

## **A Predator-Prey Model with a Time Lag in the Migration**

**Adu A.M. Wasike**

Department of Mathematics  
Masinde Muliro University of Science and Technology  
P.O. Box 190 Kakamega, Kenya

**Samwel A. Bonga'ng'a**

Department of Mathematics  
Masinde Muliro University of Science and Technology  
P.O. Box 190 Kakamega, Kenya

**Lawi, G.O.**

Department of Mathematics  
Masinde Muliro University of Science and Technology  
P.O. Box 190 Kakamega, Kenya

**Mulati O. Nyukuri**

Department of Mathematics  
Kibabii University College  
P.O. Box 1699 Bungoma, Kenya

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### **Abstract**

We develop a two-patch migration model of the classical Lotka-Volterra predator-prey system with a time lag in the migration between patches. We show that when the migration rate is less than the prey growth rate the species in at least one patch survives. When the migration rate is greater than the prey growth rate, the species in both

patches do not survive. Furthermore, when the migration rate is equal to the prey growth rate, the population will oscillate.

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## 1 Introduction

The Lotka-Volterra model assumes that the environment is homogeneous, see for instance [14], [15], [18], but that is not the case since the environment is made up of many patches which are connected by a diffusion-like process.

In predator prey theory, diffusion will represent migration of either the prey, predator population or both. Migration occurs when a species moves from one patch to another due to some unfavourable conditions in its initial patch, for example, lack of food (for both the predator and prey), lack of security mainly for the prey population, bad climatic conditions, overpopulation of either the predator or prey species in a patch, among others, see for instance [17]. There is abundant literature on Lotka-Volterra models with migration, see for instance [6],[13],[1],[15]. However, these models are overly restrictive, they assume that cause and effect are instantaneous; that is local interaction of the predator and prey and their migration is instantaneous. This is not the case in real life. Predators and prey need some “experience” before migrating. Thus a time lag in the migration terms of the equations describing the dynamics of the interacting populations.

Very little attention has been given to the models that consider a time delay in the migration of the predator and prey due to the fact that the prey do not migrate immediately after being preyed on and the predator do not migrate immediately after lacking their source of food. Hence there is need to formulate a model that takes into consideration the time lags in the migration of both the predator and prey.

This is how this paper is organised. In §2, we develop a model similar to that proposed by Mchich *et. al* [13] and Abdllaoui *et. al*, [1] by introducing time lags in the migration of the prey and predator. In §3, we analyze the model by determining the Exponential bound of the model and its characteristic equation. In §3.2, we use an approach adopted from [19], [20] by taking advantage of the symmetry in the model to break the linear part of the model into two invariant manifolds and analyse the stability of solutions on the two manifolds.

## 2 The Model

A simple Predator-Prey model in a two-patches dynamics is described by the Lotka-Volterra Equation, thus:

$$\begin{aligned} \dot{n}_i &= r_i n_i - a_i n_i p_i, \\ \dot{p}_i &= -s_i p_i + b_i n_i p_i, \quad i = 1, 2, \end{aligned} \tag{1}$$

where  $i$  indicates a patch and the variable  $n_i := n_i(t)$  is the prey population at time  $t$ ,  $p_i := p_i(t)$  is the predator population at time  $t$ ,  $r_i$  is the intrinsic growth rate of the prey population,  $a_i$  and  $b_i$  are predation parameters. The constant  $s_i$  is the natural mortality rate of the predator population. Aside from the usual assumptions in Equation (1) see for instance [14], we assume that the species of predator and prey are of the same type regardless of the patch.

We now introduce in Equation (1) a migration, that we assume takes a linear diffusion-like form. Equation (1) now becomes,

$$\begin{aligned} \dot{n}_i(t) &= D_N(n_j(t - \tau) - n_i(t)) + r_i n_i(t) - a_i n_i(t) p_i(t), \\ \dot{p}_i(t) &= D_P(p_j(t - \tau) - p_i(t)) - s_i p_i(t) + b_i n_i(t) p_i(t), \quad i, j = 1, 2, i \neq j, \end{aligned} \tag{2}$$

where  $D_N$  represents the prey migration rate,  $D_P$  represents the predator migration rate and  $\tau$  represents a time lag in the migration of both the prey and predator. Let  $z_i(t) := (n_i(t), p_i(t))$ ,  $i = 1, 2$ , and for simplicity, we assume that  $D_N = D_P$  and is equal to some constant,  $\beta > 0$ . Thus Equation (2) becomes,

$$\dot{z}_i(t) = \beta(z_j(t - \tau) - z_i(t)) + f_i(z_i(t)), \quad i, j = 1, 2, i \neq j, \tag{3}$$

where,

$$f_i(z_i(t)) = \begin{pmatrix} r_i n_i(t) - a_i n_i(t) p_i(t) \\ -s_i p_i(t) + b_i n_i(t) p_i(t) \end{pmatrix}. \tag{4}$$

