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ON A NEW MODEL OF TWO-PATCH PREDATOR-PREY SYSTEM WITH MIGRATION OF BOTH SPECIES

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Abstract In this paper we explore the dynamics of predator-prey in a two patch system. The two patches of the system are coupled with both the migration of the predator and the prey. The purpose of this exploration is to find upper and lower bounds for the populations and get an insight on the different possibilities with the three types of Holling functional responses. Also we discuss the stability and instability of the equilibrium solutions found in earlier papers. Numerical simulations are provided to graphically demonstrate the population dynamics of the system.

Keywords Predator-prey models, two-patch migrations, extinction or co-existence, stability and asymptotic behavior, numerical simulations.

MSC(2000) Primary: 35K55, 35B40; Secondary: 92B05.

1. Introduction

In many years, the Lotka-Volterra equations have been studied in various models that involve the interactions of several populations (for examples, see [1]-[5], [15]-[17]), including the predator-prey interaction of more than two populations. Other ecological concepts such as functional responses, diffusion and time delays have been added to the Lotka-Volterra equations to gain more accurate description and better understanding for the dynamics of population interactions (for examples, see [2], [5], [6], [7],[8]-[13], [14], [16], [17]. The model proposed and discussed in this paper originates from the Rosenzweig-MacArthur (1963) model. The prey in the Rosenzweig-MacArthur model has a logistic growth rate, (*i.e.* the growth rate is resource-limited [8]) and the predator has a Holling type II functional response. Jansen [9, 12, 13] further extended the Rosenzweig-MacArthur model by allowing the predator and prey to inhabit two separate patches coupled by the migration of the predator. In Jansen's models, it was assumed that the prey does not migrate and the predator in the patch with a higher density will migrate to the patch with

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a lower density[9]:

$$\begin{aligned} \frac{dN_i}{dt} =& rN_i\left(1-\frac{N_i}{K}\right)-\frac{bN_iP_i}{b+N_i} \\ \frac{dP_i}{dt} =& \frac{bN_iP_i}{b+N_i}-\mu P_i+d(P_j-P_i) \\ & i,j\in\{1,2\}: i\neq j. \end{aligned} \tag{1.1}$$

where [9, 10, 11, 12] the variables N_i and P_i denote the densities of the prey and predator, respectively, in patch $i=1,2$. The parameter d denotes the per capita predator migration rate. The parameter r is the prey growth rate at low prey densities; K is the environmental carrying capacity of the prey population in each patch. The parameter μ is the predator death rate in the absence of prey, and b is the saturation value of the functional response. Jansen had found nine equilibrium solutions for the expanded Rosenzweig-MacArthur model (1) and discussed the conditions for stability and instability in some of the equilibrium solutions [13]. Further results on the dynamics and stability (for seven of the twelve equilibrium) in (1) were also obtained by Feng and Hinson([4], 2005).

Motivated by the above predator-prey model for the dynamics of the two-patch migration of the predator, in this paper we propose a more complex model for the two-patch predator-prey interactions, with migration of both species:

$$\begin{aligned} \frac{dN_i}{dt} =& rN_i\left(1-\frac{N_i}{K}\right)-\frac{bN_iP_i}{b+N_i}+m(N_j-N_i) \\ \frac{dP_i}{dt} =& \frac{bN_iP_i}{b+N_i}-\mu P_i+d\left(\frac{P_j}{1+N_j}-\frac{P_i}{1+N_i}\right) \\ & i,j\in\{1,2\}: i\neq j. \end{aligned} \tag{1.2}$$

The parameters of this model and that in the previous are the same, except that m is the per capita migration rate of the prey. This model is constructed to allow the migration of both the predator and the prey, and to have the migration of the predator dependent on the population of the prey in each patch.

The first term in the equation for prey, $rN_i\left(1-\frac{N_i}{K}\right)$ comes from the simple logistic equation which models the competition for resources among the prey species. The second term, $-\frac{bN_iP_i}{b+N_i}$, is depleting the prey population under Holling type II consumption of the prey by the predator. The last term $m(N_j-N_i)$ represents the migration of the prey from one patch to another, dependent on the migration constant m and the number of prey in each patch.

