Persistence of Predators in a Two Predators-One Prey Model with Non-Periodic Solution

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Abstract

A model of two competing predators sharing one prey in homogeneous environment with Holling type-II functional response is introduced. It is cast as a Kolmogorov-type system of differential equations. The stability of the equilibrium points of the system is studied and discussed. The conditions of coexistence and extinction of the predators in the case of non-periodic solution are obtained in terms of efficiency of predator conversion of prey biomass into predator offspring.

Keywords: Prey- predator model; Competition; Extinction; Coexistence

1 Introduction

Systems of differential equations have, to a certain extent, successfully described the interactions between species. The basic system is the Lotka-Volterra model, which model the interaction between a predator and a prey. There exists a huge literature documenting ecological and mathematical results from this model. In particular, various dynamical relations between predators and their prey in ecology and mathematical ecology have been studied [9]. Parameters involved in the Lotka-Volterra system include birth rate of prey, death rate of predator, encounter rate and biomass conversion rate. This in

turn gives the functional and numerical responses, when combined with the prey and predator population.

The systems of interactions involving more than two species have been proposed for certain ecological phenomena. Three species interactions show very complex dynamical behavior [7, 10, 14, 15, 17]. The interactions of species involving persistence and extinction have been studied by some researchers [1, 6, 8, 10]. In addition, the coexistence and extinction in three species systems have been studied. Most of these systems can be written as a Kolgomorov-type equation [2], where a certain number of conditions must be satisfied in order a number of dynamical properties to be true.

In this paper, a mathematical model of two competing predators sharing one prey is proposed and investigated. The motivation is to answer the question of persistence of the system and extinction of one the predators based on the efficient conversion of prey biomass. It is explained analytically and numerically in the case of non periodic solution.

2 Mathematical Model

The dynamical interactions of a three species food chain model is presented, where two predators competing on one prey. The growth rates of prey and two predators are described by logistic law which the carrying capacity of predators depend on available amount of prey. The Holling type-II functional response is used to describe feeding of the two predators y and z on prey x. The model can be written as:

$$\frac{dx}{dt} = rx(1 - \frac{x}{k}) - \frac{\alpha xy}{1 + h_1 \alpha x} - \frac{\beta xz}{1 + h_2 \beta x},$$

$$\frac{dy}{dt} = -uy + R_1 y \left(1 - \frac{y}{k_y}\right) - c_1 yz,$$

$$\frac{dz}{dt} = -wz + R_2 z \left(1 - \frac{z}{k_z}\right) - c_2 yz,$$
(1)

The initial conditions of system are:

$$x(0) = x_0, y(0) = y_0, z(0) = z_0$$

The intrinsic growth rate of prey is r; α and β measure efficiency of the searching and the capture of predators y, z respectively. h_1 and h_2 represents handling and digestion rates of predators. In the absence of prey x constants, u and w are the death rates of predators y, z respectively. $R_1 = \frac{\alpha x e_1}{1 + h_1 \alpha x}$, $R_2 = \frac{\beta x e_2}{1 + h_2 \beta z}$; R_1 and R_2 represent numerical responses of the predators y, z respectively, which describe change in the population of predators by prey consumption.

 e_1 and e_2 represent efficiency of converting consumed prey into predator births. The carrying capacities $k_y=a_1x$, $k_z=a_2x$ are proportional to the available amount of prey, as first proposed by Leslie [5]. c_1 and c_2 measure interspecific competition factors that are interference competition of the predator z on predator y and vice versa. All the parameters and initial conditions of the model are assumed positive values.

