TWO–PREDATOR AND TWO–PREY SPECIES GROUP DEFENCE MODEL WITH SWITCHING EFFECT

Qamar J.A. Khan,* Edamana V. Krishnan,* and Easwaran Balakrishnan*

Abstract

A model which describes the interaction of two prey species with two predators is analysed. Prey species are of large size and exhibit group defence. Both predators are of same species and they select prey species which are numerically less and have insufficient defending capability. We found conditions for nontrivial equilibrium to be asymptotically stable and corresponding numerical results are also presented.

Key Words

Prey, predator, switching, asymptotically stable

1. Introduction

In prey–predator environment, when a prey species of small size with little defence capability with respect to predator decreases in abundance, the population of predators also reduces drastically by an amount proportional to the interaction strength. However, it is likely that in many cases a predator will consume more individuals of other species when one of its preys becomes relatively less abundant. This behaviour is termed predator switching. With predator switching, the interaction strength depends on the relative abundance of the prey species. Mathematical models involving one predator and two prey species have been generally studied in which the predator feeds more intensively on the more abundant species. One may refer to [1–12].

Prey species of large size such as wildebeest, zebra, and Thomson's gazelle live in huge herds and are dependent upon self-defence, group defence, and group alertness and consolidate themselves to fight back or scare away the predator. Here, the predator will switch towards the prey species which are fewer in number. For example, pairs of musk-oxen can be successfully attacked by wolves but groups are rarely attacked [13]. There are many such examples of group defence [14, 15]. Mathematical models of the prey–predator interaction where the prey exhibits group defence have been studied by Freedman and Walkowicz [16], Ruan and Freedman [17], and Khan *et al.* [18].

Mukherjee and Roy [19] studied a complex prey–predator system consisting of two prey species and two types of predators (dominant and mutant of the same species) with predatory switching. They considered that a predator would prey more heavily on some species if other prey species decline in relative abundance, i.e., the predator interacts with the prey species which are in abundance. This is found to be the case when prey species are relatively smaller in size with little or insignificant defence capability. We consider a similar type of prey-predator system where prey species are of large sizes and live in huge herds. They have the ability of group defence but it will be effective when the population of prey species is large. The predators will feed on both prey species. Because of group defence ability of the prey, predator will switch towards those prey species which are fewer in number. Stability analysis has been carried out for nontrivial equilibrium state to obtain a condition for a feasible equilibrium to be asymptotically stable. We use direct method of Lyapunov to study stability subject to large perturbations of the initial state.

Tansky [7] considers a general volterra type of two prey–one predator model that may be expressed as follows:

$$\frac{dx_1}{dt} = \left(\gamma_1 - \frac{b_1 y}{1 + (x_2/x_1)^n}\right) x_1$$
$$\frac{dx_2}{dt} = \left(\gamma_2 - \frac{b_2 y}{1 + (x_1/x_2)^n}\right) x_2$$
$$\frac{dy}{dt} = \left(-\mu + \frac{b_1 x_1}{(x_2/x_1)^n} + \frac{b_2 x_2}{1 + (x_1/x_2)^n}\right) y$$

where $x_1(t)$, $x_2(t)$, and $y(t)$ denote the abundances of the two prey species and the predator species, respectively. γ_1 and γ_2 are the specific growth rates of the prey species in the absence of predation and μ is the per capita death rate of the predator. The functions $\frac{b_1}{1 + (x_2/x_1)^n}$ and $\frac{b_2}{1 + (x_1/x_2)^n}$ possess the characteristic property of switching through functional response of relative abundance of the

* Department of Mathematics and Statistics, College of Science, Sultan Qaboos University, P.O. Box 36, Al-Khod, P.C. 123, Muscat, Sultanate of Oman; e-mail: {qjalil, krish, balak}@squ.edu.om
Recommended by Dr. P. Ren
(10.2316/J.2010.210-1003)

prey species. When $n = 1$, this is a simple multiplicative effect, whereas for $n > 1$, the effect is stronger [8].

This paper is organized as follows. The model is formulated in Section 2 and coexisting state is given in Section 4. Stability of equilibrium points is discussed in Section 5. Section 6 includes the asymptotic stability analysis of the coexisting equilibrium. Section 7 describes the numerical approach and the final discussion and results are summarized in Section 8.

2. Formulation

We study here a complex prey–predator system consisting of two prey species of large sizes, which exhibit group defence and compete with each other for the use of a common resource. We are considering that both prey species obey logistic growth, i.e., the population density of each prey is resource limited. There are two predators feeding on both of them and these predators switch towards that habitat where prey species are numerically less [20]. The model is described by:

$$\begin{aligned}
\frac{dx_1}{d\tau} &= \gamma_1 x_1 - \alpha_1 x_1^2 - \eta_{12} x_1 x_2 - \frac{\beta_1 x_1 x_2 z_1}{x_1 + x_2} - \frac{\beta_2 x_1 x_2 z_2}{x_1 + x_2} \\
\frac{dx_2}{d\tau} &= \gamma_2 x_2 - \alpha_2 x_2^2 - \eta_{21} x_1 x_2 - \frac{q_1 x_1 x_2 z_1}{x_1 + x_2} - \frac{q_2 x_1 x_2 z_2}{x_1 + x_2} \\
\frac{dz_1}{d\tau} &= \left(-d + \frac{l\,\beta_1 x_1 x_2}{x_1 + x_2} + \frac{l\,q_1 x_1 x_2}{x_1 + x_2}\right) z_1 \\
\frac{dz_2}{d\tau} &= \left(-d + \frac{l\,\beta_2 x_1 x_2}{x_1 + x_2} + l\,\frac{q_2 x_1 x_2}{x_1 + x_2}\right) z_2
\end{aligned} \tag{1}$$

where,

$x_i =$ population density of the prey species in two different habitats;
$z_i =$ population density of predator species;
$\beta_1, \beta_2 =$ encounter rates of predators y_1 and y_2 with prey x_1;
$q_1, q_2 =$ encounter rates of predators y_1 and y_2 with prey x_2;
$\alpha_i =$ intraspecific competition coefficient of prey i;
$\eta_{12}, \eta_{21} =$ interspecific competition coefficient between the prey species;
$\gamma_i =$ per capita birth rate of prey species in two different habitats;
$d =$ death rate of the predators;
$l =$ the rate of conversion of prey to predator.

To avoid mathematical complexity and to reduce the number of parameters, we consider here the conversion rates of predators 1 and 2 to be the same. Furthermore, if we transform the variables and parameters by:

$$\frac{\gamma_1}{l} = \varepsilon_1,\ \frac{\gamma_2}{l} = \varepsilon_2,\ \frac{\alpha_1}{l} = k_1,\ \frac{\alpha_2}{l} = k_2,\ \frac{\eta_{12}}{l} = a_{12},$$
$$\frac{\eta_{21}}{l} = a_{21},\ \frac{z_1}{l} = y_1,\ \frac{z_2}{l} = y_2,\ \frac{d}{l} = \mu,$$

and $l\tau = t$, we obtain the equations:

$$\frac{dx_1}{dt} = \varepsilon_1 x_1 - k_1 x_1^2 - a_{12} x_1 x_2 - \frac{\beta_1 x_1 x_2 y_1}{x_1 + x_2} - \frac{\beta_2 x_1 x_2 y_2}{x_1 + x_2} \tag{2a}$$

$$\frac{dx_2}{dt} = \varepsilon_2 x_2 - k_2 x_2^2 - a_{21} x_1 x_2 - \frac{q_1 x_1 x_2 y_1}{x_1 + x_2} - \frac{q_2 x_1 x_2 y_2}{x_1 + x_2} \tag{2b}$$

$$\frac{dy_1}{dt} = \left(-\mu + \frac{\beta_1 x_1 x_2}{x_1 + x_2} + \frac{q_1 x_1 x_2}{x_1 + x_2}\right) y_1 \tag{2c}$$

$$\frac{dy_2}{dt} = \left(-\mu + \frac{\beta_2 x_1 x_2}{x_1 + x_2} + \frac{q_2 x_1 x_2}{x_1 + x_2}\right) y_2 \tag{2d}$$

We assume all parameters considered here are positive.