The first term in the equation for predator, $\frac{bN_iP_i}{b+N_i}$, shows an increase in the predator population due to the consumption of the prey. This is followed by a decrease in the population of μP_i, the natural death of the predator. The new term in the predator equation, $d\left(\frac{P_j}{1+N_j}-\frac{P_i}{1+N_i}\right)$, is the migration of the predators according to the size of the prey in each patch.

The purpose of this paper is to analyze and demonstrate the population dynamics of various species in model (2) by

1. finding the ultimate upper and lower bounds for the interacting populations;
2. exploring the stability and instability of the all the equilibrium solutions;
3. obtaining numerical simulations for the pattern of dynamics in the model.

In Section 2, we give some preliminary results on the dynamics and ultimate bounds of the predator and prey populations. The stability analysis of the equilibrium solutions take place in Section 3, along with conditions that ensure the non-negativity of the equilibrium solutions. Through the method of linearization we will find conditions for asymptotic stability and instability for all the equilibrium solutions. In the last section we will graphically display the dynamics and pattern of the populations in the ecological system by utilizing the conditions for stability and instability obtained in Section 3.

2. Ultimate Bounds for the Populations

In this section we focus on finding the upper and lower bounds of the predator and prey populations. These bounds will provide us with crucial information on extinction, co-existence, and exponential behavior of the species.

The following comparison argument [5] will be employed in the proofs associated the upper and lower bounds of the populations. Consider the respective solutions u_1 and u_2 of the initial-value problem

$$u_i' = f_i(t, u_i) \text{ in } (0, T],\ u_i(0) = u_{i,\,0} \tag{2.1}$$

where $i = 1, 2$. f_1 and f_2 are continuous functions in $[0, T] \times R$. We have

Lemma 2.1. ***The Comparison Argument.***
Assume that both $\frac{\partial f_1}{\partial u}$ *and* $\frac{\partial f_2}{\partial u}$ *are continuous in* $[0, T] \times R$. *If* $f_1(t, u) \le f_2(t, u)$ *in* $(0, T] \times R$ *and* $u_{1,\,0} \le u_{2,\,0}$, *then the respective solutions* u_1 *and* u_2 *of* (2) *satisfy* $u_1(t) \le u_2(t)$ *on* $[0, T]$.

We first give the result for ultimate bounds of the total prey population.

Theorem 2.1. ***Ultimate Bounds for Prey Populations.***
The total prey population $N(t) = N_1(t) + N_2(t)$ *satisfies*

$$0 \le N(t) \le \left[\left(\frac{1}{N(0)} - \frac{1}{2K}\right)e^{-rt} + \frac{1}{2K}\right]^{-1}. \tag{2.2}$$

Proof. Recall in (2) that the prey populations satisfy the equations

$$\frac{dN_i}{dt} = rN_i\left(1 - \frac{N_i}{K}\right) - \frac{bN_iP_i}{b + N_i} + m(N_j - N_i) \quad i, j = 1, 2.$$

The non-negativity of the density functions leads to

$$\frac{d}{dt}(N_1 + N_2) \le rN_1 + rN_2 - \left(\frac{rN_1^2}{K} + \frac{rN_2^2}{K}\right) \le rN_1 + rN_2 - \frac{r(N_1 + N_2)^2}{2K}.$$

Now by letting $N = N_1 + N_2$ we obtain the inequality,

$$\frac{dN}{dt} \le rN\left(1 - \frac{N}{2K}\right).$$

This inequality corresponds to a solvable Bernoulli type two differential equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{2K}\right)$$

with solution

$$\left[\left(\frac{1}{N(0)}-\frac{1}{2K}\right)e^{-rt}+\frac{1}{2K}\right]^{-1}.$$

By the comparison argument in Lemma 2.1 we obtain the estimates in (4). □

The above theorem shows that the total prey population is dominated by the logistic growth with capacity $2K$ as its ultimate bound,

$$\lim_{t\to\infty}N(t)\le\lim_{t\to\infty}\left[\left(\frac{1}{N(0)}-\frac{1}{2K}\right)e^{-rt}+\frac{1}{2K}\right]^{-1}=2K. \tag{2.3}$$

And, $N(t)\le 2K$ for $0<t<\infty$ as long as $N(0)\le 2K$.

We next show that the total predator population is dominated by exponential growth or decay, with rate determined by environmental coefficients μ, b and K.

