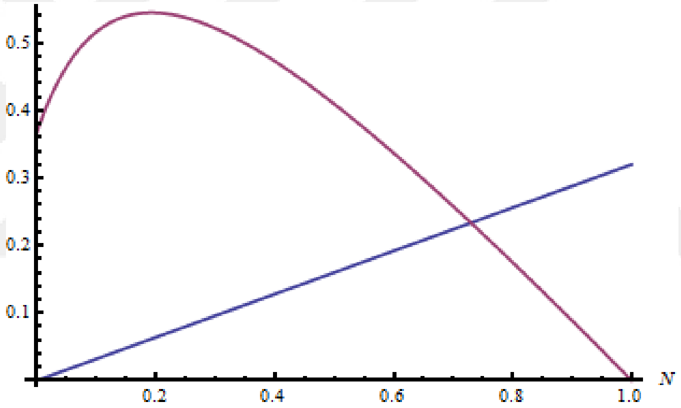
where

$$Q(N,P) = 1 - a(1-d)P + e^{-\frac{\beta}{1+Ns}}(1-N)r - e^{-\frac{\beta}{1+Ns}}Nr + \frac{e^{-\frac{\beta}{1+Ns}}(1-N)Nrs\beta}{(1+Ns)^2},$$

and



(a) Two positive fixed points exist.



(b) Only one positive fixed point exists.

Figure 4.2: For the case $s > \frac{1}{\beta}$ (a) for $\beta = 10$, $a = 2$, $r = 1$, $s = 4$, and $d = 0.9$. (b) for $\beta = 1$, $a = 2$, $r = 1$, $s = 8$, and $d = 0.6$

$$\Phi(N,P) = 1 - \frac{a((1-d)N-P)P^2}{(m+P)^2} + \frac{2a((1-d)N-P)P}{m+P} - \frac{aP^2}{m+P}.$$

Hence, we obtain

$$J(E_0)=\begin{pmatrix} 1+re^{-\beta} & 0 \\ 0 & 1 \end{pmatrix},$$

with the eigenvalues $\lambda_1 = 1 + re^{-\beta} > 1$ and $\lambda_2 = 1$. Thus (0,0) is unstable fixed point.

The Jacobian matrix at $E_1 = (1, 0)$ is

$$J(E_1) = \begin{pmatrix} 1 - re^{-\frac{\beta}{1+s}} & -a(1-d) \\ 0 & 1 \end{pmatrix}.$$

Since the eigenvalues are $\lambda_1 = 1 - re^{-\frac{\beta}{1+s}}$ and $\lambda_2 = 1$, then the point $(1,0)$ is a non-hyperbolic fixed point;

(i) If $\beta/(1+s) < \ln(r/2)$, then $|\lambda_1| > 1$, and $(1,0)$ is not stable.

(ii) If $\beta/(1+s) = \ln(r/2)$, then $|\lambda_1| = |\lambda_2| = 1$, and the stability can not be analyzed via current methods.

(iii) If $\beta/(1+s) > \ln(r/2)$, then $|\lambda_1| < 1$, and the Center Manifold Theorem can be used.

If a non-hyperbolic map is defined on $\mathbb{R}^2$, then its dynamics may be analyzed by studying the dynamics on an associated one-dimensional center manifold M_c [10]. This theorem is applicable only for the fixed point (0,0). Hence, we get the following new system by setting $x_t = N_t - 1$ and $y_t = P_t$:

$$\begin{aligned} x_{t+1} &= x_t - e^{-\frac{\beta}{1+s(1+x_t)}} r x_t(1+x_t) - a(1-d)(1+x_t)y_t \\ y_{t+1} &= y_t + \frac{a((1-d)(1+x_t) - y_t)y_t^2}{m + y_t}. \end{aligned} \tag{4.6}$$

Let J^* be the Jacobian matrix of the system (4.6). Then

$$J^*(0,0)= \begin{pmatrix} 1 - re^{-\frac{\beta}{1+s}} & -a(1-d) \\ 0 & 1 \end{pmatrix}.$$

Rewriting the system (4.6), we obtain

$$\begin{aligned} x_{t+1} &= (1 - re^{-\frac{\beta}{1+s}})x_t - ay_t(1-d) + \tilde{f}(x_t, y_t) \\ y_{t+1} &= y_t + \tilde{g}(x_t, y_t), \end{aligned} \tag{4.7}$$

where

$$\tilde{f}(x,y) = x(re^{-\frac{\beta}{1+s}} - re^{-\frac{\beta}{1+s+sx}}(1+x) + a(-1+d)y),$$

and

$$\tilde{g}(x,y) = \frac{a((1-d)(1+x)-y)y^2}{m+y}.$$

By using the Taylor series expansion of $e^{-\frac{\beta}{1+s+sx}}$ at the point $x=0$, we approximate

$$e^{-\frac{\beta}{1+s+sx}} \approx e^{-\frac{\beta}{1+s}} + \frac{ae^{-\frac{\beta}{1+s}}sx}{(1+s)^2} + \frac{\beta e^{-\frac{\beta}{1+s}}(-2+\beta-2s)s^2x^2}{2(1+s)^4} + O(x^3)$$

For simplification, let $k = e^{-\frac{\beta}{1+s}}$. Then

$$\tilde{f}(x,y) \approx x\left(kr - \left(k + \frac{\beta ksx}{(1+s)^2} + \frac{\beta k(-2+\beta-2s)s^2x^2}{2(1+s)^4}\right)r(1+x) + a(-1+d)y\right).$$

Since the invariant manifold is tangent to the corresponding eigenspace by the Theorem 2.7, assume that the map h takes the form

$$h(y) = \frac{a(d-1)}{rk}y + c_1y^2 + c_2y^3 + O(y^4).$$

To compute c_1 and c_2, the following functional equation should be solved:

$$h(y+\tilde{g}(h(y),y)) \approx (1-re^{-\frac{\beta}{1+s}})h(y) - a(1-d)y + \tilde{f}(h(y),y).$$

We have

$$c_1 \approx -\frac{a^2(-1+d)^2\left(-1-2s-s^2+ms\beta\right)}{k^2mr^2(1+s)^2},$$

and

$$c_2 \approx \frac{a^2(-1+d)}{2k^3m^2r^3(1+s)^4}(2k(1-d+m)r(1+s)^4 + a(-1+d)^2(4(1+s)^4 + 2ms(1+s)$$
$$(-4+(-4+m)s)\beta + 3m^2s^2\beta^2)).$$

This leads to the equation

$$P(y) \approx y - \frac{a(-1+d)y^2}{m} - \frac{a\left(a(-1+d)^2m + k(1-d+m)r\right)y^3}{km^2r} + \frac{a\left(1-d+m+\frac{a(-1+d)^2m}{kr} - \frac{a^2(-1+d)^3m\left((1+s)^2-ms\beta\right)}{k^2r^2(1+s)^2}\right)y^4}{m^3}.$$

We have $P'(0) = 1$, and $P''(0) = 2a(1-d)/m > 0$ for $a > 0$, $m > 0$, and $d \in [0, 1)$. Hence by Theorem 2.2, E_1 is semistable fixed point if $\beta/(1+s) > \ln(r/2)$.

