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Efficient Biomass Conversion and its Effect on the Existence of Predators in a Predator-Prey System

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Abstract: Understanding the dynamics of predator-prey species can lead us to insights in the species interactions. In this study, a Mathematical Model of two predators sharing a prey in a homogeneous environment is introduced where different functional responses are used to describe rates of consumption of the prey. The model represents a Kolmogorov Type Prey Predator System. The equilibrium points of the system are obtained and their stability is discussed. The conditions of coexistence and extinction for the predators are obtained for a non-periodic solution and this depends on the conversion efficiency of prey biomass into predator offspring.

Key words: Predator-Prey Model, efficiency conversion, Kolmogorov, coexistence, biomass

INTRODUCTION

The basic Prey Predator Model describes an interaction of two species by a system of non-linear coupled first order ordinary differential equations and has been studied extensively. Interactions involving more than two species have been proposed for certain ecological phenomena. These interactions can show complex dynamical behaviours (Hsu et al., 2001, 2003; Lv and Zhao, 2008; Upadhyay and Naji, 2009; Upadhyay and Chattopadhyay, 2005; Upadhyay et al., 2007; Naji and Balasim, 2007; Mougi, 2010; Kuang and Beretta, 1998).

Research which involve coexistence and extinction of the interacting species has been investigated by some researchers (Dubey and Upadhyay, 2004; Huo et al., 2009; Kar and Batabyal, 2010). The coexistence and extinction in three species systems have been studied in particular, a two predator one prey model of Kolgomorov type was studied by Freedman and Waltman (1984) and he proposed a number of conditions to be satisfied in order for the system to coexist.

In this study, a Mathematical Model of interactions two predators competing on one prey is introduced different functional responses; Holling type I and II functional responses are used. The coexistence and extinction of species are studied theoretically to answer the question of coexistence of the system and extinction of one of the predators in two and three dimension models and how they depend on the efficiency of biomass conversion is introduced as research problem in this study. Researchers use the numerical simulations to explain the coexistence and extinction in the case of non-periodic solution.

THE MODEL

A system of autonomous differential equations is used to describe the dynamical interactions of a three Species Food Chain Model in which two predators compete on a prey. The logistic law describes the growth rates of the prey and both predators with the carrying capacity of predators depending on available amount of prey. It was indicated in case two species (prey predator model) through some researchers as May and recently through Murray but we add the term (-uy) which have been used in many Prey Predator Models to be more realistic. Researchers have used this model in case two predators one prey model to study some dynamical behaviours with similar functional responses have been used to describe the consumption rate of prey by a predator in study (Alebraheem and Abu-Hasan, 2011, 2012). However, in this study, different functional responses are used to describe the rates of consumption of the prey x by the predators y, z, the Holling type I and the Holling type II for the predators y, z, respectively. The system can be written as follows:

$$\begin{split} \frac{dx}{dt} &= rx \left(1 - \frac{x}{k} \right) - \alpha xy - \frac{\beta xz}{1 + h_1 \beta x} \\ \frac{dy}{dt} &= -uy + R_1 y \left(1 - \frac{y}{k_y} \right) - c_1 yz \\ \frac{dz}{dt} &= -wz + R_2 z \left(1 - \frac{z}{k_z} \right) - c_2 yz \end{split} \tag{1}$$

All the parameters and initial conditions of the model are assumed positive. Here, r is the intrinsic growth rate of

prey; α and β measure efficiency the searching and the capture by predators y, z, respectively h, signifies handling and digestion rate of predator z. In the absence of the prey x, constants u and w are the death rates of predators y, z respectively. $R_1 = e_1 \alpha x$, $R_2 = e_2 \beta x/1 + h_1 \beta x$ represent the numerical responses of the predators y and z, respectively which describe the change in the population of predators due to prey consumption. Further, e₁ and e₂ indicate the efficiency of conversion of consumed prey into predator births. The carrying capacities $k_y = \alpha_1 x$, $k_z = \alpha_2 z$ are proportional to the available amount of prey as proposed by Leslie (Gazi and Bandyopadhyay, 2008). Lastly, c₁ and c₂ measure the interspecific competition between predators that is the interference competition of the predator z on predator y and vice versa.

