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Existence of chaos in two-prey, one-predator system

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Abstract

A two-prey, one-predator model incorporating nonlinear functional response is investigated analytically as well as numerically. The system appears to exhibit chaos for a range of parametric values when long time behavior studied.

1. Introduction

Two-species continuous time models of interacting species have been extensively investigated in literature. Mathematically these models can exhibit only two basic patterns: approach to equilibrium or to a limit cycle [1]. However, ecological communities in nature are observed to exhibit very complex behaviors. Price et al. [2] argued that community behavior must be based on three or more trophic levels. Three-species continuous time models are reported to have more complicated patterns. The research of the last two decades demonstrates that very complex dynamics can arise in continuous time food chain models with three or more species [3–8], while similar results are obtained for multi-species food web models [9–11]. Fujii [12] suggests the existence of a limit cycle for two-prey, one-predator Lotka–Volterra system with linear type of functional response. Vance [13] discovered a quasi-cyclic motion for this system, which was named spiral chaos [10]. Later, the Klebanoff and Hastings argued for chaotic dynamics in two-prey, one-predator through bifurcation theory [11].

The effect of nonlinearity often renders a periodic solution unstable for certain parametric choices. While these conditions do not guarantee chaos, they do make its existence possible. Chaotic dynamics may occur in a continuous dynamic system with at least three dependent variables, involving a nonlinear term that couples several of the variables. Another key feature of chaotic dynamics is a sensitive dependence on initial conditions. Even a very small change in initial conditions can lead to different results in chaotic systems. Indeed, the divergence between results grows exponentially in time for virtually all pairs of starting conditions.

We investigate in this paper a logically consistent, continuous time, food web model, consisting of two competing preys, and one predator. The model satisfies simple set of criteria for a logically credible food web models [14]. It incorporates the modified Holling type II functional response in each prey or predator equation. The local stability conditions for the system have been obtained and analyzed. Numerically simulations have been carried out to study the complex behavior of the system for biologically reasonable ranges of parameters.

2. The model system

The dynamics of the three-species system consisting of two competing preys and one predator is governed by the following system of differential equations:

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$$\begin{aligned}\frac{\mathrm{d}X_1}{\mathrm{d}T}&=r_1X_1\left(1-\frac{X_1}{K_1}-\frac{c_{12}X_2}{K_1}\right)-F_1(X_1,X_2)X_3,\\ \frac{\mathrm{d}X_2}{\mathrm{d}T}&=r_2X_2\left(1-\frac{X_2}{K_2}-\frac{c_{21}X_1}{K_2}\right)-F_2(X_1,X_2)X_3,\\ \frac{\mathrm{d}X_3}{\mathrm{d}T}&=e_1F_1(X_1,X_2)X_3+e_2F_2(X_1,X_2)X_3-dX_3,\end{aligned}\tag{1}$$

where r_i, K_i, e_i, d and c_{ij} ($i = 1, 2, j \neq i$) are model parameters assuming only positive values, and $F_i(X_1, X_2)$ represents the functional response. This system models a simple ecological situation of food web where X_1 and X_2 are the densities of two-prey species, while X_3 is the density of a predator species that preys upon X_1 and X_2. The predator consumes the prey X_i according to the functional response [15]

$$F_i(X_1,X_2)=A_iX_i/(1+B_1X_1+B_2X_2),\quad i=1,2,$$

where A_i is the maximum harvest rate of predator from prey X_i and $(B_i)^{-1}$ is the half saturation constant. The constants e_i, $i = 1, 2$ are conversion rates of prey X_i to predator X_3.

For a biological food web model to be logically credible, it must satisfy the following criteria:

- Criterion 1: The equations must be invariant under identification of identical species.
- Criterion 2: The system of equations for a food web must separate into independent subsystems if the community splits into disconnected subwebs.

The interaction of two competing prey and one common predator given by system (1) obey these two criteria. So that, if X_1 and X_2 are identical species, then $r_1 = r_2 = r$, $c_{12} = c_{21} = 1$, $A_1 = A_2 = A$, $K_1 = K_2 = K$, $B_1 = B_2 = B$, and $e_1 = e_2 = e$.