The model can be written in non-dimensional form to reduce the number of parameters. This makes the mathematical analysis less complicated. We write

By removing the bar from all parameters, then the system become

$$\frac{dx}{dt} = x (1 - x) - \frac{\alpha xy}{1 + h_1 \alpha x} - \frac{\beta xz}{1 + h_2 \beta x} = x L(x, y, z),$$

$$\frac{dy}{dt} = -uy + \frac{e_1 \alpha xy}{1 + h_1 \alpha x} - \frac{e_1 \alpha}{(1 + h_1 \alpha x)} y^2 - c_1 yz = y M_1(x, y, z) \qquad (2)$$

$$\frac{dz}{dt} = -wz + \frac{e_2 \beta xz}{1 + h_2 \beta x} - \frac{e_2 \beta}{(1 + h_2 \beta x)} z^2 - c_2 yz = z M_2(x, y, z),$$

The functions L, M_i ; i=1,2 are smooth continuous functions on $R_+^3=\{(x,y,z)\in R^3: x\geq 0,\ y\geq 0,\ z\geq 0\}.$

Equations (2) are of Kolgomorov type.

Theorem 2.1 The solution of the system in R^3_+ for $t \ge 0$ is bounded.

Proof. The first equation of the system that represents the prey equation is bounded through

$$\frac{dx}{dt} \le x(1-x) \tag{3}$$

The solution of the equation is $x(t) = \frac{1}{1+be^{-t}}$, $b = \frac{1}{x_0-1}$ is the constant of integration.

then $x(t) \leq 1 \ \forall t > 0$.

The solutions of y, z are bounded, since the boundedness follows the boundedness of x.

3 Kolmogorov analyses and equilibrium analysis

the Kolmogorov theorem contains many conditions; however it is applicable to a two-dimensional system only [2]. the system (2) is divided into two subsystems to use the Kolgomorov conditions.

The first subsystem is obtained by assuming the absence of second predator z.

$$\frac{dx}{dt} = x((1-x) - \frac{\alpha y}{1 + h_1 \alpha x}))$$

$$\frac{dy}{dt} = y(-u + \frac{e_1\alpha x}{1 + h_1\alpha x} - \frac{e_1\alpha}{(1 + h_1\alpha x)}y) \tag{4}$$

By applying the Kolmogorov theorem, we have the condition

$$0 < \frac{u}{e_1 \alpha - u h_1 \alpha} < 1 \tag{5}$$

The subsystem (4) has three non-negative equilibrium points. The equilibrium point $E_{40} = (0, 0)$ always exists and it is saddle point. The equilibrium point $E_{41} = (1, 0)$ always exists and it is locally asymptotically stable point with the following condition

$$u > \frac{e_1 \alpha}{1 + h_1 \alpha} \tag{6}$$

If the condition is violated then the equilibrium point E_{41} is a saddle point. The equilibrium point $E_{42}(\tilde{x}, \tilde{y})$ of subsystem is given where \tilde{x} is obtained through the positive root of the quadratic equation

$$\tilde{x}^2 + \left(\frac{1}{h_1} - \frac{u}{e_1} - 1 + \frac{1}{h_1 \alpha}\right) \tilde{x} - \left(\frac{1}{h_1 \alpha} + \frac{u}{e_1 h_1 \alpha}\right) = 0 \tag{7}$$

and

$$\tilde{y} = \frac{1}{\alpha} (1 - \tilde{x}) (1 + h_1 \alpha \tilde{x}) \tag{8}$$

The equilibrium point $E_{42}(\tilde{x}, \tilde{y})$ is locally asymptotically stable if it satisfies the following conditions:

$$\tilde{x} + \frac{e_1 \alpha \tilde{y}}{1 + h_1 \alpha \tilde{x}} > \frac{h_1 \alpha^2 \tilde{y} \tilde{x}}{(1 + h_1 \alpha \tilde{x})^2} \tag{9}$$

By assuming the absence of the first predator y, the second subsystem is obtained.

$$\frac{dx}{dt} = x((1-x) - \frac{\beta z}{1 + h_2 \beta x})$$

$$\frac{dz}{dt} = z(-w + \frac{e_2\beta x}{1 + h_2\beta x} - \frac{e_2\beta}{(1 + h_2\beta x)}z)$$
 (10)