Researchers rewrite the system of Eq. 1 in a non-dimensional form to reduce the number of parameters from 13-9 which make the analysis less complicated. Researchers use the following transformations:

$$\begin{split} &\overline{t}=rt,\,\overline{x}=\frac{x}{k},\,\overline{y}=\frac{y}{\alpha_1k},\,\,\overline{z}=\frac{z}{\alpha_2k},\,\overline{\alpha}=\frac{k\alpha_1\alpha}{r},\,\overline{\beta}=\frac{k\alpha_2\beta}{r},\,\overline{e}_1=\frac{e_1}{\alpha_1}\\ &\overline{e}_2=\frac{e_2}{\alpha_2},\,\overline{u}=\frac{u}{r},\,\,\overline{w}=\frac{w}{r},\,\,\overline{h}_1=\frac{rh_1}{\alpha_2},\,\,\overline{c}_1=\frac{\alpha_2kc_1}{r},\,\,\overline{c}_2=\frac{\alpha_1kc_2}{r} \end{split}$$

Researchers then have:

$$\begin{split} \frac{dx}{dt} &= x(1-x) - \alpha xy - \frac{\beta xz}{1+h_1\beta x} = xL(x,y,z) \\ \frac{dy}{dt} &= -uy + e_1\alpha xy - e_1\alpha y^2 - c_1yz = S_1(x,y,z) \\ \frac{dz}{dt} &= -wz + e_2\beta xz - e_2\beta z^2 - c_2yz = S_2(x,y,z) \end{split} \tag{2}$$

The initial conditions of system (2) are:

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

Where:

$$0 < x_0, y_0, z_0 \le 1$$

The functions, L, S_i; i =1, 2 are smooth continuous functions on $R_+^3 = \{x, y, z\} \in R^3$:

Boundedness:

Theorem 1: The solution of the system (2) for $t \ge 0$ in R_{+}^{3} is bounded.

Proof: The first equation of the system (2) that represents the prey equation is bounded through:

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

The solution of the Eq. 3 is $x(t) \le 1/1 + be^{-t}$, where $b = 1-x_0/x_0 = (1/x_0)-1>0$ is the constant of integration. Hence:

$$x(t) \le 1, \forall t \ge 0$$

Next, reserachers prove that:

$$x(t) + y(t) + z(t) \le L, \forall t \ge 0$$

Researchers define the function:

$$P(t) = x(t) + y(t) + z(t)$$

Taking the time derivative of the function P, researchers have:

$$\begin{split} \frac{dP}{dt} &= \frac{dx}{dt} + \frac{dy}{dt} + \frac{dz}{dt} \\ &= \left((1\text{-}x) - \alpha y - \frac{\beta z}{1 + h_1 \beta x} \right) x + (\text{-}u + e_1 \alpha x - e_1 \alpha y - c_1 z) y + \\ &\left(-w + \frac{e_2 \beta x}{1 + h_1 \beta x} - \frac{e_2 \beta z}{1 + h_1 \beta x} - c_2 y \right) z \end{split} \tag{4}$$

Since, the solutions initiating in remain R_{+}^{3} in nonnegative quadrant and all the parameters are positive, researchers can assume the following:

$$\begin{split} \frac{dP}{dt} &\leq (1\text{-}x)x + (-u\text{+}e_1\alpha x\text{-}e_1\alpha y)y + \\ &\left(-w\text{+}\frac{e_2\beta x}{1\text{+}h_1\beta x} - \frac{e_2\beta z}{1\text{+}h_1\beta x}\right)z \end{split} \tag{5}$$

However:

$$\max_{R_{+}} \{x(1-x)\} = \frac{1}{4}$$
 (6)

So, by substituting, Eq. 5 becomes as follows:

$$\begin{split} \frac{dP}{dt} &\leq \frac{1}{4} + (-u + e_1 \alpha x - e_1 \alpha y)y + \\ &\left(-w + \frac{e_2 \beta x}{1 + h_1 \beta x} - \frac{e_2 \beta z}{1 + h_1 \beta x} \right) z \end{split} \tag{7}$$

Rewrite this as:

$$\begin{split} \frac{dP}{dt} &\leq \frac{1}{4} + (-u + e_1 \alpha x - e_1 \alpha y)y + \\ &\left(-w + \frac{e_2 \beta x}{1 + h_1 \beta x} - \frac{e_2 \beta z}{1 + h_1 \beta x} \right) z + P(t) - P(t) \end{split} \tag{8}$$