Theorem 2.2. ***Ultimate Bounds for Predator Populations.***
The total predator population $P(t)=P_1(t)+P_2(t)$ satisfies,

$$P(0)e^{-\mu t}\le P(t)\le P(0)e^{(\frac{2bK}{2b+K}-\mu)t}. \tag{2.4}$$

Proof. Since

$$\frac{dP_i}{dt}=\frac{bN_iP_i}{b+N_i}-\mu P_i+d\left(\frac{P_j}{1+N_j}-\frac{P_i}{1+N_i}\right)$$

where $i,j=1,2$. Then by adding the two predator equations and using the estimate $N_i\le N\le 2K$ from Theorem 2.2, we can obtain

$$\frac{dP}{dt}=\frac{bN_1P_1}{b+N_1}-\mu P_1+\frac{bN_2P_2}{b+N_2}-\mu P_2$$

$$\le\frac{2bKP_1}{b+2K}-\mu P_1+\frac{2bKP_2}{b+2K}-\mu P_2=\left(\frac{2bK}{b+2K}-\mu\right)P$$

and

$$\frac{dP}{dt}\ge-\mu p.$$

Again, by the comparison argument in Lemma 2.1, this leads to the estimate in (6). □

This theorem leads us to the next corollary on the conditions for the boundedness or extinction of the predator populations.

Corollary 2.1. Boundedness or Extinction of Predator Populations.
If $\frac{2bK}{b+2K}\le\mu$, then the predator population remains bounded with $P(t)\le P(0)$.
If $\frac{2bK}{b+2K}<\mu$, then the predator population satisfies $\lim_{t\to\infty}P(t)=0$ globally with exponential rate $\frac{2bK}{b+2K}-\mu$.

The above theorem and corollary indicate that the total predator population remains positive at any finite time, and if $\frac{2bK}{b+2K}<\mu$ than the predator population goes to extinction in both patches as $t\to\infty$. Thus, one can see that the long-term survival of the predator is dependent on the following ecological parameters: the carrying capacity of the prey, the saturation value in the functional response, and the death rate of the predator.

3. Stability Analysis for the Equilibriums

The two-patch model (2) has three equilibrium solutions representing different outcomes of the ecological system.

$E_1 = (0, 0, 0, 0)$, extinction of both the predator and prey in each of the patches;

$E_2 = (K, 0, K, 0)$, extinction of the predator and persistence of the prey in each of the patches;

$E_3 = \left(\frac{b\mu}{b-\mu}, \left(\frac{rb}{b-\mu}\right)\left(1 - \frac{b\mu}{K(b-\mu)}\right), \frac{b\mu}{b-\mu}, \left(\frac{rb}{b-\mu}\right)\left(1 - \frac{b\mu}{K(b-\mu)}\right)\right)$, persistence of both the predator and prey in each of the patches.

We will now discuss the stability of the equilibrium solutions E_1-E_3. Through the method of linearization, it is known that an equilibrium solution is asymptotically stable if all the eigenvalues of the Jacobian matrix have negative real parts. The Jacobian matrix for our model (2) is represented by,

$$J = \begin{bmatrix} r - \frac{2rN_1}{K} - \frac{b^2P_1}{(b+N_1)^2} - m & -\frac{bN_1}{b+N_1} & m & 0 \\ \frac{b^2P_1}{(b+N_1)^2} - \frac{dP_1}{(1+N_1)^2} & J_{22} & \frac{dP_2}{(1+N_2)^2} & \frac{d}{1+N_2} \\ m & 0 & r - \frac{2rN_2}{K} - \frac{b^2P_2}{(b+N_2)^2} - m & -\frac{bN_2}{b+N_2} \\ \frac{dP_1}{(1+N_1)^2} & \frac{d}{1+N_2} & \frac{b^2P_2}{(b+N_2)^2} - \frac{dP_2}{(1+N_2)^2} & J_{44} \end{bmatrix}. \tag{3.1}$$

where, $j_{22} = \frac{bN_1}{b+N_1} - \mu - \frac{d}{1+N_1}$ and $J_{44} = \frac{bN_2}{b+N_2} - \mu - \frac{d}{1+N_1}$.

The first theorem in this section gives the instability of the equilibrium E_1 which represents extinction of all species.