In such a case, the model (1) transfers to the consistent model:

$$\begin{aligned}\frac{\mathrm{d}X}{\mathrm{d}T}&=rX\left(1-\frac{X}{K}\right)-F(X)X_3,\\ \frac{\mathrm{d}X_3}{\mathrm{d}T}&=eF(X)X_3-dX_3,\end{aligned}\tag{2}$$

with $F(X) = AX/(1 + BX)$, $X = X_1 + X_2$.

Also, system (1) separates into two independent subsystems. The first subsystem is obtained by assuming the absence of the second prey X_2:

$$\begin{aligned}\frac{\mathrm{d}X_1}{\mathrm{d}T}&=r_1X_1\left(1-\frac{X_1}{K_1}\right)-F_1(X_1)X_3,\\ \frac{\mathrm{d}X_3}{\mathrm{d}T}&=e_1F_1(X_1)X_3-dX_3.\end{aligned}\tag{3}$$

The second subsystem is obtained when the first prey X_1 is absent:

$$\begin{aligned}\frac{\mathrm{d}X_2}{\mathrm{d}T}&=r_2X_2\left(1-\frac{X_2}{K_2}\right)-F_2(X_2)X_3,\\ \frac{\mathrm{d}X_3}{\mathrm{d}T}&=e_2F_2(X_2)X_3-dX_3,\end{aligned}\tag{4}$$

with $F_i(X_i) = A_iX_i/(1 + B_iX_i)$, $i = 1, 2$.

To reduce the number of parameters in system (1), the following nondimensional variables are introduced:

$$y_1=X_1/K_1,\quad y_2=X_2/K_2,\quad y_3=X_3/K_1,\quad t=r_1T.$$

The nondimensionalised equations are:

$$\begin{aligned}\frac{\mathrm{d}y_1}{\mathrm{d}t}&=y_1(1-y_1-w_1y_2)-\left(\frac{w_2y_1}{1+w_3y_1+w_4y_2}\right)y_3,\\ \frac{\mathrm{d}y_2}{\mathrm{d}t}&=w_5y_2(1-y_2-w_6y_1)-\left(\frac{w_7y_2}{1+w_3y_1+w_4y_2}\right)y_3,\\ \frac{\mathrm{d}y_3}{\mathrm{d}t}&=\left(\frac{w_8y_1}{1+w_3y_1+w_4y_2}\right)y_3+\left(\frac{w_9y_2}{1+w_3y_1+w_4y_2}\right)y_3-w_{10}y_3.\end{aligned}\tag{5}$$

Here $w_1 = c_{12}K_2/K_1$, $w_2 = A_1K_1/r_1$, $w_3 = B_1K_1$, $w_4 = B_2K_2$, $w_5 = r_2/r_1$, $w_6 = c_{21}K_1/K_2$, $w_7 = A_2K_1/r_1$, $w_8 = e_1w_2$, $w_9 = (e_2K_2/K_1)w_7$, and $w_{10} = d/r_1$, represent the nondimensional parameters. It is observed that the nondimensional form reduces the number of the parameters from 13 in system (1) to 10 in system (5).

Accordingly, the nondimensional form of subsystems (3) and (4) can be written respectively as follow:

$$\begin{aligned}\frac{dy_1}{dt} &= y_1(1-y_1) - \left(\frac{w_2y_1}{1+w_3y_1}\right)y_3,\\ \frac{dy_3}{dt} &= \left(\frac{w_8y_1}{1+w_3y_1}\right)y_3 - w_{10}y_3,\end{aligned} \tag{6}$$

and

$$\begin{aligned}\frac{dy_2}{dt} &= w_5y_2(1-y_2) - \left(\frac{w_7y_2}{1+w_4y_2}\right)y_3,\\ \frac{dy_3}{dt} &= \left(\frac{w_9y_2}{1+w_4y_2}\right)y_3 - w_{10}y_3.\end{aligned} \tag{7}$$

3. Analysis

The Kolmogorov theorem assumes the existence of either a stable equilibrium point or stable limit cycle behavior in the positive quadrant of phase space of a two-dimensional (2D) dynamic system, provided certain conditions are satisfied [16,17]. An application of the theorem to a given 2D dynamical subsystems may impose constraints on parametric values. These conditions ensure that the parametric values are biologically relevant. Applying the Kolmogorov theorem to the two subsystems, it is observed that subsystem (6) is a Kolmogorov system under the constraint:

$$w_{10} < \frac{w_8}{1+w_3}. \tag{8}$$

Also, subsystem (7) is a Kolmogorov system when

$$w_{10} < \frac{w_9}{1+w_4}. \tag{9}$$

Further, linear stability analysis of the first Kolmogorov subsystem (6) gives the following results:

1. The equilibrium point $E_{20} = (0,0)$ is a saddle point.
2. The equilibrium point $E_{21} = (1,0)$ is a saddle point.
3. The nontrivial positive equilibrium point $E_{22} = (\bar{y}_1, \bar{y}_3)$ for system (6) always exists (Kolmogorov system), and is given by:

$$\begin{aligned}\bar{y}_1 &= w_{10}/(w_8 - w_3w_{10}),\\ \bar{y}_3 &= (1-\bar{y}_1)(1+w_3\bar{y}_1)/w_2.\end{aligned} \tag{10}$$

The necessary condition for linear stability of E_{22} is:

$$w_{10} > \frac{(w_3-1)w_8}{(w_3+1)w_3}. \tag{11}$$

Thus E_{22} is the only stable equilibrium point if

$$\frac{(w_3-1)w_8}{(w_3+1)w_3} < w_{10} < \frac{w_8}{(1+w_3)}, \tag{12}$$

while subsystem (6) will have a limit cycle for

$$w_{10} < \frac{(w_3-1)w_8}{(w_3+1)w_3} < \frac{w_8}{(1+w_3)}, \quad w_3 > 1. \tag{13}$$

Table 1
Behavior of subsystems (6) and (7) for a range of parameters

Parameters kept constant	Parameter varied	Analytical behavior	Numerical behavior
For subsystem (6)			
$w_2 = 6.001$	$0 < w_{10} < 0.450075$	Unstable	Limit cycle
$w_3 = 4.0$	$0.450075 \leqslant w_{10} < 0.6001$	Stable	Stable
$w_8 = 3.0005$			
For subsystem (7)			
$w_4 = 4.0$	$0 < w_{10} < 0.45$	Unstable	Limit cycle
$w_5 = 1.0001$	$0.45 \leqslant w_{10} < 0.6$	Stable	Stable
$w_7 = 6.0$, $w_9 = 3.0$			

Similar results are obtained for a Kolmogorov subsystem (7):

1. The equilibrium point $E_{10} = (0, 0)$ is a saddle point.
2. The equilibrium point $E_{11} = (1, 0)$ is saddle point.
3. The nontrivial positive equilibrium point $E_{12} = (\bar{y}_2, \bar{y}_3)$ for system (7) is given by:

$$\begin{aligned} \bar{y}_2 &= w_{10}/(w_9 - w_4 w_{10}), \\ \bar{y}_3 &= w_5(1 - \bar{y}_2)(1 + w_4\bar{y}_2)/w_7. \end{aligned} \tag{14}$$

The necessary condition for linear stability of E_{12} is:

$$w_{10} > \frac{(w_4 - 1)w_9}{(w_4 + 1)w_4}. \tag{15}$$

Thus E_{12} is the only stable equilibrium point if:

$$\frac{(w_4 - 1)w_9}{(w_4 + 1)w_4} < w_{10} < \frac{w_9}{(1 + w_4)}. \tag{16}$$

While subsystem (7) will have limit cycle for:

$$w_{10} < \frac{(w_4 - 1)w_9}{(w_4 + 1)w_4} < \frac{w_9}{(1 + w_4)}, \quad w_4 > 1. \tag{17}$$

Therefore, if we select our parametric values in such a way that conditions (13) and (17) are fulfilled, then we would expect the subsystems (6) and (7) to display a stable limit cycle in the positive quadrant of phase space.

Table 1 shows the behavior of the equilibrium point of subsystems (6) and (7) in the positive quadrant for a range of parameter values. The results in column 3 are based on theoretical considerations, and the results in column 4 are obtained by solving the subsystems (6) and (7) numerically using 6th order Runge–Kutta method/predictor–corrector method. The presence of a limit cycle is shown in Fig. 1(a) and (b) for $w_2 = 6.001$, $w_3 = 4.0$, $w_8 = 3.0005$, $w_{10} = 0.2$.