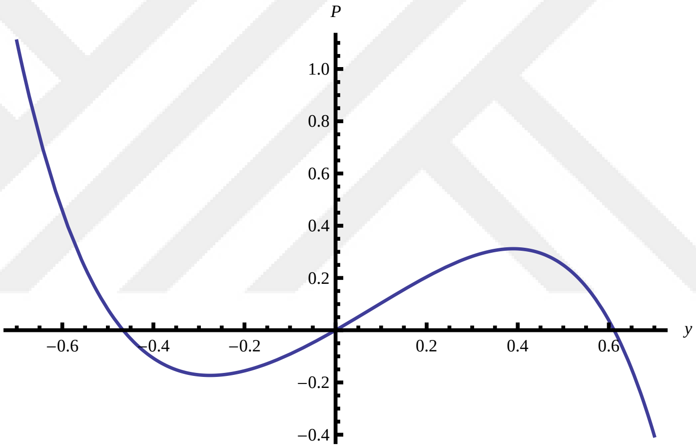


Figure 4.3: The map P on $x = h(y)$ for $\beta = 4$, $a = 2$, $r = 5$, $s = 1$, $m = 2$, and $d = 0.4$.

In order to find the stability conditions of the coexistence fixed point E_2, we substitute $(1-d)N^* = P^*$, and obtain

$$J(E_2)= \begin{pmatrix} G(N^*) & -abN^* \\ \frac{ab^3N^{*2}}{m+bN^*} & 1-\frac{ab^2N^{*2}}{m+bN^*} \end{pmatrix},$$

where $F(N^*) = e^{-\frac{\beta}{1+N^*s}}$, $b = 1-d$, and

$$G(N^*) = \frac{F(N^*)\left(F(N^*)(1+N^*s)^2 - (2N^*-1)r(1+N^*s)^2 - (N^*-1)N^*rs\beta\right)}{(1+N^*s)^2} - ab^2N^*$$

We will use the Trace-Determinant Plane Theorem to examine the stability. E_2 is stable if the Jacobian matrix at E_2 satisfies the following condition:

$$|\mathrm{tr}J| - 1 < \det J < 1$$

We find $\det(J(E_2)) = \dfrac{a^2b^4N^{*3} + G(N^*)(m + bN^*(1 - abN^*))}{m + bN^*}$,
and $\mathrm{tr}(J(E_2)) = 1 + G(N^*) - \dfrac{ab^2N^{*2}}{m + bN^*}$.

i) $\det J < 1$ if $G(N^*)(m + bN^*(1 - abN^*)) < m + bN^* - a^2b^4N^{*3}$

ii) $\mathrm{tr}J < 1 + \det J$ if $G(N^*) < 1 + ab^2N^*$

iii) $-1 - \det < \mathrm{tr}J$ if $G(N^*)(2m + bN^*(2 - abN^*)) > -2(m + bN^*) + ab^2N^{*2} - a^2b^4N^{*3}$

Hence E_2 is stable if the conditions i, ii, and iii are satisfied.

4.3 Numerical Simulations

In this section, we present the dynamic behavior of the system (4.3) about the positive fixed point under different parameter values. To compare the resulting models, we give phase-plane diagrams, time series diagrams, and bifurcation diagrams. Although there is no explicit solution of the equation $0 = r(1 - N^*)exp(-\beta/(1 + sN^*)) - a(1 - d)^2N^*$, by assigning numerical values to the parameters, the fixed point can be found approximately. By substituting this positive fixed point into the Jacobian matrix, the corresponding eigenvalues can also be found to decide the stability type of the model. The following tables represent these approximate values.

In Table 4.1, we assume that $d = 0$, which means that no prey can escape from its predators without encountering them first. For different values of predator's mate limitation coefficient m, the behavior of the system is presented under the assumption $d = 0$, $a = 1$, $\beta = 1$, $s = 0.5$, and $r = 5$. For these values we have $s < 1/\beta$, so there is unique positive fixed point, which is approximately $(0.705, 0.705)$. The values of a, β, s, d and r are sufficient to find the coexistence fixed point approximately. However, in the Jacobian, there is also an Allee effect coefficient m, which does not affect the value of the point, but may affect the stability. If there is no mate limitation Allee effect ($m = 0$) or m is small enough, then the system exhibits spiral sink behavior. As m increases, the system begins to oscillate, but remains stable. Figures 4.4, 4.5 and 4.6 consist of phase diagrams and time series graphs associated with Table 4.1. Additionally, in the tables below, we provide eigenvalues as reference, for which certain stability types are observed. For instance, as given in Table 4.1, when $|\lambda_2| < 1$ and $\lambda_1 < -1$, we observe oscillatory saddle behavior.

m	Positive Fixed Point	Eigenvalues	Stability Type
0	$(0.705, 0.705)$	$\lambda_{1,2} = -0.125 \pm 0.565i$ with $\lvert\lambda\rvert = 0.578662$	spiral sink
0.4	$(0.705, 0.705)$	$\lambda_{1,2} = -0.002 \pm 0.127i$ with $\lvert\lambda\rvert = 0.127016$	spiral sink
0.5	$(0.705, 0.705)$	$\lambda_1 = 0.197$, $\lambda_2 = -0.155$	oscillatory stable
1	$(0.705, 0.705)$	$\lambda_1 = 0.304$, $\lambda_2 = -0.231$	oscillatory stable
5	$(0.705, 0.705)$	$\lambda_1 = 0.515$, $\lambda_2 = -0.353$	oscillatory stable

Table 4.1: Effects of m for the model (4.3) with $a = 1$, $\beta = 1$, $s = 0.5$, $r = 5$, and $d = 0$

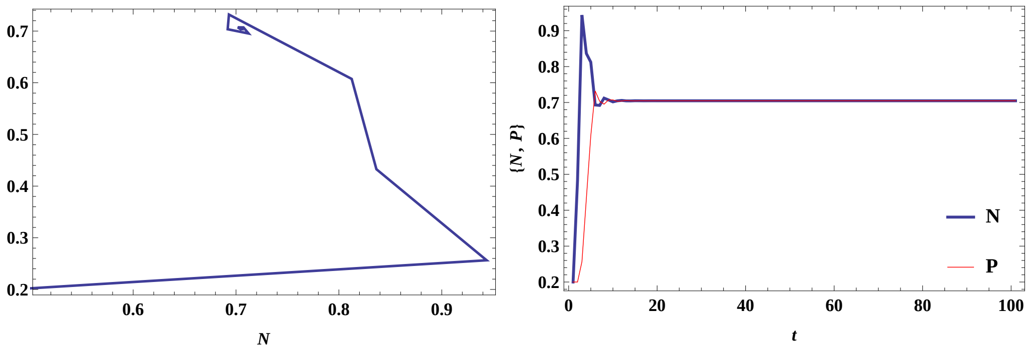


Figure 4.4: Phase Diagrams and Time Series Diagrams for the model (4.3) for $d = 0$ and $m = 0$

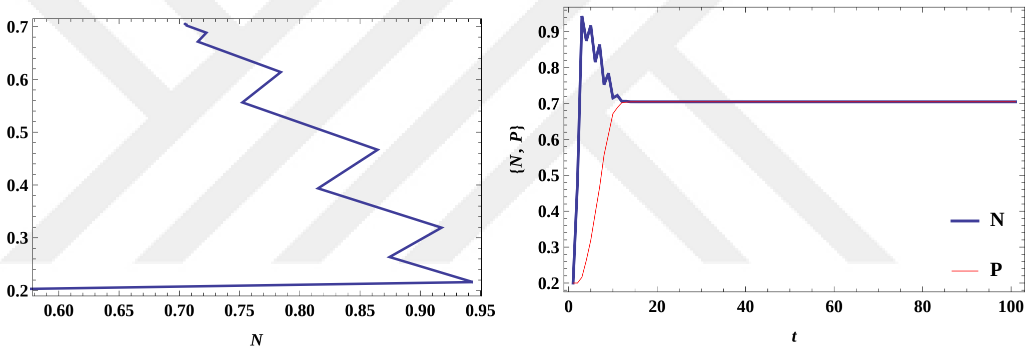


Figure 4.5: Phase Diagrams and Time Series Diagrams for the model (4.3) for $d = 0$ and $m = 0.5$

