

**A PREDATOR-PREY MODEL WITH LOGISTIC GROWTH FOR CONSTANT  
AND DENSITY-DEPENDENT DELAYED MIGRATION**

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A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Applied Mathematics of Masinde Muliro University of Science and Technology.

December 2020

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## ABSTRACT

Predator-prey models describe the interaction between two species, the prey which serves as a food source to the predator. The migration of the prey for safety reasons after a predator attack and the predator in search of food, from a patch to another may not be instantaneous. This may be due to barriers such as a swollen river or a busy infrastructure through the natural habitat. Recent predator-prey models have either incorporated a logistic growth for the prey population or a time delay in migration of the two species. Predator-prey models with logistic growth that integrate time delays in migration of both species have been given little attention. In this study, a logistic predator-prey model integrating a time delay in the migration of both species is developed and analyzed. The developed model was solved using two invariant manifolds; the symmetric manifold and the asymmetric manifold. Analysis of the model shows that when the prey growth rate is less than or equal to the prey migration rate, the two species coexist, otherwise both species become extinct. Numerical simulations show that during migration of the species, a longer time delay makes the model to stabilize at a slower rate compared to when the time delay is shorter. It is also shown that the prey migration due to the predator density does not greatly affect the prey density and existence compared to factors, such as logging, bad climatic conditions and limited food resources in a patch, that cause the prey to migrate. In the interest of species conservation, policies should be developed and enacted which address factors which prolong time delays during migration of the species by minimizing human activities and settlement in natural habitat.

## **DEDICATION**

To my father, the late Zachary Aero Apima, who on his deathbed told me "Sam, make sure you complete your PhD studies." I have done it dad.

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## CHAPTER 1

### INTRODUCTION

#### 1.1 Background of the study

Ecology is the study of interrelationship between species and their environment. Some of the branches in ecology include predator-prey systems, competition interactions, plant-herbivore systems, multi-species societies among others [23]. Given at least two species (especially animals), and considering the fact that all animals must eat to live, then all these species must interact either with other animals or with plants. Therefore when the prey species acts as a food source to the predator species, the model describing these dynamics is referred to as a predator-prey model [4, 13, 23, 29].

In 1925, Alfred J. Lotka proposed a simple classical predator-prey model using differential equations. The model is described using the following equations:

$$\begin{aligned}\dot{x}(t) &= x(\beta - \alpha y), \\ \dot{y}(t) &= y(\gamma x - \delta),\end{aligned}\tag{1.1}$$

where  $x := x(t)$  is the prey population at time  $t$ ,  $y := y(t)$  is the predator population,  $\beta$ ,  $\alpha$ ,  $\gamma$  and  $\delta$  are positive constants. The change in the prey density with respect to time is denoted by  $\dot{x}(t)$  while  $\dot{y}(t)$  is the change in the predator density with respect to time. The prey intrinsic growth rate is denoted by  $\beta$ ,  $\alpha$  and  $\gamma$  are predation parameters and  $\delta$  is the predator natural mortality rate.

The model in Equation (1.1) was derived independently by Vito Volterra in 1926 when he developed a simple predation model of one species by another to explain the fluctuations in the sizes of population of commercially desirable fish  $x(t)$  and that of larger fish  $y(t)$  which fed on the latter ( $x(t)$ ) in the Adriatic Sea in the decade from 1914 to 1923. Since the model in Equation (1.1) was proposed exclusively by Volterra and Lotka, it was then named the Lotka-Volterra Model.

The assumptions in Equation (1.1) are:

- (i) In the absence of predation, the prey density unboundedly grows; this is represented by  $\beta x$  in Equation (1.1).
- (ii) Predation reduces the intrinsic growth rate of the prey species by a term proportional to the predator and prey densities; this is the  $-\alpha xy$  term.
- (iii) In the absence of prey density, the predator density dies exponentially, that is, the  $-\delta y$  term in Equation (1.1).
- (iv) The predator density grows by a rate denoted by  $\gamma xy$ , this rate is proportional to the prey and predator density.

The Lotka-Volterra model assumes that the environment will always be homogeneous, but that may not be the case since the environment is made up of many different patches which are connected by a diffusion-like process [1, 2, 22, 23, 30].

Diffusion is a process by which matter is transported from one part of a system to another as a result of molecular motions [23]. In predator-prey theory, diffusion is usually referred to as migration or dispersal of either the predator, prey or both species [7, 17]. In a given patch, when a species encounters some hostile conditions, for example, intraspecific competition, predation, overpopulation of a species in a patch, environmental factors like drought, human activities like logging among others, the species may move from that given patch to another. This process is known as migration [2, 26].

Migration can either be constant or variable [16]. If the number of species moving per unit time is a constant fraction of the population of the species from a patch then the migration rate is constant, otherwise it is variable. The prey species may migrate at high rates from a given patch if there are more predators in that patch at that given time. Similarly, if there are more prey in a given patch, then predators will migrate at low rates to the other patch where the prey density is unknown and may be small. Thus considering density-dependent migration rates may be more

realistic [2]. Therefore, migration is an important aspect when dealing with the dynamics of a predator-prey system [2, 26]. Some examples of models which have incorporated migration in the Lotka-Volterra equation include [5, 22].

Another assumption in the Lotka-Volterra model is that the prey will grow unboundedly in the absence of predation. This may not be true because, apart from predation, other factors such as limited food resources and diseases may affect the prey population (as suggested by [30]). This necessitates an inclusion of a variable that will make the model to be bounded from above (the population not to explode). This variable is known as the carrying capacity. The carrying capacity is usually determined by the available sustaining resources. The resulting model is referred to as a predator-prey model with logistic growth [23]. Examples of predator-prey models with logistic growth are Verhulst Model [4, 23] and Rosenzweig-MacArthur Model [1, 16, 27].

The Rosenzweig-MacArthur predator-prey model is given by,

$$\begin{aligned} \dot{r} &= sr \left(1 - \frac{r}{k}\right) - \frac{\alpha rp}{1 + \alpha hr} \\ \dot{p} &= p \left(-\mu + \frac{\beta r}{1 + \alpha hr}\right) \end{aligned} \quad (1.2)$$

assumes that prey will grow logistically without predators, while predators have a Holling type II functional response to prey density. The prey and predator densities are denoted by  $r$  and  $p$ , respectively. The prey carrying capacity is denoted by  $k$  while  $s$  denotes the prey intrinsic growth rate. The predator death rate is represented by  $\mu$ ,  $\alpha$  denotes the predator searching efficiency and  $h$  is the predator handling time per prey. The conversion efficiency of prey to predators is  $\frac{\beta}{\alpha}$ . This model assumes that the species do not migrate because it only considers a homogeneous environment [16, 27, 28]. Some of the recent studies on the Rosenzweig-MacArthur model which incorporate migration of the two species include [2, 10].

A functional response refers to the relationship between the number of prey eaten per predator per unit time and prey density [18]. A functional response can be categorized into three main types [14, 15], namely:

- (i) Type I functional response: The prey consumption rate is proportional to the product of the concentration of the prey and the predator. An example of the Type I functional response is the Lotka-Volterra Model.
- (ii) Type II functional response: The prey consumption rate by a predator increases with an increase in the prey density, but finally stabilizes; the consumption rate remains constant irrespective of the prey density. An example of the Type II functional response is the Rosenzweig-MacArthur model.
- (iii) Type III functional response: The prey consumption rate by a predator falls or rises as the prey density decreases or increases respectively.

### 1.1.1 Time Delays

Laplace and Condorcet [9] in the 18th century introduced delay differential equations. However, rapid advances of the concept and application of delay equations did not come up until after the First World War. Delays usually arise when a species or a machine observes the system's state and makes the necessary changes to the system centered on its observations. These changes may not occur promptly, as a result a time delay arises between the observation and action period. Models incorporating time delays are becoming more common and appearing in technology, biology and economics. Delays represent transport delays, gestations times; incubation periods, maturity period among other processes [3, 8, 19, 21].

In a heterogeneous environment coupled via migration, the prey usually migrate from one patch to another in search of safety and food while the predator migrate from one patch to another mainly in search of food (the prey) [30]. Some models, for example [2, 5, 22], assume that there is no delay in the migration of the species, that is, either the prey species migrate instantly after facing a predator attack or the predator species migrate instantly after lacking their food source. In reality, this may not be the case since the species can meet different barriers like a swollen river or an infrastructure through the natural habitat. These barriers, therefore dictate

the inclusion of a time delay in migration of these species [24, 30].

A time delay can be included in the migration of either species to account for the fact that these species may not migrate immediately after facing unfavorable conditions in their current patch due to some reason. For instance the prey have to wait for their way to be predator-free for them to migrate or the species have to wait for a swollen river to subside for them to cross to the other side. When time delays are incorporated in a predator-prey model, they mostly affect the species population negatively. If the prey species takes time before they migrate to safety after facing a predator attack, then they will be prone to more attacks thus affecting their density negatively. Similarly, if there is a time delay when the predators are migrating after facing a shortage of food, then the species will still face a shortage of food and this will affect its population negatively [20]. Models with time delays and constant migration rates have been analyzed by [24, 30] while [20] analyzed a Lotka-Volterra model with a time delay in the migration of both species with predator-density-dependent dispersal for the prey.

## **1.2 Statement of the problem**

The interaction between the prey and the predator species is described by the classical predator-prey models. Recent predator-prey models have either incorporated a logistic growth for the prey population or delayed migration of the two species. Little attention has been given to predator-prey models with logistic growth and delayed migration of both species, which are realities that govern species behavior. In this study, we will develop and analyze a predator-prey model with logistic growth incorporating constant and density-dependent delayed migration of both species. The factors that affect the survival of the two species will be investigated.

## **1.3 Main Objective**

The main objective of this study is to develop and analyze the dynamics of a predator-prey model with logistic growth incorporating constant and density-dependent



delayed migration of both species.

#### **1.4 Specific Objectives**

The specific objectives of this study are as follows;

- (i) To develop and analyze a heterogeneous predator-prey model with logistic growth for both species and constant delayed migration of these species.
- (ii) To develop and analyze a heterogeneous predator-prey model with logistic growth for both species and density-dependent delayed migration of these species.
- (iii) To perform numerical simulations so as to verify and give more insight to the analytical solutions obtained in objectives (i) and (ii) above.

#### **1.5 Justification of the study**

This study is motivated by findings such as that of [10] which show that the environmental carrying capacity of the species has a great effect on the population of the species and the findings of [30] which show that time delay in migration of the prey and predator species affects the population of these species. It's worth investigating how time delays in migration of the species would affect the dynamics of a logistic predator-prey model.

#### **1.6 Significance of the Study**

Incorporating time delays in the migration part of a predator-prey model with logistic growth is a biological reality. Analysis of the model will give an insight into the parameters that affect its stability and therefore the survival or extinction of species. Thus, the results of this study may be used by ecologists in predicting more accurately the behaviors of both the prey and predator in view of conserving these species.

## CHAPTER 2

### LITERATURE REVIEW

#### 2.1 Lotka-Volterra models

An extension of the Lotka-Volterra model is given by [5],

$$\begin{aligned}\dot{N}_i(t) &= D_N(N_j - N_i) + N_i(a_i - b_i P_i), \\ \dot{P}_i(t) &= D_P(P_j - P_i) + P_i(c_i N_i - d_i).\end{aligned}\tag{2.1}$$

Where  $i, j = 1, 2, i \neq j$ . The subscripts indicate the patch number,  $N_i := N_i(t)$  represents the prey density and  $P_i := P_i(t)$ , represents the predator density,  $a_i$  is the prey intrinsic growth rate,  $d_i$  is the predator natural mortality rate,  $b_i$  and  $c_i$  denote the predation parameters,  $D_P$  and  $D_N$  are the predator and prey migration rates respectively.

In the analysis of the Model in Equation (2.1), it is assumed that the prey are immobile because the predators are often more mobile than the prey. Equation (2.1) also assumes that the predator will migrate promptly after lacking food source. However, this may not be the case in real life because in some situations both species usually migrate with or without a time delay,

A two patch Lotka-Volterra model was considered by [22]:

$$\begin{aligned}\dot{n}_i(\tau) &= (q_j(p_j)n_j(\tau) - q_i(p_i)n_i(\tau)) + \varepsilon(r_i n_i - a_i n_i p_i), \\ \dot{p}_i(\tau) &= (k_j p_j(\tau) - k_i p_i(\tau)) + \varepsilon(-m_i p_i + b_i n_i p_i),\end{aligned}\tag{2.2}$$

where  $i \neq j, i, j = 1, 2$  represents a patch,  $n_i(t)$  denotes the prey density and  $p_i(t)$  represents the predator density. The migration rates of prey and predators are represented by  $q_i(p_i)$  and  $k_i$  respectively. The prey intrinsic growth rate is denoted by  $r_i$ , the predator natural mortality rate is represented by  $m_i$ ,  $\varepsilon$  is a small dimensionless parameter,  $t$  is time for the interaction between the two species,  $\tau$  is the rapid time

for migration of both species between the two patches i.e.  $\tau = t/\varepsilon$ ,  $a_i$  and  $b_i$  are predation rates.

Equation (2.2) assumes that migration is instantaneous, however, in real life, physical barriers (e.g. a swollen river or busy infrastructure in the natural habitat) will be available when either the prey or predator want to migrate. These barriers dictate the inclusion of a time delay in migration of these species. Equation (2.2) also assumes that the rate of migration of the predator species does not depend on the prey density population.

## 2.2 Predator-Prey Models with Logistic Growth

A two-patch Rosenzweig-MacArthur model with migration of both species, examined by [10], is given by

$$\begin{aligned}\dot{n}_i &= rn_i \left(1 - \frac{n_i}{K}\right) - \frac{bn_i p_i}{b + n_i} + m(n_j - n_i), \\ \dot{p}_i &= \frac{bn_i p_i}{b + n_i} - \mu p_i + d \left( \frac{p_j}{1 + n_j} - \frac{p_i}{1 + n_i} \right)\end{aligned}\quad (2.3)$$

where  $i$  and  $j$  represent patch numbers,  $i \neq j$ ,  $i, j = 1, 2, \dots$ . The variable  $n_i$  represents the prey density and the predator density is denoted by  $p_i$ . The parameters  $d$  and  $m$  denote the predator and prey migration rates, respectively. The parameter  $r$  is the prey intrinsic growth rate while the prey carrying capacity is denoted by  $K$ . The parameter  $\mu$  is the predator mortality rate and the functional response's saturation value is denoted by  $b$ .

The Model in Equation (2.3) assumes that migration of these species will be instantaneous and it does not address the need to include a time delay in the migration.

A two-patch Rosenzweig-MacArthur model with migration of the predator species, examined by [16], is given by

$$\begin{aligned}\dot{v}_i &= rv_i \left(1 - \frac{v_i}{k}\right) - \frac{\alpha v_i p_i}{1 + \alpha h v_i} \\ \dot{p}_i &= -\mu p_i + \frac{\beta v_i p_i}{1 + \alpha h v_i} + D \left( \frac{\delta + \theta \alpha h v_j}{1 + \alpha h v_j} p_j - \frac{\delta + \theta \alpha h v_j}{1 + \alpha h v_i} p_i \right)\end{aligned}\quad (2.4)$$

where  $i$  denotes the patch number,  $i, j = 1, 2, i \neq j$ ,  $v_i$  and  $p_i$  denote the prey and predator population respectively. The maximum prey growth rate is represented by  $r$ ,  $k$  is the prey carrying capacity,  $\alpha$  denotes predator searching efficiency,  $h$  is the predator handling time per prey,  $\mu$  is the predator mortality rate,  $\beta$  is the conversion efficiency of the prey to predators,  $D$  is the diffusion rate,  $\delta$  corresponds to the predator mobility in its searching and  $\theta$  denotes predator mobility in its time handling.