3. Boundedness of the Positive Solutions

Set $D := (x_1, x_2, y_1, y_2) \in \mathbb{R}_+^4$ such that $x_i \in (0, \varepsilon_i / k_i)$ and $y_i > 0$ for $i = 1, 2$.

Lemma 1. *All trajectories of* (2) *with initial conditions from D remain bounded.*
Proof: Choose the function:

$$u(t) = x_1(t) + x_2(t) + y_1(t) + y_2(t) \tag{3}$$

and calculating the derivative of $u(t)$ along the solution of (2), we have:

$$\begin{aligned}\dot{u} &= (\varepsilon_1 x_1 - k_1 x_1^2 - a_{12} x_1 x_2) + (\varepsilon_2 x_2 - k_2 x_2^2 - a_{21} x_1 x_2) \\ &\quad - \mu y_1 - \mu y_2\end{aligned}$$

For a positive constant ρ, we have:

$$\begin{aligned}\dot{u} + \rho u &\le x_1(\varepsilon_1 - k_1 x_1 + \rho) + x_2(\varepsilon_2 - k_2 x_2 + \rho) \\ &\quad + (\rho - \mu) y_1 + (\rho - \mu) y_2\end{aligned}$$

If $\rho < \mu$, then there is a constant $c_1 = \frac{1}{4}\left[\frac{(\rho+\varepsilon_1)^2}{k_1} + \frac{(\rho+\varepsilon_2)^2}{k_2}\right]$ such that $\dot{u} + \rho u < c_1$ for all $(x_1, x_2, y_1, y_2) \in \mathbb{R}_+^4$.
This leads to $0 \le u \le \frac{c_1}{\rho} + u(0)e^{-\rho t}$ and for $t \to \infty$, $0 \le u \le \frac{c_1}{\rho}$.
Hence, we obtain the boundedness of the positive solutions for the system (2).

4. Coexisting State

We will study the coexisting state of (2) given by $E = (\overline{x}_1, \overline{x}_2, \overline{y}_1, \overline{y}_2)$. We can find such equilibrium point by assuming that the total energy intake of predators at equilibrium which search for prey 1 is the same as that of predators which search for prey 2. This is a natural assumption because we are considering two types of predators of the same species with the same death rate and same conversion rate. Therefore,

$$\beta_1 \overline{y}_1 + \beta_2 \overline{y}_2 = q_1 \overline{y}_1 + q_2 \overline{y}_2 \tag{4}$$

Proposition 1. *If $q_2\beta_1 - q_1\beta_2 \neq 0$ and* (4) *is satisfied, then at least one coexisting state $E \in D$.*

We find the coexisting state of system (2) in the usual manner by equating the derivatives on the left hand sides to zero and solving the resulting algebraic equations. Let us define $\overline{x}=\overline{x}_1/\overline{x}_2$. The equilibrium $E=(\overline{x}_1,\overline{x}_2,\overline{y}_1,\overline{y}_2)$ is given by:

$$\overline{x}_1=\frac{(1+\overline{x})\mu}{\beta_1+q_1},\quad \overline{x}_2=\frac{(1+\overline{x})\mu}{\overline{x}(\beta_1+q_1)}$$

From (2a) and (2b) at equilibrium we get:

$$\beta_1\overline{y}_1+\beta_2\overline{y}_2=\frac{\overline{x}_1+\overline{x}_2}{\overline{x}_2}[\varepsilon_1-k_1\overline{x}_1-a_{12}\overline{x}_2]$$

$$q_1\overline{y}_1+q_2\overline{y}_2=\frac{\overline{x}_1+\overline{x}_2}{\overline{x}_1}[\varepsilon_2-k_2\overline{x}_2-a_{21}\overline{x}_1]$$

Multiplying the first equation by q_2 and the second equation by β_2 and subtracting, we obtain:

$$\begin{aligned}\overline{y}_1(\beta_1q_2-\beta_2q_1)&=(\overline{x}_1+\overline{x}_2)\left[\frac{q_2}{\overline{x}_2}(\varepsilon_1-k_1\overline{x}_1-a_{12}\overline{x}_2)\right.\\&\qquad\left.-\frac{\beta_2}{\overline{x}_1}(\varepsilon_2-k_2\overline{x}_2-a_{21}\overline{x}_1)\right]\\&=\frac{\overline{x}_2(1+\overline{x})}{\overline{x}_1\overline{x}_2}[q_2\overline{x}_1(\varepsilon_1-k_1\overline{x}_1-a_{12}\overline{x}_2)\\&\qquad-\beta_2\overline{x}_2(\varepsilon_2-k_2\overline{x}_2-a_{21}\overline{x}_1)]\end{aligned}$$

or

$$\begin{aligned}\overline{y}_1=&\frac{(1+\overline{x})}{\overline{x}_1(\beta_1q_2-\beta_2q_1)}[q_2\overline{x}_1(\varepsilon_1-k_1\overline{x}_1-a_{12}\overline{x}_2)\\&-\beta_2\overline{x}_2(\varepsilon_2-k_2\overline{x}_2-a_{21}\overline{x}_1)]\end{aligned}$$

Similarly, we find the value of $\overline{y}_2$ which is:

$$\begin{aligned}\overline{y}_2=&\frac{(1+\overline{x})}{\overline{x}_1(q_1\beta_2-q_2\beta_1)}[q_1\overline{x}_1(\varepsilon_1-k_1\overline{x}_1-a_{12}\overline{x}_2)\\&-\beta_1\overline{x}_2(\varepsilon_2-k_2\overline{x}_2-a_{21}\overline{x}_1)]\end{aligned}\tag{5}$$

From (2c) and (2d), a steady state with coexistence of all four types of individuals require:

$$\beta_1+q_1=\beta_2+q_2\tag{6}$$

This means that the mutant and wild-type predators are equally efficient to interact with both prey species. If they are not, then steady state will not exist and presumably one of the predator will become extinct. From (6) we get that the equilibrium will exist if $\beta_1=q_2$ and $\beta_2=q_1$. We note that $\overline{y}_1$ and $\overline{y}_2$ will not exist if $\beta_1=\beta_2$ and $q_1=q_2$.