Similar results are presented for subsystem (7) in Fig. 2(a) and (b) a limit cycle is obtained for subsystem (7) when $w_4 = 4.0$, $w_5 = 1.0001$, $w_7 = 6.0$, $w_9 = 3.0$, and $w_{10} = 0.2$.

For the complete three-dimensional (3D) dynamical system, the following conjecture is made: "*If two 2D subsystems of a 3D system separately are in oscillatory mode then the complete 3D system would exhibit either a stable limit cycle or chaotic dynamics*".

4. Analysis of the 3D dynamic system

In this section we shall study the dynamic behavior of the solution of the nondimensional three-species food web model (5). Consider the general form of system (5) as:

$$\frac{dy_i}{dt} = G_i(y_1, y_2, y_3), \quad y_i(0) \geqslant 0; \quad i = 1, 2, 3. \tag{18}$$

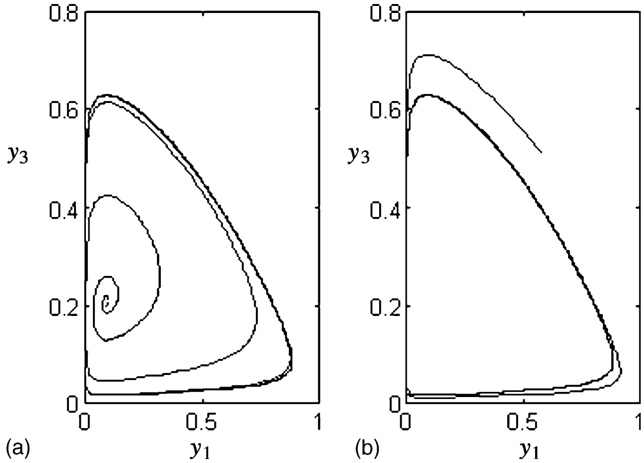

Fig. 1. For subsystem (6): (a) converge to a limit cycle from inside; (b) converge to the same limit cycle from outside.

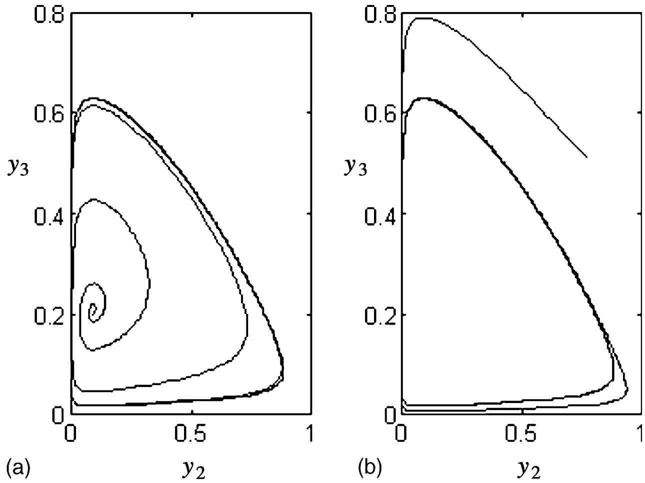

Fig. 2. For subsystem (7): (a) converge to a limit cycle from inside; (b) converge to the same limit cycle from outside.

Obviously, these functions are continuous on the positive octant $R_+^3 = \{(y_1, y_2, y_3), y_i \geqslant 0, i = 1, 2, 3\}$. Moreover, they are Lipschizian on R_+^3. Therefore, solution of system (18) with nonnegative initial condition exists and unique. Indeed, if $y_1(0) > 0$, then uniqueness of solution of initial value problems keeps the trajectory in R_+^3, $y_1(t) > 0$ for all $t > 0$. Same is true for $y_i(t)$, $i = 2, 3$. Hence, the interior of R_+^3 is invariant for model (18). In the following lemma we prove the boundedness of the solution of the system (5).

Lemma 1. *The solution* $y_1(t)$, $y_2(t)$, $y_3(t)$ *of system* (5) *is bounded for all* $t \geqslant 0$.