That is:

$$\frac{dP}{dt} + P(t) \le \frac{1}{4} + x + (-u + e_1 \alpha x - e_1 \alpha y + 1)y +$$

$$\left(-w + \frac{e_2 \beta x}{1 + h_1 \beta x} - \frac{e_2 \beta z}{1 + h_1 \beta x} + 1 \right)z$$

$$(9)$$

Since, $x(t) \le 1$, researchers have:

$$\begin{split} \frac{dP}{dt} + P(t) &\leq \frac{5}{4} + (-u + e_1 \alpha x - e_1 \alpha y + 1)y + \\ &\left(-w + \frac{e_2 \beta x}{1 + h_1 \beta x} - \frac{e_2 \beta z}{1 + h_1 \beta x} + 1 \right) z \end{split} \tag{10}$$

But:

$$max_{R_{+}}\{(-u+e_{1}\alpha-e_{1}\alpha y+1)y\}=\frac{(1+e_{1}\alpha-u)^{2}}{4e_{1}\alpha}\quad \ (11)$$

And:

$$\begin{split} & \max_{R_{+}} \left\{ \left(-w + \frac{e_{2}\beta x}{1 + h_{1}\beta x} - \frac{e_{2}\beta z}{1 + h_{1}\beta x} + 1 \right) z \right\} \\ & = \frac{(e_{2}\beta + (-1 + h_{1}\beta)(-1 + w)) + (e_{2}\beta - (1 + h_{1}\beta)(-1 + w))}{4e_{2}\beta} \end{split}$$

$$(12)$$

Nonnegative values are taken in Eq. 11 and 12. Hence, Eq. 10 becomes:

$$\frac{\mathrm{dP}}{\mathrm{dt}} + \mathrm{P}(\mathrm{t}) \le \mathrm{Q} \tag{13}$$

Where:

$$Q = \frac{1}{4} \left(5 + \frac{(1 + e_1 \alpha - u)^2}{4e_1 \alpha} + \frac{(e_2 \beta + (-1 + h_1 \beta)(-1 + w)) + (e_2 \beta - (1 + h_1 \beta)(-1 + w))}{e_2 \beta} \right)$$
(14)

Thus, $P(t) \le Q + \gamma e^{-t}$, γ is a constant of integration. As $t \to \infty$ researchers have $P(t) \le Q$.

CONVERSION EFFICIENCY

In this study, researchers present some ecological reasons to support the research problem in this research. The time varying flows of biomass and energy in a species can be examined through the construction of a dynamic mass-energy budget specific to the species but such a budget depends on efficiencies of metabolic conversion which are unknown. These efficiencies of conversion determine the overall yields when food or storage tissue is converted into body tissue or into metabolic energy (Pastor, 2008).

There are some ecological reasons that affect the conversion efficiency in prey predator systems. This includes the proportion of the kill preys which are consumed by predators. Environmental variations, considered the exogenous mechanisms, affect indirectly on the predator attack rate or the conversion efficiency. The prey is also influenced through co-vary with the environmental variation (Brassil, 2006).

ANALYSES OF TWO DIMENSION SYSTEMS

The system of Eq. 2 is in a form similar to a Kolmogorov type model which is a more general framework to model the dynamics of ecological systems with predator-prey interactions, competition, disease and mutualism. Results based on the Kolmogorov Model are applicable to two-dimensional systems only (Freedman, 1980). Researchers divide the system (2) into two subsystems. The Kolmogorov analysis is useful to obtain some scenarios of extinction of the predators in these subsystems and some results will be used in the study.

The first subsystem: By assuming the absence of the second predator z, the first subsystem is as follows:

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

$$\frac{dy}{dt} = -y(u+e_1\alpha x-e_1\alpha y)$$
(15)

By applying the Kolmogorov theorem, researchers have the following conditions:

$$e_1 > \frac{u}{\alpha}$$
 (16)

If this condition is satisfied then the predator y coexist with the prey x. However, if:

$$\mathbf{e}_{1} \le \frac{\mathbf{u}}{\alpha} \tag{17}$$

then the predator y will go to extinct.

Example 1: If the values, u = 0.47, $\alpha = 1.3$, $e_1 = 0.35$ are taken where the value of $e_1 = 0.35$ is less than the value of $u/\alpha = 0.361538$ the condition (17) is satisfied therefore, the predator y will be extinct as it is shown in Fig. 1.

However, if $e_1 = 0.5$ with the values of u and α fixed as before where the value of $e_1 = 0.5$ is bigger than the value of $u/\alpha = 0.361538$ the condition (16) is satisfied and the predator y will coexist with the prey x.