Equating the two equivalent relations:

$$\beta_1\overline{y}_1+\beta_2\overline{y}_2=(1+\overline{x})[\varepsilon_1-k_1\overline{x}_1-a_{12}\overline{x}_2]$$

and

$$q_1\overline{y}_1+q_2\overline{y}_2=\frac{(1+\overline{x})}{\overline{x}}[\varepsilon_2-k_2\overline{x}_2-a_{21}\overline{x}_1]$$

we get the resulting equation for $\overline{x}$:

$$\begin{aligned}&\overline{x}^3k_1+\overline{x}^2(k_1+a_{12}-\varepsilon_1S-a_{21})\\&\quad+\overline{x}(a_{12}+\varepsilon_2S-k_2-a_{21})-k_2=0\end{aligned}\tag{7}$$

where $S=\frac{\beta_1+q_1}{\mu^2}$. As the leading and absolute terms are positive and negative, respectively, there is at least one positive root of (7). This equilibrium exists if either ($q_2>\beta_2$ and $q_1<\beta_1$) or ($q_2<\beta_2$ and $q_1>\beta_1$) is satisfied. Moreover, the equilibrium is always positive (see Appendix).

We note that the function $f(\overline{x})$ given by (7) will have only one positive root if $B>0$ and $C>0$ or $B^2<3k_1C$ where $B=k_1+a_{12}-\varepsilon_1S-a_{21}$ and $C=a_{12}+\varepsilon_2S-k_2-a_{21}$.

5. Stability

5.1 Behaviour of the System around Zero Equilibrium $\overline{E}_0(0, 0, 0, 0)$

The stability matrix is not defined at the zero equilibrium $\overline{E}_0$. However, it is simple to prove that this equilibrium is unstable. The system cannot approach this equilibrium for large time if $x_{10}>0$ or $x_{20}>0$, where $x_{10}=x_1(0)$ and $x_{20}=x_2(0)$.

Lemma 2. (i) *If $x_{10}>0$ or $x_{20}>0$ then no trajectory can approach the origin for large times. Hence, $\overline{E}_0$ is unstable.*

(ii) *If $x_{10}=0$ or $x_{20}=0$ then all trajectories will approach the origin for large times.*

Proof: (i) From (2a), $\frac{d}{dt}(\ln x_1)\to\epsilon_1$ as $x_1\to 0$, $x_2\to 0$, $y_1\to 0$, and $y_2\to 0$.

Hence, there is a small ball with centre $\overline{E}_o$ and radius ϵ_1, such that within this ball $\frac{d}{dt}(\ln x_1)\geq\frac{\epsilon_1}{2}$.

If $(x_1,x_2,y_1,y_2)\to(0,0,0,0)$ as $t\to\infty$ then there exist t_0 such that $x_{10}>0$ and we get $x_1\geq x_{10}e^{\frac{\epsilon_1}{2}(t-to)}$. This shows that as $t\to\infty$, $x_1\to\infty$. Similarly, we can show for x_2 from (2). Hence, no trajectory will approach towards origin.

(ii) If $x_{10}=x_{20}=0$ then $x_1(t)$ and $x_2(t)=0$ for all t. Let $y_{10}=y_1(0)$ and $y_{20}=y_2(0)$.

(a) If $y_{10}>0$ and $y_{20}=0$ then $y_1(t)\to 0$ as $t\to\infty$ and $y_2(t)=0$ for all t.
(b) If $y_{10}=0$ and $y_{20}\geq 0$ then $y_1(t)=0$ for all t and $y_2(t)\to 0$ as $t\to\infty$.
(c) If $y_{10}>0$ and $y_{20}>0$ then $y_1(t)\to 0$ and $y_2(t)\to 0$ as $t\to\infty$.

5.2 Behaviour of the System around $\overline{E}_1(\overline{x}_1, 0, 0, 0)$ and $\overline{E}_2(0, \overline{x}_2, 0, 0)$

It can be easily shown that the other possible equilibrium points $\overline{E}_1(\overline{x}_1,0,0,0)$ and $\overline{E}_2(0,\overline{x}_2,0,0)$ will be neutrally stable and $\overline{E}_3(\overline{x}_1,\overline{x}_2,0,0)$ will be stable if:

$$\mu=\text{Max}\left(\frac{\beta_1\overline{x}_1\overline{x}_2}{\overline{x}_1+\overline{x}_2}+\frac{q_1\overline{x}_1\overline{x}_2}{\overline{x}_1+\overline{x}_2},\frac{\beta_2\overline{x}_1\overline{x}_2}{\overline{x}_1+\overline{x}_2}+\frac{q_2\overline{x}_1\overline{x}_2}{\overline{x}_1+\overline{x}_2}\right)$$

and unstable otherwise.

5.3 Behaviour of the System around $\overline{E}_4(\overline{x}_1, \overline{x}_2, \overline{y}_3, \overline{y}_4)$

The stability matrix reduces to:

$$J(\overline{E}_4) = \begin{pmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ b_{11} & b_{12} & b_{13} & b_{14} \\ c_{11} & c_{12} & 0 & 0 \\ d_{11} & d_{12} & 0 & 0 \end{pmatrix} \quad (8)$$

where,

$$\begin{aligned}
a_{11} &= -k_1\overline{x}_1 + \frac{\beta_1\overline{x}_1\overline{x}_2\overline{y}_1}{(\overline{x}_1+\overline{x}_2)^2} + \frac{\beta_2\overline{x}_1\overline{x}_2\overline{y}_2}{(\overline{x}_1+\overline{x}_2)^2} \\
a_{12} &= -a_{12}\overline{x}_1 - \frac{\beta_1\overline{x}_1^2\overline{y}_1}{(\overline{x}_1+\overline{x}_2)^2} - \frac{\beta_2\overline{x}_1^2\overline{y}_2}{(\overline{x}_1+\overline{x}_2)^2} \\
a_{13} &= -\frac{\beta_1\overline{x}_1\overline{x}_2}{\overline{x}_1+\overline{x}_2}, \quad a_{14} = -\frac{\beta_2\overline{x}_1\overline{x}_2}{\overline{x}_1+\overline{x}_2} \\
b_{11} &= -a_{21}\overline{x}_2 - \frac{q_1\overline{x}_2^2\overline{y}_1}{(\overline{x}_1+\overline{x}_2)^2} - \frac{q_2\overline{x}_2^2\overline{y}_2}{(\overline{x}_1+\overline{x}_2)^2} \\
b_{12} &= -k_2\overline{x}_2 + \frac{q_1\overline{x}_1\overline{x}_2\overline{y}_1}{(\overline{x}_1+\overline{x}_2)^2} + \frac{q_2\overline{x}_1\overline{x}_2\overline{y}_2}{(\overline{x}_1+\overline{x}_2)^2} \\
b_{13} &= -\frac{q_1\overline{x}_1\overline{x}_2}{\overline{x}_1+\overline{x}_2}, \quad b_{14} = -\frac{q_2\overline{x}_1\overline{x}_2}{\overline{x}_1+\overline{x}_2} \\
c_{11} &= \frac{\beta_1\overline{x}_2^2\overline{y}_1}{(\overline{x}_1+\overline{x}_2)^2} + \frac{q_1\overline{x}_2^2\overline{y}_1}{(\overline{x}_1+\overline{x}_2)^2}, \\
c_{12} &= \frac{\beta_1\overline{x}_1^2\overline{y}_1}{(\overline{x}_1+\overline{x}_2)^2} + \frac{q_1\overline{x}_1^2\overline{y}_1}{(\overline{x}_1+\overline{x}_2)^2} \\
d_{11} &= \frac{\beta_2\overline{x}_2^2\overline{y}_1}{(\overline{x}_1+\overline{x}_2)^2} + \frac{q_2\overline{x}_2^2\overline{y}_2}{(\overline{x}_1+\overline{x}_2)^2}, \\
d_{12} &= \frac{\beta_2\overline{x}_1^2\overline{y}_2}{(\overline{x}_1+\overline{x}_2)^2} + \frac{q_1\overline{x}_1^2\overline{y}_2}{(\overline{x}_1+\overline{x}_2)^2}
\end{aligned} \quad (9)$$