Similarly, by applying the Kolmogorov theorem to the subsystem, we have

$$0 < \frac{w}{e_2\beta - wh_2\beta} < 1 \tag{11}$$

There are three non-negative equilibrium points of the subsystem (10). The equilibrium point $E_{100} = (0, 0)$ always exists and it is a saddle point. The equilibrium point $E_{101} = (1, 0)$ always exists and it is locally asymptotically stable with the following condition

$$w > \frac{e_2 \beta}{1 + h_2 \beta} \tag{12}$$

But, if the condition is violated then the equilibrium point E_{101} is a saddle point.

The equilibrium point $E_{102}(\hat{x}, \hat{z})$ of subsystem is given, where \hat{x} is specified by the positive root of the quadratic equation

$$\hat{x}^2 + \left(\frac{1}{h_2} - \frac{w}{e_2} - 1 + \frac{1}{h_2\beta}\right)\hat{x} - \left(\frac{1}{h_2\beta} + \frac{w}{e_2h_2\beta}\right) = 0$$
 (13)

and

$$\hat{z} = \frac{1}{\beta} (1 - \hat{x}) (1 + h_2 \beta \hat{x})$$
 (14)

The equilibrium point $E_{102}(\hat{x}, \hat{z})$ is locally asymptotically stable, provided the following condition holds:

$$\hat{x} + \frac{e_2 \beta \hat{z}}{1 + h_2 \beta \hat{x}} > \frac{h_2 \beta^2 \hat{z} \hat{x}}{(1 + h_2 \beta \hat{x})^2}$$
 (15)

4 Equilibrium Points and Stability Analysis of Three Dimension System

It is observed that the system (2) has five nonnegative equilibrium points. $E_0 = (0, 0, 0)$ and $E_1 = (1, 0, 0)$ exist obviously (i.e. they exist without conditions on parameters). On the coordinate axis y or z there are no equilibrium points. There are two equilibrium points for the two species, the equilibrium point $E_2 = (\tilde{x}, \tilde{y}, 0)$ where \tilde{x} and \tilde{y} are given according to equations (7) and (8). The equilibrium point E_2 exists in the interior of positive quadrant of x - y plane if condition (5) holds and

$$0 < \tilde{x} < 1 \tag{16}$$

The equilibrium point $E_3 = (\hat{x}, 0, \hat{z})$, where \hat{x} and \hat{z} are specified by the equations (13) and (14). The equilibrium point E_3 exists in the interior of positive quadrant of x - z plane if it holds condition (11) and

$$0 < \hat{x} < 1 \tag{17}$$

The local dynamical behavior of equilibrium points are investigated where the results are obtained by computing the variational matrices corresponding to each equilibrium point.

The equilibrium point E_0 is an unstable manifold along x-direction, but it is a stable manifold along y-direction and along z-direction because the eigenvalue of x-direction is positive, while the eigenvalues of y-direction and z-direction is negative; consequently the equilibrium point E_0 is saddle point. The equilibrium point $E_1 = (1, 0, 0)$ is locally asymptotically stable, if the conditions (6) and (12) hold. However, if one of the conditions or both (6) and (12) are not satisfied then the equilibrium point E_1 is a saddle point because it is stable in the x-direction (the eigenvalue of x-direction is negative in all cases).

The equilibrium point $E_2 = (\tilde{x}, \tilde{y}, 0)$ has the same stability behaviour of the equilibrium point $E_{42}(\tilde{x}, \tilde{y})$ of subsystem (4) inside x - y plane; in the z-direction (i.e. orthogonal direction to the x - y direction) is stable provided the following condition holds

$$w + c_2 \tilde{y} > \frac{e_2 \beta \tilde{x}}{1 + h_2 \beta \tilde{x}} \tag{18}$$