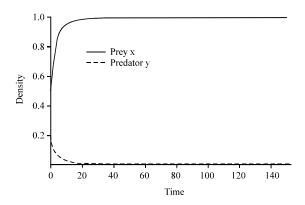


Fig. 1: Time series of dynamical behaviour of the subsystem (21) at w = 0.52, $h_1 = 0.04$, $\beta = 1.65$, $e_2 = 0.28$

The subsystem (15) has three non-negative equilibrium points. The equilibrium point $E_{150} = (0, 0)$ always exists and it is a saddle point. The equilibrium point $E_{151} = (1, 0)$ always exists and it is a locally asymptotically stable point with the following condition:

$$u > e_{,}\alpha$$
 (18)

If the condition (18) is violated then the equilibrium point $E_{\scriptscriptstyle{151}}$ is a saddle point. The equilibrium point:

$$E_{152} = (\tilde{x}, \tilde{y}) = \left(\frac{u + e_1}{e_1 \alpha + e_1}, \frac{e_1 \alpha - u}{e_1 \alpha^2 + e_1 \alpha}\right)$$

of subsystem (15) is positive if the following condition holds:

$$e_i \alpha > u$$
 (19)

The equilibrium $E_{152}(\tilde{x},\tilde{y})$ point is locally asymptotically stable if the following condition is satisfied:

$$e_1^2 \alpha + u + e_1 > u e_1$$
 (20)

However, it is observed that this condition is always satisfied since researchers have $e_1\alpha>u$ for a positive equilibrium point and it is derived from Kolmogorov condition. Hence, the equilibrium point $E_{132}(\tilde{x},\tilde{y})$ is always locally asymptotically stable it is not only locally stable but globally asymptotically stable. The following theorem proves this assertion.

Theorem 2: The equilibrium point $E_{152}(\tilde{x},\tilde{y})$ is globally asymptotically stable inside the positive quadrant of x-y plane.

Proof: Let G (x,y) = 1/xy G is a Dulac function it is continuously differentiable in the positive quadrant of x-y plane, $A = \{(x, y) | x>0, y>0\}$.

Let:

$$\begin{aligned} N_1(x,y) &= x(1\text{-}x)\text{-}\alpha xy, \\ N_2(x,y) &= -uy\text{+}e_1\alpha xy\text{-}e_1\alpha y^2 \end{aligned}$$

Thus:

$$\Delta(GN_1,GN_2) = \frac{\partial(GN_1)}{\partial x} + \frac{\partial(GN_2)}{\partial y} = \frac{-1}{y} - \frac{e_i\alpha}{x}$$

It is observed that Δ (GN₁, GN₂) is not identically zero and does not change sign in the positive quadrant of x-y plane A. So, by Bendixson-Dulac criterion there is no periodic solution inside the positive quadrant of x-y plane. The E₂ is globally asymptotically stable inside the x-y positive quadrant of plane.

The second subsystem: By assuming the absence of the first predator y, the second subsystem is as follows:

$$\frac{dx}{dt} = x \left((1-x) - \frac{\beta z}{1+h_1 \beta x} \right)$$

$$\frac{dz}{dt} = z \left(-w + \frac{e_2 \beta x}{1+h_1 \beta x} - \frac{e_2 \beta z}{1+h_1 \beta x} \right)$$
(21)

Similarly, by applying the Kolmogorov theorem to the subsystem (21), the following conditions are obtained:

$$e_2 > \frac{wh_1\beta + w}{\beta} \tag{22}$$

If this condition is satisfied then the predator z coexist with the prey x:

$$e_2 \le \frac{wh_1\beta + w}{\beta} \tag{23}$$

However, if then the predator z will go to extinct.

Example 2: The values w = 0.52, $h_1 = 0.04$, $\beta = 1.65$, $e_2 = 0.28$ are assumed where the value of $e_2 = 0.28$ is less than the value of:

$$\frac{wh_1\beta+w}{\beta}=0.317232$$

The condition (23) is satisfied; consequently the predator z will be extinct.

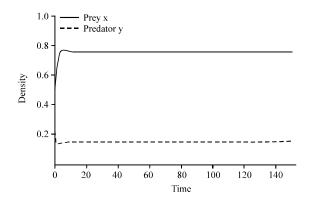


Fig. 2: Time series of dynamical behaviour of the subsystem (21) at w = 0.52, $h_1 = 0.04$, $\beta = 1.65$, $e_2 = 0.55$

However, if the value of e_2 is changed to become 0.55 with the same fixed values of w, h_1 and β where the value of e_2 = 0.55 is bigger than the value of wh₁ β +w/ β = 0.317232, the condition (22) is satisfied and the predator z will coexist with the prey.