Let  $z(t) := (z_1(t), z_2(t))$  and  $f(z(t), z(t - \tau))$  represent the vector field on the right hand side of Equation (3), thus Equation (3) becomes,

$$\dot{z}(t) = f(z(t), z(t - \tau)). \tag{5}$$

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,

$$\varphi(t) := z(t) |_{[-\tau, 0]}, \tag{6}$$

where  $\varphi \in C$ . Since  $f(z(t), z(t - \tau)) \in \mathcal{C}(\mathbb{R}^4 \times C, \mathbb{R}^4)$ , Equation (5) subject to Equation (6) has a unique solution. For more on existence and uniqueness of solutions, see for instance Hale & Lunel [9].

### 3 Analysis of the Model

In this section, we analyze Equation (3) using the same method as the one used in [19],[20] where a system of coupled oscillators with a time lag in the coupling was studied.

We wish to exploit the symmetries in the coupling terms of Equation (3); that is,

$$\dot{z}_i(t) = \beta(z_j(t - \tau) - z_i(t)), \quad i, j = 1, 2, i \neq j, \quad (7)$$

We show that Equation (7) generates semiflows on two invariant manifolds. To this end we shall apply Laplace transform methods in complex variables to the terms describing migration in Equation (3). To this end, an exponential estimate of the solution of the Equation (7) should be bounded.

#### 3.1 Exponential Boundedness

We now prove that Equation (7) is exponentially bounded.

**Lemma 3.1.** *The solution of Equation (7) subject to the initial condition in Equation (6) for  $t \geq 0$ , satisfies,*

$$|z(t)| \leq \alpha(\tau)e^{b\tau}|\varphi|, \quad (8)$$

where  $\alpha(\tau) = 1 + |\beta|\tau$ ,  $b = 2|\beta|$  and  $|\cdot|$  denotes a sup norm in  $\mathbb{R}^4$  as well as a matrix norm.

*Proof.* The solution of Equation (7) subject to initial condition in Equation (6) satisfy,

$$z(t) = \varphi(0) + \beta \int_{-\tau}^0 \begin{pmatrix} 0 & I_2 \\ I_2 & 0 \end{pmatrix} \varphi(s) ds + \beta \int_0^t \left\{ \begin{pmatrix} 0 & I_2 \\ I_2 & 0 \end{pmatrix} z(s - \tau) - \begin{pmatrix} I_2 & 0 \\ 0 & I_2 \end{pmatrix} z(s) \right\} ds. \quad (9)$$

Therefore,

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

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

$$\begin{aligned} |z(t)| &\leq (1 + \beta\tau) \exp\left(\int_0^t 2\beta ds\right) |\varphi| \\ &= (1 + \beta\tau) \exp(2\beta t) |\varphi|. \end{aligned}$$

□

Since Equation (7) is exponentially bounded, we will now find the characteristic equation so that we can be able to show that Laplace Transform of Equation (7) exists.

The Characteristic Equation of the Coupling terms, in Equation (7) is given by,

$$(\beta + \lambda - \beta e^{-\lambda\tau})(\beta + \lambda + \beta e^{-\lambda\tau}) = 0. \tag{10}$$

The multiplicities of the roots in Equation (10) will be doubled.

### 3.2 Invariant Manifold

We now show that solutions of Equation (7) define two semi-flows on two two-dimensional invariant subspaces of  $\mathbb{R}^4$ . Taking the Laplace transform of Equation (7), we get

$$\begin{pmatrix} (-\lambda - \beta)I_2 & \beta e^{-\lambda\tau}I_2 \\ \beta e^{-\lambda\tau}I_2 & (-\lambda - \beta)I_2 \end{pmatrix} \begin{pmatrix} z_1(\lambda) \\ z_2(\lambda) \end{pmatrix} = \begin{pmatrix} z_1(0) \\ z_2(0) \end{pmatrix}, \tag{11}$$