The equilibrium point $E_3 = (\hat{x}, 0, \hat{z})$ has the same stability of the equilibrium point $E_{102}(\hat{x}, \hat{z})$ of subsystem (10) in x - z, while in the y-direction (i.e. orthogonal direction to the x - z plane) is stable with following condition

$$u + c_1 \hat{z} > \frac{e_1 \alpha \hat{x}}{1 + h_1 \alpha \hat{x}} \tag{19}$$

For non-trivial equilibrium points $E_4 = (\overline{x}, \overline{y}, \overline{z})$, it is given through the positive solution of system of algebraic solution as follows:

$$(1-x) - \frac{\alpha y}{1 + h_1 \alpha x} - \frac{\beta z}{1 + h_2 \beta x} = 0$$

$$-u + \frac{e_1 \alpha x}{1 + h_1 \alpha x} - \frac{e_1 \alpha}{1 + h_1 \alpha x} y - c_1 z = 0$$

$$-w + \frac{e_2 \beta x}{1 + h_2 \beta x} - \frac{e_2 \beta}{(1 + h_2 \beta x)} z - c_2 y = 0$$
(20)

The variational matrix of E_4 is

$$= \begin{bmatrix} \overline{x} \left(-1 + \frac{h_1 \alpha^2 \overline{y}}{(1 + h_1 \alpha \overline{x})^2} + \frac{h_2 \beta^2 \overline{z}}{(1 + h_2 \beta \overline{x})^2}\right) & -\overline{x} \left(\frac{\alpha}{1 + h_1 \alpha \overline{x}}\right) & -\overline{x} \left(\frac{\beta}{1 + h_2 \beta \overline{x}}\right) \\ \overline{y} \left(\frac{e_1 \alpha + h_1 e_1 \alpha^2 \overline{y}}{(1 + h_1 \alpha \overline{x})^2}\right) & -\overline{y} \left(\frac{e_1 \alpha}{1 + h_1 \alpha \overline{x}}\right) & -c_1 \overline{y} \\ \overline{z} \left(\frac{e_2 \beta + e_2 h_2 \beta^2 \overline{z}}{(1 + h_2 \beta \overline{x})^2}\right) & -c_2 \overline{z} & -\overline{z} \left(\frac{e_2 \beta}{1 + h_2 \beta \overline{x}}\right) \end{bmatrix}$$

$$= \left[\begin{array}{ccc} h_{11} & h_{12} & h_{13} \\ h_{21} & h_{22} & h_{23} \\ h_{31} & h_{32} & h_{33} \end{array} \right]$$

where

$$h_{11} = \overline{x} \left(-1 + \frac{h_1 \alpha^2 \overline{y}}{(1 + h_1 \alpha \overline{x})^2} + \frac{h_2 \beta^2 \overline{z}}{(1 + h_2 \beta \overline{x})^2} \right), \ h_{12} = -\overline{x} \left(\frac{\alpha}{1 + h_1 \alpha \overline{x}} \right), \ h_{13} = -\overline{x} \left(\frac{\beta}{1 + h_2 \beta \overline{x}} \right)$$

$$h_{21} = \overline{y} \left(\frac{e_1 \alpha + h_1 e_1 \alpha^2 \overline{y}}{(1 + h_1 \alpha \overline{x})^2} \right), \ h_{22} = -\overline{y} \left(\frac{e_1 \alpha}{1 + h_1 \alpha \overline{x}} \right), \ h_{23} = -c_1 \overline{y}$$

$$h_{31} = \overline{z} \left(\frac{e_2 \beta + e_2 h_2 \beta^2 \overline{z}}{(1 + h_2 \beta \overline{x})^2} \right), \ h_{32} = -c_2 \overline{z}, \ h_{33} = -\overline{z} \left(\frac{e_2 \beta}{1 + h_2 \beta \overline{x}} \right),$$

