

**MODELLING DELAY IN MIGRATION FOR CONSTANT PREDATOR
AND PREDATOR-DENSITY-DEPENDENT PREY MIGRATION**

BY

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DECLARATION

This thesis is my own work and has not been presented elsewhere for a degree in any other institution.

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This thesis has been submitted for examination with our approval as the university supervisors.

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May God bless you all.

DEDICATION

To my father, the late Bendickto Mabwago Kenyaga, my mother Askah Nyangweso Mabwago, my brothers and sisters. You have made me what I am today.

ABSTRACT

Predator-prey models describe the dynamics of ecological systems in which two species, the predator and the prey, interact. The classical Lotka-Volterra model is the simplest predator-prey model. Migration of species, due to predation and other factors, in predator-prey systems has been studied. In reality the prey do not migrate instantly upon being preyed on neither do the predators migrate immediately they lack food. Delay in the migration of species in such systems for constant rates has been investigated. However, if the migration of the prey is largely due to predation, then it is expected that the prey migration rate will depend on the density of the predators. The objective of this study is to formulate and analyze a predator-prey mathematical model, based on a system of delay differential equations that takes into consideration time delay in migration, with a prey migration rate that depends on the predator density and other factors like availability of its food. Analysis of the formulated model shows that for both the Symmetric and Asymmetric manifolds, the system is unstable when the prey migration rate is less than the prey growth rate. This means that the predator and prey species will become extinct in either patches. On the other hand, when the prey migration rate is greater than the prey growth rate, then the resulting system is stable. This implies that the two species in both patches will coexist. Furthermore, when the prey migration rate is equal to the prey growth rate, a periodic solution occurs. This means that the two populations will fluctuate by rising or falling almost in equal measure. Numerical analysis show that delay has a stabilizing effect on the system and in the presence of delay, the species populations decrease at a faster rate compared to the case without delay. It is shown that the population density mainly depends on the migration rate which may be affected by factors such as infrastructure through natural habitat, destruction of the natural habitat through logging, natural disasters like fire-outbreaks among others. In view of this, relevant agencies like the Kenya Wildlife Service and the government should employ measures which will deal with factors which cause barriers during migration for example reducing natural habitat land allocation to human settlement, agriculture or infrastructure.

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CHAPTER 1

INTRODUCTION

1.1 Background of the Study

The classical Lotka-Volterra predator-prey model is mostly used in describing the dynamics of ecological systems in which, the prey and predator (feeding on the prey as its main food) interact, Brauer and Chaves [3], Hastings [6], Murray [10]. In nature three factors are likely to promote the coexistence and stability in the environment. They include first the prey, which in the absence of any predators grows exponentially. Secondly the predators, which in the absence of prey, their main food, decay exponentially. The third factor is the presence of both the predator and prey species, in which case the growth of the prey is limited by the predators, and the predators grow proportionately to the amount of prey available.

The classical Lotka-Volterra model assumes a homogeneous (single patch) ecological environment, which is not the case since the environment is made up of many patches. This assumption of a single patch implies that species essentially do not migrate. Migration occurs when the predator or the prey move from their initial patch to another patch in search of food, security mainly for the prey due to predation and due to other unfavorable conditions, Pillai *et. al.*[13].

Let the prey and predator population be denoted by $N_i(t)$, $P_i(t)$, respectively at time t in patch i , $i = 1, 2$. The migration equation for the predator- prey system from one patch to another is given by;

$$\begin{aligned}\dot{N}_i(t) &= D_N(N_j(t) - N_i(t)), \\ \dot{P}_i(t) &= D_P(P_j(t) - P_i(t)), \quad i, j = 1, 2, i \neq j,\end{aligned}\tag{1.1}$$

where D_N represents prey migration rates, and D_P represents the predator migration rate, see for instance Abdllaoui *et. al.* [1], Mchich *et. al.* [9] and Wasike *et. al.* [15]. Most predator-prey models, for instance Abdllaoui *et. al.* [1], and Mchich *et. al.* [9] assume the migration is at a constant rate. However, this may not be ecologically realistic because of the nature of the factors that cause migration. These factors include lack of

security, mainly for the prey species due to predation, unfavorable climatic conditions and intraspecific competition in a patch, see for instance Brauer and Chaves [3], Murray [10]. Migration can either be constant or variable [10]. 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 [1, 2, 13].

In a predator-prey system, delay in migration is the duration of time taken by one species before they relocate from one patch to another in a heterogeneous environment after facing an unfavorable condition in the initial patch. The unfavorable conditions which cause delay may include, barriers which may be caused by natural habitat land allocation to human settlement, agriculture or infrastructure. Other factors may include adverse weather conditions like long dry spells or heavy rains which may lead to swollen rivers. Some models for migration at constant rates with delay are for instance Apima [2], Neubert *et. al* [11], Wasike *et. al.*[15].

1.2 Statement of the problem.

In a predator-prey system, the prey do not migrate instantly upon being preyed on neither do the predators migrate immediately they lack food. There is delay in migration which has often been assumed to be at constant rate. However, if the migration of the prey is largely due to predation, then it is expected that the migration rate will not be constant, instead it may be dependent on the density of the predators. The study therefore formulates and analyzes a mathematical model for the delayed migration of both species with predator-density-dependent dispersal for the prey.

1.3 Objectives of the Study

1.3.1 Main objective

The main objective of this study is to develop and analyze a predator-prey model with delay in migration, where the prey migration rate is dependent on the predator-density among other factors.

1.3.2 Specific objectives

The specific objectives of this study are as follow;

1. Develop a system of delay differential equation for the migration of species in a two patch environment.
2. Analyze long term solution of the proposed model in (1) above
3. To perform numerical simulations so as to verify and give more insight to the analytical solutions obtained in objectives (2) above.

1.4 Justification of the study

This study is motivated by findings such as that of Kramer and Drake [6] which show that predation can drive prey species with low density to extinction. It's worth investigating the dynamics of the system, since predator-density-dependent prey migration with time delays has a profound effect on such system.

1.5 Significance of the study

An understanding of the long term dynamics of the system may provide useful insights to ecologists on conservation measures where the prey is an endangered species. The novelty of the mathematical formulations and analysis is expected to contribute to the body of mathematical knowledge in the area of study.

CHAPTER 2

LITERATURE REVIEW

2.1 The Lotka-Volterra Model

Lotka in the year 1925 and Volterra in the year 1926 proposed a simple classical predator-prey model. They used a system of ordinary differential equations regularly used in describing the dynamics of the interaction between the predator and prey in homogeneous ecological environment. The system is given by;

$$\begin{aligned}\frac{dN}{dt} &= N(a - bP) \\ \frac{dP}{dt} &= P(cN - d)\end{aligned}\tag{2.1}$$

Where N represents the prey population, P represents the predator population, a , denotes the prey growth rate, d denotes the predator mortality rate b , and c are non- negative parameters which describe the interaction between the predator and prey species. Lotka used herbivores and plants species to come up with a simple classical predator-prey model. On the other hand Volterra used the predation of one species of fish by another to explain fluctuation in size of population of commercially desirable fish $N(t)$ and that of larger fish $P(t)$ which fed on the latter $N(t)$ in the Adriatic Sea. Since model (2.1) was derived exclusively by Lotka and Volterra it was then called Lotka-Volterra predator-prey model. The assumptions in Model (2.1) are:

- (i) The prey population grows exponentially in the absence of the predator (Malthus law). It is represented by the term aN in the model (2.1)
- (ii) The total number of prey predation per unit time and the amount of predator produced per unit time is assumed to be proportional to the number of predator and prey encounters (the rate at which they are preyed on). It is represented by the term $-bP$
- (iii) The prey's contribution to the predators growth rate is cNP ; that is, it is proportional to the available prey as well as to the size of the predator population.