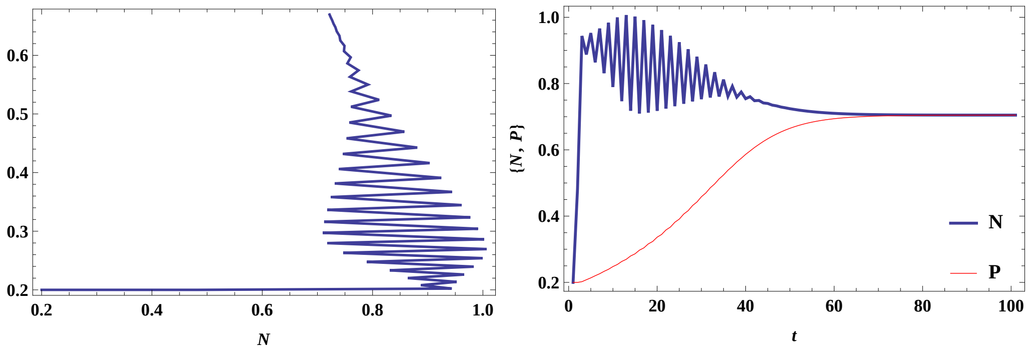


Figure 4.6: Phase Diagrams and Time Series Diagrams for the model (4.3) for $d = 0$ and $m = 5$

Table 4.2 and Figures 4.7, 4.8 and 4.9 show how the change of m affects the dynamic behavior of the system, while the parameters $a = 1$, $\beta = 1$, $s = 0.5$, $r = 5$ and $d = 0.5$ are kept fixed. The positive fixed point is an oscillatory saddle. The systems have a two-periodic stable cycle for all values of m, but the amplitude of the cycle of the predator decreases as m increases. The initial values are taken as $N = 0.2$ and $P = 0.2$.

m	Positive Fixed Point	Eigenvalues	Stability Type	2 Periodic Cycles
0	$(0.91, 0.455)$	$\lambda_1 = -1.178$ $\lambda_2 = -0.485$	oscillatory saddle	{(0.72,0.46),(1.04,0.41)}
0.5	$(0.91, 0.455)$	$\lambda_1 = -1.214$ $\lambda_2 = -0.759$	oscillatory saddle	{(0.7,0.44),(1.05,0.42)}
1	$(0.91, 0.455)$	$\lambda_1 = -1.223$ $\lambda_2 = 0.842$	oscillatory saddle	{(0.7,0.44),(1.05,0.43)}
5	$(0.91, 0.455)$	$\lambda_1 = -1.234$ $\lambda_2 = 0.95$	oscillatory saddle	{(0.7,0.43),(1.05,0.43)}

Table 4.2: Effects of m for the model (4.3) with $a = 1$, $\beta = 1$, $s = 0.5$, $r = 5$, and $d = 0.5$.

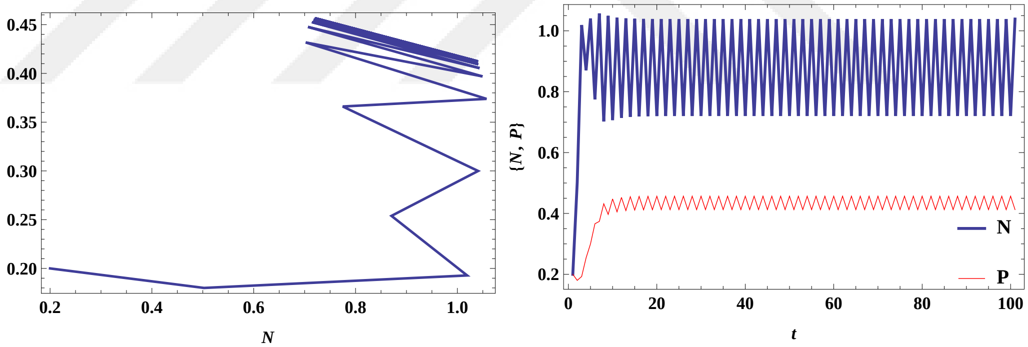


Figure 4.7: Phase Diagrams and Time Series Diagrams for the model (4.3) for $d = 0.5$ and $m = 0$

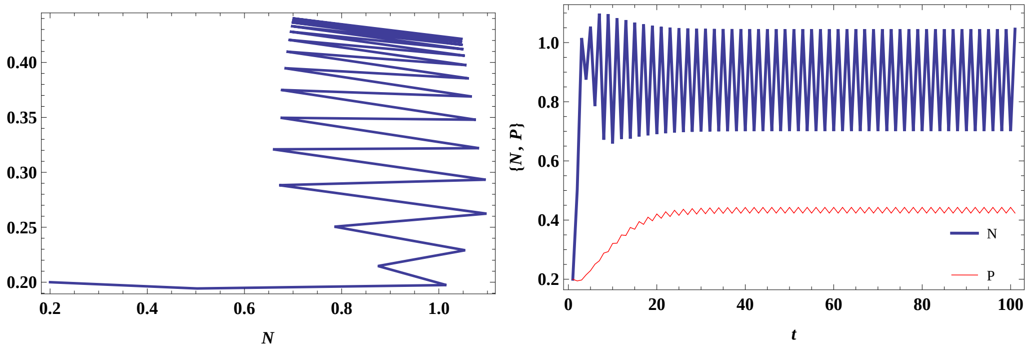


Figure 4.8: Phase Diagrams and Time Series Diagrams for the model (4.3) for $d = 0.5$ and $m = 0.5$

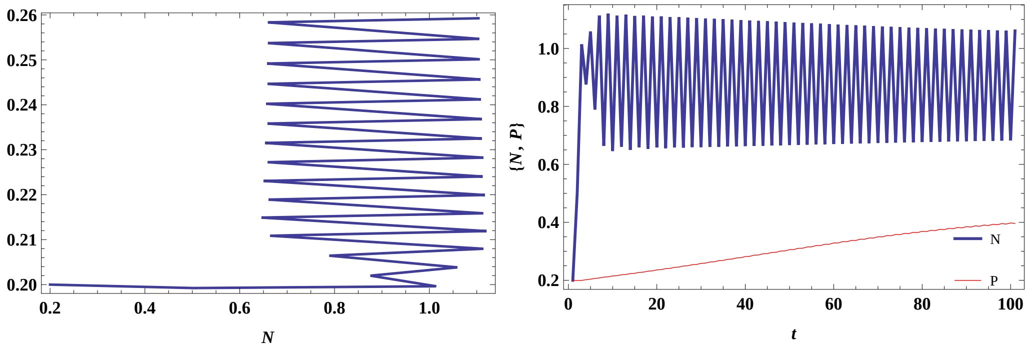


Figure 4.9: Phase Diagrams and Time Series Diagrams for the model (4.3) for $d = 0.5$ and $m = 5$

Table 4.3 and Figures 4.10, 4.11 and 4.12 show the effects of m when there is a high amount of refuge ($d = 0.8$). The other parameters are set to the same values as those in the previous tables.

m	Positive Fixed Point	Eigenvalues	Stability Type	4 Periodic Cycle
0	$(0.985, 0.197)$	$\lambda_1 = -1.507$ $\lambda_2 = 0.8$	oscillatory saddle	{(1.177,0.175),(0.58,0.186), (1.112,0.173),(0.728,0.181)}
0.5	$(0.985, 0.197)$	$\lambda_1 = -1.509$ $\lambda_2 = -0.943$	oscillatory saddle	{(1.177,0.179),(0.579,0.181), (1.112,0.178),(0.728,0.18)}
5	$(0.985, 0.197)$	$\lambda_1 = -1.51$ $\lambda_2 = -0.99$	oscillatory saddle	{(1.177,0.182),(0.579,0.183), (1.119,0.182),(0.728,0.183)}

Table 4.3: Effects of m for the model (4.3) with $a = 1$ $\beta = 1$, $s = 0.5$, $r = 5$, and $d = 0.8$.