The limitation of the Model in Equation (2.4) is that the prey is assumed to be immobile and there is no time delay when the predator population are migrating.

A two-patch predator-prey model which assumed that the prey growth, predator mortality and predator prey interactions is slow than migration was considered by [2]. The following model was studied:

$$\begin{aligned}\dot{n}_i(\tau) &= (f_j(p_j)n_j(\tau) - f_i(p_i)n_i(\tau)) + \epsilon[\phi_i(n_i)n_i(t) - \Phi_i(n_i)p_i(t)], \\ \dot{p}_i(\tau) &= (g_j(n_j)p_j(\tau) - g_i(n_i)p_i(\tau)) + \epsilon(-\psi_i(p_i) + \Psi_i(n_i)p_i(t)) \quad , i \neq j, i, j = 1, 2,\end{aligned}\tag{2.5}$$

where  $t = \epsilon\tau$  the slow time scale and the fast time scale is given by  $\tau$ . The patch number is represented by  $i = 1, 2$ . Prey density is denoted by  $n_i := n_i(t)$  and the corresponding predator density is  $p_i := p_i(t)$ . The function  $f_i(p_i)$  represent prey migration rates and  $g_i(n_i)$  represent the predator migration rates,  $\phi_i(n_i)$  represents the prey growth rate,  $\psi_i(n_i)$  is the predator mortality rate,  $\Phi_i(n_i)$  is the functional responses and  $\Psi_i(n_i)$  is the predator growth rate.

Equation (2.5) assumes that migration of the predator and prey will occur instantaneously after being triggered by an event and as a consequence it does not include time delays.

### 2.3 Lotka-Volterra models involving time delay in migration

The following model was considered by [24],

$$\begin{aligned}\frac{dn(t)}{dt} &= (R - Ap(t))n(t) + D_n \left[ \int_0^\infty G_n(S)e^{M_n S} n(t-S) dS - n(t) \right], \\ \frac{dp(t)}{dt} &= (Bn(t) - M)p(t) + D_p \left[ \int_0^\infty G_p(S)e^{M_p S} p(t-S) dS - p(t) \right],\end{aligned}\quad (2.6)$$

where  $n$  represents the prey density and  $p$  denotes the predator density.  $G_d(S) \geq 0$ , (where  $d = n, p$ ) is a probability density function. The  $\exp(M_d S)$  is the survival probability during a trip of duration  $S$  (the time delay). The parameters  $R, A, B$  and  $M$  are taken to be positive and  $D_n, D_p, M_n$  and  $M_p$  are non-negative constants.

The limitation in this model is that only one species has the ability to disperse while the other is confined to its patch,

A two patch Lotka-Volterra model with delayed migration was considered by [30]. The following model was studied,

$$\begin{aligned}\dot{n}_i &= D_N(n_j(t-\tau) - n_i(t)) + r_i n_i - a_i n_i p_i, \\ \dot{p}_i &= D_P(p_j(t-\tau) - p_i(t)) - s_i p_i + b_i n_i p_i.\end{aligned}\quad (2.7)$$

where a patch number is denoted by  $i, i \neq j, i, j = 1, 2$ , and the prey is represented by the variable  $n_i := n_i(t)$ . The predator density is given by  $p_i := p_i(t)$ . The prey per capita growth rate is represented by  $r_i$  while  $a_i$  and  $b_i$  are predation parameters. The constant  $s_i$  is the predator natural mortality rate. The prey and predator migration rates are given by  $D_N$  and  $D_P$  respectively. A time delay in the migration of both species is denoted by  $\tau$ .

The analysis of both the asymmetric and synchronization manifold showed that the model is stable when prey growth rate is less than the coupling term. The model is unstable when the prey growth rate is greater than coupling term, and there is a periodic solutions when coupling term and the prey growth rate are equal.

Equation (2.7) assumes that the only factor affecting the prey population is predation which is not the case since the prey population is affected by the environ-

mental carrying capacity.

A Lotka-Volterra equation in a two patch environment with delayed migration was considered by [20] given by,

$$\begin{aligned}\dot{n}_i(t) &= (\alpha_j p_j + \alpha_0) n_j(t - \tau) - (\alpha_i p_i + \alpha_0) n_i(t) + r_i n_i - a_i n_i p_i, \\ \dot{p}_i(t) &= \beta(p_j(t - \tau) - p_i(t)) + b_i n_i p_i - s_i p_i,\end{aligned}\tag{2.8}$$

Where  $i$  indicates the patch number,  $i, j = 1, 2, i \neq j$ ,  $p_i = p_i(t)$  and  $n_i = n_i(t)$  are the predator and prey densities, respectively. The per capita growth rate is denoted by  $r_i$ , whereas  $a_i$  and  $b_i$  are predation parameters. The constant  $s_i$  is the predator natural mortality rate. The predator migration rate taken to be constant, i.e.  $D_P = \beta$ . The density dependent prey migration rate is given by  $D_N = (\alpha_i p_i + \alpha_0)$ . A time delay in the migration of both the prey and predator is represented by  $\tau$ .

The results obtained show that a time delay in migration greatly affects the density of both species; a longer time delay negatively affects the population density. The results also show that when the migration rate is high, the species will coexist. Equation (2.8) assumes that the predator migration rate is constant and that the carrying capacity does not affect the stability of a species.

From the literature stated above, the Lotka-Volterra model assumed that the environment is homogeneous and therefore the species do not migrate in search of food or safety. The model also assumed that in the absence of the predator species, the prey will grow unboundedly. The Rosenzweig-MacArthur model improved the Lotka-Volterra model by including a carrying capacity for the prey species to account for the fact that the prey will grow governed by the available sustaining resources in the absence of the predation in a homogeneous environment.

Recent Lotka-Volterra models like [5, 22] have addressed instantaneous migration of the predator and prey species. The two models fail to address the fact that the prey species density is dictated by both the predator density and the available sustaining resources. The two models also fail to address the fact that there may be a time delay when these species are migrating due to a number of factors, for

example, barriers like a busy infrastructure in the natural habitat or a swollen river.

Models which address time delays in migration have also been developed and examined, for example, [24, 20, 30]. Their main limitation is that in the absence of predation, the prey density will grow unboundedly. These two models also do not consider density-dependent migration rate for both species. Models like [2, 10] have addressed both migration of the species and a carrying capacity for the prey species. These models assume that migration is instantaneous irrespective of the barriers faced during migration. Since there may be barriers during migration, this study incorporates time delays in the migration of both species. Similarly, given the fact that the prey species will grow bounded by the sustaining available resources, this study assumes a logistic growth for the prey species.

## CHAPTER 3

### A PREDATOR-PREY MODEL WITH LOGISTIC GROWTH AND CONSTANT DELAYED MIGRATION

#### 3.1 Model Formulation

The proposed model uses the framework of the Rosenzweig-MacAurthur predator-prey system with a Holling-type II predator functional response, given by,

$$\begin{aligned}\dot{n}_i(t) &= n_i \left( r_i \left( 1 - \frac{n_i}{K_i} \right) - \frac{A_i p_i}{n_i + B_i} \right), \\ \dot{p}_i(t) &= \frac{p_i n_i}{B_i + n_i} - d_i p_i, \quad \text{where } i = 1, 2\end{aligned}\tag{3.1}$$

Where  $n_i = n_i(t)$  and  $p_i = p_i(t)$  are the prey and predator densities at time  $t$  in patch  $i$ , respectively. The parameter  $r_i$  denotes the prey intrinsic growth rate. The prey carrying capacity is denoted by  $K_i$ . The constant  $d_i$  is the predator natural mortality rate. The predation parameter is denoted by  $B_i$  and the prey capturing rate is denoted by  $A_i$ .

The assumptions in Equation (3.1) are as follows:

- (i) In the absence of predation, the prey species grows bounded by carrying capacity  $K$ ;
- (ii) Predation reduces the prey's intrinsic growth rate by a term proportional to the predator and prey densities;
- (iii) The death rate of the predator density assumes an exponential decay in the absence of the prey density;
- (iv) The density of the prey and predator is proportional to the predators' growth rate;
- (v) The species are assumed to be of the same type. The only difference could be due to different families that is typical of ecological systems.



The net migrated prey and predator density is denoted by  $m_{ni}$  and  $m_{pi}$ , respectively, and are defined as:

$$\begin{aligned} m_{ni} &= D_N(n_j(t - \tau) - n_i(t)) \\ m_{pi} &= D_P(p_j(t - \tau) - p_i(t)), \end{aligned} \quad (3.2)$$

Where  $i \neq j$ ,  $i, j = 1, 2$ ,  $D_N$  is the prey migration rate,  $D_P$  is the predator migration rate, and  $\tau$  represents a time delay in the migration of both the prey and predator.

Equation (3.1) describes how the predator and prey species interact within their respective patches and Equation (3.2) describes how the species migrate from one patch to another. Therefore introducing the migration Equation (3.2) into the interaction Equation (3.1), we obtain.

$$\begin{aligned} \dot{n}_1 &= D_N(n_2(t - \tau) - n_1) + n_1 \left( r_1 \left( 1 - \frac{n_1}{K_1} \right) - \frac{A_1 p_1}{n_1 + B_1} \right), \\ \dot{p}_1 &= D_P(p_2(t - \tau) - p_1) + \frac{p_1 n_1}{B_1 + n_1} - d_1 p_1 \\ \dot{n}_2 &= D_N(n_1(t - \tau) - n_2) + n_2 \left( r_2 \left( 1 - \frac{n_2}{K_2} \right) - \frac{A_2 p_2}{n_2 + B_2} \right), \\ \dot{p}_2 &= D_P(p_1(t - \tau) - p_2) + \frac{p_2 n_2}{B_2 + n_2} - d_2 p_2 \end{aligned} \quad (3.3)$$

### 3.2 Model Analysis

Let  $Y_i(t) := (n_i(t), p_i(t))$ ,  $i = 1, 2$  and let the prey migration rate  $D_N$  and the predator migration rate  $D_P$  be equal to some constants  $\alpha$  and  $\beta$ , respectively, then Equation (3.3) becomes,

$$\dot{Y}_i(t) = (Y_j(t - \tau) - Y_i(t))\gamma + f_i(Y_i(t)), \quad i \neq j, i, j = 1, 2, \quad (3.4)$$

where,  $\gamma = (\alpha \quad \beta)^T$  and

$$f_i(Y_i(t)) = \begin{pmatrix} n_i \left( r_i \left( 1 - \frac{n_i}{K} \right) - \frac{A_i p_i}{n_i + B_i} \right) \\ \frac{p_i n_i}{B_i + n_i} - d_i p_i \end{pmatrix}.$$

Let  $Y(t) := (Y_1(t), Y_2(t))$  and  $f(Y(t), Y(t - \tau))$  represent the vector field on the right hand side of Equation (3.4), thus Equation (3.4) becomes,

$$\dot{Y}(t) = f(Y(t), Y(t - \tau)). \quad (3.5)$$

Let  $C = \mathcal{C}([-\tau, 0], \mathbb{R}^4)$  be a Banach space equipped with the sup norm,  $\|\phi\| = \sup|\phi(\theta)| \leq r, (0 \leq r < \infty)$ , for  $\theta \in [-\tau, 0]$  and where  $|\phi(\theta)|$  denotes a Euclidean norm of  $\phi(\theta)$ .

Let the initial condition be given by,

$$\varphi(t) := Y(t) |_{[-\tau, 0]}, \quad (3.6)$$

where  $\varphi \in C$ . Since  $f(Y(t), Y(t - \tau)) \in \mathcal{C}(\mathbb{R}^4 \times C, \mathbb{R}^4)$ , Equation (3.5) subject to Equation (3.6) has a unique solution. For more on existence and uniqueness of solutions, see for instance [11].

We wish to exploit the symmetries in the linear part of Equation (3.4), that is;

$$\dot{Y}_i(t) = (Y_j(t - \tau) - Y_i(t))\gamma, \quad i \neq j, i, j = 1, 2, \quad (3.7)$$

which can be represented by two invariant manifolds. We will study the dynamics of these two invariant manifolds. To obtain these invariant manifolds, an application of the Laplace transform methods in complex variables to the migration terms in Equation (3.4) is required. For us to get the Laplace transform, an exponential estimate of the solution of the Equation (3.7) should be bounded.

### 3.2.1 Exponential Boundedness

The following definition, which is found in [12], will be used in proving that the exponential estimate of the solution of the Equation (3.7) is bounded

**Definition 3.2.1** (Gronwall's Inequality). *If  $\varphi, \psi$  are real-valued and continuous functions on  $[0, c]$  and  $\varphi \geq 0$  is integrable on  $[0, c]$ , and*

$$z(t) \leq \varphi(t) + \int_0^t \psi(s)z(s)ds,$$

*we have,*

$$z(t) \leq \varphi(t) + \int_0^t \varphi(s)\psi(s)[\exp \int_s^t (\psi(\xi)d\xi)]ds$$

*moreover, if  $\varphi(t)' \geq 0$  then*

$$z(t) \leq \varphi(t)\exp(\int_0^t \psi(s)ds).$$

The exponential boundedness of Equation (3.7) is shown in the following Lemma.

**Lemma 3.2.1.** *The solution of Equation (3.7) subject to the initial condition in Equation (3.6) for  $t \geq 0$ , satisfies,*

$$\|Y(t)\| \leq (1 + A\tau)e^{2At} \|\varphi\|, \quad (3.8)$$

where  $\|\cdot\|$  denotes a sup norm in  $\mathbb{R}$  as well as a matrix norm.

*Proof.* Equation (3.7) can be written as,

$$\begin{aligned} \begin{pmatrix} \dot{n}_1 \\ \dot{p}_1 \\ \dot{n}_2 \\ \dot{p}_2 \end{pmatrix} &= \begin{pmatrix} -\alpha_1 & 0 & 0 & 0 \\ 0 & -\beta_1 & 0 & 0 \\ 0 & 0 & -\alpha_2 & 0 \\ 0 & 0 & 0 & -\beta_2 \end{pmatrix} \begin{pmatrix} n_1 \\ p_1 \\ n_2 \\ p_2 \end{pmatrix} \\ &+ \begin{pmatrix} 0 & 0 & \alpha_1 & 0 \\ 0 & 0 & 0 & \beta_1 \\ \alpha_2 & 0 & 0 & 0 \\ 0 & \beta_2 & 0 & 0 \end{pmatrix} \begin{pmatrix} n_1(t-\tau) \\ p_1(t-\tau) \\ n_2(t-\tau) \\ p_2(t-\tau) \end{pmatrix}. \end{aligned}$$

Where  $n_i := n_i(t)$  and  $p_i := p_i(t)$ ,  $i = 1, 2$ . Let  $\begin{pmatrix} \alpha_i & 0 \\ 0 & \beta_i \end{pmatrix} = A_i$

$$\dot{Y}(t) = \begin{pmatrix} -A_1 & 0 \\ 0 & -A_2 \end{pmatrix} Y(t) + \begin{pmatrix} 0 & A_1 \\ A_2 & 0 \end{pmatrix} Y(t-\tau).$$

The solutions of Equation (3.9) subject to initial condition in Equation (3.6) satisfy,

$$\begin{aligned} Y(t) &= \varphi(0) + \int_{-\tau}^0 \begin{pmatrix} 0 & A_1 \\ A_2 & 0 \end{pmatrix} \varphi(s) ds + \int_0^t \left\{ \begin{pmatrix} 0 & A_1 \\ A_2 & 0 \end{pmatrix} Y(s-\tau) \right. \\ &\quad \left. - \begin{pmatrix} A_1 & 0 \\ 0 & A_2 \end{pmatrix} Y(s) \right\} ds. \end{aligned} \quad (3.9)$$

Therefore,

$$\begin{aligned} \|Y(t)\| &\leq \|\varphi\| + A \|\varphi\| \tau + 2A \int_0^t \|Y(s)\| ds \\ &= (1 + A\tau) \|\varphi\| + 2 \int_0^t A \|Y(s)\| ds. \end{aligned}$$

Where  $\begin{pmatrix} A_1 & 0 \\ 0 & A_2 \end{pmatrix} = A$ . Since  $(1 + A\tau)\varphi$  is nondecreasing, by Grownwall's inequality,

$$\|Y(t)\| \leq (1 + A\tau) \exp\left(\int_0^t 2A ds\right) \|\varphi\| = (1 + A\tau) \exp(2At) \|\varphi\|.$$

□

Since the exponential boundedness of Equation (3.7) has been proved, the characteristic equation will be obtained. This will help to prove that the Laplace Transform of Equation (3.7) exists.