(iv) In the absence of any prey for sustenance the predators death rate results in exponential decay. It is represented by the term $-dP$.

The predator population, in the Lotka-Volterra model, grows exponentially when the population of prey is high, ultimately, reduces their main food supply. Also prey population will increase as the predator size reduces. The assumption in model (2.1) that the environment is homogenous is not realistic, since the environment is made up of more than one patch and both species can migrate from one patch to another patch. For more on the Lotka Volterra model see Brauer and Chaves [3], Hastings [6] and Murray [10]

2.2 Models involving migration of predator and prey species

An extension of the Lotka-Volterra model to a simple two patch model was given by Comins and Blatt [4],

$$\begin{aligned}\dot{N}_i(t) &= N_i(a_i - b_i P_i) + D_N(N_j - N_i), \\ \dot{P}_i(t) &= P_i(c_i N_i - d_i) + D_P(P_j - P_i), \quad \text{where } i, j = 1, 2 \quad i \neq j\end{aligned}\quad (2.2)$$

where $N_i = N_i(t)$ represents the prey population and $P_i = P_i(t)$ represents the predator population, a_i and d_i is the prey intrinsic growth and natural mortality rate of the predator respectively, b_i and c_i represent the predation parameters, D_N is the prey migration rate and D_P the predator migration rate. The analysis of model (2.2) was done with the assumption that $D_N = 0$, because the predator are often more mobile than the prey. This assumption may not be the case because of factors like; insecurity due to predation, intraspecific competition for resources among others. It also assumed that the predator will migrate immediately after lacking their main food source. The assumption that the predator will move immediately is not entirely realistic.

Mchich *et. al.* [10] examined the predator-prey equation in a two patch system, using the system below

$$\begin{aligned}\dot{n}_i(\tau) &= (q_j(p_j)n_j(\tau) - q_i(p_i)n_i(\tau)) + \varepsilon(r_i n_i(t) - a_i n_i p_i(t)), \\ \dot{p}_i(\tau) &= (k_j p_j(\tau) - k_i p_i(\tau)) + \varepsilon(-m_i p_i(t) + b_i n_i p_i(t)), \quad \text{where } i, j = 1, 2 \quad i \neq j\end{aligned}\quad (2.3)$$

The prey population is represented by n_i and the predator population is presented by p_i at time t on the two patches. r_i represents the prey intrinsic growth rate in patch i . The

natural mortality rate of the predator in patch i is represented by the term m_i . The terms $g_i(p_i)$ and k_i represent the prey and the predator migration rates respectively from one patch to another patch. ε is a small dimensionless parameter, t is the slow time scale for interaction between the prey and predator while τ is the rapid time for migration of the species from one patch to another patch i.e. $\tau = t/\varepsilon$, a_i and b_i are predation rates. The model (2.3) assumes that migration occurs immediately, which is not the case in real life due to factors such as physical barriers (e.g. infrastructure and human settlement in natural habitat), unfavorable climatic conditions and security due to predation which may cause delay in migration.

Abdllaoui *et. al.* [1] considered a general two patch model of the predator-prey system and assumed that the migration between the two patches is rapid than the predator-prey interaction. The model below was used in the study:

$$\begin{aligned}\dot{n}_i(\tau) &= (f_j(p_j)n_j(\tau) - f_i(p_i)n_i(\tau)) + \varepsilon(\phi_i n_i(t) - \bar{\phi}_i n_i p_i(t)) \\ \dot{p}_i(\tau) &= (k_j p_j(\tau) - k_i p_i(\tau)) + (\varphi_i p_i(t) + \bar{\varphi}_i n_i p_i(t)), \quad \text{where } i, j = 1, 2 \quad i \neq j \quad (2.4)\end{aligned}$$

where τ is the rapid time scale and $t = \tau\varepsilon$ is the slow time scale. The two patches are represented by $i = 1, 2$. The prey density is denoted by $n_i(t)$ and the predator density is denoted by $p_i(t)$ in patch i . $f_i(p_i)$ is the migration rates for prey from one patch to another which assumes that the more the predators are found in a patch the more the prey will migrate. $g_i(n_i)$ is the migration rates for predator from one patch to another which assumes that the predator will stay in the patch where prey population is high. $\phi_i n_i$ and $\varphi_i(n_i)$ are the prey growth rate and predator death respectively, $\bar{\phi}_i(n_i)$ represents functional responses and $\bar{\varphi}_i(n_i)$ represent the predator growth rate. Model (2.4) assumes that both species will migrate immediately which is not realistic, because of security due to predation, intraspecific competition and also unfavorable climatic conditions which may cause time delays.

2.3 Predator-prey models involving delay in migration

Wasike *et. al.* [15] developed a two patch Lotka-Volterra model with a time delay in the migration between two patches. The following model was studied,

$$\dot{z}_i(t) = \beta(z_j(t - \tau) - z_i(t)) + f_i(z_i(t)), \quad \text{where } i, j = 1, 2, \quad i \neq j, \quad (2.5)$$

where τ represents a delay in the migration of the two species. The predator-prey density in the two patches are represented by $z_i(t) := (n_i(t), p_i(t))^T$, $i = 1, 2$, β represents the migration rate. The term $f_i(z_i(t))$ represents the prey and predator interaction, i.e.

$$f_i(z_i(t)) = \begin{pmatrix} r_i n_i(t) - a_i n_i(t) p_i(t) \\ -s_i p_i(t) + b_i n_i(t) p_i(t) \end{pmatrix} \quad (2.6)$$

Equation (2.5) assumes that migration for the prey and predator is constant which is not the case since the prey and the predator migration depend on a number of factors and therefore a constant rate is not realistic.

Neubert *et. al.* [11] considered the model below.

$$\begin{aligned} \frac{dN(t)}{dt} &= (R - AP(t))N(t) + D_N \left[\int_0^\infty G_N(S) e^{M_N S} N(t-S) dS - N(t) \right] \\ \frac{dP(t)}{dt} &= (BN(t) - M)P(t) + D_P \left[\int_0^\infty G_P(S) e^{M_P S} P(t-S) dS - P(t) \right] \end{aligned} \quad (2.7)$$

where N represent prey population and P represent predator population in the two patches, $G_d(S) \geq 0$, where $d = N, P$ is the probability density function. The $\exp(M_d S)$ is the predator probability of surviving a trip. The parameters A , B , M and R are assumed to be non- negative values and D_N , D_P , M_N and M_P are positive constants. The results obtained by Neubert. *et. al.* [11] from this study show that for both the distributed and discrete delay, the delay has a stabilizing effect. The dispersal tends to synchronize the dynamics in a heterogeneous environment, while delay decouples immigration rates from local densities in the patches. The restrictions in this predator-prey model is that only the prey or the predator has the ability to disperse while the other is confined to its patch. Due to the interaction of the two species, the migration of one necessarily results in the migration of the other.