There are three non-negative equilibrium points of the subsystem (21). The equilibrium point $E_{210} = (0, 0)$ always exists and it is a saddle point. The equilibrium point $E_{211} = (1, 0)$ always exists and it is a locally asymptotically stable point with the following condition (Fig. 1 and 2):

$$w > \frac{e_2 \beta}{1 + h_1 \beta} \tag{24}$$

If the condition (24) is violated then the equilibrium point E_{211} is a saddle point. The equilibrium point $E_{212}(\hat{x},\hat{z})$ of subsystem (21) is obtained which \hat{x} is specified by the positive root of the quadratic equation:

$$\hat{x}^2 + \left(\frac{1}{h_1} - \frac{w}{e_2} - 1 + \frac{1}{h_1 \beta}\right) \hat{x} - \left(\frac{1}{h_1 \beta} + \frac{w}{e_2 h_1 \beta}\right) = 0$$
 (25)

And:

$$\hat{z} = \frac{1}{\beta} (1 - \hat{x})(1 + h_1 \beta \hat{x})$$
 (26)

The equilibrium point $E_{212}(\hat{x},\hat{z})$ is locally asymptotically stable provided the following conditions hold:

$$\hat{\mathbf{x}} + \frac{\mathbf{e}_2 \beta \hat{\mathbf{z}}}{1 + \mathbf{h}_1 \beta \hat{\mathbf{x}}} > \frac{\mathbf{h}_1 \beta^2 \hat{\mathbf{x}} \hat{\mathbf{z}}}{(1 + \mathbf{h}_1 \beta \hat{\mathbf{x}})^2}$$
 (27)

Theorem 3: The coexistence equilibrium points of subsystems (15) and (21) are locally asymptotically stable under the condition (20) of the first subsystem and the condition (27) of the second subsystem.

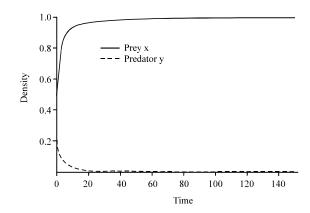


Fig. 3: Time series of dynamical behaviour of the subsystem (15) at u = 0.47, $\alpha = 1.3$, $e_1 = 0.35$

Proof: The theorem can be proved by applying Routh-Hurwitz criteria of characteristic equations that are obtained through the variational matrices.

STABILITY ANALYSIS OF THREE DIMENSION SYSTEM

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). However, on the coordinate axis y or z, there are no equilibrium points. There are two equilibrium points for two species, the first being the equilibrium point:

$$E_2 = (\tilde{\mathbf{x}}, \, \tilde{\mathbf{y}}, \, 0) = \left(\frac{\mathbf{u} + \mathbf{e}_1}{\mathbf{e}_1 \alpha + \mathbf{e}_1}, \frac{\mathbf{e}_1 \alpha - \mathbf{u}}{\mathbf{e}_1 \alpha^2 + \mathbf{e}_1 \alpha}, 0\right)$$

The equilibrium point E_2 exists in the interior of positive quadrant of x-y plane if it satisfies the Kolmorogov condition and the condition (Eq. 19).

At the equilibrium point $E_3(\hat{x},0,\hat{z})$, \hat{x} and \hat{z} are specified by Eq. 25 and 26. The equilibrium point E_3 exists in the interior of positive quadrant of x-y plane if it satisfies the Kolmorogov condition and:

$$0 < \hat{\mathbf{x}} < 1 \tag{28}$$

By computing the variational matrices corresponding to each equilibrium point, the local dynamical behaviour of equilibrium points are investigated.

Figure 3 and 4 the equilibrium point $E_0 = (0,\,0,\,0)$ is an unstable manifold along the x-direction but a stable manifold along y-direction and along z-direction because the eigenvalue in the x-direction is positive while the eigenvalues in the y-direction and z-direction are negative; consequently the equilibrium point E_0 is a saddle point.

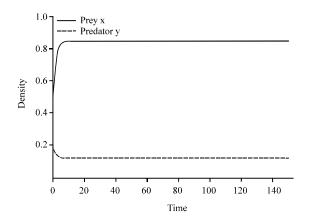


Fig. 4: Time series of dynamical behaviour of the subsystem (15) at u = 0.47, $\alpha = 1.3$, $e_1 = 0.5$

The equilibrium point $E_0 = (1, 0, 0)$ is locally asymptotically stable, provided the conditions (18) and (24) are satisfied. However, if the conditions (18) and/or (24) are not satisfied then the equilibrium point E_1 is a saddle point because it is stable in the x-direction because the eigenvalue in x-direction is negative for all cases.