The characteristic equation of the variational matrix D_4 is

$$\lambda^{3} + H_{1}\lambda^{2} + H_{2}\lambda + H_{3} = 0$$

$$H_1 = -(h_{11} + h_{22} + h_{33})$$

$$H_2 = (h_{11}h_{22} + h_{11}h_{33} + h_{22}h_{33} - h_{12}h_{21} - h_{13}h_{31} - h_{23}h_{32})$$

$$H_3 = (h_{13}h_{31}h_{22} + h_{12}h_{21}h_{33} + h_{11}h_{23}h_{32} - h_{12}h_{23}h_{31} - h_{13}h_{21}h_{32} - h_{11}h_{22}h_{33})$$

According to Routh-Hurwitz criterion, $E_4 = (\overline{x}, \overline{y}, \overline{z})$ is locally asymptotically stable if it holds the following conditions.

$$H_1 > 0 \tag{21}$$

$$H_3 > 0 \tag{22}$$

$$H_1H_2 > H_3 \tag{23}$$

We have thus proved the following theorem.

Theorem 4.1 (i) The equilibrium point $E_0 = (0, 0, 0)$ is a saddle point with locally stable manifold in the y-z plane and with locally unstable manifold in the x-direction.

(ii) The positive equilibrium point $E_1 = (1, 0, 0)$ is locally asymptotically stable in x-direction, but it is locally asymptotically stable in y-z plane if it holds the conditions (6) and (12). The equilibrium point E_1 is a saddle point if the

conditions (6) and/or (12) are not satisfied.

(iii) The equilibrium points $E_2 = (\tilde{x}, \tilde{y}, 0)$ and $E_3 = (\hat{x}, 0, \hat{z})$ are positive under the conditions (16) and (17) respectively. The equilibrium point E_2 is locally asymptotically stable provided the conditions (9) and (18) hold, while the equilibrium point E_3 is locally asymptotically stable provided the conditions (15) and (19) hold.

(iv) The non-trivial positive equilibrium point $E_4 = (\overline{x}, \overline{y}, \overline{z})$ is given through the positive solution of system (20); it is locally asymptotically stable provided the conditions (21), (22), and (23) hold.

Corollary. The equilibrium points E_2 and E_3 are unstable the in z-direction (i.e. orthogonal direction to the x-y plane) and in the y-direction (i.e. orthogonal direction to the x-z plane) respectively, if the condition (18) of E_2 and the condition (19) of E_3 are not satisfied.

5 Theoretical Approach of Persistence and Extinction

The analysis of persistence was carried by Freedman and Waltman [3] for equations of Kolgomorov type. The persistence is defined as follows: if x(0) > 0 and $\liminf_{t\to\infty} x(t) > 0$, x(t) persist. The system is said to persist if each component of the system persists. The analysis for non periodic solution (i.e. no limit cycles) is presented, where the system (2) has non periodic solution under conditions (9) and (15) of planar equilibriums in respective planes. The boundedness of the system (2) was proved (theorem 1). The stability in positive orthogonal directions of x-y plane, x-z plane are given by the conditions (17), (18) respectively.

(C1) x is a prey population and y,z are competing predators, living exclusively on the prey, i.e.

$$\frac{\partial L}{\partial y_i} < 0, \frac{\partial M_i}{\partial x} > 0, M_i(0, y, z) < 0, \frac{\partial M_i}{\partial y_j} \le 0 \quad i, j = 1, 2.$$

(C2) In the absence of predators, the prey species x grows to carrying capacity, i.e.

$$L\left(0,0,0\right)>0,\frac{\partial L}{\partial x}\left(x,\ y,\ z\right)=-1\leq0,$$

 $\exists k > 0 \ni J(k, 0, 0) = 0$. Here k = 1.