We propose to formulate a delay predator-prey migration model in which the rate of migration of the prey is dependent on the density of the predators.

CHAPTER 3

MODEL FORMULATION AND ANALYSIS

3.1 Research Methodology

To achieve the objectives of the study, a mathematical model based on a system of delay differential equations for the dynamics of a predator-prey system with delay in migration and predator-density-dependent prey migration was formulated. The stability of the long term solutions of the model were studied. The parameters and conditions for stability were investigated analytically. Numerical simulations were performed to verify the analytical results obtained.

3.2 Model Formulation

Consider the Lotka-Volterra equation in a two patch environment, where these two patches are coupled via migration, given by,

$$\begin{aligned}\dot{n}_i(t) &= r_i n_i - a_i n_i p_i, \\ \dot{p}_i(t) &= b_i n_i p_i - s_i p_i, \quad \text{where } i = 1, 2\end{aligned}\tag{3.1}$$

where i indicates the patch number, $n_i = n_i(t)$ and $p_i = p_i(t)$ are the prey and predator populations at time t , respectively. The intrinsic growth rate of the prey population is denoted by r_i , whereas a_i and b_i are predation parameters. The constant s_i is the natural mortality rate of the predator population.

The net migrated prey and predator density is denoted by m_{ni} and m_{pi} , respectively, where $i = 1, 2$, are defined as:

$$\begin{aligned}m_{n1} &= D_N(n_2(t - \tau) - n_1(t)) \\ m_{n2} &= D_N(n_1(t - \tau) - n_2(t)) \\ m_{p1} &= D_P(p_2(t - \tau) - p_1(t)) \\ m_{p2} &= D_P(p_1(t - \tau) - p_2(t))\end{aligned}\tag{3.2}$$

where D_P is the predator migration rate, it is taken to be constant, i.e. $D_P = \beta$. D_N is the prey migration rate, it is dependent on the predator density and other factors, i.e.

$D_N = (\alpha_i p_i + \alpha_0)$. A time delay in the migration of both the prey and predator is represented by τ .

Introducing the migration equation (3.2) into the interaction equation (3.1), we obtain.

$$\begin{aligned}
\dot{n}_1(t) &= (\alpha_2 p_2 + \alpha_0) n_2(t - \tau) - (\alpha_1 p_1 + \alpha_0) n_1(t) + r_1 n_1 - a_1 n_1 p_1, \\
\dot{n}_2(t) &= (\alpha_1 p_1 + \alpha_0) n_1(t - \tau) - (\alpha_2 p_2 + \alpha_0) n_2(t) + r_2 n_2 - a_2 n_2 p_2, \\
\dot{p}_1(t) &= \beta(p_2(t - \tau) - p_1(t)) + b_1 n_1 p_1 - s_1 p_1, \\
\dot{p}_2(t) &= \beta(p_1(t - \tau) - p_2(t)) + b_2 n_2 p_2 - s_2 p_2
\end{aligned} \tag{3.3}$$

Let $X(t) = (n_1(t), n_2(t), p_1(t), p_2(t))$ and $f(X(t), X(t - \tau))$ represent the vector field on the right hand side of equation (3.3), thus equation (3.3) becomes,

$$\dot{X}(t) = f(X(t), X(t - \tau)) \tag{3.4}$$

Let $C = \mathbb{C}([- \tau, 0], \mathbb{R}^4)$ be a Banach space. Let the initial condition be given by

$$\varphi(t) := X(t) |_{[- \tau, 0]} \tag{3.5}$$

where $\varphi \in C$. Since $f(X(t), X(t - \tau)) \in \mathbb{C}(\mathbb{R}^4 \times C, \mathbb{R}^4)$, equation (3.4) subject to equation (3.5) has a unique solution, Hale & Lunel [7]

3.2.1 Exponential Boundedness

The linear part of equation (3.3) can be written as,

$$\dot{X}(t) = \begin{pmatrix} -\alpha_0 + r & 0 & 0 & 0 \\ 0 & -\beta - s & 0 & 0 \\ 0 & 0 & -\alpha_0 + r & 0 \\ 0 & 0 & 0 & -\beta - s \end{pmatrix} X(t) + \begin{pmatrix} 0 & \beta & 0 & 0 \\ \alpha_0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \beta \\ 0 & 0 & \alpha_0 & 0 \end{pmatrix} X(t - \tau) \tag{3.6}$$

Equation (3.6) can be represented by two manifolds. In order to study the dynamics of these manifolds, an application of the Laplace transform methods in complex variables to equation (3.6) is required. For a Laplace transform, an exponential estimate of the solution of equation (3.6) should be bounded. The following definition will be used in proving that the exponential estimate of the solution of equation (3.6) is bounded

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

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

we have,

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

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

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

Lemma 3.2.1. *The solution of equation (3.3) subject to the initial condition in equation (3.4) for $t \geq 0$, satisfies*

$$|X(t)| \leq \alpha(\tau)e^{b\tau}|\varphi| \quad (3.7)$$

where $\alpha(\tau) = 1 + \gamma_1\tau$, $b = 2\gamma_1$, $\gamma_1 = (\alpha_0 \ \beta)^T$ and $|\cdot|$ denotes a sup norm in \mathbb{R} as well as a matrix norm.

Proof. The solutions of equation (3.6) subject to initial condition stated in equation (3.5) satisfy,

$$\begin{aligned} X(t) = \varphi(0) + \int_{-\tau}^0 \begin{pmatrix} 0 & \beta & 0 & 0 \\ \alpha_0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \beta \\ 0 & 0 & \alpha_0 & 0 \end{pmatrix} \varphi(s)ds + \int_0^t \left\{ \begin{pmatrix} 0 & \beta & 0 & 0 \\ \alpha_0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \beta \\ 0 & 0 & \alpha_0 & 0 \end{pmatrix} X(s-\tau) \right. \\ \left. - \begin{pmatrix} \alpha_0 - r & 0 & 0 & 0 \\ 0 & \beta + s & 0 & 0 \\ 0 & 0 & \alpha_0 - r & 0 \\ 0 & 0 & 0 & \beta + s \end{pmatrix} X(s) \right\} ds. \end{aligned} \quad (3.8)$$

Therefore,

$$\begin{aligned} |X(t)| &\leq |\varphi| + \gamma_1 |\varphi| \tau + 2\gamma_1 \int_0^t |X(s)| ds \\ &\leq (1 + \gamma_1\tau) |\varphi| + 2 \int_0^t \gamma_1 |X(s)| ds. \end{aligned}$$

Since $(1 + \gamma_1\tau)\varphi$ is nondecreasing, by Grownwall's inequality,

$$|X(t)| \leq (1 + \gamma_1\tau)\exp(\int_0^t 2\gamma_1 ds) |\varphi| = (1 + \gamma_1\tau)\exp(2\gamma_1 t) |\varphi|.$$

□

Therefore equation (3.3) is exponentially bounded. The characteristic equation will be obtained so that it can be shown that Laplace Transform of equation (3.3) exists.