The equilibrium point $E_2 = (\tilde{x}, \tilde{y}, 0)$ has the same stability behavior as the equilibrium point $E_{152}(\tilde{x}, \tilde{y})$ of subsystem (15) on the x-y plane but in the z-direction (i.e., orthogonal direction to the x-y direction) of equilibrium point E_2 it is stable provided the following condition holds:

$$w + c_2 \tilde{y} > \frac{e_2 \beta \tilde{x}}{1 + h_1 \beta \tilde{x}}$$
 (29)

The equilibrium point $E_3 = (\hat{x}, 0, \hat{z})$ is stable in the x-z plane if the condition (27) is satisfied while in the y direction (i.e., orthogonal direction to the x-z plane) of equilibrium point E_3 is stable with condition:

$$\mathbf{u} + \mathbf{c}, \hat{\mathbf{z}} > \mathbf{e}, \alpha \hat{\mathbf{x}} \tag{30}$$

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

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

$$-u + e_1\alpha x - e_1\alpha y - c_1 z = 0$$

$$-w + \frac{e_2\beta x}{1+h_1\beta x} - \frac{e_2\beta}{1+h_1\beta x} z - c_2 y = 0$$
(31)

The variational matrix of E4 is:

$$\begin{split} D_4 = & \begin{pmatrix} \overline{x} \bigg(-1 + \frac{h_i \beta^2 \overline{z}}{(1 + h_i \beta \overline{x})^2} \bigg) & -\alpha \overline{x} & -\overline{x} \bigg(\frac{\beta}{1 + h_i \beta \overline{x}} \bigg) \\ & e_i \alpha \overline{y} & -e_i \alpha \overline{y} & -c_i \overline{y} \\ & \bigg(\frac{e_2 \beta + e_2 h_i \beta^2 \overline{z}}{(1 + h_i \beta \overline{x})^2} \bigg) \overline{z} & -c_2 \overline{z} & -\overline{z} \bigg(\frac{e_2 \beta}{1 + h_i \beta \overline{x}} \bigg) \bigg) \\ = & \begin{pmatrix} h_{11} & h_{12} & h_{13} \\ h_{21} & h_{22} & h_{23} \\ h_{31} & h_{32} & h_{33} \end{pmatrix} \end{split}$$

Where:

$$\begin{split} h_{11} &= \overline{x} \Bigg(-1 + \frac{h_1 \beta^2 \overline{z}}{(1 + h_1 \beta \overline{x})^2} \Bigg), \, h_{12} = -\alpha \overline{x}, \, h_{13} = -\overline{x} \Bigg(\frac{\beta}{1 + h_1 \beta \overline{x}} \Bigg), \\ h_{21} &= e_1 \alpha \overline{y}, h_{22} = -e_1 \alpha \overline{y}, \, h_{23} = -e_1 \overline{y}, \, h_{31} = \Bigg(\frac{e_2 \beta + e_2 h_1 \beta^2 \overline{z}}{(1 + h_1 \beta \overline{x})^2} \Bigg) \overline{z}, \\ h_{32} &= -e_2 \overline{z}, h_{33} = -\overline{z} \Bigg(\frac{e_2 \beta}{1 + h_1 \beta \overline{x}} \Bigg) \end{split}$$

The characteristic equation of the variational matrix is:

$$\begin{split} \lambda^3 + H_1 \lambda^2 + H_2 \lambda + H_3 &= 0 \\ H_1 &= -(h_{11} + h_{22} + h_{33}) \\ H_2 &= (h_{11} h_{22} + h_{22} h_{33} + h_{11} h_{33} + h_{22} h_{33} - \\ &\quad h_{12} h_{21} - h_{13} h_{31} - h_{32} h_{23}) \\ H_3 &= (h_{13} h_{31} h_{22} + h_{12} h_{21} h_{33} + h_{11} h_{23} h_{32} - \\ &\quad h_{11} h_{22} h_{33} - h_{21} h_{32} h_{13} - h_{12} h_{23} h_{31}) \end{split}$$

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

$$H_1 > 0 \tag{32}$$

$$H_3 > 0 \tag{33}$$

$$H_1H_2 > H_3$$
 (34)

Researchers suppose the following theorem which is proved through the earlier analysis.