Proof. Since $\mathrm{d}y_1/\mathrm{d}t \leqslant y_1(1 - y_1)$ and $\mathrm{d}y_2/\mathrm{d}t \leqslant w_5 y_2(1 - y_2)$, then

$$\lim_{t\to\infty} \sup y_i(t) \leqslant 1, \quad i = 1, 2. \tag{19}$$

Consider

$$z = \frac{w_8}{w_2} y_1 + \frac{w_9}{w_7} y_2 + y_3$$

then from system (5), we get

$$\frac{dz}{dt} \leqslant \frac{w_8}{w_2}y_1 + \frac{w_5 w_9}{w_7}y_2 - w_{10}y_3.$$

Further simplifications yield

$$\frac{dz}{dt} \leqslant \frac{w_8}{w_2}y_1 - \min(1, w_{10})\left[\frac{w_9}{w_7}y_2 + y_3\right] + \frac{w_9}{w_7}y_2(1 + w_5).$$

Using (19), we get

$$\frac{dz}{dt} \leqslant \alpha - \beta z,$$

where

$$\alpha = \frac{w_8}{w_2}[1 + \min(1, w_{10})] + \frac{w_9}{w_7}[1 + w_5] \quad \text{and} \quad \beta = \min(1, w_{10}).$$

Hence $z(t) \leqslant (\alpha/\beta) + ce^{-\beta t}$, c is the constant of integration.

Thus for t sufficiently large, there is a small positive number ε so that:

$$z(t) \leqslant \frac{\alpha}{\beta} + \varepsilon.$$

Since y_1 and y_2 are bounded, this implies that there exists a bound for y_3 in R^3_+ . That is: $y_3(t) \leqslant B$ for some positive number B, and hence the solution is bounded. □

The following theorem provides necessary condition for survival of the common predator for system (5).

Theorem 1. *A necessary condition for predator species y_3 to survive is*

$$w_{10} < \frac{w_8}{1 + w_3} + \frac{w_9}{1 + w_4}. \tag{20}$$

Proof. Consider

$$\begin{aligned}\frac{dy_3}{dt} &= y_3\left[\frac{w_8 y_1}{1 + w_3 y_1 + w_4 y_2} + \frac{w_9 y_2}{1 + w_3 y_1 + w_4 y_2} - w_{10}\right],\\ &\leqslant y_3\left[\frac{w_8 y_1}{1 + w_3 y_1} + \frac{w_9 y_2}{1 + w_4 y_2} - w_{10}\right],\\ &\leqslant y_3\left[\frac{w_8}{1 + w_3} + \frac{w_9}{1 + w_4} - w_{10}\right], \quad \text{using (19)}.\end{aligned}$$

This yield $y_3(t) \leqslant y_3(0)e^{At}$, where

$$A = \left[\frac{w_8}{1 + w_3} + \frac{w_9}{1 + w_4} - w_{10}\right].$$

Clearly, if $A < 0$, then $\lim_{t\to\infty} y_3(t) = 0$.

Hence, A should be positive and (20) is the necessary condition for survival of the predator. Moreover, according to Lemma 1, there is a positive number B and T so that for all $t > T$, $y_3(t) \leqslant B < y_3(0)e^{At}$. □

It is concluded that the predator faces extinction if condition (20) not satisfied. According to the criterion 2, model (5) is logically correct if it can be reduced to two independent subsystems in the absence of other prey. Further these two subsystems have to be Kolmogorov if they are biologically feasible. Accordingly, for the food web under consideration, the condition (20) will always be satisfied.

At most, seven nonnegative equilibrium points are possible for system (5). The existence and local stability conditions of these equilibrium points are given below:

(1) The equilibrium points $E_0 = (0, 0, 0)$, $E_1 = (1, 0, 0)$, and $E_2 = (0, 1, 0)$ always exist for system (5), and they are saddle points. However, the point $(0, 0, \alpha)$ with $\alpha > 0$ does not exist.