3.2.2 Characteristic equation of the Migration Terms

To obtain solutions of equation (3.3), let

$$X(t) = e^{\lambda t} c, \quad (3.9)$$

where $c \in \mathbb{R}^4$ with c a nonzero 4 by 1 column vector. Substituting equations (3.9) into the linear part of equation (3.3), the following equation is obtained

$$\lambda I_4 e^{\lambda t} c = \begin{pmatrix} -\alpha_0 e^{\lambda t} & \alpha_0 e^{\lambda(t-\tau)} & 0 & 0 \\ \alpha_0 e^{\lambda(t-\tau)} & -\alpha_0 e^{\lambda t} & 0 & 0 \\ 0 & 0 & -\beta e^{\lambda t} & \beta e^{\lambda(t-\tau)} \\ 0 & 0 & \beta e^{\lambda(t-\tau)} & -\beta e^{\lambda t} \end{pmatrix} c \quad (3.10)$$

where I_4 denotes the identity matrix of order 4. The following characteristic equation from equation (3.10) is obtained

$$(\alpha_0 + \lambda)^2 (\beta + \lambda)^2 - \alpha_0^2 \beta^2 e^{-4\lambda\tau} = 0 \quad (3.11)$$

3.3 Invariant Manifold

Taking Laplace transform of the linear part of equation (3.3), we get

$$\begin{pmatrix} -\lambda I_2 - I_2 \gamma_1 & e^{-\lambda\tau} I_2 \gamma_1 \\ e^{-\lambda\tau} I_2 \gamma_1 & -\lambda I_2 - I_2 \gamma_1 \end{pmatrix} \begin{pmatrix} X_1(\lambda) \\ X_2(\lambda) \end{pmatrix} = \begin{pmatrix} X_1(0) \\ X_2(0) \end{pmatrix}. \quad (3.12)$$

Equation (3.12) is symmetric in nature. On simplifying it, adding (respectively subtracting) the set of equations involving $X_2(0)$ to (respectively from) $X_1(0)$ in equation (3.12), we obtain

$$\begin{aligned} (-I_2 \lambda - I_2 \gamma_1 + I_2 \gamma_1 e^{-\lambda\tau})(X_1(\lambda) + X_2(\lambda)) &= X_1(0) + X_2(0), \\ (-I_2 \lambda - I_2 \gamma_1 - I_2 \gamma_1 e^{-\lambda\tau})(X_1(\lambda) - X_2(\lambda)) &= X_1(0) - X_2(0), \end{aligned} \quad (3.13)$$

The matrix $(-I_2 \lambda - I_2 \gamma_1 + I_2 \gamma_1 e^{-\lambda\tau})$ is non-singular when λ is such that $(-I_2 \lambda - \gamma_1 + \gamma_1 e^{-\lambda\tau}) \neq 0$ and $(-\lambda - \gamma_1 - \gamma_1 e^{-\lambda\tau}) I_2$ is non-singular when λ is such that $(-\lambda - \gamma_1 - \gamma_1 e^{-\lambda\tau}) \neq 0$, thus the inverse Laplace transform is

$$\begin{aligned} (X_1(\lambda) + X_2(\lambda)) &= \mathcal{L}^{-1}\{(-\lambda - \gamma_1 + \gamma_1 e^{-\lambda\tau}) I_2\}^{-1} (X_1(0) + X_2(0)), \\ (X_1(\lambda) - X_2(\lambda)) &= \mathcal{L}^{-1}\{(-\lambda - \gamma_1 - \gamma_1 e^{-\lambda\tau}) I_2\}^{-1} (X_1(0) - X_2(0)), \end{aligned} \quad (3.14)$$

We have two manifolds; the symmetric manifold where $X_1(t) = X_2(t)$ and the asymmetric manifold where $X_1(t) = -X_2(t)$.

To simplify the study of equation (3.3), we introduce the change of coordinates,

$$\begin{aligned} u_1 &:= 1/2(n_1 + n_2), & u_2 &:= 1/2(n_1 - n_2), \\ v_1 &:= 1/2(p_1 + p_2), & v_2 &:= 1/2(p_1 - p_2), \end{aligned} \quad (3.15)$$

Introducing these coordinates in equation (3.3) and with the assumption that the predator and prey species are of the same type regardless of the patch, we take $r_1 = r_2 = r$, $a_1 = a_2 = a$, $b_1 = b_2 = b$, $s_1 = s_2 = s$, and $\alpha_1 = \alpha_2 = \alpha$ then

$$\begin{aligned} \dot{u}_1(t) &= (u_1(t - \tau) - u_1)(\alpha_0 + \alpha v_1) + \alpha(u_2(t - \tau) - u_2)v_2 + ru_1 - a(u_1v_1 + u_2v_2), \\ \dot{u}_2(t) &= -(u_2(t - \tau) + u_2)(\alpha_0 + \alpha v_1) - \alpha(u_1(t - \tau) + u_1)v_2 + ru_2 - a(u_1v_2 + u_2v_1), \\ \dot{v}_1(t) &= \beta(v_1(t - \tau) - v_1(t)) - sv_1 + b(u_1v_1 + u_2v_2), \\ \dot{v}_2(t) &= -\beta(v_2(t - \tau) + v_2(t)) - sv_2 + b(u_1v_2 + u_2v_1), \end{aligned} \quad (3.16)$$

Reducing equation (3.16) to a two dimensional system, we get

$$\begin{aligned} \dot{u}_1(t) &= -(\alpha_0 + \alpha v_1)(u_1 - u_1(t - \tau)) + ru_1 - au_1v_1 \\ \dot{v}_1(t) &= \beta(v_1(t - \tau) - v_1(t)) - sv_1 + bu_1v_1, \end{aligned} \quad (3.17)$$

and

$$\begin{aligned} \dot{u}_2(t) &= -\alpha_0(u_2(t - \tau) + u_2) + ru_2, \\ \dot{v}_2(t) &= -\beta(v_2(t - \tau) + v_2(t)) - sv_2, \end{aligned} \quad (3.18)$$

3.4 Asymmetric Manifold

On solving the system in equation (3.17), we let $U_1 = (u_1, v_1)^T$ and $\dot{U}_1 = (\dot{u}_1, \dot{v}_1)^T$, then the system in equation (3.17) becomes

$$\dot{U}_1 = \begin{pmatrix} \alpha v_1 + \alpha_0 & 0 \\ 0 & \beta \end{pmatrix} U_1(t - \tau) + \begin{pmatrix} -\alpha_0 + r & -(\alpha + a)u_1 \\ 0 & -\beta - s + bu_1 \end{pmatrix} U_1 \quad (3.19)$$

Let $U_1(t) = e^{\lambda t} C_1$, then we obtain the following characteristic equation from equation (3.19),

$$(\alpha_0 e^{-\lambda \tau} - \alpha_0 + r - \lambda)(\beta e^{-\lambda \tau} - \beta - s - \lambda) = 0 \quad (3.20)$$

Using the first factor of equation (3.20), we have

$$(\alpha_0 e^{-\lambda \tau} - \alpha_0 + r - \lambda) = 0 \quad (3.21)$$

Let

$$z = (\lambda + \alpha_0 - r)\tau \quad (3.22)$$

Therefore we have $\frac{z}{\tau} = \lambda + \alpha_0 - r$ which can be written as $\lambda = \frac{z}{\tau} - \alpha_0 + r$. Equation (3.22) can be written as

$$(\alpha_0 e^{-(\frac{z}{\tau} - \alpha_0 + r)\tau} - \frac{z}{\tau}) = 0, \quad (3.23)$$

$$\alpha_0 \tau e^{-z} e^{(\alpha_0 - r)\tau} = z, \quad (3.24)$$

The following lemma, which is found in [5], will be used to simplify equation (3.22)

Lemma 3.4.1. *The equation $z = be^{-z}$ has simple pure imaginary roots,*
 $z = i(\pi/2 + 2m\pi),$ *for $b = -(\pi/2 + 2m\pi)$*
 $z = 0,$ *for $b = 0$*
 $z = i(\pi/2 + (2m + 1)\pi),$ *for $b = (\pi/2 + (2m + 1)\pi)$*
where $m = 0, 1, 2, \dots$ and there are no other purely imaginary roots.