Theorem 3.1. ***Instability of the Equilibrium*** E_1***.***

The equilibrium solution $E_1 = (0, 0, 0, 0)$ *is unstable.*

Proof. After inserting the trivial equilibrium solution into the Jacobian matrix (8) we obtain,

$$J_{(0,0,0,0)} = \begin{bmatrix} r-m & 0 & m & 0 \\ 0 & -\mu-d & 0 & d \\ m & 0 & r-m & 0 \\ 0 & d & 0 & -\mu-d \end{bmatrix}.$$

The determinant of $[J_{(0,0,0,0)} - \lambda I]$ gives the characteristic polynomial which can be factored as

$$\det\left|J_{(0,0,0,0)} - \lambda I\right| = (\lambda + 2d + \mu)(\lambda + \mu)(\lambda - r)(\lambda + 2m - r). \tag{3.2}$$

Thus we see that the roots of this characteristic polynomial are $-2d - \mu$, $-\mu$, r , and $r - 2m$. The Jacobian matrix has at least one positive root which leads to the conclusion of instability. □

We next show that the prey-only equilibrium E_2 has a complex stability pattern affected by various ecological parameters.

Theorem 3.2. ***Stability of the Equilibrium*** E_2***.***

The equilibrium solution $E_2 = (K, 0, K, 0)$ *solution is*

(i) globally exponentially stable if $\frac{2bK}{b+2K} < \mu$ *and* $N(0) \neq 0$*;*

(ii) asymptotically stable if $\frac{bk}{b+K} < \mu$;

(iii) stable if $\frac{bk}{b+K} \leq \mu$;

(iv) unstable if $\frac{bK}{b+K} > \mu$.

Proof. In Corollary 1 we have derived that $\frac{2bK}{b+2K} < \mu$ is a global condition for the extinction of the predators, namely,

$$\lim_{t\to\infty} P_1(t) = \lim_{t\to\infty} P_2(t) = 0.$$

Hence the preys N_1 and N_2 will both converge (as $t \to \infty$) to K, which is the global attracting equilibrium in the logistic equation

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}).$$

This proves (i).

After inserting the equilibrium solution E_2 into the Jacobian matrix (8) we obtain,

$$J_{(K,0,K,0)} = \begin{bmatrix} -r-m & -\frac{bK}{b+K} & m & 0 \\ 0 & \frac{bK}{b+K} - \mu - \frac{d}{1+K} & 0 & \frac{d}{1+K} \\ m & 0 & -r-m & -\frac{bK}{b+K} \\ 0 & \frac{d}{1+K} & 0 & \frac{bK}{b+K} - \mu - \frac{d}{1+K} \end{bmatrix}.$$

This gives a characteristic polynomial of

$$\det\left|J_{(K,0,K,0)} - \lambda I\right| = -\frac{1}{(1+K)(b+K)^2} f_1(\lambda) f_2(\lambda) f_3(\lambda) f_4(\lambda),$$

where f_n $(n = 1, 2, 3, 4)$ is one of the factors for the characteristic polynomial.

$$f_1(\lambda) = -b\lambda - K\lambda + bK - b\mu - K\mu$$
$$f_2(\lambda) = b(-K^2 + K\mu + K\lambda - K + 2d + \lambda + \mu) + K^2(\mu + \lambda) + K(2d + \lambda + \mu)$$
$$f_3(\lambda) = r + \lambda$$
$$f_4(\lambda) = r + 2m + \lambda$$

We see that the roots of the characteristic polynomial are

$$\begin{aligned} \lambda_1 &= \frac{bK - b\mu - K\mu}{b+K}, \\ \lambda_2 &= \frac{bK^2 + bK - 2db - 2dK}{(K+1)(b+K)} - \mu, \\ \lambda_3 &= -r, \\ \lambda_4 &= -2m - r. \end{aligned}$$

Clearly, the roots λ_3 and the λ_4 are already negative, and $\lambda_1 \leq (<) 0$ if $\frac{bK}{b+K} \leq (<) \mu$. In order to ensure that $\lambda_2 <\leq (<) 0$, we need to confirm that $\frac{bK^2+bK-2db-2dK}{(K+1)(b+K)} \leq (<) \mu$. Taking a closer look, this condition is equivalent to

$$\frac{bK}{b+K} - \frac{2d}{K+1} \leq (<) \mu,$$

which will hold as long as $\frac{bK}{b+K} \leq (<)\mu$. Thus, we can conclude that the only condition for the (asymptotic) stability of E_2 solution is $\frac{bK}{b+K} \leq (<)\mu$. This proves $(ii)-(iii)$.