The characteristic equation associated to system(2) around $\overline{E}_4$ takes the general form:

$$\lambda^4 + e_1\lambda^3 + e_2\lambda^2 + e_3\lambda + e_4 = 0 \quad (10)$$

where,

$$\begin{aligned}
e_1 &= -a_{11} - b_{12} \\
e_2 &= a_{11}b_{12} - b_{13}c_{12} - b_{14}a_{12} - a_{12}b_{11} - a_{13}c_{11} + a_{14}d_{11} \\
e_3 &= a_{11}b_{13}c_{12} + a_{11}b_{14}d_{12} - a_{12}c_{11}b_{13} - a_{12}b_{14}d_{11} \\
&\quad - a_{13}b_{11}c_{12} + a_{13}b_{12}c_{11} + a_{14}b_{11}d_{12} - a_{14}b_{12}d_{11} \\
e_4 &= a_{13}b_{14}c_{11}d_{12} - a_{13}b_{14}c_{12}d_{11} + a_{14}b_{13}d_{12}c_{11} \\
&\quad - a_{14}b_{13}c_{12}d_{11}
\end{aligned} \quad (11)$$

By Routh–Hurwitz criterion, we need to show the following statements:
(i) $e_i > 0$ for $i = 1, 2, 3, 4$.
(ii) $e_1e_2 - e_3 > 0$.
(iii) $e_3(e_1e_2 - e_3) - e_4e_1^2 > 0$.

If the above conditions are satisfied then the non-zero equilibrium $\overline{E}_4$ will be locally stable.

6. Asymptotic Stability of Coexisting State $\overline{E}_4(\overline{x}_1, \overline{x}_2, \overline{y}_1, \overline{y}_2)$

An ecosystem model is asymptotically stable if every trajectory of the model which begins at a positive octant state remains in the positive octant for all finite values of the time variable t and converges to positive equilibrium as $t \to \infty$. We make use of the general Lyapunov function:

$$\begin{aligned}
V(x_1, x_2, y_1, y_2) &= \sum_{i=1}^{2}\left[(x_i - \overline{x}_i) - \overline{x}_i \ln\left(\frac{x_i}{\overline{x}_i}\right)\right] \\
&\quad + \sum_{i=1}^{2}\left[(y_i - \overline{y}_i) - \overline{y}_i \ln\left(\frac{y_i}{\overline{y}_i}\right)\right]
\end{aligned} \quad (12)$$

Calculating the derivative along each solution of system (2), we have:

$$\frac{dV}{dt} = \sum_{i=1}^{2}\left(\frac{dx_i}{dt} - \frac{\overline{x}_i}{x_i}\frac{dx_i}{dt}\right) + \sum_{i=1}^{2}\left(\frac{dy_i}{dt} - \frac{\overline{y}_i}{y_i}\frac{dy_i}{dt}\right) \quad (13)$$

The assumption:

$$\frac{x_1}{x_2} \approx \overline{x}, \text{ the root of (7) for all } t \geq 0 \quad (14)$$

reduces (13) to:

$$\begin{aligned}
\frac{dV}{dt} &\approx (x_1 - \overline{x}_1)[-k_1(x_1 - \overline{x}_1) - a_{12}(x_2 - \overline{x}_2)] \\
&\quad - (x_2 - \overline{x}_2)[-k_2(x_2 - \overline{x}_2) - a_{21}(x_1 - \overline{x}_1)] \\
&\quad + \frac{x_1\overline{x}_2 - x_2\overline{x}_1}{(x_1+x_2)(\overline{x}_1+\overline{x}_2)}[(\beta_1\overline{y}_1 + \beta_2\overline{y}_2)(x_1 - x_2) \\
&\quad - (\beta_1 y_1 + \beta_2 y_2)(\overline{x}_1 - \overline{x}_2)]
\end{aligned}$$

and finally we get:

$$\begin{aligned}
\frac{dV}{dt} &\approx -k_1(x_1 - \overline{x}_1)^2 - k_2(x_2 - \overline{x}_2)^2 \\
&\quad - a_{12}(x_1 - \overline{x}_1)(x_2 - \overline{x}_2) - a_{21}(x_1 - \overline{x}_1)(x_2 - \overline{x}_2) \\
&= -(x_1 - \overline{x}_1, x_2 - \overline{x}_2)\begin{bmatrix} k_1 & a_{12} \\ a_{21} & k_2 \end{bmatrix}\begin{pmatrix} x_1 - \overline{x}_1 \\ x_2 - \overline{x}_2 \end{pmatrix} \\
&= -\mathbf{P}^T\mathbf{QP}
\end{aligned}$$

where,

$$\mathbf{Q} = \begin{bmatrix} k_1 & a_{12} \\ a_{21} & k_2 \end{bmatrix}, \quad \mathbf{P} = \begin{bmatrix} x_1 - \overline{x}_1 \\ x_2 - \overline{x}_2 \end{bmatrix} \text{ and } p_i = x_i - \overline{x}_i, i = 1, 2$$

Hence,

$$\begin{aligned}
\frac{dV}{dt} &\leq 0 \quad \text{if} \quad k_1p_1^2 + k_2p_2^2 + (a_{12} + a_{21})p_1p_2 \geq 0 \\
&\text{or} \quad \frac{(a_{12} + a_{21})^2}{k_1k_2} \leq 4
\end{aligned} \quad (15)$$

Here the equality holds if $x_1 = \overline{x_1}$ and $x_2 = \overline{x_2}$.

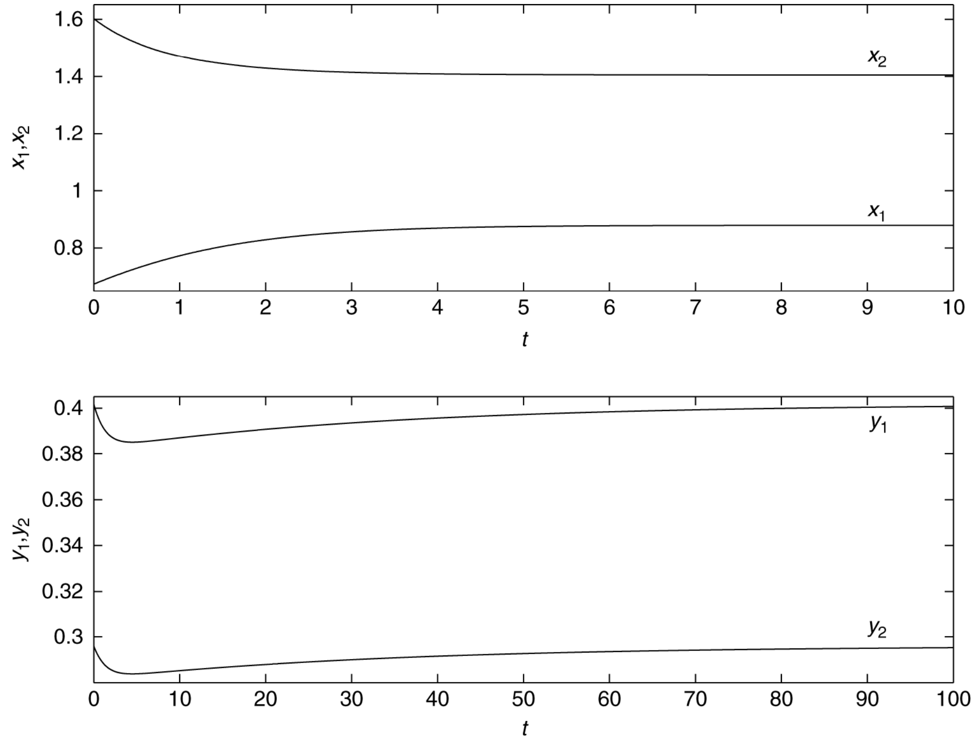

Figure 1. The graph of x_1, x_2, y_1, and y_2 versus t for the first set of parameter values given in Section 7 for the first set of initial conditions.