Using Lemma (3.4.1), and $b = \alpha_0 \tau e^{(-r + \alpha_0)\tau} > 0$ and therefore $z = i(\pi/2 + (2m + 1)\pi)$ for $\alpha_0 \tau e^{(-r + \alpha_0)\tau} = (\pi/2 + (2m + 1)\pi)$. Equation (3.22) becomes

$$\lambda = \frac{i(\pi/2 + (2m + 1)\pi)}{\tau} - \alpha_0 + r \quad (3.25)$$

Equation (3.25) has

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

For the second factor of equation (3.20),

$$(\beta e^{-\lambda\tau} - \beta - s - \lambda) = 0. \quad (3.26)$$

Let

$$z = (\lambda + \beta + s)\tau \quad (3.27)$$

Therefore we have $\frac{z}{\tau} = \lambda + \beta + s$ which can be written as $\lambda = \frac{z}{\tau} - \beta - s$. Equation (3.26) can be written as

$$(\beta e^{-(\frac{z}{\tau} + \beta + s)\tau} - \frac{z}{\tau}) = 0, \quad (3.28)$$

$$\beta\tau e^{-z} e^{-(\beta+s)\tau} = z, \quad (3.29)$$

From Lemma (3.4.1), equation (3.27) becomes

$$\lambda = \frac{i(\pi/2 + 2m\pi)}{\tau} - (\beta + s) \quad (3.30)$$

All roots of equation (3.30) have negative real parts regardless of β and s . Therefore from equation (3.20) there is:

- (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 the prey density becomes extinct leading to the predator population becoming extinct because of lack of food.
- (ii) a sink at the origin for $\alpha_0 > r$, that implies that, when the migration rate is greater than the prey growth rate, then the prey and predator species will not become extinct, regardless of the mortality of the predator and the predator migration rate.
- (iii) a periodic solution 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 prey density will be dependent on the predator density and vice versa; the prey density is governed by the availability of sustainable resources and the predator density in a given patch while the predator density is dependent on the availability of their food source.

3.5 Symmetric Manifold

Similarly, on solving the system in equation (3.18), let $U_2 = (u_2, v_2)^T$ and $\dot{U}_2 = (\dot{u}_2, \dot{v}_2)^T$, then the system in equation (3.18) becomes

$$\dot{U}_2 = \begin{pmatrix} -\alpha_0 & 0 \\ 0 & -\beta \end{pmatrix} U_2(t - \tau) + \begin{pmatrix} -\alpha_0 + r & 0 \\ 0 & -\beta - s \end{pmatrix} U_2 \quad (3.31)$$

Let $U_2(t) = e^{\lambda t} C_2$, then the following characteristic equation is obtained from equation (3.31),

$$(\alpha_0 e^{-\lambda\tau} + \alpha_0 - r + \lambda)(\beta e^{-\lambda\tau} + \beta + s + \lambda) = 0 \quad (3.32)$$

Using the first factor of equation (3.32), we have

$$(\alpha_0 e^{-\lambda\tau} + \alpha_0 - r + \lambda) = 0 \quad (3.33)$$

Let $z = (\alpha_0 - r + \lambda)\tau$. Therefore we have $\frac{z}{\tau} = \lambda + \alpha_0 - r$ which can be written as $\lambda = \frac{z}{\tau} - \alpha_0 + r$.
in equation (3.33). Equation (3.33) can be written as

$$(\alpha_0 e^{-(\frac{z}{\tau} - \alpha_0 + r)\tau} + \frac{z}{\tau}) = 0, \quad (3.34)$$

$$-\alpha_0 \tau e^{-z} e^{(\alpha_0 - r)\tau} = z, \quad (3.35)$$

From Lemma 3.4.1, since $b = -\alpha_0 \tau e^{(-r + \alpha_0)\tau} < 0$, then

$$z = i(\pi/2 + 2m\pi) \text{ for } \alpha_0 \tau e^{(-r + \alpha_0)\tau} = \frac{\pi}{2} + 2m\pi. \quad (3.36)$$

Substituting equation (3.35) in equation (3.33) we obtain,

$$\lambda = \frac{i(\pi/2 + 2m\pi)}{\tau} - (\alpha_0 - r). \quad (3.37)$$

Therefore equation (3.33);

- (i) has roots with negative real parts when $\alpha_0 > r$,
- (ii) has roots with positive real parts when $\alpha_0 < r$,
- (iii) has a periodic solution when $\alpha_0 = r$.

For the second factor of equation (3.32); that is,

$$(\beta e^{-\lambda\tau} + s + \beta + \lambda) = 0, \quad (3.38)$$

Therefore we have $\frac{z}{\tau} = \lambda - \beta - s$ which can be written as $\lambda = \frac{z}{\tau} + \beta + s$. Equation (3.38) can be written as

$$(\beta e^{-(\frac{z}{\tau} + \beta + s)\tau} - \frac{z}{\tau}) = 0, \quad (3.39)$$

$$\beta \tau e^{-z} e^{-(\beta + s)\tau} = z, \quad (3.40)$$

From Lemma 3.4.1, equation (3.38) becomes,

$$\lambda = \frac{i(\pi/2 + 2m\pi)}{\tau} - (\beta + s) \quad (3.41)$$

From equation (3.41) all the roots of equation (3.38) have negative real parts, and thus the system of equation (3.38) is asymptotically stable.

From the results of equation (3.33) and equation (3.38), equation (3.31) has;

- (i) a sink at the origin for $\alpha_0 > r$ because equation (3.33) is stable for $\alpha_0 > r$ while equation (3.38) is stable for all β and s ,
- (ii) a saddle at the origin for $\alpha_0 < r$ because equation (3.33) is unstable for $\alpha_0 < r$ while equation (3.38) is stable for all β and s
- (iii) a periodic solution for $\alpha_0 = r$ because equation (3.33) is a center for $\alpha_0 = r$ while equation (3.38) is stable for all β and s

The results for equation (3.31) show that, when the system has a saddle at the origin, then the prey population becomes extinct making the predator population to become extinct. When the system has a sink at the origin, the predator and prey populations coexist. When the prey migration rate is the same as the prey growth rate then a periodic solution occurs and therefore the population fluctuates.