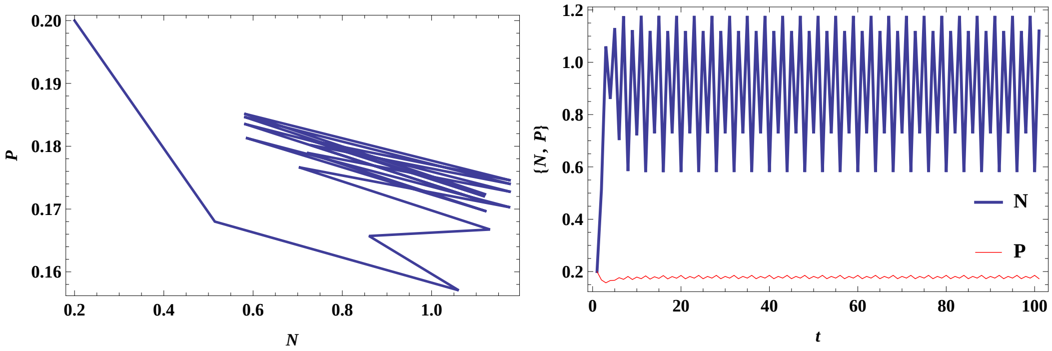


Figure 4.10: Phase Diagrams and Time Series Diagrams for the model (4.3) for $d = 0.8$ and $m = 0$

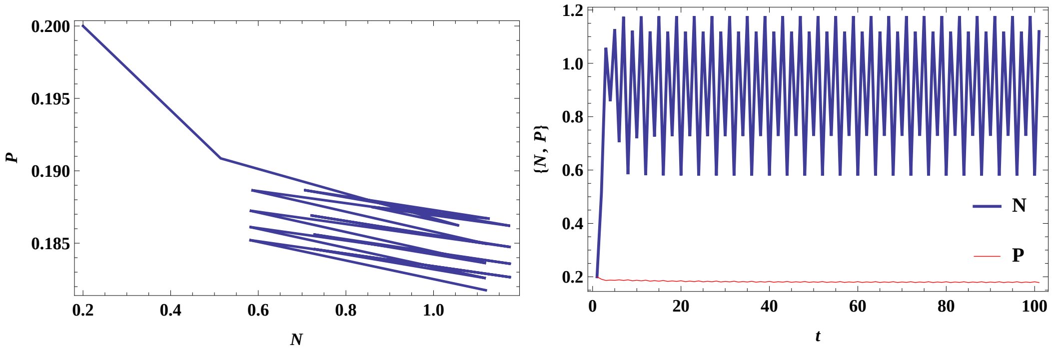


Figure 4.11: Phase Diagrams and Time Series Diagrams for the model (4.3) for $d = 0.8$ and $m = 0.5$

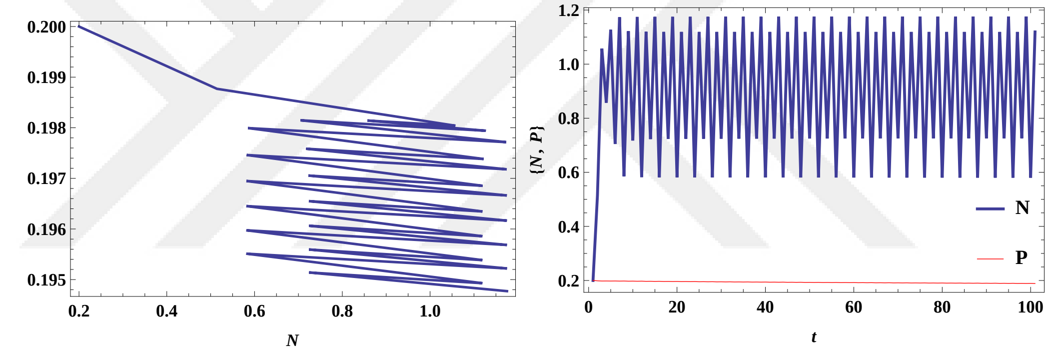


Figure 4.12: Phase Diagrams and Time Series Diagrams for the model (4.3) for $d = 0.8$ and $m = 5$

Tables and diagrams given in this section show that when the value of d changes, the dynamic behavior changes, and the system doubles the periods of cycles. If $d = 0$, then the positive fixed point is stable. With a moderate d value, there is a two-periodic cycle, while with a great value of d the period of the cycle is four. If the system has a cycle, then the positive fixed point loses its stability. The predator population oscillates, but the amplitude is so small that P^* seems stable. On the other hand, the magnitude of the oscillation is greater for prey, hence N^* is unstable. As a result, the fixed point (N^*, P^*) is a saddle fixed point. As m increases, the oscillation amplitude of the predator decreases. The system goes through a period doubling bifurcation with respect to d. The bifurcation plots are given in Figure 4.13 at the values $a = 1$, $\beta = 1$, $s = 0.5$, and $r = 5$.