### 3.2.2 Characteristic Equation of the Coupling Terms

To obtain solutions of Equation (3.3), we assume a solution of the form

$$Y(t) = e^{\lambda t} c, \quad (3.10)$$

where  $c \in \mathbb{R}^4$  with  $c$  a nonzero 4 by 1 column vector. Substituting Equation (3.10) into the Equation (3.7), we obtain the characteristic equation

$$\lambda I_4 e^{\lambda t} c = \begin{pmatrix} -\alpha e^{\lambda t} & 0 & \alpha e^{\lambda(t-\tau)} & 0 \\ 0 & -\beta e^{\lambda t} & 0 & \beta e^{\lambda(t-\tau)} \\ \alpha e^{\lambda(t-\tau)} & 0 & -\alpha e^{\lambda t} & 0 \\ 0 & \beta e^{\lambda(t-\tau)} & 0 & -\beta e^{\lambda t} \end{pmatrix} c \quad (3.11)$$

where  $I_4$  denotes the identity matrix of order 4.

We obtain the following characteristic equation from Equation (3.11)

$$(-\beta - \lambda)^2 (\alpha^2 - \alpha^2 e^{-2\lambda\tau} + a\alpha\lambda + \lambda^2) + e^{-\lambda\tau} \beta (e^{-2\lambda\tau} \beta \alpha^2 - e^{-\lambda\tau} \beta \alpha^2 - 2e^{-\lambda\tau} \beta \alpha \lambda - e^{-\lambda\tau} \beta \lambda^2) = 0 \quad (3.12)$$

### 3.2.3 Invariant Manifold

A manifold is topological space that is homeomorphic to a Euclidean space near each point. Given  $E \subset \mathbb{R}^n$ ,  $E$  is a  $n$ -manifold if it can be locally represented as the graph of a smooth function defined on a  $n$ -dimensional affine subspace of  $\mathbb{R}^n$ . An  $n$ -manifold  $E \subset \mathbb{R}^n$  is said to be invariant under the flow of a vector field  $X$  if for  $x \in E$ ,  $F_t(x) \in E$  for small  $t > 0$ , where  $F_t(x)$  is the flow of  $X$  [25].

We now show that solutions of Equation (3.7) define two semi-flows on two two-dimensional invariant subspaces of  $\mathbb{R}^4$ . Taking the Laplace transform of Equation (3.7), we get

$$\begin{pmatrix} -\lambda I_2 - I_2 \gamma & e^{-\lambda\tau} I_2 \gamma \\ e^{-\lambda\tau} I_2 \gamma & -\lambda I_2 - I_2 \gamma \end{pmatrix} \begin{pmatrix} Y_1(\lambda) \\ Y_2(\lambda) \end{pmatrix} = \begin{pmatrix} Y_1(0) \\ Y_2(0) \end{pmatrix}. \quad (3.13)$$

where  $\gamma = \begin{pmatrix} \alpha & 0 \\ 0 & \beta \end{pmatrix}$ . Equation (3.13) is symmetric in nature. On simplifying Equation (3.13), adding the set of equations involving  $Y_2(0)$  to  $Y_1(0)$  in Equation (3.13), we obtain

$$(-I_2\lambda - I_2\gamma + I_2\gamma e^{-\lambda\tau})(Y_1(\lambda) + Y_2(\lambda)) = Y_1(0) + Y_2(0), \quad (3.14)$$

On simplifying Equation (3.13) by subtracting the set of equations involving  $Y_2(0)$  from  $Y_1(0)$  in Equation (3.13), we obtain

$$(-I_2\lambda - I_2\gamma - I_2\gamma e^{-\lambda\tau})(Y_1(\lambda) - Y_2(\lambda)) = Y_1(0) - Y_2(0), \quad (3.15)$$

The Matrix  $(-I_2\lambda - I_2\gamma + I_2\gamma e^{-\lambda\tau})^{-1}$  is non-singular when  $\lambda$  is such that  $(-I_2\lambda - \gamma + \gamma e^{-\lambda\tau}) \neq 0$  and  $(-\lambda - \gamma - \gamma e^{-\lambda\tau})^{-1}I_2$  is non-singular when  $\lambda$  is such that  $(-\lambda - \gamma - \gamma e^{-\lambda\tau}) \neq 0$ , thus the inverse Laplace transform for Equation (3.14) and Equation (3.15) is

$$\begin{aligned} (Y_1(\lambda) + Y_2(\lambda)) &= \mathcal{L}^{-1}\{(-\lambda - \gamma + \gamma e^{-\lambda\tau})I_2\}^{-1}(Y_1(0) + Y_2(0)), \\ (Y_1(\lambda) - Y_2(\lambda)) &= \mathcal{L}^{-1}\{(-\lambda - \gamma - \gamma e^{-\lambda\tau})I_2\}^{-1}(Y_1(0) - Y_2(0)), \end{aligned} \quad (3.16)$$

We have two manifolds; the symmetric manifold denoted by  $\Theta$ -manifold where  $Y_1(t) = Y_2(t)$  and the asymmetric manifold denoted by  $\Pi$ -manifold where  $Y_1(t) = -Y_2(t)$ .

Let us now define two linear subspaces of  $\mathbb{R}^4$

$$\begin{aligned} \Theta &= \{(Y_1(t), Y_2(t)), Y_i(t) \in \mathbb{R}^2 : Y_1(t) - Y_2(t) = 0\}, \\ \Pi &= \{(Y_1(t), Y_2(t)), Y_i(t) \in \mathbb{R}^2 : Y_1(t) + Y_2(t) = 0\}. \end{aligned} \quad (3.17)$$

We reduce the dimension of the system in Equation (3.3) by the introduction of change of coordinates defined by,

$$\begin{aligned} u_1 &:= \frac{1}{2}(n_1 + n_2), \quad v_1 := \frac{1}{2}(p_1 + p_2), \\ u_2 &:= \frac{1}{2}(n_1 - n_2), \quad v_2 := \frac{1}{2}(p_1 - p_2). \end{aligned} \quad (3.18)$$

With the assumption that the predator and prey species are of the same type regardless of the patch, we take  $r_i := r$ ,  $A_i := A$ ,  $B_i := B$ ,  $d_i := d$ ,  $\alpha_i := \alpha$ ,  $K_i := K$  and  $\beta_i := \beta$ ,  $i = 1, 2$ . Substituting the transformation in Equation (3.18) in Equation (3.3), we obtain,

$$\begin{aligned}
\dot{u}_1 &= \alpha(u_1(t - \tau) - u_1) + \frac{r}{K} \left( Ku_1 - u_1^2 - u_2^2 \right) - A \left( \frac{Bu_1v_1 + u_1^2v_1 - u_2(-u_2v_1 + Bv_2)}{(u_1 + B)^2 - u_2^2} \right), \\
\dot{v}_1 &= \beta(v_1(t - \tau) - v_1) + \frac{Bu_2v_2 + (u_1(B + u_1) - u_2^2)v_1}{(B + u_1)^2 - u_2^2} - dv_1, \\
\dot{u}_2 &= -\alpha(u_2(t - \tau) + u_2) + \frac{r}{K} \left( Ku_2 - 2u_1u_2 \right) - A \left( \frac{Bu_2v_1 + u_1(B + u_1)v_2 - u_2^2v_2}{(u_1 + B)^2 - u_2^2} \right), \\
\dot{v}_2 &= -\beta(v_2(t - \tau) + v_2) + \frac{Bu_2v_1 + (u_1(B + u_1) - u_2^2)v_2}{(B + u_1)^2 - u_2^2} - dv_2.
\end{aligned} \tag{3.19}$$

where  $u_i = u_i(t)$  and  $v_i = v_i(t)$ ,  $i = 1, 2$ . The linear subspace in Equation (3.17) becomes

$$\begin{aligned}
\Pi &= \{(u_1, v_1, 0, 0) \in \mathbb{R}^4 : (u_1, v_1) \in \mathbb{R}^2\}, \\
\Theta &= \{(0, 0, u_2, v_2) \in \mathbb{R}^4 : (u_2, v_2) \in \mathbb{R}^2\}.
\end{aligned}$$

On both  $\Pi$  and  $\Theta$  the system reduces to two dimensional systems of the form

$$\begin{aligned}
\dot{u}_1 &= \alpha(u_1(t - \tau) - u_1) + ru_1 \left( 1 - \frac{u_1}{K} \right) - A \left( \frac{u_1v_1}{u_1 + B} \right), \\
\dot{v}_1 &= \beta(v_1(t - \tau) - v_1) + \frac{u_1v_1}{B + u_1} - dv_1,
\end{aligned} \tag{3.20}$$

and

$$\begin{aligned}
\dot{u}_2 &= -\alpha(u_2(t - \tau) + u_2) + ru_2 + A \left( \frac{u_2^2v_2}{B^2 - u_2^2} \right), \\
\dot{v}_2 &= -\beta(v_2(t - \tau) + v_2) - \frac{u_2^2}{B^2 - u_2^2} - dv_2,
\end{aligned} \tag{3.21}$$

respectively.

Next we examine the stability of solutions on the two manifolds, this will help us predict long-term behaviors of solutions of Model (3.3).

### 3.2.4 Asymmetric Manifold

On solving the system in Equation (3.20), we let  $U_1 = (u_1, v_1)^T$ , then the system in Equation (3.20) becomes

$$\dot{U}_1 = \begin{pmatrix} \alpha & 0 \\ 0 & \beta \end{pmatrix} U_1(t - \tau) + \begin{pmatrix} -\alpha + r - \frac{ru_1}{K} & -\beta - \frac{v_1}{u_1 + B} \\ 0 & \end{pmatrix} U_1 \quad (3.22)$$

Let  $U_1(t) = e^{\lambda t} C_1$ , then we obtain the following characteristic equation from Equation (3.22),

$$(\alpha e^{-\lambda\tau} - \alpha + r - \lambda)(\beta e^{-\lambda\tau} - \beta - d - \lambda) = 0 \quad (3.23)$$

The analysis of Equation (3.22) is summarized in the following proposition,

**Theorem 3.2.1.** *For all values of the predator migration rate and the predator mortality rate, Equation (3.22) has*

- (i) *a sink when the prey growth rate is less than the prey migration rate,*
- (ii) *a saddle when the prey growth rate is greater than the prey migration rate,*
- (iii) *a periodic solution when the prey growth rate and the prey migration rate are equal*

*Proof.* Using the first factor of Equation (3.23), we have

$$(\alpha e^{-\lambda\tau} - \alpha + r - \lambda) = 0 \quad (3.24)$$

Let

$$x = (\lambda + \alpha - r)\tau \quad (3.25)$$

Then Equation (3.24) becomes

$$x = \alpha\tau e^{-x} e^{(-r+\alpha)\tau} \quad (3.26)$$

The following lemma which is found in [6] will be used to solve Equation (3.26)

**Lemma 3.2.2.** *The equation  $x = be^{-x}$  has simple pure imaginary roots,*

$$x = i\left(\frac{\pi}{2} + 2m\pi\right), \quad \text{for } b = -\left(\frac{\pi}{2} + 2m\pi\right)$$

$$x = 0, \quad \text{for } b = 0$$

$$x = i\left(\frac{\pi}{2} + (2m + 1)\pi\right), \quad \text{for } b = \left(\frac{\pi}{2} + (2m + 1)\pi\right)$$

where  $m = 0, 1, 2, \dots$  and there are no other purely imaginary roots.

*Proof.* Let  $x = a + ib$ , thus

$$a + ib = \beta e^{-(a+ib)} \quad (3.27)$$

$$a + ib = \beta e^{-a}(\cos b - i \sin b) \quad (3.28)$$

Therefore

$$a = \beta e^{-a} \cos b \quad (3.29)$$

$$b = -\beta e^{-a} \sin b \quad (3.30)$$

For  $x$  to have purely imaginary roots, then  $a = 0$ . Equation (3.29) and Equation (3.30) become

$$0 = \beta \cos b \quad (3.31)$$

and

$$b = -\beta \sin b \quad (3.32)$$

respectively. For Equation (3.31) to hold, then  $b = \frac{\pi}{2} + k\pi$ . This yields  $\beta = \frac{\pi}{2} + k\pi$  when  $k$  is odd and  $\beta = -\left(\frac{\pi}{2} + k\pi\right)$  when  $k$  is even. This proves Lemma 3.2.2.  $\square$

Using Lemma (3.2.2) where  $b = \alpha\tau e^{-(r-\alpha)\tau} > 0$ , let  $\alpha\tau e^{-(r-\alpha)\tau} = \left(\frac{\pi}{2} + (2m+1)\pi\right)$ , then  $x = i\left(\frac{\pi}{2} + (2m + 1)\pi\right) = i\alpha\tau e^{-(r-\alpha)\tau}$ . Equation (3.25) becomes

$$\lambda = i\alpha e^{-(r-\alpha)\tau} - \alpha + r \quad (3.33)$$

Then for

(i)  $\alpha < r$ , Equation (3.33) has roots that have positive real parts

(ii)  $\alpha > r$ , Equation (3.33) has roots that have negative real parts



(iii)  $\alpha = r$ , Equation (3.33) has purely imaginary roots.

For the second factor of Equation (3.23),

$$(\beta e^{-\lambda\tau} - \beta - d - \lambda) = 0. \quad (3.34)$$

Let

$$x = (\lambda + \beta + d)\tau \quad (3.35)$$

From Lemma (3.2.2), Equation (3.35) becomes

$$\lambda = i\beta e^{(\beta+d)\tau} - \beta - d \quad (3.36)$$

Equation (3.35) has roots with negative real parts for all positive values of  $d$  and  $\beta$

The results for Equation (3.23) therefore becomes

(i) a saddle when the prey growth rate is greater than the prey migration rate, then either,

**(a)** the prey population becomes extinct, as a result of the prey not migrating in high rates after facing an unfavorable condition like a predator attack leaving a big fraction of the prey density vulnerable to other predator attacks and thus diminishing the prey density to extinction after some time. This will lead to the extinction of the predator population after some time due to their lack of food, or,

**(b)** the predator population is led to extinction which leads the prey density to grow bounded by the carrying capacity. If the prey density is high, it will make the predator density to grow and with low prey density, the predator density will be also decrease. The predator density might decrease to extinction when the prey density is low or when the predator density is high, this makes the prey density to reduce thus making the predator density to reduce possibly to extinction. Then in the absence of predation, the prey population grows bounded by the carrying capacity.