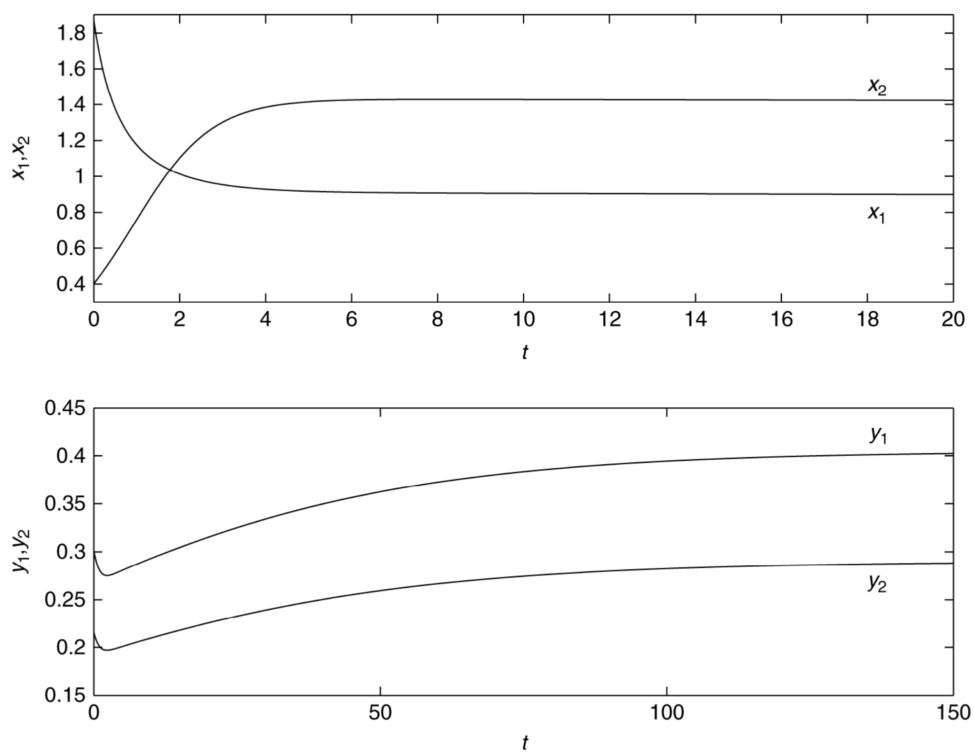

Figure 2. The graph of x_1, x_2, y_1, and y_2 versus t for the first set of parameter values given in Section 7 for the second set of initial conditions.

We summarize the preceding details in the following theorem.

Theorem 1. *Suppose* $\overline{E}_4 = (\overline{x}_1, \overline{x}_2, \overline{y}_1, \overline{y}_2)$ *exists, the condition (14) is satisfied and* $\overline{x}$ *is the real positive root of (7), then the positive equilibrium* $\overline{E}_4$ *is asymptotically stable provided (15) is satisfied.*

7. Numerical Results

The system (2) is integrated using the standard routines available in Matlab for different sets of realistic parameter

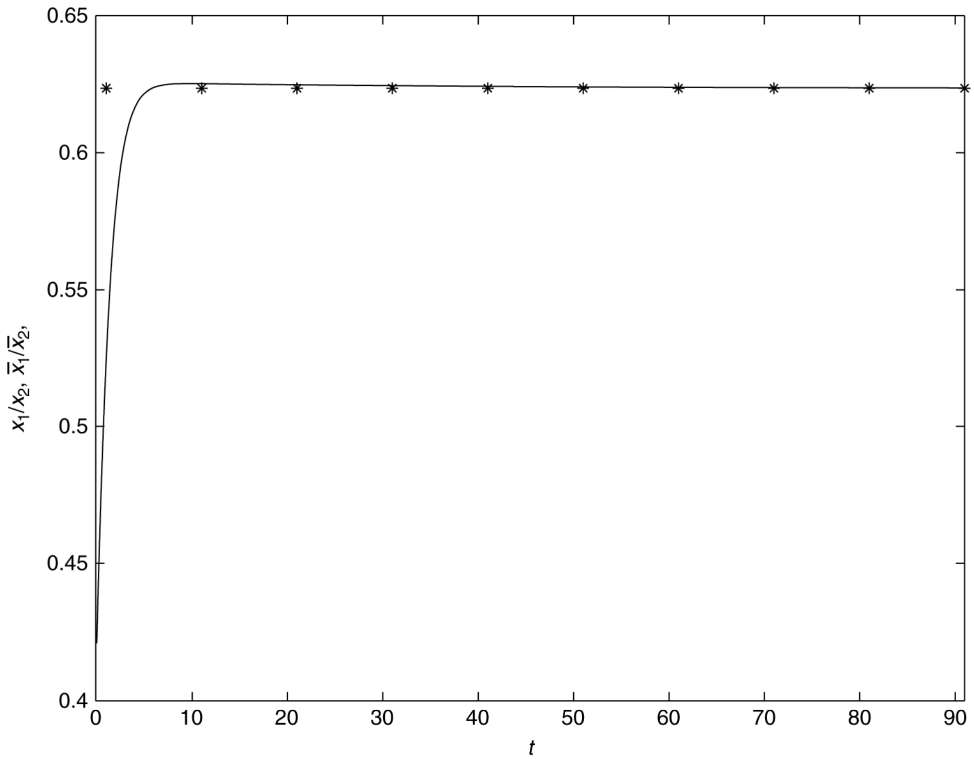

Figure 3. The graph of x_1/x_2 versus t and $\overline{x_1}/\overline{x_2}$ versus t for the parameter values given in Section 7 for the first set of initial conditions. $\overline{x_1}/\overline{x_2}$ is given in $*$.