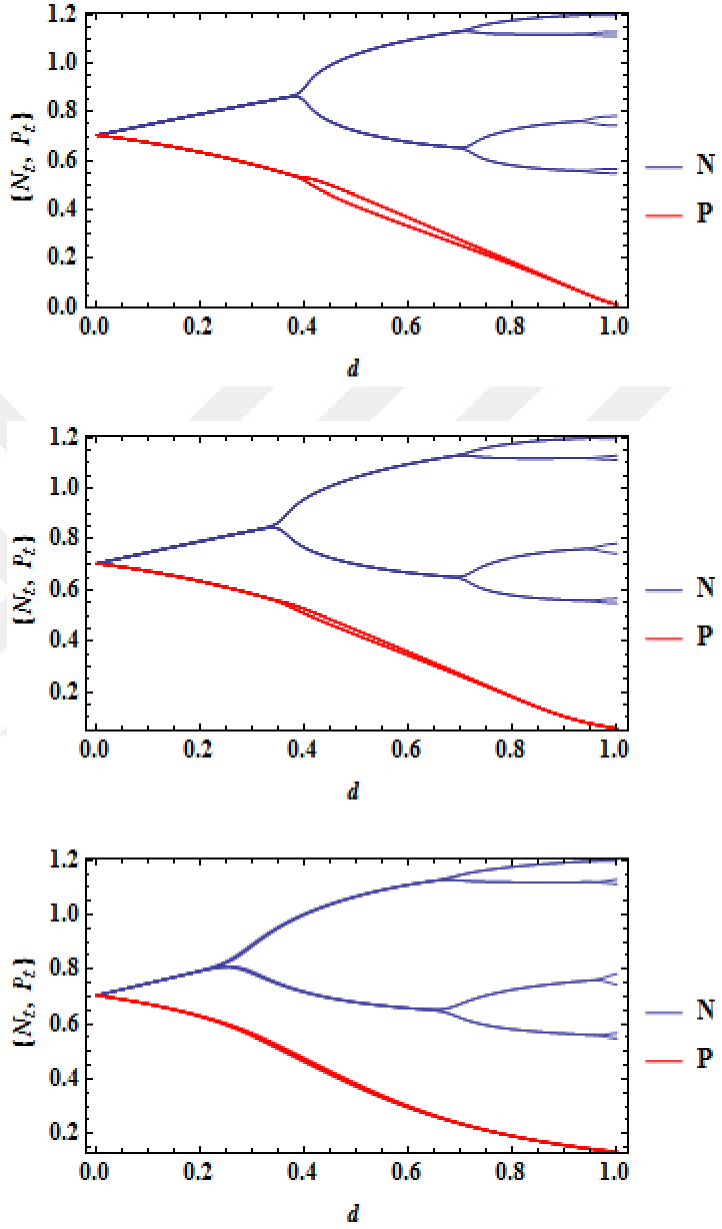


Figure 4.13: The bifurcation diagrams of the model (4.3) for $m = 0$, $m = 0.5$, and $m = 5$, respectively.

4.4 Results

In [37], the model (4.2) was formulated. They also extended the model (4.2) by incorporating Allee effect in prey, Allee effect in predator, and Allee effect in both populations. By analyzing these four models, they concluded that if the refuge effect is not sufficiently dominant, then the Allee effect can stabilize the system. In the paper [37], they incorporated Allee effects which are caused by mate limitation. In this chapter, we formulated a new model in which the predator saturation mechanism is taken into consideration. We extend the model (4.2) by incorporating predator saturation of prey as well as the mate limitation of predator. The fixed points and the existence conditions are similar with the results of [37], but we have one more parameter due to the predator saturation term. Moreover, our findings indicate an interesting fact that the equilibria, even the predator value in the equilibria of our model, depend on the dynamics of prey and the interaction between predator and prey. Biologically this corresponds to the case where the predator population is closely defined by the prey. As a result, the effects added to prey dominantly impact the model.

Chapter 5

The Holling Type II Prey-Predator Model

In this chapter, we formulate discrete-time Holling type II prey-predator models with Allee and the refuge effects. The study of the dynamical properties of resulting models allows us to have information about the future behavior of prey predator populations.

The following prey-predator model with the Holling type II functional response [19] has been studied by many authors [1, 17, 26].

$$\begin{aligned} x' &= ax(1-x) - \alpha\frac{mxy}{1+\varepsilon x}, \\ y' &= (\frac{mx}{1+\varepsilon x} - \beta)y, \end{aligned} \tag{5.1}$$

where all the parameters are positive, and

- α is conversion,
- β is predator's death rates,
- a is prey intrinsic growth parameter,

- m is half saturation parameter,
- ε is limitation of the growth velocity of the predator population with increase in the number of prey.

We refer to the works in [11, 26, 38]. Equilibrium points of this model are stable or limit cycles.

The discrete prey-predator model with Holling type II given by [1] is as follows:

$$\begin{aligned} x_{n+1} &= a x_n(1-x_n) - \frac{b x_n y_n}{1+\varepsilon x_n}, \\ y_{n+1} &= \frac{d x_n y_n}{1+\varepsilon x_n}, \end{aligned} \tag{5.2}$$

where all parameters are nonnegative. This map is non-invertible map.

We first study this model with a fixed number of prey in refuge, then with an Allee effect.

5.1 Holling type II model with a refuge effect

We study the following model obtained by adding a refuge effect R to prey in the model given by [1]:

$$\begin{aligned} x_{n+1} &= a x_n(1-x_n) - \frac{b(x_n-R)y_n}{1+e(x_n-R)}, \\ y_{n+1} &= \frac{d(x_n-R)y_n}{1+e(x_n-R)}, \end{aligned} \tag{5.3}$$

where the parameters are positive.

5.1.1 Fixed points of the model (5.3) and their stability

In this section, we investigate the fixed points of the map (5.3) and their stability conditions. The solution of the following system of equations gives us three non-negative fixed points:

$$\begin{aligned} x &= ax(1-x) - b\frac{(x-R)y}{1+e(x-R)}, \\ y &= \frac{d(x-R)y}{1+e(x-R)}. \end{aligned} \tag{5.4}$$

The fixed points are :

a. for any values of parameters, there exists extinction fixed point $E_0 = (0,0)$.

b. there exists one exclusion fixed point $E_1 = (\frac{a-1}{a}, 0)$ for $a > 1$.

c. there exists one positive fixed point $E_2 = (\frac{\Phi}{Q}, -\frac{d\Phi(Q+a\Phi-aQ)}{bQ^2})$ for

- $Q < \Phi < 0$ and $a > \frac{Q}{Q-\Phi}$, or
- $0 < \Phi < Q$ and $a > \frac{Q}{Q-\Phi}$,

where $Q = d - e$ and $\Phi = 1 + RQ$.

The Jacobian matrix of the map (5.3) is as follows:

$$J(x,y) = \begin{pmatrix} -2xa + a - \frac{by}{(e(x-R)+1)^2} & \frac{b(x-R)}{e(R-x)-1} \\ \\ \frac{dy}{(e(x-R)+1)^2} & \frac{d(x-R)}{e(x-R)+1} \end{pmatrix}.$$

For the fixed point E_0 ;

$$J(E_0) = \begin{pmatrix} a & \frac{bR}{1-eR} \\ 0 & \frac{dR}{eR-1} \end{pmatrix}.$$

The eigenvalues are $\lambda_1 = a$ and $\lambda_2 = \frac{dR}{eR-1}$. Then E_0 is

a. a stable fixed point (sink) if $a < 1$, $d < \frac{eR-1}{R}$, and $R > \frac{1}{e}$,

b. oscillatory stable if $a < 1$, $d < \frac{1-eR}{R}$, and $e < \frac{1}{R}$,

c. non-hyerbolic if one of the following conditions is hold:

   - $a = 1$
   - $d = \frac{eR-1}{R}$
   - $d = \frac{1-eR}{R}$

We consider only the case $a = 1$. We need to write the system in the following form to use the Center Manifold Theorem:

$$\begin{aligned} x_{n+1} &= Ax_n + f(x_n, y_n), \\ y_{n+1} &= By_n + g(x_n, y_n). \end{aligned} \tag{5.5}$$

Furthermore $f(0,0) = 0, g(0,0) = 0, Df(0,0) = 0, Dg(0,0) = 0$. If we substitute the parameters $a = 1$, $b = 0.2$, $d = 3.5$, $e = 0.9$, and $R = 1/9$, then we obtain the following Jacobian matrix at E_0:

$$\mathrm{J(0,0)}=\begin{pmatrix} 1 & 0.0246914 \\ 0 & -0.432099 \end{pmatrix}.$$

Hence, the fixed point $E_0 = (0,0)$ is non-hyperbolic. Now, we can rewrite the system (5.3) as follows:

$$\begin{aligned} x_{n+1} &= x_n + 0.0246914 y_n + f(x_n, y_n) \\ y_{n+1} &= -0.432099 y_n + g(x_n, y_n), \end{aligned} \tag{5.6}$$

where

$$f(x,y) = -x^2 - 0.0246914y - \frac{0.2y\left(x - \frac{1}{9}\right)}{1 + 0.9\left(x - \frac{1}{9}\right)}, \tag{5.7}$$

and

$$g(x,y) = 0.432099y + \frac{3.5y\left(x-\frac{1}{9}\right)}{1+0.9\left(x-\frac{1}{9}\right)}. \tag{5.8}$$