- (C3) There are no equilibrium points on the y or z coordinate axes and no equilibrium point in y-z plane.
- (C4) The predator y and the predator z can survive on the prey; this means that there exist points $\tilde{E}: (\tilde{x}, \ \tilde{y}, 0)$ and $\hat{E}: (\hat{x}, \ 0, \hat{z})$ such that $L(\tilde{x}, \ \tilde{y}, \ 0) = M_1(\tilde{x}, \ \tilde{y}, \ 0) = 0$ and $L(\hat{x}, \ 0, \hat{z}) = M_2(\hat{x}, \ 0, \hat{z}) = 0, \tilde{x}, \ \tilde{y}, \ \hat{x}, \hat{z} > 0$ and $\tilde{x} < k, \ \hat{x} < k$. If the above hypotheses hold, there is no limit cycles and if in addition

$$M_1(\hat{x}, 0, \hat{z}) > 0, M_2(\tilde{x}, \tilde{y}, 0) > 0$$
 (24)

then system (2) persists.

Inequalities (24) implies that

$$-u + \frac{e_1 \alpha \hat{x}}{1 + h_1 \alpha \hat{x}} - c_1 \hat{z} > 0$$

$$\Rightarrow e_1 > \frac{(u + c_1 \hat{z})(1 + h_1 \alpha \hat{x})}{\alpha \hat{x}}$$

$$-w + \frac{e_2 \beta \tilde{x}}{1 + h_2 \beta \tilde{x}} - c_2 \tilde{y} > 0$$

$$\Rightarrow e_2 > \frac{(w + c_2 \tilde{y})(1 + h_2 \beta \tilde{x})}{\beta \tilde{x}}$$
(25)

The necessary conditions for (24) include the following [4]

$$M_1(\hat{x}, 0, \hat{z}) \ge 0, M_2(\tilde{x}, \tilde{y}, 0) \ge 0$$
 (27)

If the conditions (25) and (26) are satisfied then the system (2) persists. In case the condition (25) is satisfied and on the other hand the condition (26) is not satisfied, then the second predator z will tend to extinct, while the first predator y survives. In the same manner, if the condition (26) is satisfied but the condition (25) is not satisfied, then the first predator y will tend to extinct while the second predator y survives.

6 Numerical simulations

By considering different values of the parameters e_1 and e_2 , it can be shown numerically the existence or extinction of one of the predators in a non-periodic solution (i.e. no limit cycles). The parameters e_1 and e_2 are important parameters because are contained in the functional and numerical responses that formed the main components of prey predator models [13]; in addition, they are involved in determining intraspecific competition coefficients in our model.

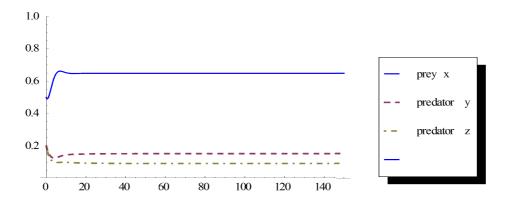


Figure 1: Time series of dynamical behaviour of the system (2) at $e_1 = 0.8$

The functional responses play an important role in interactions between prey and predator [12]. e_1 , e_2 measure the efficiency converting of predators.

The values of parameters are chosen to satisfy the stability conditions (9) and (15) in a non-periodic solution (i.e. no limit cycles). The other parameters are fixed as follows:

$$\alpha = 1.41, \beta = 1.5, u = 0.55, h_1 = 0.005, h_2 = 0.004, c_1 = 0.08, c_2 = 0.05, w = 0.65, x(0) = 0.5, y(0) = 0.2, z(0) = 0.2.$$

Two different sets of numerical simulations were executed. In the first set, the value of e_2 are fixed at 0.79, while e_1 is changed to show the effects of the efficiency of biomass conversion on existence and extinction of one the predators. It is observed that in Fig. 1.1 there is coexistence of three species when the values of e_1 ($e_1 = 0.8$), and e_2 are near to each other. However, if the value of e_1 ($e_1 = 1.8$)is increased, the predator z tends to extinct, as shown in figure 1.2. In another case, when the value of e_1 ($e_1 = 0.45$) is decreased, the predator y goes to extinction, as shown in figure 1.3. The results show the important role of efficiency of conversion on predators' survival.