where

$$z_i(\lambda) := \int_0^\infty e^{-\lambda t} z_i(t) dt$$

is analytic for  $\Re\lambda > b$ . Equation (11) is symmetric in nature, on simplifying it, adding (respectively subtracting) the set of equations involving  $z_2(0)$  to (respectively from)  $z_1(0)$  in Equation (11), we obtain

$$\begin{aligned} (-\lambda - \beta + \beta e^{-\lambda\tau})I_2(z_1(\lambda) + z_2(\lambda)) &= z_1(0) + z_2(0), \\ (-\lambda - \beta - \beta e^{-\lambda\tau})I_2(z_1(\lambda) - z_2(\lambda)) &= z_1(0) - z_2(0). \end{aligned} \tag{12}$$

The matrices  $(-\lambda - \beta + \beta e^{-\lambda\tau})I_2$  and  $(-\lambda - \beta - \beta e^{-\lambda\tau})I_2$  are invertible for  $\Re\lambda > b$ . Thus the inverse Laplace transform exists and is given by

$$\begin{aligned} z_1(\lambda) + z_2(\lambda) &= (-\lambda - \beta + \beta e^{-\lambda\tau})^{-1}I_2(z_1(0) + z_2(0)), \\ z_1(\lambda) - z_2(\lambda) &= (-\lambda - \beta - \beta e^{-\lambda\tau})^{-1}I_2(z_1(0) - z_2(0)). \end{aligned} \tag{13}$$

Let

$$\begin{aligned} \Theta &= \{(z_1(t), z_2(t)), z_i(t) \in \mathbb{R}^2 : z_1(t) - z_2(t) = 0\}, \\ \Pi &= \{(z_1(t), z_2(t)), z_i(t) \in \mathbb{R}^2 : z_1(t) + z_2(t) = 0\}. \end{aligned} \tag{14}$$

The  $\Theta$ -manifold is referred to as the Synchronization Manifold while  $\Pi$ -manifold is called Asymmetric. These manifolds are invariant with respect to the semi-flow defined by (2) see [19]. To simplify the study of Equation (2) on these manifolds, we introduce a change of coordinates defined by,

$$u_1 := \frac{1}{2}(n_1 + n_2), \quad v_1 := \frac{1}{2}(p_1 + p_2), \quad u_2 := \frac{1}{2}(n_1 - n_2), \quad v_2 := \frac{1}{2}(p_1 - p_2). \tag{15}$$

Since the species are assumed to be of the same type, we shall assume  $r_1 = r_2 := r$ ,  $a_1 = a_2 := a$ ,  $b_1 = b_2 := b$ ,  $s_1 = s_2 := s$ . Using the transformation in Equation (15) in Equation (2), we obtain,

$$\begin{aligned}\dot{u}_1(t) &= \beta(u_1(t - \tau) - u_1(t)) + ru_1(t) - a(u_1(t)v_1(t) + u_2(t)v_2(t)), \\ \dot{v}_1(t) &= \beta(v_1(t - \tau) - v_1(t)) - sv_1(t) + b(u_1(t)v_1(t) + u_2(t)v_2(t)). \\ \dot{u}_2(t) &= -\beta(u_2(t - \tau) + u_2(t)) + ru_2(t) - a(u_1(t)v_2(t) + u_2(t)v_1(t)), \\ \dot{v}_2(t) &= -\beta(v_2(t - \tau) + v_2(t)) - sv_2(t) + b(u_1(t)v_2(t) + u_2(t)v_1(t)).\end{aligned}\quad (16)$$

The linear subspace in Equation (14) becomes

$$\Pi = \{(u_1, v_1, 0, 0) \in \mathbb{R}^4 : (u_1, v_1) \in \mathbb{R}^2\},$$

$$\Theta = \{(0, 0, u_2, v_2) \in \mathbb{R}^4 : (u_2, v_2) \in \mathbb{R}^2\}.$$

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

$$\dot{U}_1(t) = \begin{pmatrix} \beta & 0 \\ 0 & \beta \end{pmatrix} U_1(t - \tau) + \begin{pmatrix} r - \beta - av_1 & 0 \\ 0 & -s - \beta + bu_1 \end{pmatrix} U_1(t), \quad (17)$$

and

$$\dot{U}_2(t) = \begin{pmatrix} -\beta & 0 \\ 0 & -\beta \end{pmatrix} U_2(t - \tau) + \begin{pmatrix} r - \beta & 0 \\ 0 & -s - \beta \end{pmatrix} U_2(t), \quad (18)$$

where  $U_i(t) = (u_i(t), v_i(t))$ ,  $i = 1, 2$ , respectively.