- (ii) a sink when the prey growth rate is less than the prey migration rate, therefore the two species will coexist. This is as a result of the prey migrating in high rates after a predator attack thus reducing the danger the prey density faces. This in turn means that availability of the food source for the predator is always granted.
- (iii) a center for  $\alpha = r$ , that means that, when the prey growth rate and the prey migration rate are equal, then a periodic solution for these species occurs. The prey and predator densities will be dependant on the other species, the prey population is governed by the availability of sustainable resources and the predator density in a given patch while the predator species is dependant on the availability of their food source.

□

### 3.2.5 Symmetric Manifold

Similarly, on solving the system in Equation (3.21), let  $U_2 = (u_2, v_2)^T$ , then the system in Equation (3.21) becomes

$$\dot{U}_2 = \begin{pmatrix} -\alpha & 0 \\ 0 & -\beta \end{pmatrix} U_2(t - \tau) + \begin{pmatrix} -\alpha + r & \frac{u_2}{B^2 - u_2^2} \\ 0 & -\beta - d \end{pmatrix} U_2 \quad (3.37)$$

Let  $U_2(t) = e^{\lambda t} C_2$ , then the following characteristic equation is obtained from Equation (3.37),

$$(-\alpha e^{-\lambda\tau} - \alpha + r - \lambda)(-\beta e^{-\lambda\tau} - \beta - d - \lambda) = 0 \quad (3.38)$$

The analysis of Equation (3.37) is summarized in the following proposition,

**Theorem 3.2.2.** *For all values of the predator migration rate and the predator mortality rate, Equation (3.37) has*

- (i) a sink when the prey migration rate is greater than the prey growth rate,
- (ii) a saddle when the prey migration rate is less than the prey growth rate,

(iii) a periodic solution when the prey growth rate and the prey migration rate are equal

*Proof.* Using the first factor of Equation (3.38), we have

$$(-\alpha e^{-\lambda\tau} - \alpha - \lambda + r) = 0 \quad (3.39)$$

Let

$$x = (-r + \lambda + \alpha)\tau \quad (3.40)$$

Then Equation (3.39) becomes

$$x = -\alpha\tau e^{-x} e^{(-r+\alpha)\tau} \quad (3.41)$$

Using Lemma (3.2.2) where  $b = -\alpha\tau e^{(-r+\alpha)\tau} > 0$ , we get  $x = i(\frac{\pi}{2} + 2m\pi)$  for  $-\alpha\tau e^{(-r+\alpha)\tau} = -(\frac{\pi}{2} + 2m\pi)$ . Equation (3.40) becomes

$$\lambda = i\alpha e^{(-r+\alpha)\tau} - \alpha + r \quad (3.42)$$

Then for

- (i)  $\alpha < r$ , Equation (3.42) has roots with positive real parts
- (ii)  $\alpha > r$ , Equation (3.42) has roots with negative real parts
- (iii)  $\alpha = r$ , Equation (3.42) has purely imaginary roots.

For the second factor of Equation (3.38),

$$(-\lambda - \beta - d - \beta e^{-\lambda\tau}) = 0. \quad (3.43)$$

Let

$$x = (\beta + \lambda + d)\tau \quad (3.44)$$

From Lemma (3.2.2), Equation (3.44) becomes

$$\lambda = i\beta e^{(\beta+d)\tau} - \beta - d \quad (3.45)$$

Equation (3.45) has roots with negative real parts for all positive values of  $d$  and  $\beta$ .

The results for Equation (3.38) therefore become

- (i) a saddle when the prey growth rate is greater than prey migration rate, and thus the model becomes unstable. Therefore, either,
  - (a) the prey population becomes extinct because they migrate in low rates after facing an unfavorable condition which makes the predator population becoming extinct after some time due to their lack of food.
  - (b) the predator population is led to extinction and the prey density grows logistically. This is as a result of the prey population decreasing when the predator density is high, this makes the predator population to reduce, possibly to extinction. Then the prey population grows logistically in the absence of the predator population.
- (ii) a sink when the prey growth rate is less than prey migration rate, implying that, the model is stable and therefore the two species will coexist.
- (iii) a center when the prey growth rate and prey migration rate are equal, and therefore a periodic solution occurs.

□

In both the symmetric and asymmetric manifolds, it has been shown when the prey migration rate is greater than the prey growth rate, the the two species can coexist.

### **3.3 Numerical Analysis for Model with constant migration for both Species**

In this section, Matlab software is used to illustrate the numerical simulations describing the theoretical results for the System of Equation (3.3). Variables and parameters values are adapted from [2, 20, 22]. In this section, time,  $t$ , is in months. The initial population is given by  $u_1$  and  $v_1$  for the asymmetric manifold and  $u_2$  and  $v_2$  for the symmetric manifold. In Section 3.3.1, the simulations for the Asym-

metric Manifold are shown, while in Section 3.3.2 the simulations for the Symmetric Manifold are shown.

### 3.3.1 Numerical analysis for Asymmetric manifold

The following parameter values are used in simulating the graphs of Equation (3.20).

**Table 3.1:** *Parameter values for the Asymmetric Manifold*

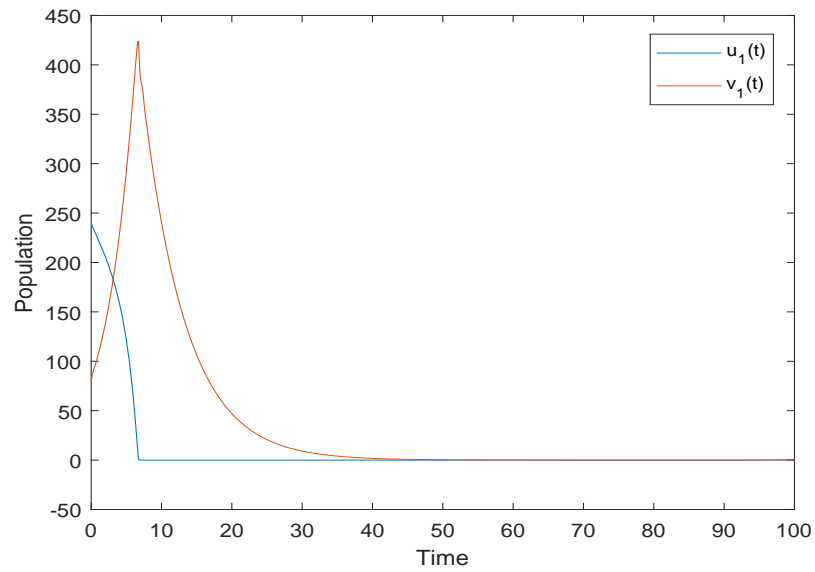
<b>Figure</b>	$r$	$\alpha$	$K$	$\beta$	$A$	$B$	$d$	$u_1$	$v_1$
3.1	1.5	0.6	250	2.792403	0.2	3	0.4	240	80
3.2	1.5	0.6	250	2.792403	0.2	3	0.4	240	80
3.3	0.1	0.6	250	2.792403	0.2	3	0.4	240	80
3.4	0.1	0.6	250	2.792403	0.2	3	0.4	240	80
3.5	0.6	0.6	250	2.792403	0.2	3	0.4	240	80
3.6	0.6	0.6	250	2.792403	0.2	3	0.4	240	80

For each scenario ( $\alpha < r$ ,  $\alpha > r$ , and  $\alpha = r$ ), we consider a case where

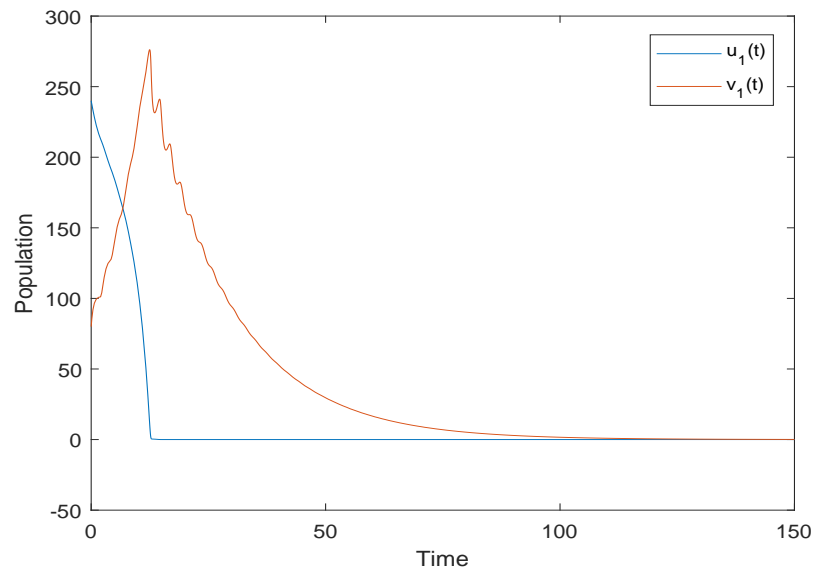
1. the time delay is short,  $\tau = 0.1$  which is equivalent to three days
2. the time delay is long,  $\tau = 1.5$  or  $\tau = 2$  which is equivalent to approximately 45 days or 60 days respectively.

This will help us see the effects delay in migration has on these species densities.

Simulations for the asymmetric manifold gives,



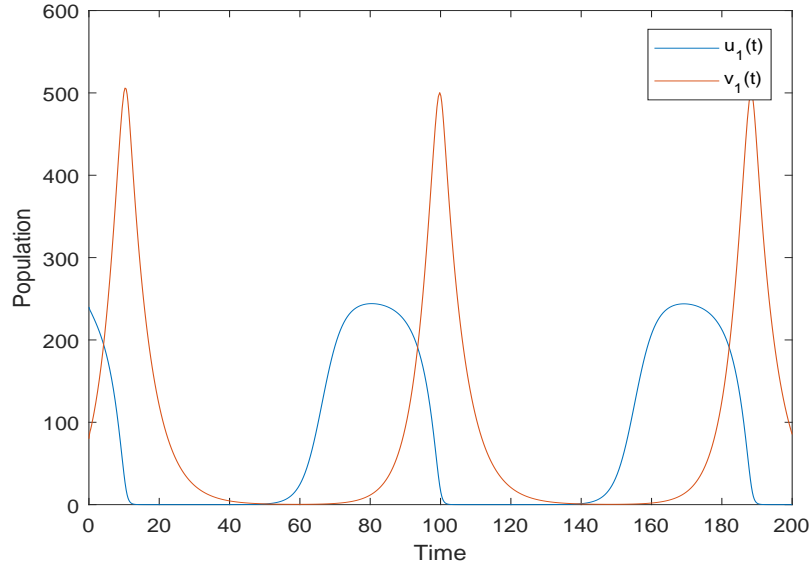
**Figure 3.1:** *Graph of asymmetric manifold for  $\alpha < r$ ,  $\tau = 0.1$ .*



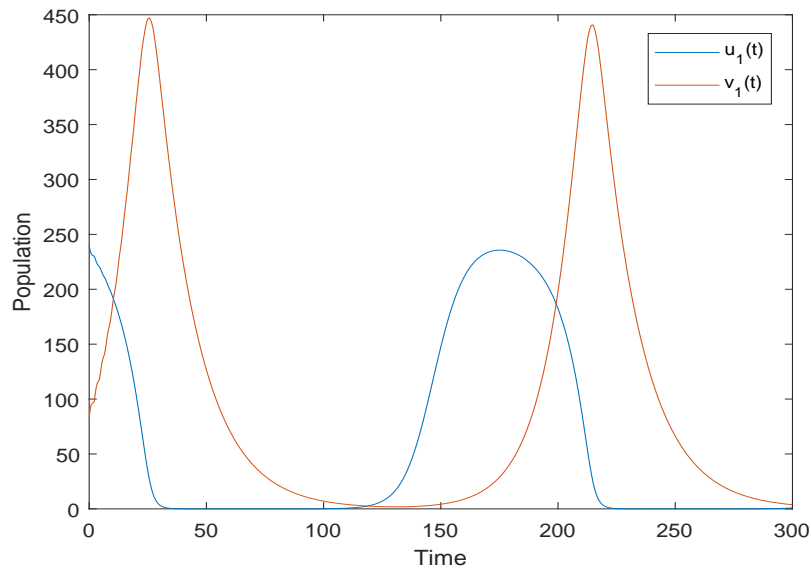
**Figure 3.2:** *Graph of asymmetric manifold for  $\alpha < r$ ,  $\tau = 2$ .*

When the prey growth rate is greater than prey migration rate ( $r > \alpha$ ), the prey density becomes extinct after some time as shown in Figure 3.1 and Figure 3.2. This leads to the predator density also becoming extinct since it does not have any source of food. A longer time delay makes the predator and prey species become extinct at a slower rate compared to when the time delay is short. This is due to the fact that the prey species migrates at a slower rate, meaning few prey migrate, and those migrating face barriers which delays their migration and thus they remain the given

patch for some more time and this in turn provides food for the predator density. With these barriers and the slow migration rates, the prey density reduces possibly to extinction.



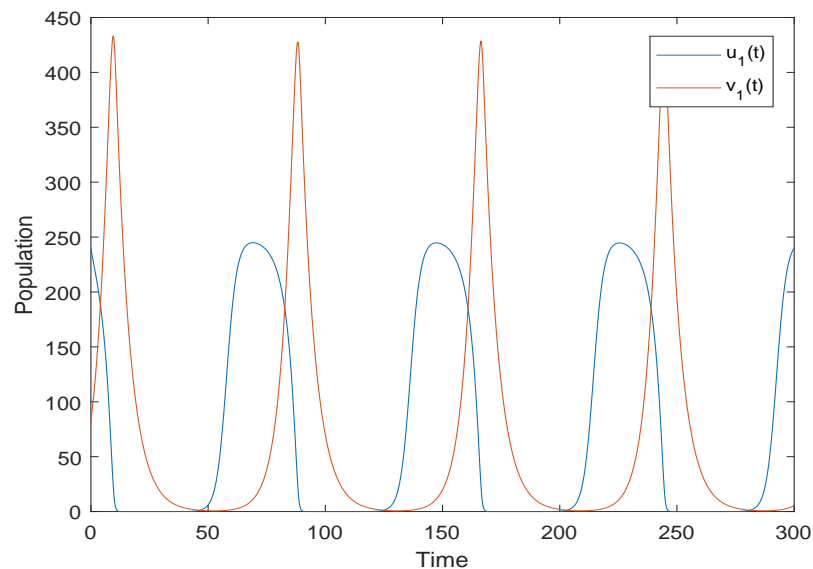
**Figure 3.3:** *Graph of asymmetric manifold for  $\alpha > r$ ,  $\tau = 0.1$ .*



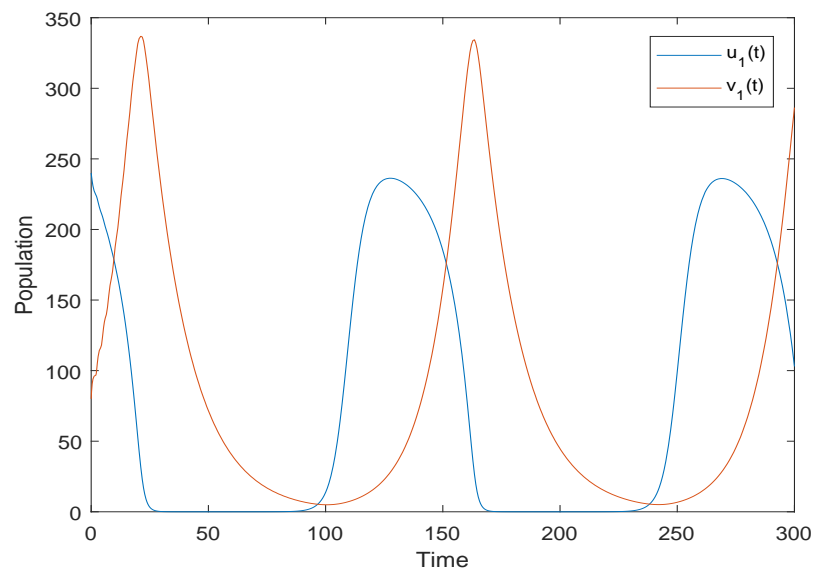
**Figure 3.4:** *Graph of asymmetric manifold for  $\alpha > r$ ,  $\tau = 2$ .*

In Figure 3.3 and Figure 3.4, when the prey intrinsic growth rate is less than prey migration rate ( $r < \alpha$ ). The predator and prey densities coexist. The two population densities oscillate, where both densities are dependant on the available sustaining resources. This is due to the fact that the prey migrate at a higher rate after facing unfavourable conditions thus leaving a small fraction of the prey species vulnerable

to the unfavorable condition being faced. These conditions may include predator attacks, limited food resources among others. With the survival of the prey species, the predator species will always have its source of food thus guaranteeing their survival. A longer time delay slows down the decrease or increase of a given species. When this species face hostile conditions, they may try to migrate to safety, if they meet barriers during migration, then they will be prone to these hostile condition for a longer period of time before finally being able to migrate. This in turn will have a negative impact on these species since they cannot be able to migrate to safety instantly.