To prove the instability result (iv), it suffices just to show that one of the eigenvalues is positive. One can see that $\lambda_1 > 0$ if $\frac{bK}{b+K} > \mu$. □

We now study the main result of this paper, concerning conditions for stability of E_3 which ensures the long-term coexistence of the predator and prey in each patch.

Theorem 3.3. ***Stability of the Equilibrium*** E_3**.**

If $\mu < \frac{bK}{b+K} < \frac{r\mu}{2m}$ *(which also implies* $b > \mu$*), then the ecological model (2) has a coexistence state at* $E_3 = \left(\frac{b\mu}{b-\mu}, \left(\frac{rb}{b-\mu}\right)\left(1-\frac{b\mu}{K(b-\mu)}\right), \frac{b\mu}{b-\mu}, \left(\frac{rb}{b-\mu}\right)\left(1-\frac{b\mu}{K(b-\mu)}\right)\right)$. *Moreover,* E_3 *is asymptotically stable.*

Proof. After substituting the equilibrium solution E_3 into the Jacobian matrix (7), we obtain

$$J_{\left(\frac{b\mu}{b-\mu},\left(\frac{rb}{b-\mu}\right)\left(1-\frac{b\mu}{K(b-\mu)}\right),\frac{b\mu}{b-\mu},\left(\frac{rb}{b-\mu}\right)\left(1-\frac{b\mu}{K(b-\mu)}\right)\right)} = \begin{bmatrix} \alpha & -\mu & m & 0 \\ \beta & -\delta & \xi & \delta \\ m & 0 & \alpha & -\mu \\ \xi & \delta & \beta & -\delta \end{bmatrix},$$

where,

$$\begin{aligned}
\alpha &= \frac{-rb^2\mu - rbK\mu + rK\mu^2 + rb\mu^2 + mKb^2 - mKb\mu}{bK(b-\mu)}, \\
\beta &= \frac{(b^2\mu^2 + b^2 + db^2 + 2b^2\mu - 2b\mu^2 - 2b\mu + \mu^2)(Kb - K\mu - b\mu)r}{bK(b-\mu+b\mu)^2}, \\
\delta &= \frac{d(b-\mu)}{b-\mu+b\mu}, \\
\xi &= -\frac{(Kb-K\mu-b\mu)brd}{K(b-\mu+b\mu)^2}.
\end{aligned}$$

The characteristic polynomial

$$\begin{aligned}
&\det\left|J_{\left(\frac{b\mu}{b-\mu},\left(\frac{rb}{b-\mu}\right)\left(1-\frac{b\mu}{K(b-\mu)}\right),\frac{b\mu}{b-\mu},\left(\frac{rb}{b-\mu}\right)\left(1-\frac{b\mu}{K(b-\mu)}\right)\right)} - \lambda I\right| \\
= \; &\lambda^4 + (-2\alpha + 2\delta)\lambda^3 + (-4\alpha\delta + 2\mu\beta - m^2 + \alpha^2)\lambda^2 \\
&+ (2\delta\xi\mu - 2\alpha\mu\beta + 2\delta\alpha^2 + 2m\mu\xi - 2m^2\delta + 2\delta\mu\beta)\lambda \\
&- 2\alpha\delta\mu\beta + 2m\delta\xi\mu - 2\alpha\delta\xi\mu - \xi^2\mu^2 + \mu^2\beta^2 + 2m\delta\mu\beta
\end{aligned}$$

can be factored into the product of two quadratics

$$\begin{aligned}
Q_1(\lambda) &= \lambda^2 + (-\alpha - m)\lambda + \xi\mu + \mu\beta, \\
Q_2(\lambda) &= \lambda^2 + (2\delta + m - \alpha)\lambda - \xi\mu + \mu\beta + 2m\delta - 2\alpha\delta.
\end{aligned}$$

Generally, let λ_1 and λ_2 be the roots of the quadratic equation

$$\lambda^2 + A\lambda + B. \tag{3.3}$$

It is well known that:
(a) When $B < 0$, λ_1 and λ_2 are both real and have opposite signs.
(b) When $B > 0$ and $A > 0$, both λ_1 and λ_2 have negative real parts.