3.6 Numerical Simulations

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 described and they are hypothetical. In Section 3.6.1, the simulations for the Asymmetric Manifold are shown, while in Section 3.6.2 the simulations for the Symmetric Manifold are shown. In Section 3.6.3, the simulations for the System of equations with delay and Predator-density-dependent prey migration, the System of equations with delay and constant prey migration and the System of equations without delay are compared so that the effects of delay and Predator-density-dependent prey migration affect a predator prey model can be shown.

3.6.1 Numerical Simulation for asymmetric manifold

The following parameter values, adapted from Apima [2] and Mchich et. al. [9], are used in simulating the graphs of equation (3.17).

Table 3.1: *Parameter values for the Asymmetric Manifold*

Figure	r	α_0	α	s	β	a	b	u_i	v_i	τ
3.1	0.2	0.1	0.2	0.291	0.251	0.2	0.3	12	8	0.1
3.2	0.1	0.62	0.2	0.291	0.251	0.2	0.3	12	8	0.1
3.3	0.1	0.1	0.2	0.291	0.251	0.2	0.3	12	8	0.1

Simulations for the asymmetric manifold gives,

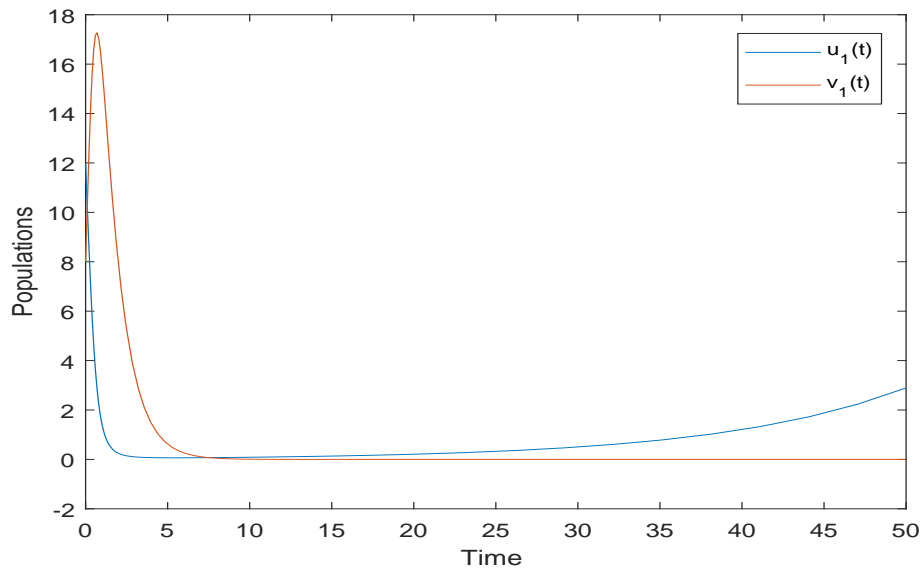


Figure 3.1: *Graph of asymmetric manifold for $(\alpha_0 < r)$*

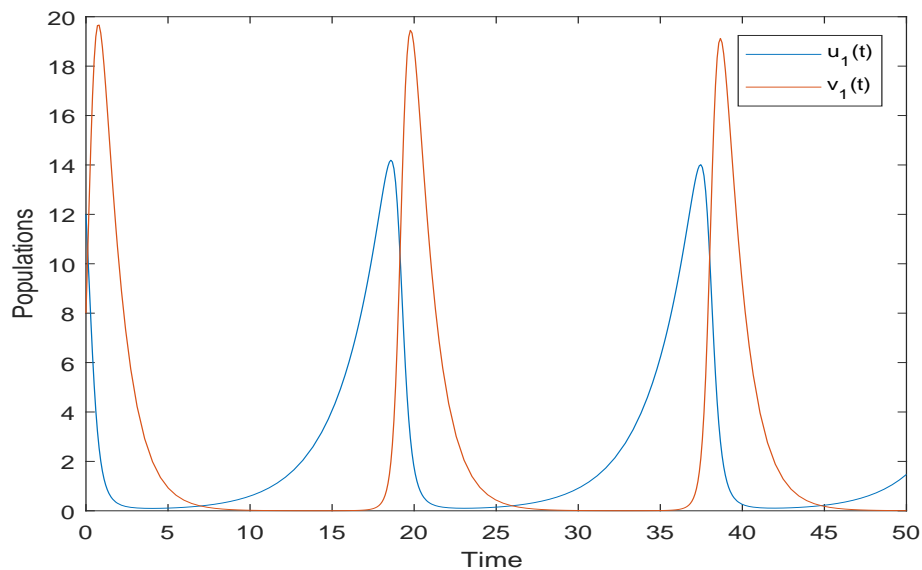


Figure 3.2: Graph of asymmetric manifold for ($\alpha_0 > r$)

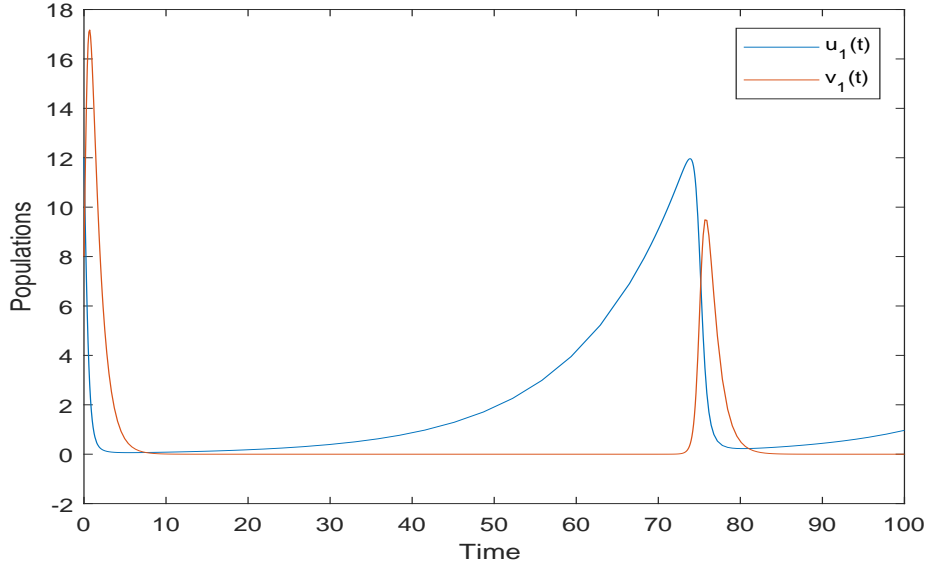


Figure 3.3: Graph of asymmetric manifold for ($\alpha_0 = r$)

Figure 3.1 shows when $\alpha_0 < r$, the prey migration rate is less than the prey growth rate, the predator density will be led into extinction after some time. This is due to the unavailability of the predator's source of food. Figure 3.2 shows when $\alpha_0 > r$, the prey migration rate is greater than the prey growth rate, then the predator and prey species coexist and are governed by the available sustaining resources. Figure 3.3 shows when $\alpha_0 = r$, the prey migration rate is equal to the prey growth rate, the predator and prey species will oscillate though the oscillation occurs after a longer period of time.

3.6.2 Numerical Simulation for symmetric manifold

The following parameter values, adapted from Apima [2] and Mchich et. al. [9], are used in simulating the results of equation (3.18).