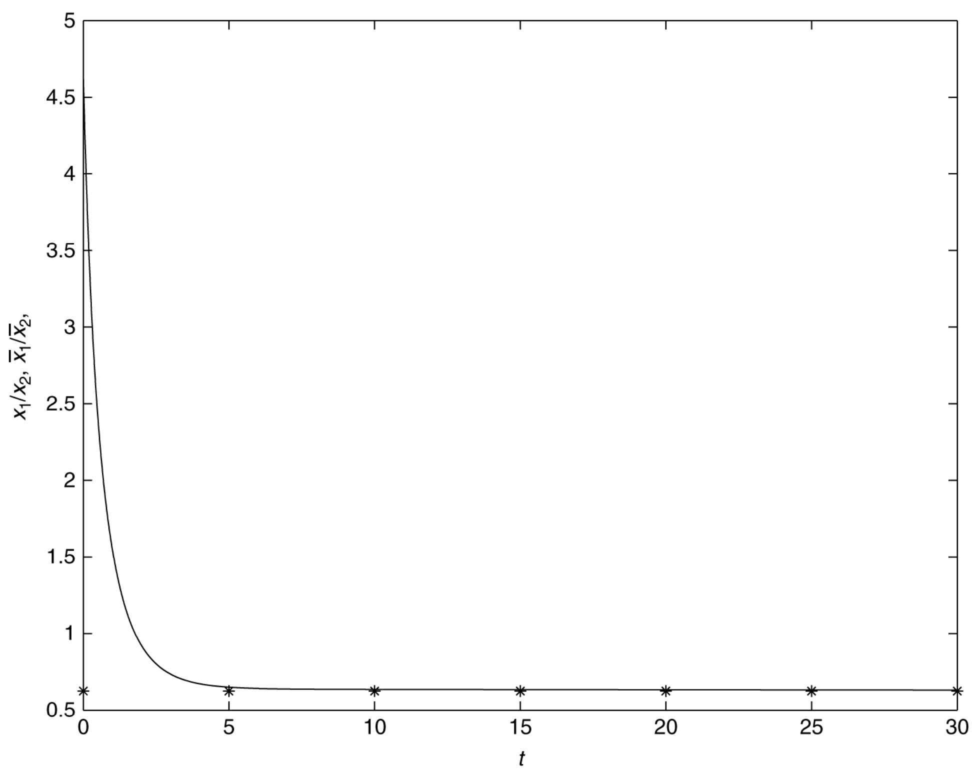

Figure 4. The graph of x_1/x_2 versus t and $\overline{x_1}/\overline{x_2}$ versus t for the parameter values given in Section 7 for the second set of initial conditions. $\overline{x_1}/\overline{x_2}$ is given in $*$.

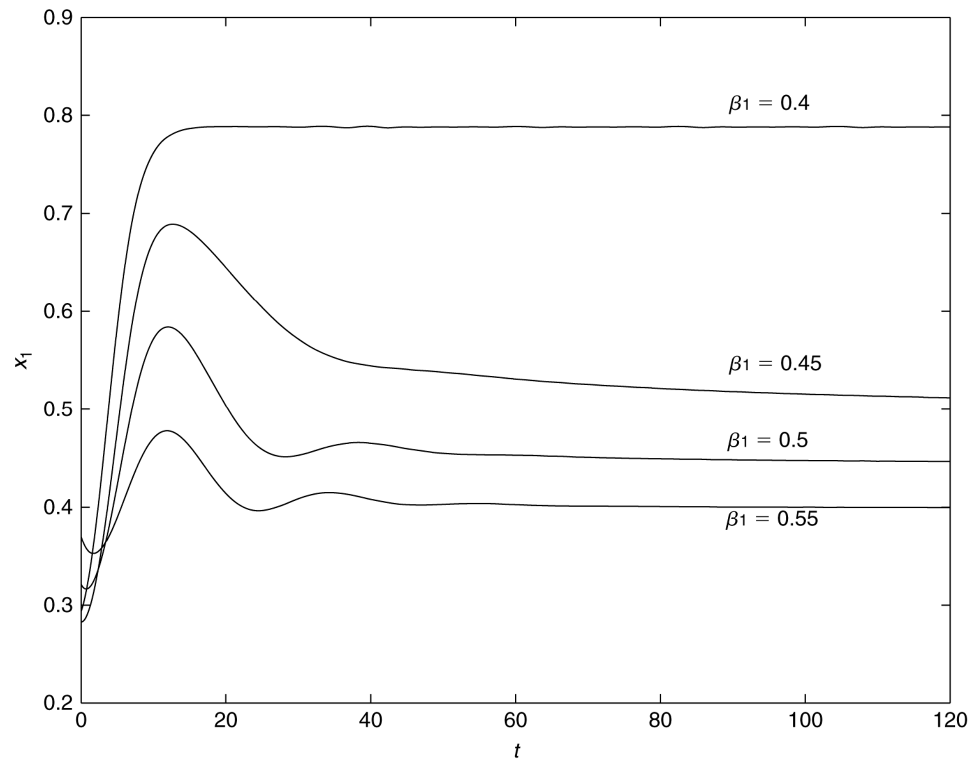

Figure 5. The graph of x_1 versus t for the second set of parameter values given in Section 7 for varying β_1 values.

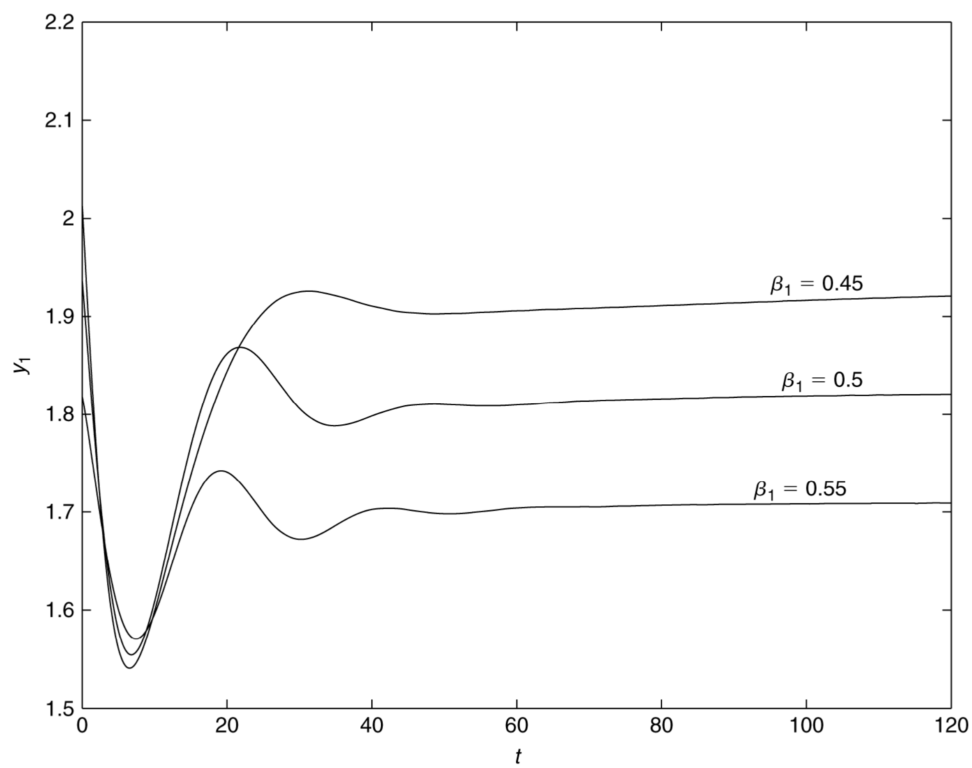

Figure 6. The graph of y_1 versus t for the second set of parameter values given in Section 7 for varying β_1 values.

values. As a result, we present below results on two sets of parameter values. These values yield a coexisting equilibrium $\overline{E}=(\overline{x}_1,\overline{x}_2,\overline{y}_1,\overline{y}_2)$ satisfying the conditions (7), (14), and $(a_{12}+a_{21})^2\leq 4k_1k_2$. The values of first such set are $k_1=1$, $\mu=0.28$, $a_{1,2}=a_{2,1}=0.01$, $\epsilon_1=1$, $\beta_1=0.4$, $q_1=0.12$, $\epsilon_2=1.2$, $k_2=0.8$, $\beta_2=0.07$, and $q_2=0.45$. The coexisting equilibrium corresponding to these values is $\overline{x}_1=0.8742$, $\overline{x}_2=1.4020$, $\overline{y}_1=0.4018$, and $\overline{y}_2=0.2960$ be-