Let

$$h(x) = c_1x^2 + c_2x^3 + O(x^4), \tag{5.9}$$

for $c_1, c_2 \in \mathbb{R}$. In order to compute the constants c_1 and c_2, the following functional equation should be solved:

$$h\left(x_n + 0.0246914h(x_n) + f\left(x_n, h(x_n)\right)\right) = -0.432099h(x_n) + g\left(x_n, h(x_n)\right). \tag{5.10}$$

By solving the equation (5.10), we find $c_1 = c_2 = 0$. Now, on the center manifold $y = h(x)$, we obtain the following one dimensional map:

$$x_{n+1} = x_n - x_n^2 + O(x_n^4). \tag{5.11}$$

Let $f(x) = x - x^2 + O(x^4)$. Since $f'(0) = 1$ and $f''(0) = -2 < 0$, hence by Theorem 2.2, the origin is semistable from right under the given set of parameters. (Similarly, we get the same result for $d = \frac{eR-1}{R}$ and $d = \frac{1-eR}{R}$.)

For the fixed point E_1 ;

$$J(E_1) = \begin{pmatrix} 2-a & \frac{b(-Ra+a-1)}{e+a(e(R-1)-1)} \\ \\ 0 & \frac{d(a(R-1)+1)}{e+a(e(R-1)-1)} \end{pmatrix}.$$

The eigenvalues are $\lambda_1 = 2-a$ and $\lambda_2 = \frac{d(a(R-1)+1)}{e+a(e(R-1)-1)}$. Then E_1 is a stable fixed point (sink) if $1 < a < 3$ and $|\lambda_2| < 1$. Otherwise, it is unstable. If $a = 3$ or $d = \frac{1+a(R-2)}{1+a(R-1)}$, then similarly, the Center Manifold theorem must be used as above.

For the fixed point E_2;

$$J(E_2) = \begin{pmatrix} a - \frac{2ap}{Q} + \frac{dp(a(p-Q)+Q)}{(Q+e(p-QR))^2} & -\frac{b}{d} \\ \\ -\frac{d^2p(a(p-Q)+Q)}{b(Q+e(p-QR))^2} & 1 \end{pmatrix}.$$

The positive fixed point is stable if the eigenvalues of the Jacobian matrix are $|\lambda_{1,2}| < 1$. This case will be investigated in the numerical simulations section.

5.1.2 Numerical simulations for (5.3)

We first study the model when we vary only the parameter R (refuge effect) and fix the others with respect to the above analytical results. Second, we study the model (5.3) for varying values of the parameter e. E_1 and E_2 are not in the positive region if $0 < a < 1$. There is no biological meaning when the trajectory of the map is oscillating on the positive and negative regions for $0 < a < 1$. Then, we will give the numerical simulation only when $a > 1$ and $d > e$.

Without loss of the generality, we fix the parameters $a = 4, b = 0.2, d = 3.5, e = 0.1$ and assume R varies. Under this set of parameter values, E_2 is a spiral sink if $0.09 < R < 0.24$, and it is an oscillatory saddle if $0.24 < R < 0.46$. For example, if $R = 1/9$, the fixed points are $E_0 = (0, 0), E_1 = (0.75, 0)$ and $E_2 = (0.405229, 9.77979)$ with the eigenvalues $\lambda_{E_0} = \{4., -0.393258\}$, $\lambda_{E_1} = \{-2., 2.10183\}$, and $\lambda_{E_2} = \{-0.0438074 \pm 0.869627i\}$, respectively. In this case E_0 is an oscillatory saddle, E_1 is an oscillatory source, and E_2 is a stable focus (spiral sink).

Next, we fix the parameters $a = 4, b = 0.2, d = 3.5, R = 1/9$ and assume e varies. The positive fixed point E_2 is a spiral sink if $0 < e < 0.92$, it is an oscillatory sink if $0.92 < e < 1.45$, otherwise it is unstable. For example, the fixed points are $E_0 = (0, 0), E_1 = (0.75, 0)$ and $E_2 = (0.495726, 8.82351)$ when $e = 0.9$. The eigenvalues are $\lambda_{E_0} = \{4., -0.432099\}$, $\lambda_{E_1} = \{-2., 1.41975\}$, and

$\lambda_{E_2} = \{0.0301804 \pm 0.18242i\}$, respectively. In this case E_0 is an oscillatory saddle, E_1 is an oscillatory source, and E_2 is a spiral sink.

Similarly, if $e = 1.2$, the fixed points are $E_0 = (0, 0), E_1 = (0.75, 0)$ and $E_2 = (0.545894, 7.79942)$ with the eigenvalues $\lambda_{E_0} = \{4., -0.448718\}$, $\lambda_{E_1} = \{-2., 1.26572\}$, and $\lambda_{E_2} = \{-0.626654, 0.585889\}$, respectively. As a result, E_0 is an oscillatory saddle, E_1 is an oscillatory source, and E_2 is an oscillatory sink. We give some phase portraits for different values of e (Figure 5.1, and Figure 5.2).

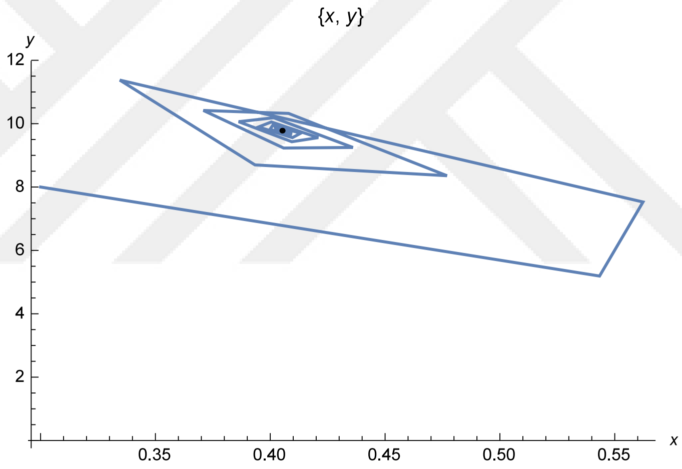


Figure 5.1: Phase portrait for the model (5.3) for $e = 0.1$

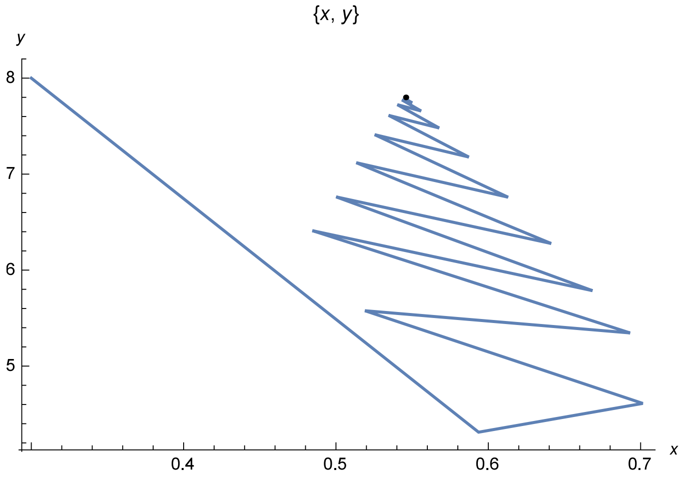


Figure 5.2: Phase portrait for the model (5.3) for $e = 1.2$

5.2 Holling type II model with an Allee effect

Let $I(x) = \frac{x}{x+K}$ be the probability of finding a mate where $1/K > 0$ is an individual's searching efficiency. We study the following model which is given by [1] by adding the mate limitation Allee effect to the prey:

$$\begin{aligned} x_{n+1} &= \left(a x_n(1-x_n) - \frac{b x_n y_n}{1+e x_n} \right) \frac{x_n}{K+x_n}, \\ y_{n+1} &= \frac{d x_n y_n}{1+e x_n}, \end{aligned} \tag{5.12}$$

where the parameters are positive.