Theorem 4:

- The equilibrium point E₀ = (0, 0, 0) is a saddle point with locally stable manifold in the y-z plane and with unstable manifold in the x direction
- The positive equilibrium point E₁ = (1, 0, 0) is locally asymptotically stable in the x-direction but it is locally asymptotically stable in x-z plane if it holds the conditions (18) and (24). The equilibrium point is a saddle point if the conditions (18) and/or (24) are not satisfied

- The equilibrium E₂ = (x̂,0,2̂) point is positive under condition (19) it is locally asymptotically stable if the condition (20) holds
- The equilibrium point E₃ = (x̂, 0, 2̂) is positive under condition (28). The equilibrium point E₃ is locally asymptotically stable provided the conditions (27) and (30) hold
- The non-trivial positive equilibrium point E₄ = (x̄, ȳ, z̄) is given through the positive solution of system (32) it is locally asymptotically stable provided the conditions (32), (33) and (34) hold

Corollary: The equilibrium points E_2 and E_3 are unstable in z-direction (i.e., orthogonal direction to the x-y plane) and in y-direction (i.e., orthogonal direction to the x-z plane), respectively if the condition (29) of E_2 and the condition (30) of E_3 are not satisfied (violated).

COEXISTENCE AND EXTINCTION

The coexistence problem was studied by Freedman and Waltman for equations of Kolgomorov type. For a population x(t), the coexistence is defined as follows: if x(0)>0 and $\lim\inf_{t\to\infty}x(t)>0$, x(t) persists. The analysis for non periodic solution (i.e., no limit cycles) is presented where the system (2) has non periodic solution under conditions (20) and (27) of planar equilibriums in the respective planes. The boundedness of the system (2) is proved (Theorem 1). The stability in positive orthogonal directions of x-y, x-z planes are given by the conditions (30) and (31), respectively.

Researchers apply the following hypothesis of Freedman and Waltman (1984) to ensure they are satisfied. Researchers use $y_1 = y$ and $y_2 = z$ to simplify the notations.

H1: x is a prey population and y, z are competing predators living exclusively on the prey, i.e.:

$$\frac{\partial L}{\partial y_i} < 0, \frac{\partial S_i}{\partial x} > 0, S_i(0, y_1, y_2) < 0, \frac{\partial S_i}{\partial y_j} \le 0, \quad i, j = 1, 2$$

H2: In the absence of predators, the prey species x grows to carrying capacity, i.e.:

$$L(0, 0, 0) > 0, \frac{\partial L}{\partial x}(x, y_1, y_2) = -1 \le 0$$

 $\exists k > 0 \ni L(k, 0, 0) = 0$

Here k = 1.

H3: There are no equilibrium points on the y or z coordinate axes and no equilibrium point in plane.

H4: The predator y and the predator z can survive on the prey; this means that there exist points $E_2: (\tilde{x}, \tilde{y}, 0)$ and $E_3 = (\hat{x}, 0, \hat{z})$ such that:

$$L(\tilde{x}, \tilde{y}, 0) = S_1(\tilde{x}, \tilde{y}, 0) = 0$$

And:

$$L(\hat{x}, 0, \hat{z}) = S_2(\hat{x}, 0, \hat{z}) = 0, \tilde{x}, \tilde{y}, \hat{x}, \tilde{z} > 0$$

And:

$$\tilde{x} < k, \hat{x} < k$$

If the above hypotheses hold, if there is no limit cycles and if:

$$S_1(\hat{x}, 0, \hat{z}) > 0, S_2(\tilde{x}, \tilde{y}, 0) > 0$$
 (35)

then system (2) coexists. Inequalities (35) implies that:

$$-u+e_{1}\alpha\hat{x}-c_{1}\hat{z} > 0$$

$$\Rightarrow e_{1} > \frac{u+c_{1}\hat{z}}{\alpha\hat{x}}$$
(36)

$$-w + \frac{e_2 \beta \tilde{x}}{1 + h_1 \beta \tilde{x}} - c_2 \tilde{y} = 0$$

$$\Rightarrow e_2 > \frac{(w + c_2 \tilde{y})(1 + h_1 \beta \tilde{x})}{\beta \tilde{x}}$$
(37)

The system (2) coexists if the conditions (36) and (37) are satisfied. In the case condition (36) is satisfied and the condition (37) is not satisfied then the second predator z will tend to extinction while the first predator y survives. In the same manner if the condition (37) is satisfied but the condition (36) is not satisfied then the first predator y will tend to extinction while the second predator z survives.

NUMERICAL SIMULATIONS

Different values of the parameters e_1 , e_2 are considered. The coexistence or extinction of one of the predators in non periodic solution (i.e., no limit cycles) can be shown numerically. The parameters e_1 , e_2 are chosen because of their importance. The parameters include numerical responses which they are with the functional responses to form the main components of prey predator models (Rockwood, 2006). Also, the parameters are involved to determine intraspecific competition coefficients in our model. In addition to e_1 , e_2 measure the efficiency of conversion.