Based on the above reasons, we see that our conditions for asymptotic stability of E_3 are that all the coefficients in both of the quadratics $Q_1(\lambda)$ and $Q_2(\lambda)$, namely A_1, A_2,B_1 and B_2, are positive. Here,

$$\begin{aligned}
A_1 &= -\alpha - m,\\
B_1 &= \mu(\xi + \beta),\\
A_2 &= 2\delta + m - \alpha,\\
B_2 &= \mu(\beta - \xi) + 2\delta(m - \alpha).
\end{aligned}$$

By the assumption $\mu < \frac{bK}{b+K} < \frac{r\mu}{2m}$, one can deduce that

$$A_1 = \frac{r\mu(b+K)}{bK} - 2m > 0,$$

$$B_1 = \frac{(Kb - K\mu - \mu b)r\mu}{Kb} > 0.$$

We will break the next two coefficients A_2 and B_2 into parts involving the two known positive coefficients A_1 and B_1. Noting that,

$$A_2 = 2\delta + m - \alpha = 2\delta + 2m + A_1.$$

Since $2\delta = \frac{2d(b-\mu)}{b-\mu+\mu b}$ is positive with $b > \mu$, which is ensured by $\frac{bK}{b+K} > \mu$, then we can conclude that $A_2 > 0$.

Lastly, we look into the condition for $B_2 > 0$. Noting that,

$$B_2 = \mu(\beta - \xi) + 2\delta(m - \alpha) = -2\mu\xi + B_1 + 2\delta(A_1 + 2m).$$

Since $-2\mu\xi = \frac{2bdr\mu(Kb-K\mu-b\mu)}{K(b-\mu+b\mu)^2} > 0$ as $\frac{bK}{b+K} > \mu$, with the facts that A_1 and B_1 are both positive we then conclude that $B_2 > 0$.

Therefore we have shown that if $\mu < \frac{bK}{b+K} < \frac{r\mu}{2m}$, then the component-wise positive equilibrium E_3 is asymptotically stable. □

4. Numerical Simulations and Discussions

In this section we will graphically display the dynamics and pattern of the predator and prey populations in the two-patch model by utilizing the conditions for stability and instability obtained in Section 3. The numerical simulations help us get an understanding of the long term behavior of the ecological system.

4.1. Stability Conditions for Equilibrium E_2.

Figure 1 shows the stability of the equilibrium E_2 when $\frac{bK}{b+K} < \mu$, which was derived in Theorem 3.2. By choosing the parameters to be $r = 0.65$, $K = 1.9$, $b = 0.75$, $m = 0.15$, $d = 0.15$, and $\mu = 0.65$, one can then see that the stability condition for E_2 is satisfied. In both patches, the prey populations converge to their carrying capacity of $K = 1.9$ and the predator populations go to extinction. In Corollary

1 we also deduced that $\frac{2bK}{b+2K} < \mu$ was a sufficient condition for global exponential stability of E_2. This is directly reflected below in the simulation with the values we have chosen. This shows that the death rate chosen for the predator is relatively large given the carrying capacity of the prey. While the total growth rate being dependent on the death rate and the functional response, it does not allow enough consumption of prey for the predator to survive. As we will see in Figure 2, a decrease on the death rate μ will lead to a different stability pattern.