Table 3.2: Parameter values for the Symmetric Manifold

Figure	r	α_0	s	β	u_i	v_i	τ
3.4	0.1	0.15	0.1	0.15	12	8	0.1
3.5	0.5	0.21	0.1	0.1	12	8	0.1
3.6	0.1	0.1	0.46	0.5	12	8	0.1

Simulations for the symmetric manifold gives,

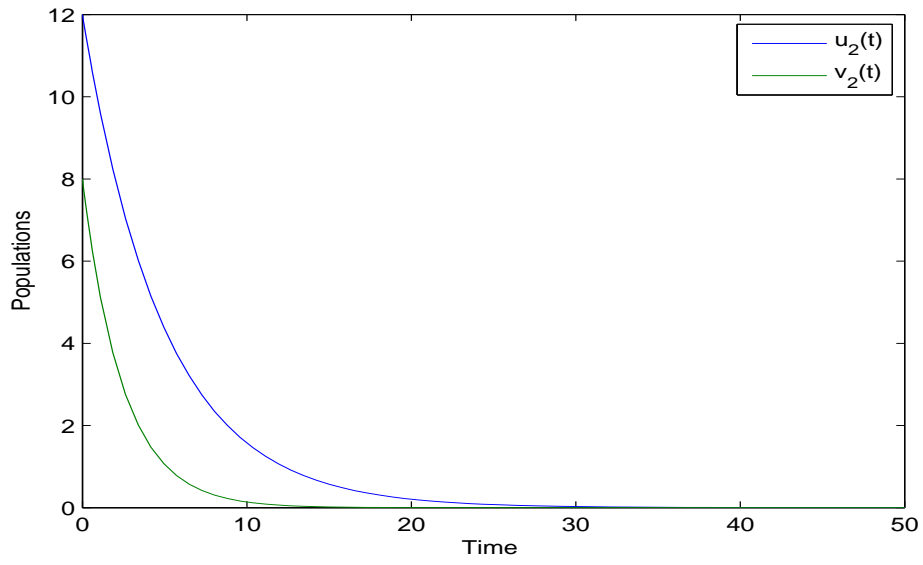


Figure 3.4: Graph of symmetric manifold for $(\alpha_0 > r)$

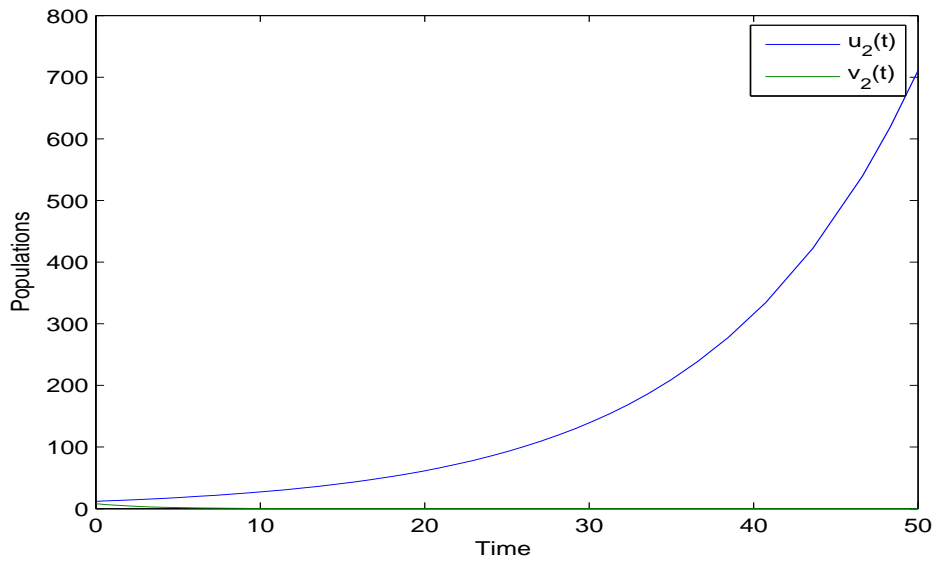


Figure 3.5: Graph of symmetric manifold for $(\text{for } \alpha_0 < r)$

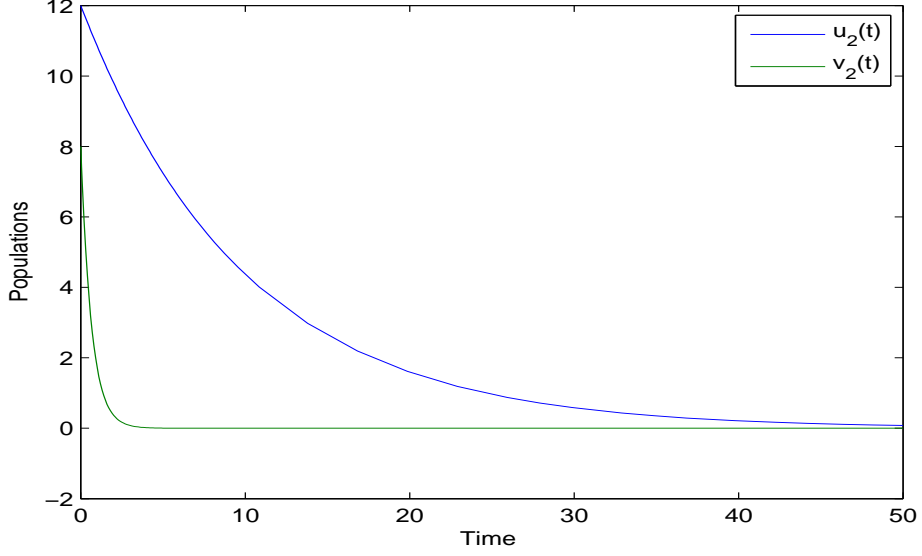


Figure 3.6: *Graph of symmetric manifold for $(\alpha_0 = r)$*

Figure 3.4 shows that the species population stabilize at 0 for $\alpha_0 > r$, that means that if the prey migration rate is greater than the prey growth rate, then, either the predator and prey species will be wiped out or the population in both patches will be equal (because of the change of coordinates in equation (3.15)). Figure 3.5 shows that for $\alpha_0 < r$, the prey migration rate is less than the prey growth rate, then the predator population will become extinct as the prey population increases in patch one. Figure 3.6 shows that the species population tends zero for $\alpha_0 = r$ as time increases, that means that if the prey migration rate is equal to the prey growth rate, then, either both species will almost be wiped out or the population in both patches will almost be equal (because of the change of coordinates in equation (3.15)).

3.6.3 Numerical Simulation for the formulated model

The following parameter values, adapted from Apima [2] and Mchich et. al. [9], are used in simulating the results of equation (3.3).