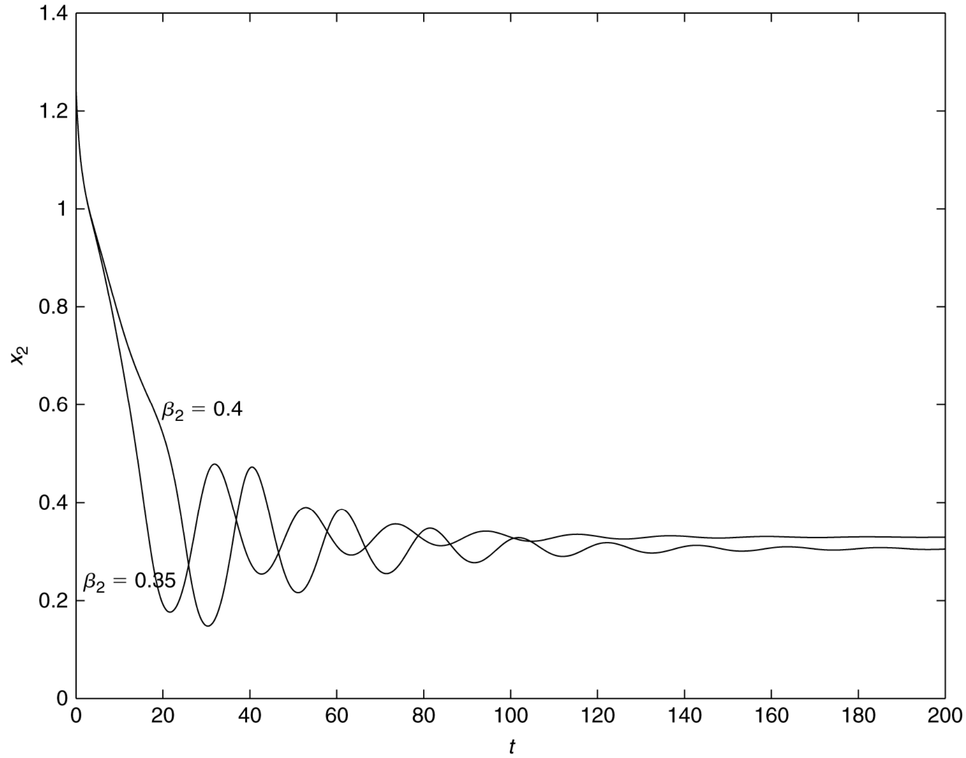

Figure 7. The graph of x_2 versus t for the second set of parameter values given in Section 7 for varying β_2 values.

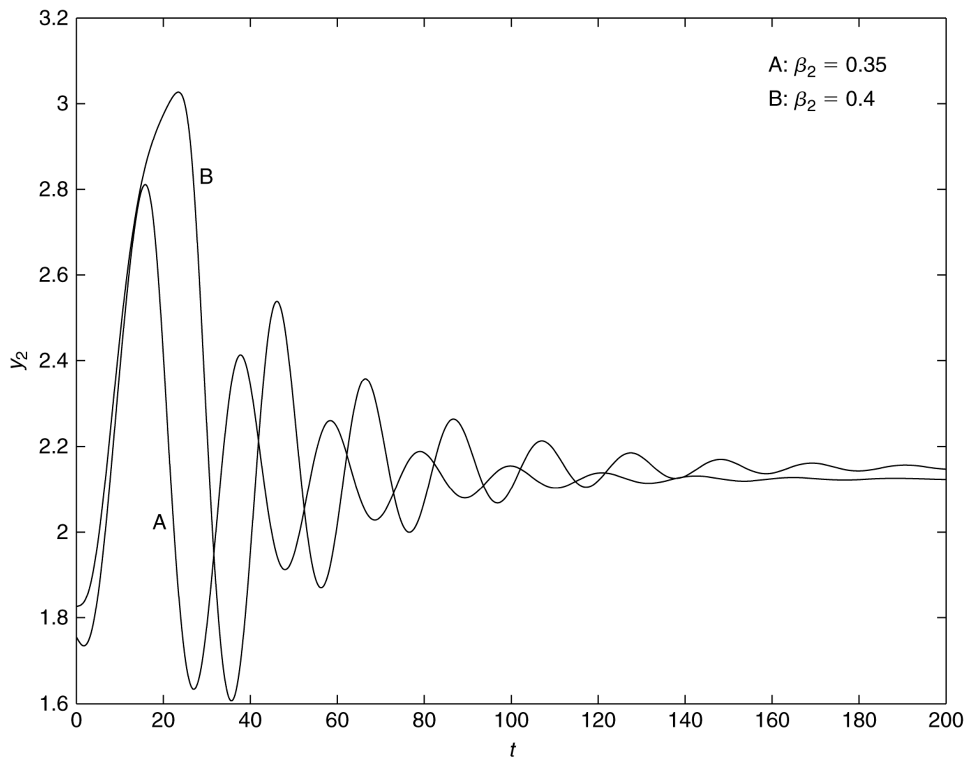

Figure 8. The graph of y_2 versus t for the second set of parameter values given in Section 7 for varying β_2 values.

cause the only real root to the cubic equation (7) is $\overline{x} = 0.6236$. The results for two different sets of initial conditions are given in Figs 1–4. Figure 1 corresponds to the first set of initial conditions and Fig. 2 corresponds to second set. In Figs 3 and 4, we demonstrate the fact that the condition (14) holds once the coexisting state is attained. In a similar way, we perform simulations for a second set of parameter values which are $k_1 = 0.95$, $\mu = 0.2$,

$a_{1,2} = 0.1$, $a_{2,1} = 0.01$, $\epsilon_1 = 1.2$, $q_1 = 0.12$, $\epsilon_2 = 1$, $k_2 = 0.8$, and $q_2 = 0.45$. The coexisting equilibrium corresponding to these values when $\beta_1 = 0.4$ and $\beta_2 = 0.07$ is $\overline{x}_1 = 0.7936$, $\overline{x}_2 = 0.7464$, $\overline{y}_1 = 1.6973$, and $\overline{y}_2 = 1.2506$ because the only real root to the cubic equation (7) is $\overline{x} = 1.0632$. In Figs. 5 and 6, we present the behaviour of x_1 and y_1 against t for varying β_1 values. Similarly, behaviour of x_2 and y_2 against t for varying β_2 values are given in Figs 7 and 8. It can be seen from these figures that the stability increases when β_1 and β_2 decreases.

8. Summary

Prajneshu and Holgate [8] studied a system involving one predator and two prey species in which the predator feeds more intensively on the more abundant species. Later Khan *et al.* [10] studied one prey and one predator model where prey lives in two different habitats separated by a barrier. In both models authors considered prey of small size having insignificant defence capability where predator feeds prey indiscriminately and feeds preferentially on the most numerous species. In this paper, we have considered a system having two predators (dominant and mutant of the same species) interacting with two prey species where interspecific and intraspecific competition hold between prey species. The predator can feed on either prey species. Both prey species have the ability of group defence to fight back or scare away the predator but it will be effective when the population of prey species is large. Because of the group defence ability of the prey, the predator will select the prey species which is numerically less because prey in less number will not be able to defend itself against the predator. Hence, switching of the predator in this model will be in opposite direction contrary to what was considered in [8, 10]. Advantage of our model over other two previous models is that it explains the interaction of prey–predator when prey is of large size like zebra, buffalo, kongoni, and Thomson's gazelle while models [8, 10] explain prey–predator interaction for prey like vole, Dik-dik, etc.