5.2.1 Fixed points of the model (5.12) and their stability

In this section, we investigate the fixed points of the map (5.12) and their stability conditions. The solution of the following system of equations gives us four non-negative fixed points:

$$\begin{aligned} x &= \left(a x(1-x) - b\frac{xy}{1+ex} \right) \frac{x}{K+x}, \\ y &= \frac{dxy}{1+ex}, \end{aligned} \tag{5.13}$$

The fixed points are

a. for any values of parameters, there exists extinction fixed point $A_0 = (0,0)$,

b. there exist two exclusion fixed points $A_{1,2} = (\frac{a-1 \pm M}{2a}, 0)$ if $a > 1$ and $K < \frac{(a-1)^2}{4a}$,

c. there exists one positive fixed point $A_3 = \left(\frac{1}{Q}, \frac{d(a(Q-1) - Q(1+QK))}{bQ^2} \right)$ for $Q > 1$ and $a > \frac{Q(1+KQ)}{Q-1}$, where $M = \sqrt{(a-1)^2 - 4aK}$ and $Q = d - e$.

The Jacobian matrix of the system (5.12) is given by

$$J(x,y) = \begin{pmatrix} -\frac{x\left(a(x(2x-1)+K(3x-2))(ex+1)^2+b(x+K(ex+2))y\right)}{(K+x)^2(ex+1)^2} & -\frac{bx^2}{(K+x)(ex+1)} \\ \frac{dy}{(ex+1)^2} & \frac{dx}{ex+1} \end{pmatrix}.$$

For the fixed point A_0;

$$J(A_0) = \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}.$$

A_0 is stable.

For the fixed point $A_1 = (\frac{a-1-M}{2a}, 0)$;

$$J(A_1) = \begin{pmatrix} \frac{M+a(-a+6K+M+4)-1}{2a(K+1)} & -\frac{b(-a+M+1)^2}{(-a(2K+1)+M+1)(Me+e-a(e+2))} \\ 0 & \frac{d(-a+M+1)}{Me+e-a(e+2)} \end{pmatrix}.$$

If $|\frac{M+a(-a+6K+M+4)-1}{2a(K+1)}| < 1$ and $|\frac{d(-a+M+1)}{Me+e-a(e+2)}| < 1$, then A_1 is stable.

For the fixed point $A_2 = (\frac{a-1+M}{2a}, 0)$;

$$J(A_2) = \begin{pmatrix} -\frac{M+a(a-6K+M-4)+1}{2a(K+1)} & -\frac{b(a+M-1)^2}{(2Ka+a+M-1)(a(e+2)+e(M-1))} \\ 0 & \frac{d(a+M-1)}{a(e+2)+e(M-1)} \end{pmatrix}.$$

If $|-\frac{M+a(a-6K+M-4)+1}{2a(K+1)}| < 1$ and $|\frac{d(a+M-1)}{a(e+2)+e(M-1)}| < 1$, then A_2 is stable.
For the fixed point A_3;

$$J(A_3) = \begin{pmatrix} \frac{(2dK-eK+1)Q^2+a(d(e-1)-e(e+1))}{dQ(KQ+1)} & -\frac{b}{QKd+d} \\ \frac{-KQ^2-Q+a(Q-1)}{b} & 1 \end{pmatrix}.$$

The stability of A_3 will be investigated in the numerical simulations section.

5.2.2 Global behavior of model (5.12)

The extinction fixed point A_0 of model (5.12) is stable for any values of parameters. By comparison we have

$$x_{n+1} = \left(ax_n(1-x_n) - \frac{bx_ny_n}{1+ex_n} \right) \frac{x_n}{K+x_n} < ax_n(1-x_n) - \frac{bx_ny_n}{1+ex_n},$$

and

$$ax_n(1-x_n) - \frac{bx_ny_n}{1+ex_n} < ax_n(1-x_n) < ax_n.$$

Hence, if $a < 1$,

$$\lim_{n\to\infty} x_n = 0.$$

Since $y_{n+1} = \frac{dx_ny_n}{1+ex_n}$,

$$\lim_{n\to\infty} y_n = 0,$$

which means A_0 is globally attracting and globally asymptotically stable if $a < 1$. Consequently, if the growth parameter is small ($a < 1$), both populations become extinct even with large initial values. On the other hand, the other fixed points A_1, A_2 and A_3 cannot be globally stable because of the local stability of A_0.

5.2.3 Numerical simulations for (5.12)

We first study the model (5.12) when we change only the parameter e and fix the others with respect to the above analytical results. We compare our results with the results of [1]. We fix the parameters $a = 4.1, b = 3, d = 3.5, K = 0.2$, and assume that e varies as in [1]. When the control parameter e varies in $(0, 0.85)$, $(0.85, 1.53)$ and $[1.53, 2.03]$ the stability/unstability of positive fixed point changes through various types of bifurcations, but A_0 is always stable, and $A_{1,2}$ are always saddle in the positive region. A_3 is unstable (spiral source) if $0 < e < 0.85$. It is stable (spiral sink) if $0.85 < e < 1.53$, and it is stable (sink) if $1.53 \leq e \leq 2.03$. If $e > 2.03$, it is not a positive fixed point anymore.

We consider the following cases :

Let $e = 1.9$ then $A_0 = (0, 0), A_1 = (0.0712257, 0), A_2 = (0.684872, 0)$ and $A_3 = (0.625, 0.158594)$ are the fixed points. Eigenvalues are $\lambda_{A_1} = \{1.66071, 0.219575\}$, $\lambda_{A_2} = \{1.04163, -0.947291\}$ and $\lambda_{A_3} = \{0.951751, -0.561167\}$, respectively. Since $|\lambda_{A_3}| < 1$, the positive fixed point is asymptotically stable (sink). A_1, and A_2 are saddles (Figure 5.3).

Let $e = 0.86$, then the positive fixed point is $A_3 = (0.378788, 0.450302)$ (the others as same as in case $e = 1.90$). Eigenvalues are $\lambda_{A_3} = \{0.746513 \pm 0.662383i\}$. Since $|\lambda_{A_3}| = 0.998015 < 1$, then the positive fixed point is stable (spiral sink) (Figure 5.4).

Now, let $e = 0.85$, then the positive fixed point is $A_3 = (0.377358, 0.450303)$ (the others as same as in case $e = 1.90$). We observe that the behavior of the model becomes very complicated including the Neimark-Sacker bifurcation. The fixed point A_3 loses its stability through a Neimark-Sacker bifurcation and an invariant closed curve is created around the fixed point when $e = 0.85$ (Figure 5.5).

When we compare these results with results of [1], we can see that Allee effect has a strong effect on the stability of system and changes the parameter intervals for stability. When e is decreased, the behavior of the system changes to a chaotic one. We give the time series diagram of x in Figure 5.6. The time series of y is also similar but only the domain is different.