**Figure 3.5:** Graph of asymmetric manifold for  $\alpha = r$ ,  $\tau = 0.1$ .





**Figure 3.6:** Graph of asymmetric manifold for  $\alpha = r$ ,  $\tau = 2$ .

In Figure 3.5 and Figure 3.6, when the prey growth rate and the prey migration rate are equal ( $r = \alpha$ ). The predator and prey densities will oscillate. The two populations will rise and fall almost in equal measures. The prey density will depend on the availability of food and its safety from predation while the predator density will depend on the availability of the food source. A longer time delay slows down the change in population of a given species.

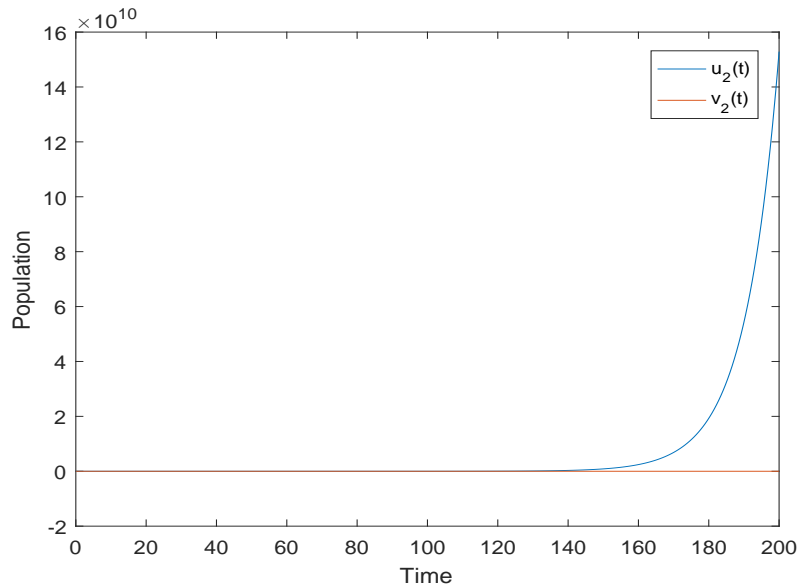
### 3.3.2 Numerical analysis for Symmetric manifold

The following parameter values are used in simulating the results of Equation (3.21).

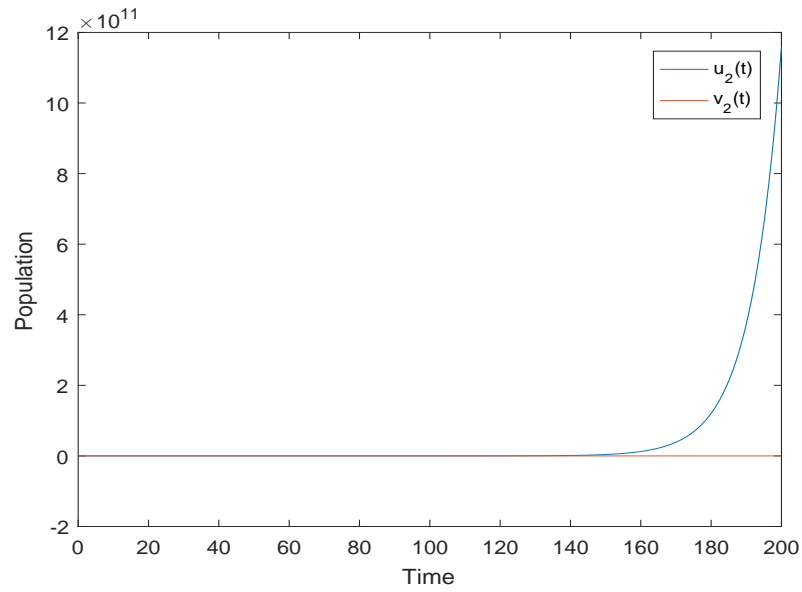
Figure	$r$	$\alpha$	$\beta$	$A$	$B$	$d$	$u_2$	$v_2$
3.7	1.5	0.6	2.792403	0.2	3	0.4	240	80
3.8	1.5	0.6	2.792403	0.2	3	0.4	240	80
3.9	0.1	0.6	2.792403	0.2	3	0.4	240	80
3.10	0.1	0.6	2.792403	0.2	3	0.4	240	80
3.11	0.6	0.6	2.792403	0.2	3	0.4	240	80
3.12	0.6	0.6	2.792403	0.2	3	0.4	240	80

**Table 3.2:** Parameter values for the Symmetric Manifold

Simulations for the Symmetric manifold gives,

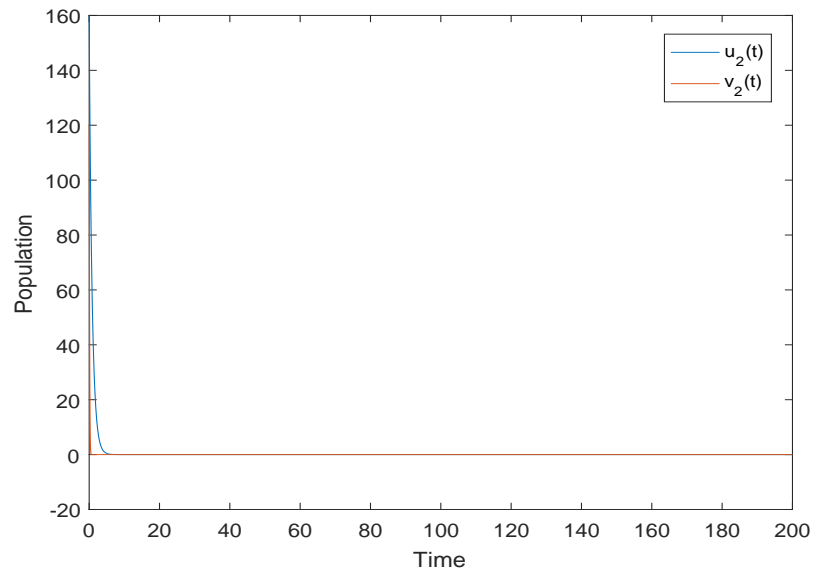


**Figure 3.7:** Graph of symmetric manifold for  $\alpha < r$ ,  $\tau = 0.1$ .

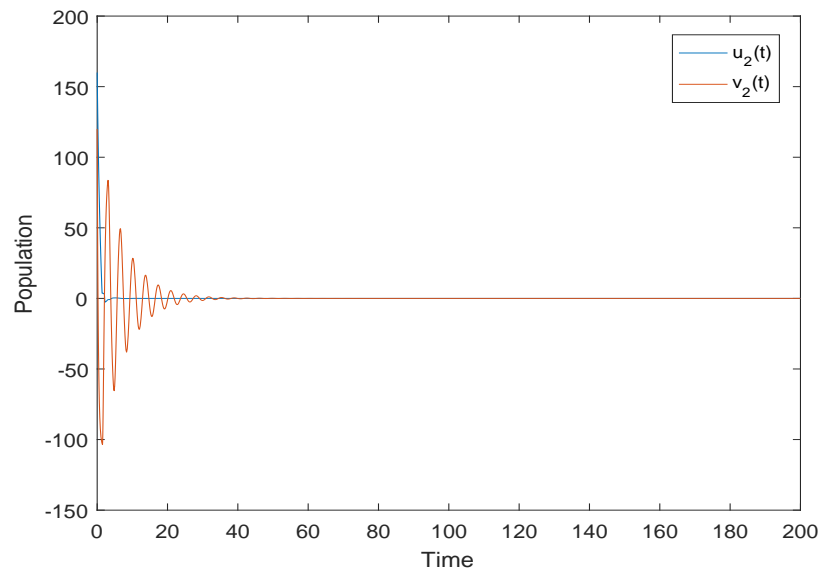


**Figure 3.8:** Graph of symmetric manifold for  $\alpha < r$ ,  $\tau = 1.5$ .

When the prey growth rate is greater than prey migration rate ( $r > \alpha$ ), the predator density becomes extinct, this makes the prey density to grow. This is as a result of the prey densities being driven almost to extinction since they cannot migrate at higher rates to safety. With the diminished numbers of the prey species, the predator species declines to extinction. The few prey remaining then reproduce and since there is no predation, the prey species grows. A longer time delay makes the population increase as seen in Figure 3.8 compared to Figure 3.7.



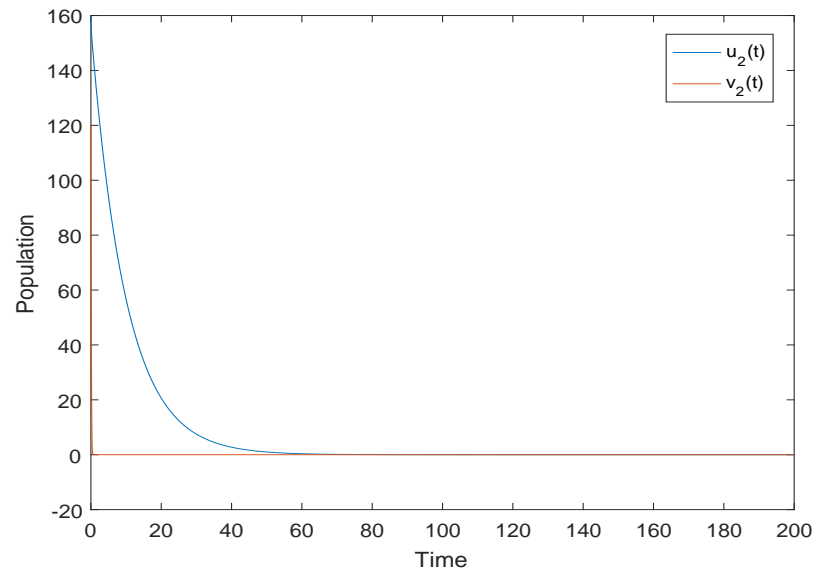
**Figure 3.9:** *Graph of symmetric manifold for  $\alpha > r$ ,  $\tau = 0.1$ .*



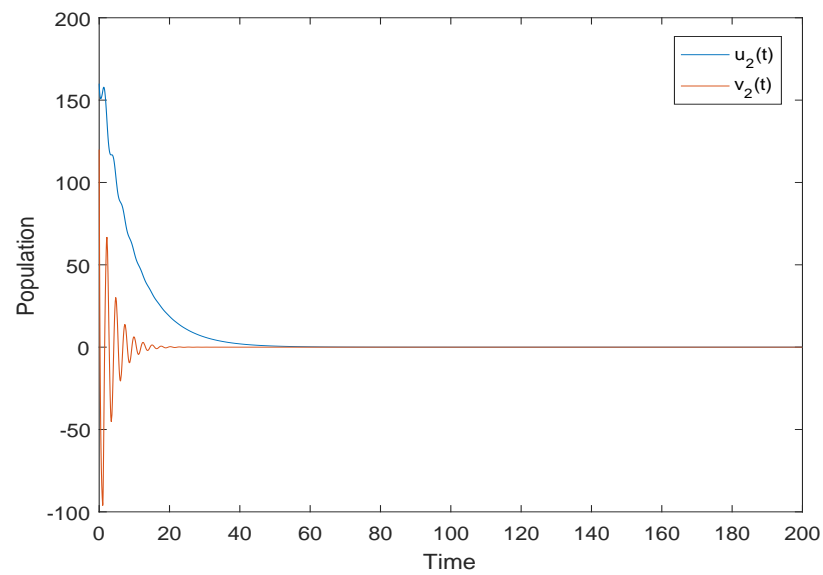
**Figure 3.10:** *Graph of symmetric manifold for  $\alpha > r$ ,  $\tau = 1.5$ .*

When the prey growth rate is less than the prey migration rate ( $r < \alpha$ ), the two densities stabilize at zero as seen in Figure 3.9. Implying that the prey and predator densities in the two patches are equal (using Equation (3.18)). This is a result of the two species moving from one patch to another in search of better conditions, especially security and availability of food. The two species will notice that the living conditions in patch one are the same as those in patch two and in as time increases, the species densities in patch one will be the same as that of patch two.

With a longer time delay, the populations oscillate as seen in Figure 3.10, when the population is positive, then the population in patch one is greater than the population in patch two and when the population is negative, then the population in patch one is less than the population in patch two.



**Figure 3.11:** Graph of symmetric manifold for  $\alpha = r$ ,  $\tau = 0.1$ .



**Figure 3.12:** Graph of symmetric manifold for  $\alpha = r$ ,  $\tau = 1.5$ .

In Figure 3.11 and Figure 3.12, when the prey growth rate and the prey migration rate are equal ( $r=\alpha$ ). The two densities stabilize at zero after some time. A longer time delay introduces oscillations and the time taken for the model to stabilize in this case increases. When the population is negative, then the population in patch

one is less than the population in patch two.