In our study, we found that if interspecific interactions $a_{12} = a_{21} = 0$ or very weak in comparison to intraspecific competition k_1 and k_2, then coexisting state will be asymptotically stable. It is quite natural because prey species living in the same habitat will interact much more than the prey species living in different habitats. If a_{12} and a_{21} are not very small in comparison to k_1 and k_2, then coexisting state will be asymptotically stable if the ratio of the sum of squares of interspecific competition and the product of intraspecific competition is less than or equal to 4 and unstable if the ratio is greater than 4. A detailed Hopf bifurcation analysis on the model (2) is expected in a follow-up study by the authors.

In the real world, ecosystem is subjected to large perturbations of the initial state and system dynamics. We have used direct method of Lyapunov for studying stability relative to finite perturbations of the initial state. We have found conditions for a feasible equilibrium to be asymptotically stable. Corresponding numerical results have also been presented.

Appendix

$\overline{y}_1$ and $\overline{y}_2$ will exist iff $q_2\beta_1 - q_1\beta_2 \neq 0$. So there are only two possibilities. Either $q_2\beta_1 > q_1\beta_2$ or $q_2\beta_1 < q_1\beta_2$. Consider $q_2\beta_1 > q_1\beta_2$. Then $\overline{y}_1 > 0$ if $q_2\overline{x}_1(\varepsilon_1 - k_1\overline{x}_1 - a_{12}\overline{x}_2) > \beta_2\overline{x}_2$ $(\varepsilon_2 - k_2\overline{x}_2 - a_{21}\overline{x}_1)$. From equations (2a) and (2b), at equilibrium we get $q_2\overline{x}_1(\beta_1\overline{y}_1 + \beta_2\overline{y}_2) > \beta_2\overline{x}_2(q_1\overline{y}_1 + q_2\overline{y}_2)\overline{x}$.

Using equation (4) and relation $\overline{x} = \overline{x}_1/\overline{x}_2$ give $q_2 > \beta_2$. Similarly, we can show that $\overline{y}_2 > 0$ if $\beta_1 > q_1$. Hence,

$$\overline{y}_1 > 0 \text{ and } \overline{y}_2 > 0 \text{ if } q_2 > \beta_2 \text{ and } \beta_1 > q_1.$$

Exactly in the same way, by considering $q_2\beta_1 < q_1\beta_2$, we can show that,

$$\overline{y}_1 > 0 \text{ and } \overline{y}_2 > 0 \text{ if } q_2 < \beta_2 \text{ and } q_1 > \beta_1.$$

References

[1] C.S. Holling, Principles of insect predation, *Annual Review of Entomology*, *6*, 1961, 163–182.

[2] F. Takahashi, Reproduction curve with two equilibrium points: A consideration on the fluctuation of insect population, *Research Population Ecology*, *47*, 1964, 733–745.

[3] R.M. May, *Some mathematical problems in biology*, Vol. 4 (Providence, RI: American Mathematical Society, 1974).

[4] W.W. Murdoch & A. Oaten, Predation and population stability, *Advances in Ecology Research*, *9*, 1975, 1–31.

[5] J. Roughgarden & M. Feldman, *Species packing and predation pressure*, *Ecology*, *56*, 1975, 489–492.

[6] M. Tansky, *Progress in theoretical biology* (Edited by R. Rosen), *4* (London: Academic Press, 1976).

[7] M. Tansky, Switching effects in prey-predator system, *Journal of Theoretical Biology*, *70*, 1978, 263–272.

[8] R. Prajneshu & P. Holgate, A prey-predator model with switching effect, *Journal of Theoretical Biology*, *125*, 1987, 61–66.

[9] J.N. McNair, A reconcillation of simple and complex models of age – dependent predation, *Theoretical Population Biology*, *32*, 1987, 383–392.

[10] Q.J.A. Khan, B.S. Bhatt, & R.P. Jaju, Stability of a switching model with two habitats and a predator, *Journal of the Physical Society Japan*, *63*, 1994, 1995–2001.

[11] F. Courchamp, M. Langlais, & G. Sugihara, Rabbits killing birds: Modelling the hyperpredation process, *Journal of Animal Ecology*, *69*, 2000, 154–164.

[12] J. Zhang, M. Fan, & Y. Kuang, Rabbits killing birds revisited, *Mathematical Biosciences*, *203*, 2006, 100–123.

[13] J.S. Tener, *Muskoxen*, (Ottawa: Queen's Printer, 1965).

[14] R.D. Yang & A.F. Humphrey, Dynamics and steady state studies of phenol biodegeneration in pure and mixed cultures, *Biotechnology and Bioengineering*, *17*, 1975, 1211–1235.

[15] R.M. May & S.K. Robinson, Population dynamics of avian brood parasitism, *American Naturalist*, *126*, 1985, 475–494.

[16] H.I. Freedman & G.S.K. Walkowicz, Predator-prey system with group defense: The paradox of enrichment revisited, *Bulletin of Mathematical Biology*, *48*, 1986, 493–508.

[17] S. Ruan & H.I. Freedman, Persistence in three species food chain models with group defence, *Mathematical Biosciences*, *111*, 1992, 73–87.

[18] Q.J.A. Khan, B.S. Bhatt, & R.P. Jaju, Switching model with two habitats and a predator involving group defence, *Journal of Nonlinear Mathematical Physical*, *5*, 1998, 212–229.

[19] D. Mukherjee & A.B. Roy, Global stability of prey-predator systems with predatory switching, *Biosystems*, *27*, 1992, 171–178.

[20] Q.J.A. Khan, E. Balakrishnan, & G.C. Wake, Analysis of a predator-prey system with predator switching, *Bulletin of Mathematical Biology*, *66*, 2004, 109–123.

Biographies

Qamar J.A. Khan, was born on 1st July, 1953. He received his Ph.D. degree in Biomathematics from Indian Institute of Technology, Kanpur, in 1980. At present, he is working as an associate professor at Sultan Qaboos University, Muscat, Oman. His research areas of interest are prey–predator and epidemic models. He has published 43 research papers in various international journals. He is an associate editor of the journal *IAENG*.

Edamana V. Krishnan, an Indian national, was born on 18th September, 1952. He received his Ph.D. degree in Nonlinear Waves from Indian Institute of Science, Bangalore, in 1979. Currently he is working as a professor at Sultan Qaboos University, Muscat, Oman. His main area of research is Analytical Solutions of Nonlinear Dispersive Waves. He has published about 60 research papers in various international journals. He is in the Editorial Board of two journals: *International Journal of Pure and Applied Mathematical Sciences* and *Global Journal of Mathematics and Mathematical Sciences.*

Easwaran Balakrishnan obtained his Ph.D. degree in Mathematics from the Massey University, New Zealand, in 1996. Currently, he is an associate professor in Mathematics at Sultan Qaboos University, Muscat, Oman. His research areas include mathematical biology, nonlinear dynamics, and computational mathematics.