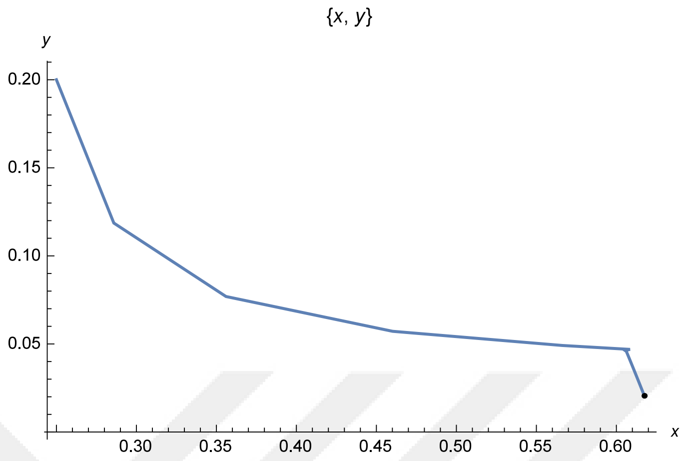


Figure 5.3: Phase portrait for the model (5.12) for $e = 1.9$

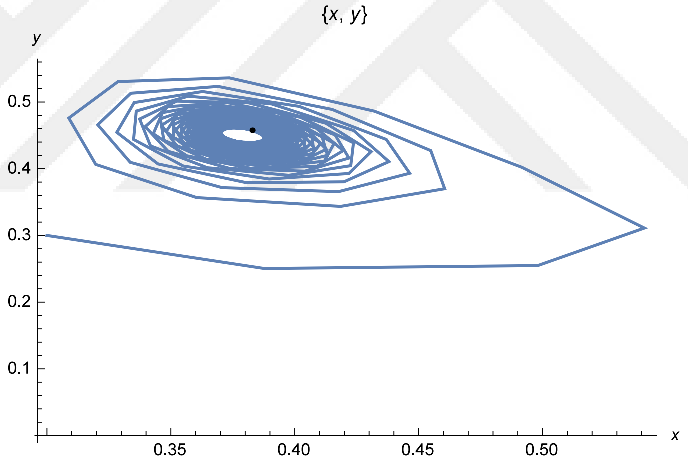


Figure 5.4: Phase portrait for the model (5.12) for $e = 0.86$

5.3 Results

A discrete-time prey-predator model with Holling type II was given in [1]. They analyzed the model (5.2) and concluded that compared to the continuous case, the discrete-time Holling type model has richer features and more complicated dynamics. In this chapter, we extend the model by incorporating the Allee and the refuge effects. We see that both the mating limitation Allee effect and refuge effect have strong impacts on the stability of the system.

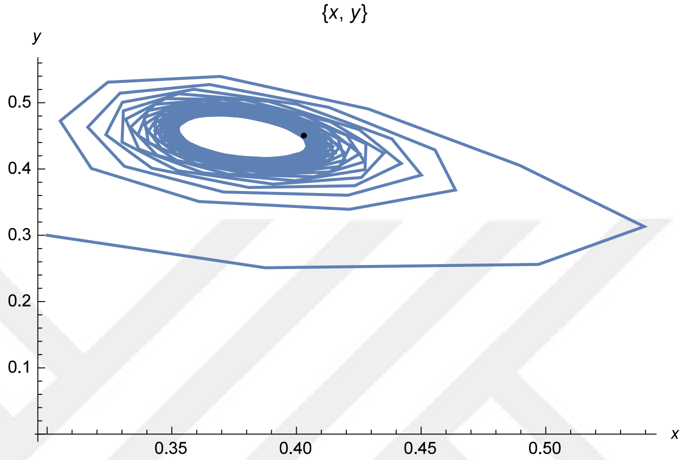


Figure 5.5: Phase portrait for the model (5.12) when a Neimark-Sacker bifurcation exists for $e = 0.85$

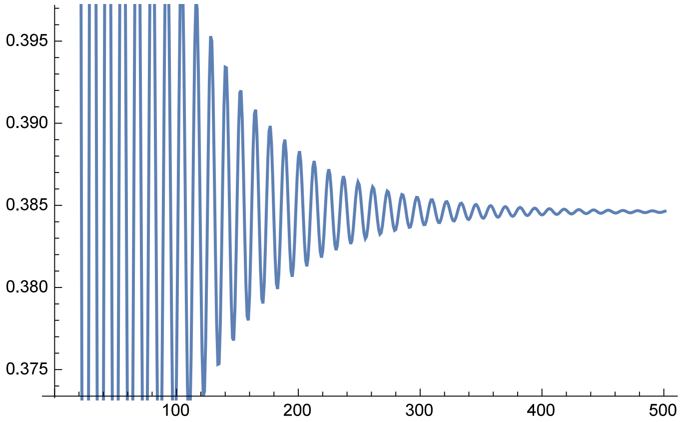


Figure 5.6: Time series of x for the model (5.12) for $e = 0.9$

Chapter 6

Conclusion and Further Studies

In this thesis, we have constructed new models for host-parasitoid and prey-predator interactions by incorporating the Allee and refuge effects. We have studied the models analytically, and performed numerical simulations to study their stability and bifurcation behaviors. We have presented rigorous proofs related to the general behavior of the dynamical equations depending on the conditions on the parameter space. Specifically, we have obtained the existence and uniqueness of positive fixed points. We have also examined the effects of the stability of the fixed points on the dynamics of the models. For some of the models, we presented the global behavior. We have shown that the populations incorporating Allee effects are more likely to become extinct as a direct consequence of Allee effect. In Chapters 3 and 4, the positive fixed points cannot be found explicitly. However, by assigning numerical values to the parameters, they can be found approximately. By substituting the positive fixed point into the Jacobian matrix, the corresponding eigenvalues can also be found to decide the stability type of the model. In the numerical simulations, we provided eigenvalues as reference, for which certain stability types are observed. In Chapter 5, the positive fixed point is explicitly found. However, due to the abundance of parameters, we also investigated it numerically. The numerical simulations have shown that our systems are capable of generating complex temporal dynamics. We have also compared the models and discussed the biological relevance. The analytical and numerical results indicate that the impacts of refuge and Allee effects for pattern formulation is substantial. We believe this understanding will enrich the dynamics of the effects on the predator-prey and host-parasitoid systems.

In this thesis, all the models we constructed are deterministic models. Studying the population dynamics in a stochastic environment needs further study. In the models, there are many parameters, which are about growth rate, capacity constraint, Allee and the refuge effects, interaction strength, etc. By making some of the parameters random, the stochasticity can be incorporated into the models. The next studies will be about stochastic population models to incorporate the randomness into the systems.

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VITA

Burçin Külahçıoğlu was born in 1988 in İzmir, Turkey. She recieved her B.Sc. degree from İzmir University of Economics, Department of Mathematics in 2011 as a high honour student. She also completed Double Major program in Department of Economics in the same university. In 2012, she started her Ph.D. with scholarship in Applied Mathematics and Statistics program in İzmir University of Economics, Turkey. She has been working as a research assistant at Department of Mathematics of the same university since February, 2012. She completed the requirements of the Ph.D. program under the guidance of Prof. Dr. Ünal Ufuktepe. Her research interests include mathematical modelling, mathematical biology, dynamical systems, and stability analysis. Since 2012, she has been awarded by The Scientific and Technological Research Council of Turkey (TÜBİTAK) with a Ph.D. scholarship.