The values of the parameters are selected where the stability conditions (20) and (27) hold that means non periodic solution (i.e., no limit cycles). The other parameters and initial conditions are fixed as follows:

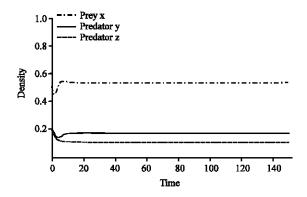


Fig. 5: Time series of dynamical behaviour of the system (3) at $e_1 = 0.78$

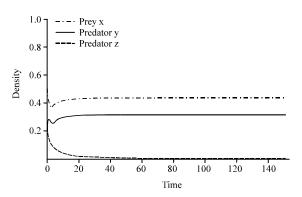


Fig. 6: Time series of dynamical behaviour of the system (3) at $e_1 = 2.4$

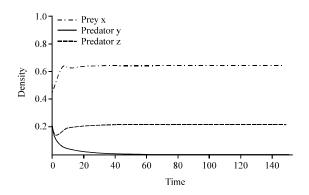


Fig. 7: Time series of dynamical behaviour of the system (3) at $e_1 = 0.4$

$$\alpha = 1.7$$
, $\beta = 1.65$, $u = 0.47$, $c_1 = 0.1$, $c_2 = 0.06$,
 $h_1 = 0.004$, $w = 0.67$, $x(0) = 0.5$, $y(0) = 0.2$, $z(0) = 0.2$

Two different sets of numerical simulations are implemented. In the first set, the value of is changed while the value of e_2 is fixed at Fig. 5-7 show the effect of the efficiency conversion on existence and extinction of one of the predators.

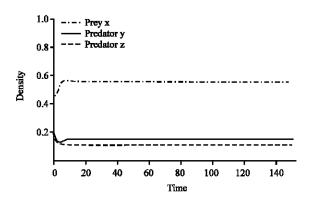


Fig. 8: Time series of dynamical behaviour of the system (2) at $e_2 = 0.72$

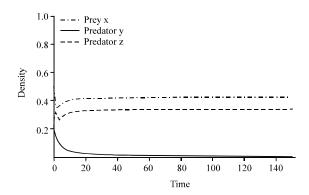


Fig. 9: Time series of dynamical behaviour of the system (3) at $e_2 = 3.75$

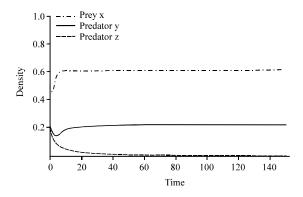


Fig. 10: Time series of dynamical behaviour of the system (3) at $e_2 = 0.5$

- There is coexistence of three species when the values of e₁ (e₁ = 2.4) and e₂ (e₂ = 0.75) are near to each other this is shown in Fig. 5
- There is extinction of predator z when the value of e₁
 (e₁ = 0.78) is increased as shown in Fig. 6
- In Fig. 7 there is extinction of predator y when $e_1 (e_1 = 0.4)$ was decreased

In the second set, different values of e₂ are used while the value of are fixed at 0.78 and the same values of other parameters are used as in the first set.

There are correspondence results for survival and extinction of the predators, depending on efficiency conversion. From Fig. 8-10 the following results are obtained:

- Three species coexists when the values of e₁ (e₁ = 0.70) and e₂ (e₂ = 0.72) were near to each other this is shown in Fig. 8
- When increasing the value of e_1 ($e_1 = 3.75$) there is extinction of predator y as is shown in Fig. 9
- There is extinction of predator z when e₂ (e₂ = 0.5) was decreased as is shown in Fig. 10

The results demonstrate the important role of efficiency conversion for predators' survival.

CONCLUSION

In this study, a continuous time model of interactions of two competing predators sharing one prey in homogenous environment is introduced in which different functional responses are used. The model is divided into two subsystems in order to apply Kolmogorov theorem; consequently the stability of equilibrium points of two subsystems are discussed. The equilibrium points and the stability of equilibrium points of three dimension system (2) are obtained. Theoretical analysis of coexistence the system and extinction one of predators is presented which explain the conditions of coexistence and extinction by depending on the efficiency conversion.

Numerical simulations show that there is extinction of one of predator, depending on the efficiency conversion in the two predators. If the value of conversion efficiency of first predator is less than the other then the first predator will go into extinction while the other survives and vice versa. However, the three species can coexist when the values of conversion efficiency for two predators are near to each other.

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