Table 3.3: *Parameter values for the formulated model*

Figure	α_1	α_2	τ	α_0	r_1	r_2	a_1	a_2	β	s_1	s_2	b_1	n_1	n_2	p_1	p_2
3.7	0.25	0.2	0.1	0.22	0.5	0.7	0.3	0.2	0.42	0.61	0.41	0.51	12	8	14	10
3.8	0	0	0.1	0.22	0.5	0.7	0.3	0.2	0.42	0.61	0.41	0.51	12	8	14	10
3.9	0.25	0.2	0	0.22	0.5	0.7	0.3	0.2	0.42	0.61	0.41	0.51	12	8	14	10

Simulations for the formulated model give,

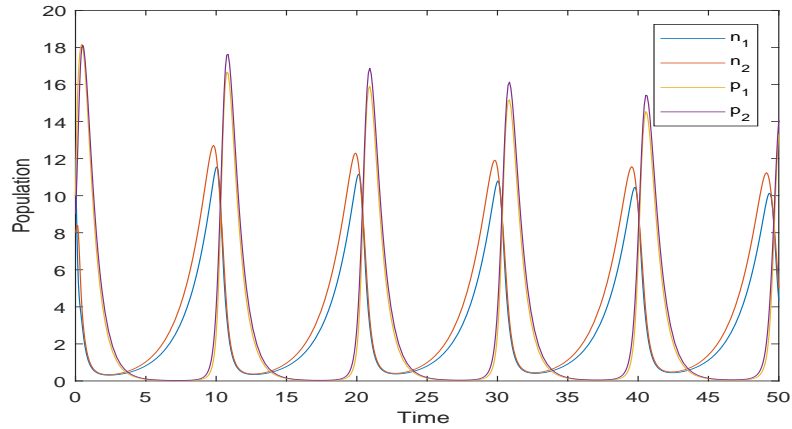


Figure 3.7: Graph of model (3.3) with delay

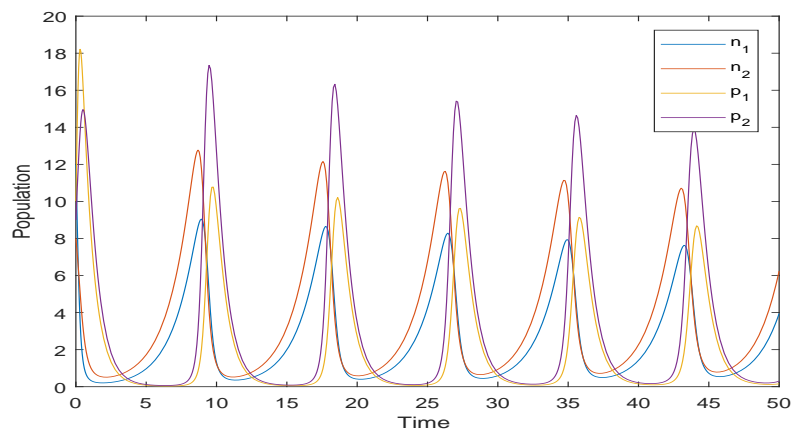


Figure 3.8: Graph of model (3.3) with constant prey migration, $\alpha_1 = \alpha_2 = 0$

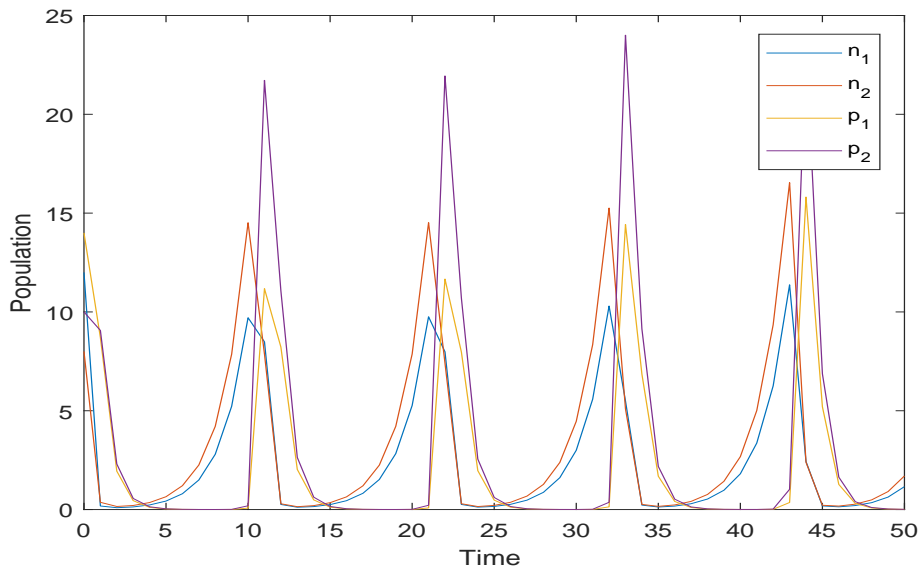


Figure 3.9: Graph of model (3.3) without delay, $\tau = 0$

Figure 3.7, Figure 3.8 and Figure 3.9 show that the prey and predator populations co-exist in both patches. Figure 3.7 and Figure 3.8 show that the delay has a stabilizing effect on equation (3.3). In the presence of delay, the species populations in both patches decreases at

a faster rate compared to the population without a delay. These oscillations tend to stabilize at some value for the model with delay, meaning that the population will not be fluctuating at a high rate unlike the model without delay.

CHAPTER 4

CONCLUSION AND RECOMMENDATION

4.1 Conclusion

A two-patch Lotka-Volterra model which incorporates a delay in the migration for both species with predator-density-dependent migration for the prey was formulated. The analysis of both the asymmetric and symmetric manifold showed that there is a sink at the origin when the prey migration rate is greater than prey growth rate, $\alpha_0 > r$. This means that the prey and predator species will not become extinct, regardless of the mortality of the predator and the predator migration rate. There is a saddle at the origin for $\alpha_0 < r$. This means that the prey and predator species will become extinct with time. There is a periodic solution for $\alpha_0 = r$ which shows that the population fluctuates. The prey density will be dependent on the predator density and vice versa; the prey density is governed by the availability of sustainable resources and the predator density in a given patch while the predator density is dependent on the availability of their food source.

Numerical analysis of the asymmetric manifold shows that when the prey migration rate is less than the prey growth rate, as shown in Figure 3.1, the predator population becomes extinct after some time while the prey population begins growing after the predator population has been wiped out. Figure 3.2 shows when the prey migration rate is greater than the prey growth rate, then the predator and prey species coexist. Figure 3.3 shows when the prey migration rate is equal to the prey growth rate, the predator and prey species will oscillate though the oscillation occurs after a longer period of time.

Numerical analysis of the symmetric manifold (Figure 3.4, Figure 3.5 and Figure 3.6) shows that if the prey migration rate is greater than the prey growth rate, then, either both species will be wiped out or the population in both patches will be equal (because of the change of coordinates in equation (3.15)). If the prey migration rate is less than the prey growth rate, then the predator population will become extinct or becomes the same in both patches as the prey population increases, and if the prey migration rate is equal to the prey growth rate, then, either the predator and prey species will be wiped out or the population

in both patches will almost be equal.

4.2 Recommendations

The results obtained show that delay in migration greatly affects the density of any species and thus the the government and relevant agencies like the Kenya Wildlife Service should employ measures which will deal with factors which cause barriers during migration for example reducing natural habitat land allocation to human settlement, agriculture or infrastructure.

The model developed herein considers a constant migration rate for the predator, however the predator migration rate may be dependent on the prey density, and migration rates may not be the same since every species in patch i , $i = 1, 2, 3 \dots$ has different dynamics. One can also examine a logistic growth predator-prey model which incorporates a delay in the migration of the system with predator-density-dependent migration for the prey. One can further add another delay to account for the fact that a predator must attain a certain age to able to hunt.

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