## CHAPTER 4

### A PREDATOR-PREY MODEL WITH LOGISTIC GROWTH AND DENSITY-DEPENDENT DELAYED MIGRATION

#### 4.1 Model Formulation and Analysis

Since the migration of the prey is largely due to predation, then the migration rate will not be constant, instead it may be dependent on the density of the predators and other factors like food availability. Similarly, since the predator migration depends on the availability of food (the prey), then the predator migration rate will be dependent on the density of the prey. Therefore in this chapter we take the migration rates as done by [2], let  $D_N = (\alpha_i p_i + \alpha_0)$  and  $D_P = \frac{1}{\beta_i n_i + \beta_0}$ . Equation (3.3) becomes

$$\begin{aligned}
 \dot{n}_1(t) &= (\alpha_2 p_2 + \alpha_0) n_2(t - \tau) - (\alpha_1 p_1 + \alpha_0) n_1 + n_1 \left( r_1 \left( 1 - \frac{n_1}{K} \right) - \frac{A_1 p_1}{n_1 + B_1} \right), \\
 \dot{p}_1(t) &= \frac{p_2(t - \tau)}{\beta_2 n_2 + \beta_0} - \frac{p_1}{\beta_1 n_1 + \beta_0} + \frac{p_1 n_1}{B_1 + n_1} - d_1 p_1 \\
 \dot{n}_2(t) &= (\alpha_1 p_1 + \alpha_0) n_1(t - \tau) - (\alpha_2 p_2 + \alpha_0) n_2 + n_2 \left( r_2 \left( 1 - \frac{n_2}{K} \right) - \frac{A_2 p_2}{n_2 + B_2} \right), \\
 \dot{p}_2(t) &= \frac{p_1(t - \tau)}{\beta_1 n_1 + \beta_0} - \frac{p_2}{\beta_2 n_2 + \beta_0} + \frac{p_2 n_2}{B_2 + n_2} - d_2 p_2
 \end{aligned} \tag{4.1}$$

In the absence of the predation, due to intraspecific competition, the prey population migrates at the same constant rate,  $\alpha_0$ . With predation, the prey population migrates at a density-dependent rate denoted by  $\alpha_i p_i + \alpha_0$ . This rate depends on the predator density in that patch. The migration rate of the predator species is denoted by  $\frac{1}{\beta_i n_i + \beta_0}$ , this rate depends on the prey density. Predators migrate from one patch to another at a constant rate,  $\frac{1}{\beta_0}$  in search of prey.

With the assumption that the predator and prey species are of the same type regardless of the patch, we take  $r_i := r$ ,  $b_i := b$ ,  $a_i := a$ ,  $s_i := s$ ,  $A_i := A$ ,  $B_i := B$ ,  $\alpha_i := \alpha$  and  $\beta_i := \beta$  where  $i = 1, 2$ . Substituting Equation (3.18) in Equation (4.1), yields,

$$\dot{u}_1 = (u_1(t - \tau) - u_1)(\alpha_0 + \alpha v_1) + \alpha(u_2(t - \tau) - u_2)v_2 + f_1(u_i, v_i),$$

$$\begin{aligned}
\dot{v}_1 &= \frac{-(\beta_0(-v_1(t-\tau) + v_1) + \beta(u_1(-v_1(t-\tau) + v_1) - u_2(v_2(t-\tau) - v_2)))}{(\beta(u_1 - u_2) + \beta_0)(\beta(u_1 + u_2) + \beta_0)} + g_1(u_i, v_i), \\
\dot{u}_2 &= -(u_2(t-\tau) + u_2)(\alpha_0 + \alpha v_1) - \alpha(u_1(t-\tau) + u_1)v_2 + f_2(u_i, v_i), \\
\dot{v}_2 &= \frac{-(-\beta u_2(-v_1(t-\tau) + v_1) + (\beta_0 + \beta(u_1)(-v_2(t-\tau) + v_2)))}{(\beta(u_1 - u_2) + \beta_0)(\beta(u_1 + u_2) + \beta_0)} + g_2(u_i, v_i).
\end{aligned} \tag{4.2}$$

where  $u_i = u_i(t)$  and  $v_i = v_i(t)$ ,  $i = 1, 2$ ,  $f_1(u_i, v_i) = \frac{r}{K}(Ku_1 - u_1^2 - u_2^2) - A\left(\frac{Bu_1v_1 + u_1^2v_1 - u_2(-u_2v_1 + Bv_2)}{(u_1+B)^2 - u_2^2}\right)$ ,  $f_2(u_i, v_i) = \frac{r}{K}(Ku_2 - 2u_1u_2) - A\left(\frac{Bu_2v_1 + u_1(B+u_1)v_2 - u_2^2v_2}{(u_1+B)^2 - u_2^2}\right)$ ,  $g_1(u_i, v_i) = \frac{Bu_2v_2 + (u_1(B+u_1) - u_2^2)v_1}{(B+u_1)^2 - u_2^2} - dv_1$ , and  $g_2(u_i, v_i) = \frac{Bu_2v_1 + (u_1(B+u_1) - u_2^2)v_2}{(B+u_1)^2 - u_2^2} - dv_2$ .

The linear subspace in Equation (3.17) reduces the  $\Pi$  and  $\Theta$  manifolds to two dimensional systems of the form

$$\begin{aligned}
\dot{u}_1 &= -(\alpha_0 + \alpha v_1)(u_1 - u_1(t-\tau)) + u_1\left(r\left(1 - \frac{u_1}{K}\right) - \frac{Av_1}{u_1 + B}\right), \\
\dot{v}_1 &= \frac{\beta_0(v_1(t-\tau) - v_1)}{\beta^2u_1^2 + 2\beta\beta_0u_1 + \beta_0^2} + \frac{u_1v_1}{B + u_1} - dv_1,
\end{aligned} \tag{4.3}$$

and

$$\begin{aligned}
\dot{u}_2 &= -\alpha_0(u_2(t-\tau) + u_2) + ru_2 + A\left(\frac{u_2^2v_2}{B^2 - u_2^2}\right), \\
\dot{v}_2 &= \frac{\beta_0(v_2(t-\tau) - v_2)}{\beta_0^2 - \beta^2u_2^2} - \frac{u_2^2v_2}{B^2 - u_2^2} - dv_2,
\end{aligned} \tag{4.4}$$

respectively. Stability analysis of solutions on the two manifolds is carried out to predict long-term behavior of solutions of the Model (4.1).

#### 4.1.1 Asymmetric Manifold

On solving the system in Equation (4.3), we let  $U_3 = (u_1, v_1)^T$ , then the system in Equation (4.3) becomes

$$\dot{U}_3 = \begin{pmatrix} \alpha_0 & 0 \\ 0 & \frac{\beta_0}{(\beta u_1 + \beta_0)^2} \end{pmatrix} U_3(t-\tau) + \begin{pmatrix} -\alpha_0 + r - \frac{ru_1}{K} & \alpha u_1(t-\tau) - \left(\alpha u_1 + \frac{-A}{u_1+B}\right)u_1 \\ 0 & -\frac{\beta_0}{(\beta u_1 + \beta_0)^2} + \frac{u_1}{u_1+B} - d \end{pmatrix} U_3 \tag{4.5}$$

The analysis Equation (4.5) is summarized in the following proposition,

**Theorem 4.1.1.** *For all values of the constant predator migration rate and the predator mortality rate, Equation (3.22) has*

- (i) *a sink when the prey growth rate is less than the prey migration rate which is not dependent on the predator density,*
- (ii) *a saddle when the prey growth rate is greater than the prey migration rate which is not dependent on the predator density,*
- (iii) *a periodic solution when the prey growth rate is equal to the prey migration rate which is not dependent on the predator density*

*Proof.* Let  $U_3(t) = e^{\lambda t}C_1$ , then we obtain the following characteristic equation from Equation (4.5),

$$(\alpha_0 e^{-\lambda\tau} - \alpha_0 + r - \lambda) \left( \frac{1}{\beta_0} (e^{-\lambda\tau} - 1) - d - \lambda \right) = 0 \quad (4.6)$$

Using the first factor of Equation (4.6), we have

$$(\alpha_0 e^{-\lambda\tau} - \alpha_0 - \lambda + r) = 0 \quad (4.7)$$

Let

$$z = (-r + \lambda + \alpha_0)\tau \quad (4.8)$$

Then Equation (4.7) becomes

$$z = \alpha_0\tau e^{-z} e^{(\alpha_0 - r)\tau} \quad (4.9)$$

Using Lemma (3.2.2) where  $b = \alpha_0\tau e^{-(\alpha_0 - r)\tau} > 0$ , we get  $z = i\left(\frac{\pi}{2} + (2m + 1)\pi\right)$  for  $\alpha_0\tau e^{-(\alpha_0 - r)\tau} = \left(\frac{\pi}{2} + (2m + 1)\pi\right)$ . Equation (4.8) becomes

$$\lambda = i\alpha_0 e^{-(r - \alpha_0)\tau} - \alpha_0 + r \quad (4.10)$$

Then for

- (i)  $\alpha_0 < r$ , Equation (4.10) has roots with positive real parts



- (ii)  $\alpha_0 > r$ , Equation (4.10) has roots with negative real parts
- (iii)  $\alpha_0 = r$ , Equation (4.10) has purely imaginary roots.

For the second factor of Equation (4.6),

$$\left(\frac{1}{\beta_0}(e^{-\lambda\tau} - 1) - d - \lambda\right) = 0. \quad (4.11)$$

Let

$$z = \left(\lambda + \frac{1}{\beta_0} + d\right)\tau \quad (4.12)$$

From Lemma (3.2.2), Equation (4.12) becomes

$$\lambda = \frac{i}{\beta_0}e^{(\frac{1}{\beta_0}+d)\tau} - \frac{1}{\beta_0} - d \quad (4.13)$$

Equation (4.12) has roots with negative real parts for all values of  $\frac{1}{\beta_0}$  and  $d$ .

The results for Equation (4.5) therefore becomes

- (i) a saddle at the origin for  $\alpha_0 < r$ , that means that, when the prey migration rate is less than the prey growth rate, then either,
  - (a) both species will be wiped out after some time. This is due to the fact that the prey migrate in low rates after facing an unfavorable condition like a predator attack or famine. Since most prey remain in the initial patch, they are still prone to more unfavorable conditions which affect their population density and leads the prey density in that patch to tend to extinction. This makes the predator density also to go to extinction due to lack of food.
  - (b) the predator population is wiped out and the prey density grows bounded by the carrying capacity. This is due to the fact that as the prey population decreases, this makes the predator population to be led to extinction. Then the prey population grows bounded by the carrying capacity in the absence of the predator population.

- (ii) a sink at the origin for  $\alpha_0 > r$ , that implies that, when the prey migration rate is greater than the prey growth rate, the two species will coexist. This is as a result of the prey migrating in high rates to safety after facing an unfavorable condition in their initial patch. This in turn will always provide a source of food to the predator density.
- (iii) a center for  $\alpha_0 = r$ , that means that, when the prey migration rate is the same as the prey growth rate then a periodic solution occurs. The two populations will rise and fall almost in equal measures. The prey and predator densities will be dependant on the other species, the prey population is governed by both the predator density and the availability of sustainable resources in a given patch while the predator species is dependant on the availability of their food source.

□

#### 4.1.2 Symmetric Manifold

Similarly, on solving the system in Equation (4.4), let  $U_4 = (u_2, v_2)^T$ , then the system in Equation (4.4) becomes

$$\dot{U}_4 = \begin{pmatrix} -\alpha_0 & 0 \\ 0 & \frac{\beta_0}{\beta_0^2 - \beta^2 u_2^2} \end{pmatrix} U_4(t - \tau) + \begin{pmatrix} r - \alpha_0 & \frac{A u_2^2}{B^2 - u_2^2} \\ 0 & \frac{\beta_0}{\beta_0^2 - \beta^2 u_2^2} - \frac{u_2^2}{B^2 - u_2^2} - d \end{pmatrix} U_4 \quad (4.14)$$

The analysis of Equation (4.14) is summarized in the following proposition,

**Theorem 4.1.2.** *For all values of the constant predator migration rate and the predator mortality rate, Equation (3.22) has*

- (i) *a sink when the prey migration rate, which is not dependent on the predator density, is greater than the prey growth rate,*
- (ii) *a saddle when the prey migration rate, which is not dependent on the predator density, is less than the prey growth rate,*

(iii) a periodic solution when the prey migration rate, which is not dependent on the predator density, is equal to the prey growth rate

*Proof.* Let  $U_4(t) = e^{\lambda t}C_2$ , then the following characteristic equation is obtained from Equation (4.14),

$$(-\alpha_0 e^{-\lambda\tau} - \alpha_0 + r - \lambda)\left(\frac{1}{\beta_0}(e^{-\lambda\tau} - 1) - d - \lambda\right) = 0 \quad (4.15)$$

Using the first factor of Equation (4.15), we have

$$(-\alpha_0 e^{-\lambda\tau} - \alpha_0 + r - \lambda) = 0 \quad (4.16)$$

Let

$$z = (\lambda + \alpha_0 - r)\tau \quad (4.17)$$

Then Equation (4.16) becomes

$$z = -\alpha_0\tau e^{-z} e^{(\alpha_0 - r)\tau} \quad (4.18)$$

Using Lemma (3.2.2), where  $b = -\alpha_0\tau e^{(\alpha_0 - r)\tau} < 0$ , in Equation (4.18) we get  $z = i\left(\frac{\pi}{2} + 2m\pi\right)$  for  $-\alpha_0\tau e^{-z} = -\left(\frac{\pi}{2} + 2m\pi\right)$ . Equation (4.17) becomes

$$\lambda = i\alpha_0 e^{(-r + \alpha_0)\tau} - \alpha_0 + r \quad (4.19)$$

Then for

- (i)  $\alpha_0 < r$ , Equation (4.19) has roots with positive real parts
- (ii)  $\alpha_0 > r$ , Equation (4.19) has roots with negative real parts
- (iii)  $\alpha_0 = r$ , Equation (4.19) has purely imaginary roots.

For the second factor of Equation (4.15),

$$\left(\frac{1}{\beta_0}(e^{-\lambda\tau} - 1) - d - \lambda\right) = 0. \quad (4.20)$$

Let

$$z = \left(\lambda + \frac{1}{\beta_0} + d\right)\tau \quad (4.21)$$

From Lemma (3.2.2), Equation (4.21) becomes

$$\lambda = \frac{i}{\beta_0} e^{(\frac{1}{\beta_0} + d)\tau} - \frac{1}{\beta_0} - d \quad (4.22)$$

Equation (4.22) has roots with negative real part for all values of  $\frac{1}{\beta_0}$  and  $d$ .

For all  $\frac{1}{\beta_0}$  and  $d$ , the results for Equation (4.15) therefore becomes

- (i) a saddle when the prey migration rate, which is not dependent on the predator density, is less than the prey growth rate, then either,
  - (a) both species will be wiped out after some time. Since the prey density do not migrate in high rates after facing an adverse condition, they remain prone to that adverse condition which may make the prey density in that patch to be extinct. Extinction of the prey density leads the predator density to extinction.
  - (b) the prey density grows logistically after the predator population is led to extinction. As the predator density makes the prey density to decline, this makes the predator density also to decline possibly to extinction as a result of a depleted source of food. Then the prey population grows governed by the available sustaining resources in the absence of the predator population.
- (ii) a sink when the prey migration rate, which is not dependent on the predator density, is greater than the prey growth rate, the two species will coexist. This is as a result of the prey moving in high rates after facing an adverse condition, and this makes the prey density not to be wipes out. With the prey density surviving, a food source to the predator density is always guaranteed thus making the two species to coexist.
- (iii) a periodic solution when the prey migration rate, which is not dependent on the predator density, is equal to the prey growth rate.

□

The obtained results show that prey migration due to the predator density does not greatly affect the prey density compared to the other factors that cause the prey to migrate. These factors include:

- (i) human activities in the natural habitats like logging
- (ii) natural causes like bad climatic conditions, limited food resources and over-population of the prey species in a patch among others.

## 4.2 Numerical Analysis for Model with density-dependent migration for both Species

In Section 4.3.1, the simulations for the Asymmetric Manifold are shown, while in Section 4.3.2 the simulations for the Symmetric Manifold are shown. The initial population is given by  $u_1$  and  $v_1$  for the asymmetric manifold and  $u_2$  and  $v_2$  for the symmetric manifold.