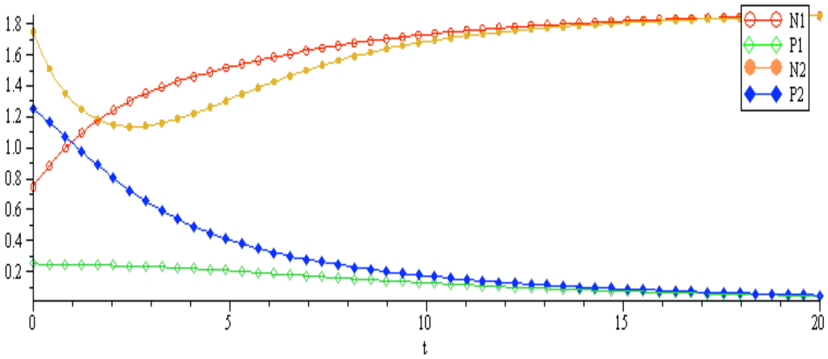

Figure 1. Stability of E_2

4.2. Stability Conditions for Equilibrium E_3.

Figure 2 shows the asymptotic stability of the coexistence equilibrium E_3, by decreasing the death rate of the predator μ in the previous simulation to satisfy the conditions given in Theorem 3.3. We choose the same parameters $r = 0.65, K = 1.9, b = 0.75, m = 0.15, d = 0.15$, as in 4.1, and reduce μ as 0.4, then the condition $\mu < \frac{bK}{b+K} < \frac{r\mu}{2m}$ will be satisfied. One can notice an initial increase of the predator population in Patch 2, due to the high number of prey in that patch. After large amount of consumption in Patch 2, the number of prey there declines sharply and also causes the predator population to decline. As the populations in both patches fluctuate over time, they tend to stabilize at the coexistence equilibrium $E_3 = \left(\frac{b\mu}{b-\mu}, \left(\frac{rb}{b-\mu}\right)\left(1 - \frac{b\mu}{K(b-\mu)}\right), \frac{b\mu}{b-\mu}, \left(\frac{rb}{b-\mu}\right)\left(1 - \frac{b\mu}{K(b-\mu)}\right)\right) = (.86, .76, .86, .76)$.

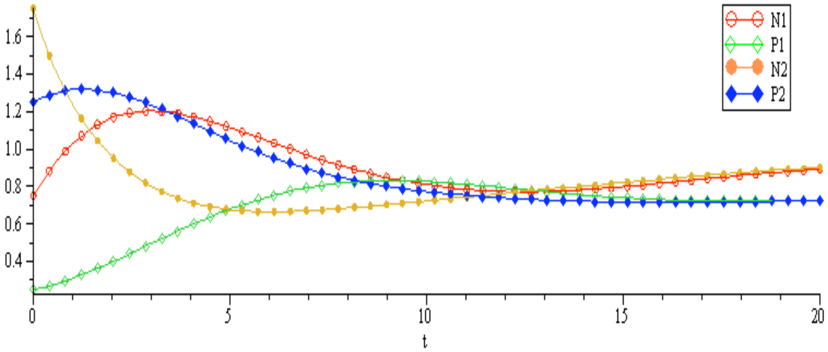

Figure 2. Stability of E_3

4.3. Instability and Oscillations When $r > 2m$.

One can observe that the stability condition given in Theorem 3.3 becomes impossible when $r > 2m$, with relatively larger intrinsic growth rate for the prey in each patch and smaller migration between the two patches. By choosing the parameters as $r = 0.7, K = 2.7, b = 0.75, m = 0.3, d = 0.5$, and $\mu = 0.4$, then the condition $\frac{bK}{b+K} > \frac{r\mu}{2m} > \mu$ holds. In this case, we cannot ensure stability of any equilibrium among the three. The pattern demonstrated in Figure 3 shows that the populations in both patches will continue to oscillate with increasing amplitudes. After a short period of time, the prey population in two patches will be fluctuating at same level, and so does the predator. The coexistence equilibrium E_3 is unstable, but the prey and predator species still have long-term persistence in both patches.

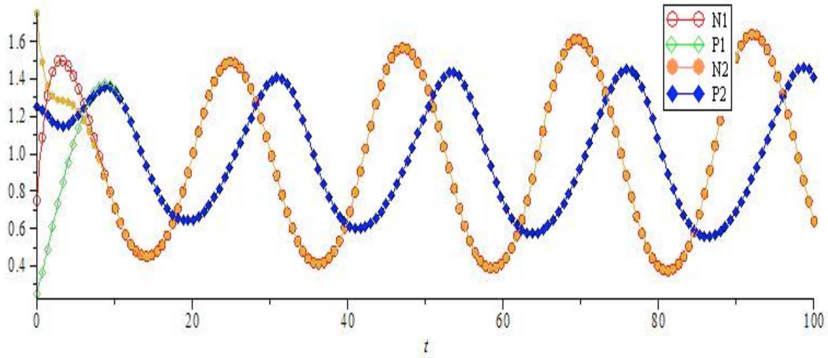

Figure 3. Instability, Periodic Behavior

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