In the second set, different values of e_2 are used while the value of e_1 are fixed at 0.68. There are corresponding results for survival and extinction of predators depending on efficiency of conversion; coexistence of three species when the values of e_1 , and e_2 ($e_2 = 0.72$) are near to each other, as shown in figure 2.1. On increasing the value of e_2 ($e_2 = 1.45$), the predator y tends to extinction, while on decreasing the value of e_2 ($e_2 = 0.45$), the predator z goes to extinction, as observed in figure 2.2, and figure 2.3 respectively.

The reasons that may affect the conversion efficiency are the metabolic conversion efficiency of predators, in addition to proportion of the kill preys which may be consumed by predators [11]. Other reason that may affect the conversion efficiency is body size of prey [18]. More ideas from biology are needed to properly model biomass conversion.

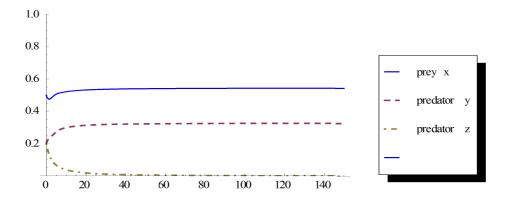


Figure 2: Time series of dynamical behaviour of the system (2) at $e_1=1.8$

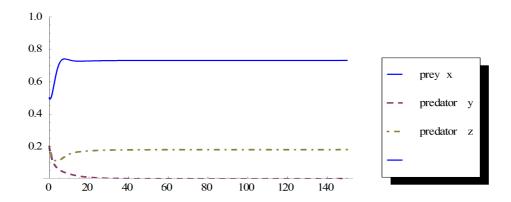


Figure 3: Time series of dynamical behaviour of the system (2) at $e_1 = 0.45$

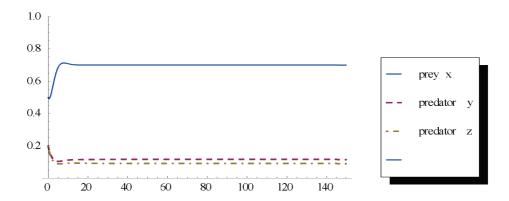


Figure 4: Time series of dynamical behaviour of the system (2) at $e_2=0.72$

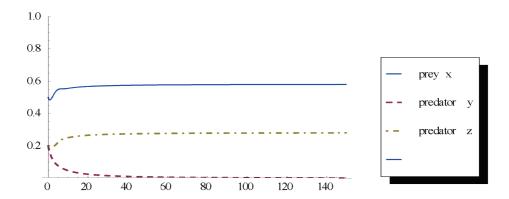


Figure 5: Time series of dynamical behaviour of the system (2) at $e_2=1.45$

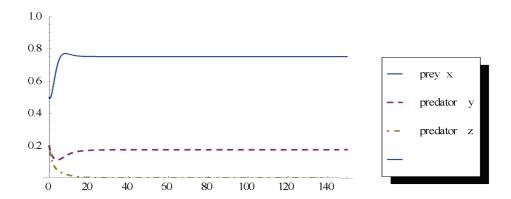


Figure 6: Time series of dynamical behaviour of the system (2) at $e_2=0.45$

7 Conclusions

In this paper, a mathematical model of continuous time of interactions two competing predators sharing one prey is introduced. The model is divided into two subsystems, consequently Kolmogorov conditions of the subsystems were found and the stability of equilibrium points of the two subsystems was discussed. The conditions of existence of equilibrium points and their stability of equilibrium points of the three dimension system (2) were obtained. Theoretical analysis of persistence the system and extinction one of predators was presented.

Numerical simulations have illustrated that the three species can coexist, when the values of efficiency conversion for the two predators are near to each other. However, the extinction of one predator depend on the value of efficiency conversion in the two predators, where if the value efficiency conversion of first predator is less than the other then the first predator go to extinction, while the other survive and vice versa.

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