Next we examine the stability of solutions on the two manifolds, this will help us predict long-term behaviours of solutions of Model (2).

### 3.3 Analysis of the Synchronization Manifold

Our main result in this section is Theorem 3.2

**Theorem 3.2.** *For all  $s$ , Equation (17) has;*

- (i) *A sink at the origin for  $\beta > r$ ;*
- (ii) *A saddle at the origin for  $\beta < r$ ;*
- (iii) *A periodic solution for  $\beta = r$ .*

We will use Lemma 3.3 and Lemma 3.4 that can be found for instance in [3] to prove Theorem 3.2.

**Lemma 3.3.** *The equation  $z = be^{-z}$  has simple pure imaginary roots,*

$$\begin{aligned} z &= i(\pi/2 + 2m\pi), & \text{for } b &= -(\pi/2 + 2m\pi), \\ z &= 0, & \text{for } b &= 0, \\ z &= i(\pi/2 + (2m + 1)\pi), & \text{for } b &= (\pi/2 + (2m + 1)\pi), \end{aligned}$$

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

**Lemma 3.4.** *If  $|b|$  is close to zero, equation  $z = be^{-z}$  has no positive real root for  $b < 0$  and precisely one if  $b > 0$ .*

*Proof.* Let  $U_1(t) = e^{\lambda t}c_1$ ,  $c_1 \in \mathbb{C}^2$ , be the nontrivial solution of Equation (17). Substituting  $U_1(t)$  in Equation (17), we obtain the characteristic equation,

$$(\beta e^{-\lambda\tau} + r - \beta - \lambda)(\beta e^{-\lambda\tau} - s - \beta - \lambda) = 0. \tag{19}$$

If we let

$$z = (\lambda + \beta - r)\tau. \tag{20}$$

in the first factor of Equation (19),

$$(-\beta e^{-\lambda\tau} - r + \beta + \lambda) = 0. \tag{21}$$

we obtain

$$z = \beta\tau e^{-z} e^{(-r+\beta)\tau}. \tag{22}$$

From Lemma 3.3, setting  $b = \beta\tau e^{(-r+\beta)\tau} > 0$ , then

$$z = i(\pi/2 + (2m + 1)\pi) \text{ for } \beta\tau e^{(-r+\beta)\tau} = \frac{\pi}{2} + (2m + 1)\pi. \tag{23}$$

Using Equation (20) in Equation (23) we obtain,

$$\lambda = \frac{i(\pi/2 + (2m + 1)\pi)}{\tau} - (\beta - r). \tag{24}$$

Thus Equation (21) has;

- (i) Roots with negative real parts for  $\beta > r$ ;
- (ii) Roots with positive real parts for  $\beta < r$  and precisely one positive real root if  $|\beta\tau e^{(\beta-r)\tau}|$  is close to zero;
- (iii) Purely imaginary roots when  $\beta = r$ .

Similarly upon applying Lemma 3.3 with  $z := (\lambda + \beta + s)\tau$  in

$$(-\beta e^{-\lambda\tau} + s + \beta + \lambda) = 0, \quad (25)$$

and upon the use of Lemma 3.3, we obtain

$$\lambda = \frac{i(\pi/2 + 2m\pi)}{\tau} - (\beta + s) \quad (26)$$

for

$$\beta\tau e^{(s+\beta)\tau} = \frac{\pi}{2} + 2m\pi.$$

All the roots of Equation (25) have negative real parts for all positive values of  $\beta$  and  $s$ .

Combining the results obtained for Equation (21) and Equation (25), the System of Equation (17) has;

- (i) A sink at the origin for  $\beta > r$ ;
- (ii) A saddle at the origin for  $\beta < r$ ;
- (iii) A Periodic solution for  $\beta = r$ .

Hence Theorem 3.2 is proved.  $\square$

### 3.4 Analysis of the Asymmetric Manifold

The main results in this section is Theorem 3.5.