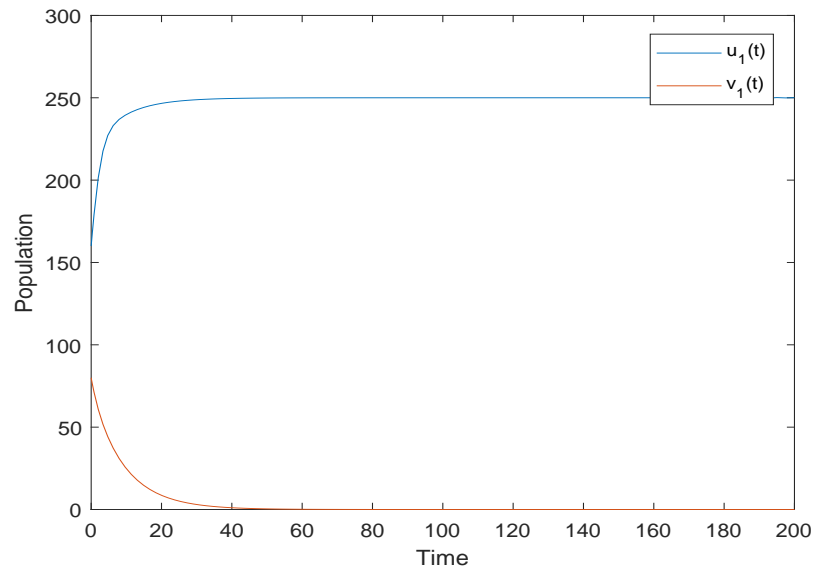
### 4.2.1 Numerical analysis for Asymmetric manifold

In this section, with the help of Matlab software, numerical simulations for Equation (4.3) are performed. Parameters values are adapted from [2, 20, 22]. In this section, time,  $t$ , is in months. The following parameter values are used in simulating the graphs of Equation (4.3).

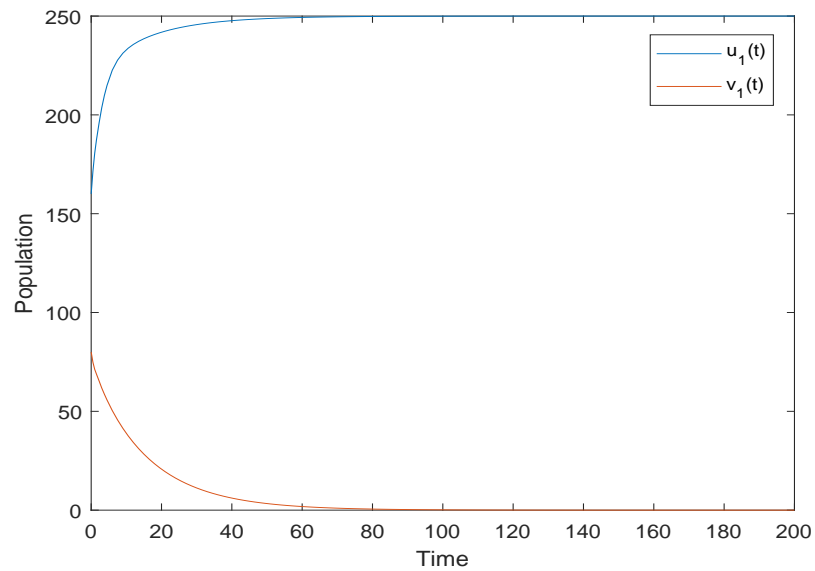
<b>Figure</b>	$r$	$\alpha_0$	$\alpha$	$K$	$d$	$A$	$\beta_0$	$\beta$	$B$	$u_i$	$v_i$
4.1	1.5	0.6	0.4	250	0.4	0.3	0.4	2.792403	3	160	80
4.2	1.5	0.6	0.4	250	0.4	0.3	0.4	2.792403	3	160	80
4.3	0.1	0.6	0.4	250	0.4	0.3	0.4	2.792403	3	160	80
4.4	0.1	0.6	0.4	250	0.4	0.3	0.4	2.792403	3	160	80
4.5	0.6	0.6	0.4	250	0.4	0.3	0.4	2.792403	3	160	80
4.6	0.6	0.6	0.4	250	0.4	0.3	0.4	2.792403	3	160	80

**Table 4.1:** *Parameter values for the Asymmetric Manifold*

Simulations for the asymmetric manifold gives,



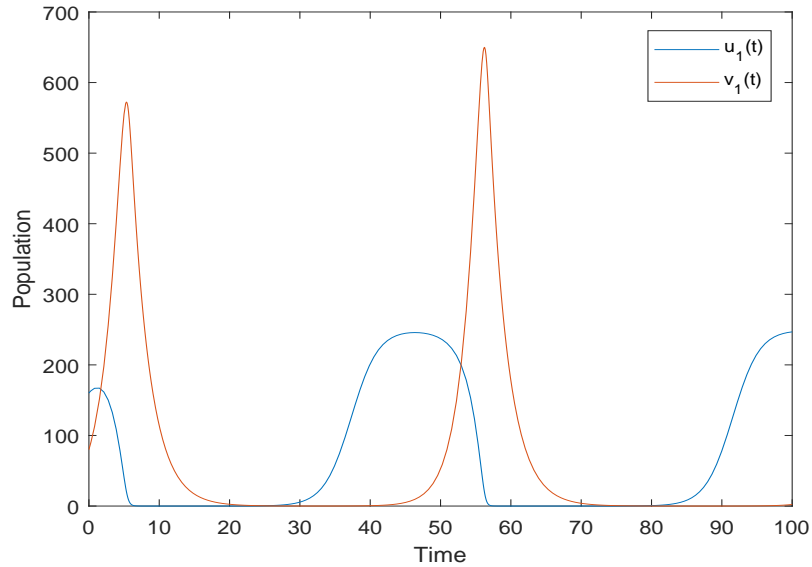
**Figure 4.1:** *Graph of asymmetric manifold for  $\alpha_0 < r$ ,  $\tau = 0.1$ .*



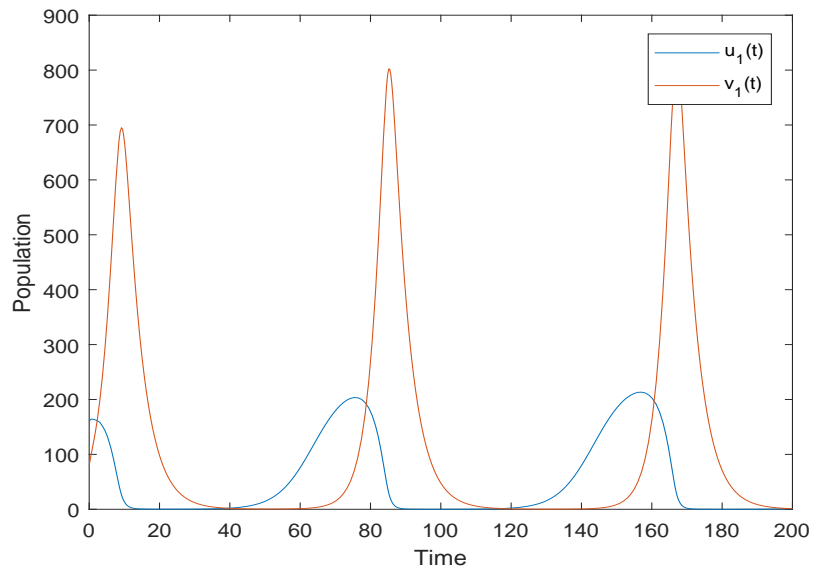
**Figure 4.2:** *Graph of asymmetric manifold for  $\alpha_0 < r$ ,  $\tau = 1.5$ .*

When the prey growth rate is greater than prey migration rate, where the prey migration rate is not dependent on the predator density, ( $r > \alpha_0$ ), the predator density becomes extinct leading to the prey density growing bounded by the carrying capacity as seen in Figure 4.1 and Figure 4.2. The prey migration rate with respect to the predator density is also low ( $\alpha p_i$ ) because the predator density is decreasing. As the predator density reduces to zero, then the prey density grows bounded by the carrying capacity. This is an unstable case since one of the species is wiped

out. A longer time delay, as shown in Figure 4.2, slows down the rate at which the predator population declines.



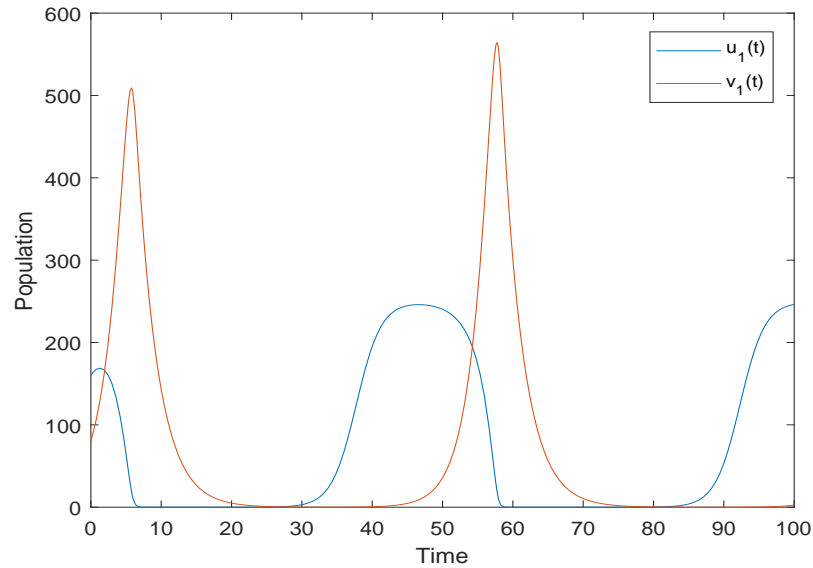
**Figure 4.3:** Graph of asymmetric manifold for  $\alpha_0 > r$ ,  $\tau = 0.1$ .



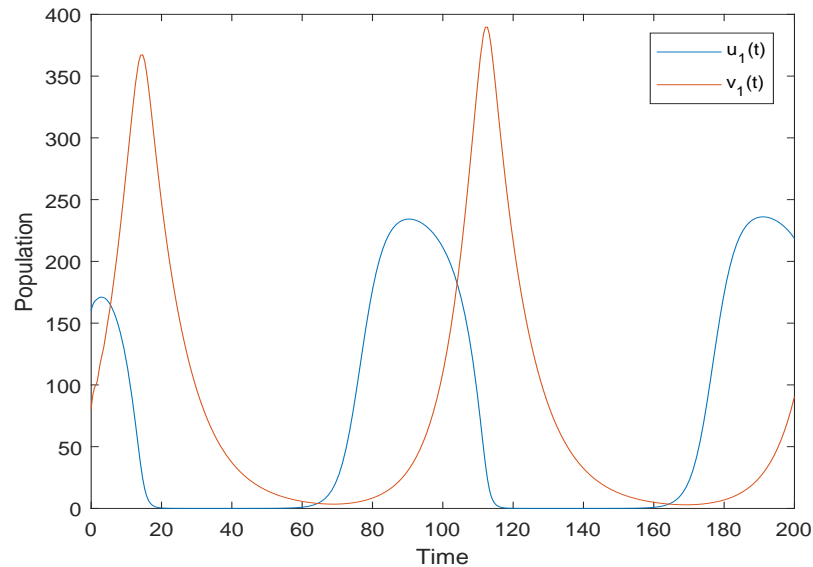
**Figure 4.4:** Graph of asymmetric manifold for  $\alpha_0 > r$ ,  $\tau = 1.5$ .

When the prey growth rate is less than prey migration rate, where the prey migration rate is not dependent on the predator density, ( $r < \alpha_0$ ), the two population densities coexist and depend on each other as shown in Figure 4.3 and Figure 4.4. The prey population is affected by the availability of sustaining resources and security while the predator population is mainly affected by the availability of the prey. When the predator density is high, this negatively affects the prey density which

in turn reduces, since predator attacks will be many. With a reduction in the prey density, the predator density also reduces due to their diminished source of food. This implies that predator attacks for the prey species will be minimized, thus the prey density increases. When the prey density increases, it makes the predator density to grow. With a high predator density, the cycle occurs again. A longer time delay slows down the increase or decrease of the predator and prey species.



**Figure 4.5:** Graph of asymmetric manifold for  $\alpha_0 = r$ ,  $\tau = 0.1$ .



**Figure 4.6:** Graph of asymmetric manifold for  $\alpha_0 = r$ ,  $\tau = 1.5$ .

In Figure 4.5 and 4.6, the prey growth rate is equal to the prey migration rate, where the prey migration rate is not dependent on the predator density, ( $r = \alpha_0$ ). Oscilla-



tions occur where the rise and fall of densities of both species occurs almost in equal measures. These two populations depend on the available sustaining resources. A longer time delay slows down the change in the predator and prey densities.

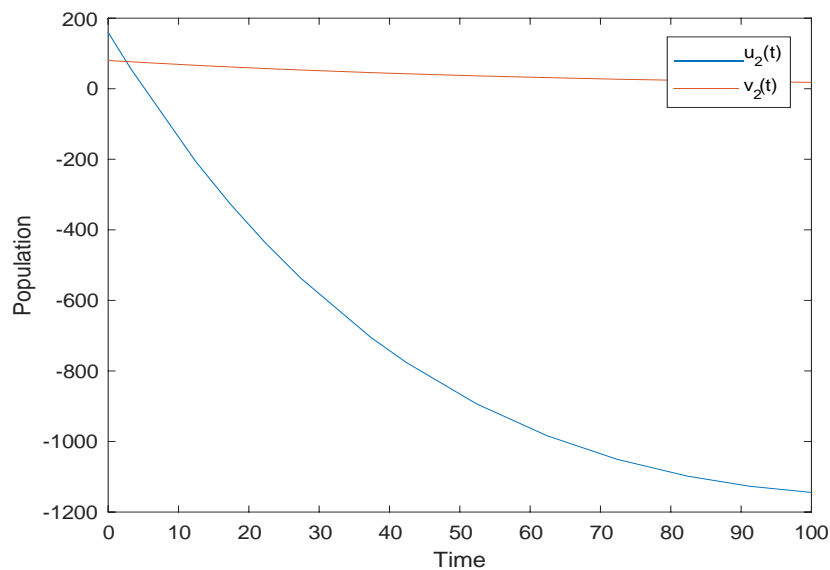
#### 4.2.2 Numerical analysis for Symmetric manifold

In this section, numerical simulations for Equation (4.4) are performed using Matlab software. Parameters values are adapted from [2, 20, 22]. In this section, time,  $t$ , is in months. The following parameter values are used in simulating the results of Equation (4.4).

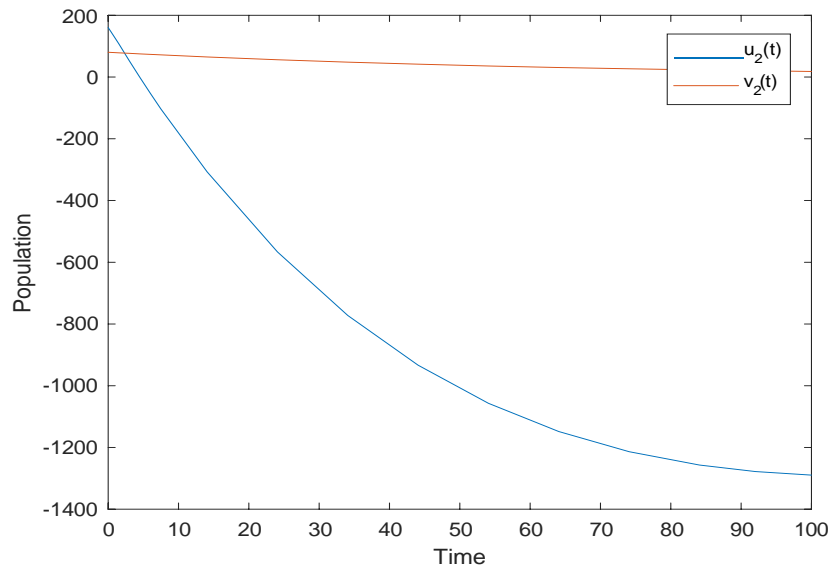
Figure	$r$	$\alpha_0$	$d$	$A$	$\beta_0$	$\beta$	$B$	$u_2$	$v_2$
4.7	1.5	0.6	0.4	0.3	0.4	2.792403	3	160	80
4.8	1.5	0.6	0.4	0.3	0.4	2.792403	3	160	80
4.9	0.1	0.6	0.4	0.3	0.4	2.792403	3	160	80
4.10	0.1	0.6	0.4	0.3	0.4	2.792403	3	160	80
4.11	0.6	0.6	0.4	0.3	0.4	2.792403	3	160	80
4.12	0.6	0.6	0.4	0.3	0.4	2.792403	3	160	80

**Table 4.2:** *Parameter values for the Symmetric Manifold*

Simulations for the symmetric manifold gives,

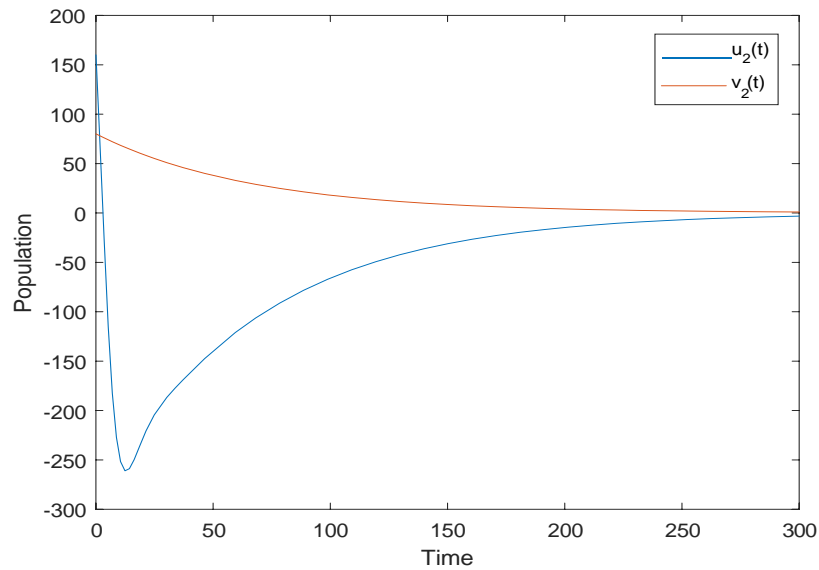


**Figure 4.7:** *Graph of symmetric manifold for  $\alpha_0 < r$ ,  $\tau = 0.1$ .*

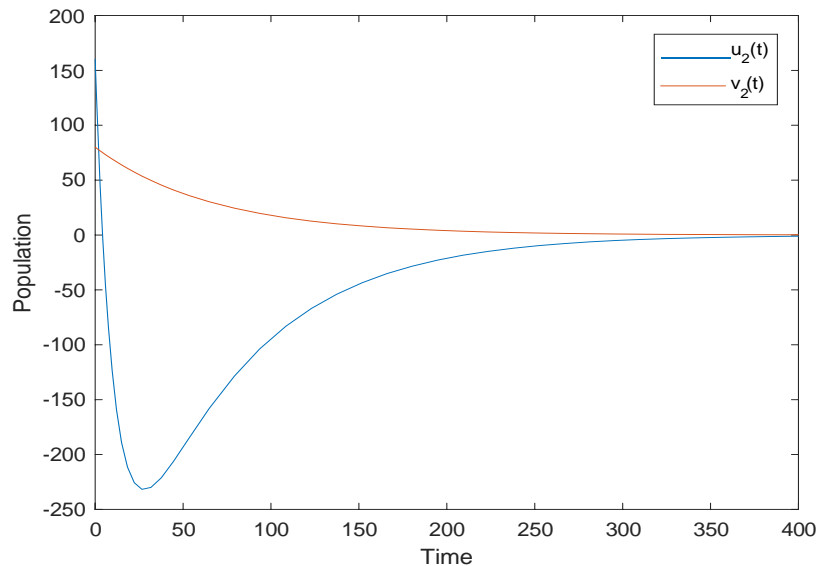


**Figure 4.8:** *Graph of symmetric manifold for  $\alpha_0 < r$ ,  $\tau = 1.5$ .*

When the prey growth rate is greater than prey migration rate, where the prey migration rate is not dependent on the predator density, ( $r > \alpha_0$ ), the predator density becomes extinct while the prey density grows in patch two hence the negative populations shown in Figure 4.7 and Figure 4.8. A longer time delay makes the prey density in patch two increase as seen in Figure 4.8. This is as a result of the prey migrating in low quantities and take time to migrate to patch one, thus an increase of the prey density in patch two. The predator in patch one will have a limited supply of food thus reducing their density. When the population is negative, then the population in patch one is less than the population in patch two.



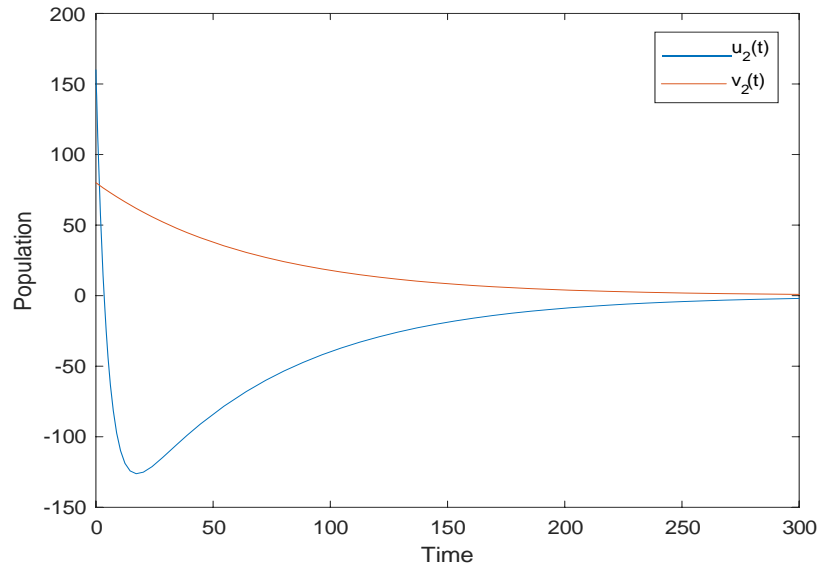
**Figure 4.9:** Graph of symmetric manifold for  $\alpha_0 > r$ ,  $\tau = 0.1$ .



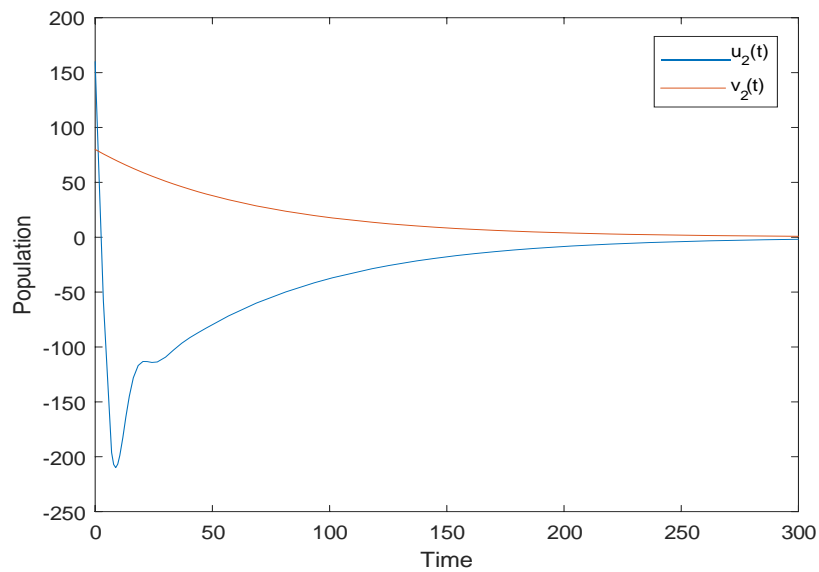
**Figure 4.10:** Graph of symmetric manifold for  $\alpha_0 > r$ ,  $\tau = 1.5$ .

In Figure 4.9 and Figure 4.10, the prey growth rate is less than prey migration rate, where the prey migration rate is not dependent on the predator density, ( $r < \alpha_0$ ). The two densities stabilize at zero after some time. Since the prey migrate in large quantities, we therefore see the prey population decreasing at a very fast rate: most of the prey population migrates from patch one to patch two thus the negative population. Some of the prey density also migrates back to patch one and

with time the prey population in the two patches. The predator population migrates slowly to patch two from patch one, to a point where the predator populations in the two patches is equal. A shorter time delay makes the population to stabilize at a slightly faster rate as shown Figure 4.9 compared to Figure 4.10.



**Figure 4.11:** Graph of symmetric manifold for  $\alpha_0 = r$ ,  $\tau = 0.1$ .



**Figure 4.12:** Graph of symmetric manifold for  $\alpha_0 = r$ ,  $\tau = 1.5$ .

In Figure 4.11 and Figure 4.12, the prey growth rate is equal to the prey migration rate, where the prey migration rate is not dependent on the predator density, ( $r = \alpha_0$ ). Both species stabilize at zero, meaning they will coexist. As the predator density tends to zero, the prey density tends away from zero (the prey density in

patch two grows) then after some time it tends to zero. Since the prey migration rate is the same as the intrinsic growth rate, the prey migrate in large quantities as seen in the sharp decline of the prey species in patch one and the prey population increasing in patch two. The predator density also tends to zero with time, meaning the predator density will be equal in the two patches. A longer time delay slows down the rate at which the prey population stabilizes.

## CHAPTER 5

### CONCLUSION AND RECOMMENDATION

#### 5.1 Conclusion

A predator prey model with logistic growth for constant and density-dependent delayed migration in a two-patch was formulated. Analysis of the model with constant migration was done on two manifolds: the symmetric manifold, where the population density in the first patch is the same as the population density in the second patch, and the asymmetric manifold, where the population density in the first patch is not the same as the population density in the second patch.

The analysis of both the asymmetric and symmetric manifold showed that when the prey growth rate is greater than the prey migration rate, then model is unstable. Either the prey population becomes extinct because they are unable to migrate to safety at a high rate, this leads to the extinction of the predator species after some time as a result of lack of food, or, the prey density grows logistically after the predator population is led to extinction. As the predator density makes the prey density to decline, this makes the predator density also to decline possibly to extinction as a result of a depleted source of food. When the prey growth rate is less than the prey migration rate, the the model is stable and therefore the two species will coexist. When prey growth rate and the prey migration rate are equal, a periodic solution occurs. This means that the two species densities will rise and fall almost in equal measures.

Numerical analysis of the asymmetric manifold shows that if the prey growth rate is greater than the prey migration rate, then both species will be wiped out as shown in Figure 3.1 and Figure 3.2. This is due to the fact that the prey density increases and that will make the predator density to increase, with an increase in the predator density and considering the fact that the prey species cannot migrate

at higher rates. Then the prey density begins declining to extinction. A longer time delay slows the rate of extinction of these species. If the prey intrinsic growth rate is greater than or equal to the prey migration rate, both species will coexist and their densities depict a periodic nature, as shown in Figure 3.3, Figure 3.4, Figure 3.5 and Figure 3.6. An increase in the prey density will lead to the predator density growing while when the prey density decreases, this makes the predator density to decrease. When the predator density declines, the prey density grows while an increase in the predator density will make the prey density to decline. A longer time delay slows down the rate at which these species densities increase or decrease.

Numerical analysis of the symmetric manifold shows that, when the prey migration rate is less than the prey growth rate, the predator species becomes extinct leading to the prey population growing as displayed in Figure 3.7 and Figure 3.8. When the prey growth rate is greater than or equal to the prey migration rate, the two densities will coexist and they will be equal in both patches after some time as seen in Figures 3.9 - 3.12. A longer time delay slows down the rate at which the two species stabilize.

Analysis of the model with density-dependent migration was also done using two manifolds: the symmetric manifold and the asymmetric manifold. The analysis of the two manifolds showed that there is a sink when the prey growth rate is less than prey migration rate. This means that two species will coexist. There is a saddle when the prey migration rate is less than prey growth rate, this makes either the extinction of both species with time or the prey density growing logistically after the extinction of the predator density. There is a periodic solution and therefore the two densities fluctuate when the prey growth rate and prey migration rate are equal. The obtained results show that prey migration due to the predator density does not greatly affect the prey density compared to the other factors that cause the prey to migrate like human activities and settlement in natural habitat, lack of food, bad climatic conditions among others.

Numerical simulations of the asymmetric manifold shows that if the prey growth rate is greater than the prey migration rate, then the predator density will be wiped out and the prey density grows bounded by its carrying capacity as shown in Figure 4.1 and Figure 4.2. A longer time delay slows down the rate at which the predator go to extinction and the rate at which the prey increase. When the prey growth rate is less than or equal to the prey migration rate, periodic solutions occur. This implies that these populations will depend on the availability of the sustaining resources. Therefore the population densities will increase when there is abundance of resources and decrease when the resources have diminished. This is shown in Figures 4.3 - 4.6.

Numerical analysis of the symmetric manifold show that when the prey growth rate is greater than the prey migration rate, the prey population in patch two increases while the predator populations is driven to extinction as shown in Figure 4.7 and Figure 4.8. A longer time delay slows down migration and thus more prey density will be in patch two. In Figure 4.9 - 4.12, the prey growth rate is less than or equal to the prey migration rate, both species densities stabilize at zero after some time. This means that both species densities will be the same in the two patches (because of the change of coordinates in Equation (3.18)). A longer time delay slows down the rate at which the two species stabilize.

It is evident from this study that survival of the species depends on the migration rates as shown in the analysis of the two models where the species will survive if the prey growth rate is less than or equal to the prey migration rate, otherwise at least one species will be extinct. The prey migration rate due to the predator density does not greatly affect the prey density and existence compared to the other factors that cause the prey to migrate. These factors include human activities in the natural habitats like logging and natural causes like bad climatic conditions, limited food resources and overpopulation of the prey density in a patch. It is also shown that when the species are migrating, a longer time delay will affect the population density



negatively because it slows down the increase or decrease of the species population.

## **5.2 Recommendations**

For the species to coexist, we recommend that factors that slow down migration rates should be addressed, for example, reducing human activities and settlement in natural habitat. Factors which also prolong time delays during migration of the species should also be addressed, for example, avoiding where possible the construction of an infrastructure through natural habitats.

For future works, it can be assumed that the prey migration rate will be high when the density of the predator is high on a patch. On the other hand, it can also be assumed that predators will migrate in low rates from a given patch with high prey density in a patch and the predators will migrate in high rates from a patch with low prey density in a patch. This leads to a repulsive effect of predators on prey and an attractive effect of the prey species on the predators. Therefore a repulsive-attractive model can be studied. Furthermore, a delay in maturity of the predator to hunting age can be incorporated since a predator species must be of a certain age to be able to hunt.

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