**Theorem 3.5.** *For all  $s$ , and  $\beta\tau e^{(-r+\beta)\tau} = \frac{\pi}{2} + 2m\pi, m = 0, 1, \dots$  Equation (18) has;*

- (i) *A sink at the origin for  $\beta > r$ ;*
- (ii) *A saddle at the origin for  $\beta < r$ ;*
- (iii) *A periodic solution for  $\beta = r$ .*

*Proof.* Let  $U_2(t) = e^{\lambda t}c_2$ , where  $c_2 \in \mathbb{C}^2$  is nonzero. Substituting  $U_2(t)$  in Equation (18), we obtain the following characteristic equation,

$$(\beta e^{-\lambda\tau} - r + \beta + \lambda)(\beta e^{-\lambda\tau} + s + \beta + \lambda) = 0. \quad (27)$$

We will analyze the factors of Equation (27) separately and then combine the results obtained.

Consider the first factor of Equation (27); that is,

$$(\beta e^{-\lambda\tau} - r + \beta + \lambda) = 0. \quad (28)$$



Let

$$z = (\lambda + \beta - r)\tau. \tag{29}$$

Equation (28) becomes,

$$z = -\beta\tau e^{-z} e^{(-r+\beta)\tau}. \tag{30}$$

From Lemma 3.3, since  $b = -\beta\tau e^{(-r+\beta)\tau} < 0$ ,

$$z = i(\pi/2 + 2m\pi) \text{ for } \beta\tau e^{(-r+\beta)\tau} = \frac{\pi}{2} + 2m\pi, m = 0, 1, 2, \dots \tag{31}$$

Using Equation (29) in Equation (31) we obtain,

$$\lambda = \frac{i(\pi/2 + 2m\pi)}{\tau} - (\beta - r). \tag{32}$$

Therefore for all  $\beta\tau e^{(-r+\beta)\tau} = \frac{\pi}{2} + 2m\pi$ , Equation (28) has:

- (i) Roots with negative real parts when  $\beta > r$ ;
- (ii) Roots with positive real parts when  $\beta < r$  and precisely one positive real root when  $|\beta\tau e^{(\beta-r)\tau}|$  is close to zero;
- (iii) A periodic solution when  $\beta = r$ .

For the second factor of Equation (19); that is,

$$(\beta e^{-\lambda\tau} + s + \beta + \lambda) = 0, \tag{33}$$

let

$$z = (\lambda + \beta + s)\tau. \tag{34}$$

Using Lemma 3.3 and Equation (34), we obtain

$$\lambda = \frac{i(\pi/2 + 2m\pi)}{\tau} - (\beta + s) \tag{35}$$

All the roots of Equation (33) have negative real parts, and thus the System of Equation (18) is asymptotically stable.

Combining the results obtained for Equation (28) and Equation (33), Equation (18) has;

- (i) A sink at the origin for  $\beta > r$ ;
- (ii) A saddle at the origin for  $\beta < r$ ;
- (iii) A periodic solution for  $\beta = r$ . Hence Theorem 3.5 is proved.

□

## 4 Conclusion and Discussion

The analysis of the Synchronization Manifold show that, regardless of the value of the mortality rate,  $s$ , when the migration coefficient  $\beta$ , is less than the growth rate of the prey, the population in one patch grows while the population in the other patch stabilizes at zero: this means that the species will not die out in both patches since one of the patches does not remain at zero for all time. When the migration coefficient is greater than the prey growth rate, the population in both patches stabilizes at zero: these two species in both patches will die out. When the coupling term is the same as the prey growth rate then a periodic solution occurs. The analysis of Asymmetric manifold show that we have sink at the origin when migration coefficient is greater than the prey growth rate,  $\beta > r$ , and  $0 < \beta\tau e^{(-r+\beta)\tau} < \pi/2$ , irrespective of the value of the predator mortality rate,  $s$ , saddle at the origin when  $\beta < r$  or  $\beta\tau e^{(-r+\beta)\tau} > \pi/2$  irrespective of the value of the predator mortality rate,  $s$ , and a periodic solutions when coupling term is equal to the prey growth rate  $\beta = r$ .

We have considered a model where the migration rate is constant, but the migration rate is usually dependent on the other species, i.e. the prey migration rate should be dependent on the predator density and the predator migration rate should be dependent on the prey density, and these migration rates should not be the same since every species in patch  $i$ ,  $i = 1, 2, 3 \dots$  has different dynamics. Model (3) can also be extended to more than two patches. One can also examine a logistic growth predator-prey model which incorporates a delay in the migration of the system. One can further add another delay in the nonlinear(interaction) part to account for the fact that a prey must attain a certain age to be preyed on and a predator must attain a certain age to able to hunt.

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