(2) The point $E_{32} = (\bar{y}_1, 0, \bar{y}_3)$, where $\bar{y}_1$ and $\bar{y}_3$ are given by Eq. (10). This point always exists for the Kolmogorov system (5). The variational matrix $J = \{a_{ij}\}$ is

$$a_{11} = \bar{y}_1\left[-1 + \frac{w_3(1-\bar{y}_1)}{(1+w_3\bar{y}_1)}\right], \quad a_{12} = \bar{y}_1\left[-w_1 + \frac{w_4(1-\bar{y}_1)}{(1+w_3\bar{y}_1)}\right], \quad a_{13} = -\frac{w_2 w_{10}}{w_8}, \quad a_{21} = 0,$$
$$a_{22} = w_5(1 - w_6\bar{y}_1) - \frac{w_7}{w_2}(1-\bar{y}_1), \quad a_{23} = 0, \quad a_{31} = \frac{w_8(1-\bar{y}_1)}{w_2(1+w_3\bar{y}_1)},$$
$$a_{32} = \frac{[w_9 + (w_3w_9 - w_4w_8)\bar{y}_1]}{w_2(1+w_3\bar{y}_1)}(1-\bar{y}_1), \quad a_{33} = 0.$$

The coefficients of the characteristic equation $|J - \lambda I| = \lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0$ are:

$$A_1 = -(a_{11} + a_{22}),$$
$$A_2 = a_{11}a_{22} - a_{13}a_{31},$$
$$A_3 = a_{13}a_{22}a_{31}.$$

Thus, $A_4 = A_1A_2 - A_3 = -(a_{11})^2 a_{22} + a_{11}a_{13}a_{31} - a_{11}(a_{22})^2$.

According to Routh–Hurwitz criterion, the necessary and sufficient conditions for local asymptotic stability of the equilibrium point are $A_i > 0, i = 1, 3, 4$ [16]. Hence, E_{32} is locally asymptotically stable if a_{11} as well as a_{22} are negative. This gives

$$\frac{(w_3 - 1)w_8}{(w_3 + 1)w_3} < w_{10}, \quad [w_7 - w_2w_5w_6 + w_3(w_7 - w_2w_5)]w_{10} < w_8(w_7 - w_2w_5). \tag{21}$$

Observe that, if $E_{22} = (\bar{y}_1, \bar{y}_3)$ is unstable, then $E_{32} = (\bar{y}_1, 0, \bar{y}_3)$ is also unstable. Further, if E_{22} stable E_{32} may become unstable for a suitable choice of parametric values.

(3) The point $E_{31} = (0, \bar{y}_2, \bar{y}_3)$, where $\bar{y}_2$ and $\bar{y}_3$ are given by Eq. (14), exists for a Kolmogorov system (5), and the coefficients of variational matrix are

$$a_{11} = (1 - w_1\bar{y}_2) - \frac{w_2w_5}{w_7}(1-\bar{y}_2), \quad a_{12} = 0, \quad a_{13} = 0,$$
$$a_{21} = \bar{y}_2\left[-w_2w_6 + \frac{w_3w_5(1-\bar{y}_2)}{(1+w_4\bar{y}_2)}\right], \quad a_{22} = \bar{y}_2\left[-w_5 + \frac{w_4w_5(1-\bar{y}_2)}{(1+w_4\bar{y}_2)}\right], \quad a_{23} = -\frac{w_7w_{10}}{w_9},$$
$$a_{31} = \frac{w_5\left[w_8 + (w_4w_8 - w_3w_9)\bar{y}_2\right]}{w_7(1+w_4\bar{y}_2)}(1-\bar{y}_2), \quad a_{32} = \frac{w_5w_9(1-\bar{y}_2)}{w_7(1+w_4\bar{y}_2)}, \quad a_{33} = 0.$$

The coefficients of the characteristic equation are:

$$A_1 = -(a_{11} + a_{22}),$$
$$A_2 = a_{11}a_{22} - a_{23}a_{32},$$
$$A_3 = a_{11}a_{23}a_{32}.$$

Therefore,

$$A_4 = -(a_{11})^2 a_{22} + a_{11}a_{23}a_{32} - a_{11}(a_{22})^2.$$

Hence, according to Routh–Hurwitz criterion, E_{31} is locally asymptotically stable if a_{11} as well as a_{22} are negative, which give:

$$[w_2w_5 - w_1w_7 + w_4(w_2w_5 - w_7)]w_{10} < w_9(w_2w_5 - w_7), \quad \frac{(w_4 - 1)w_9}{(w_4 + 1)w_4} < w_{10}, \tag{22}$$

respectively. Clearly, if $E_{12} = (\bar{y}_2, \bar{y}_3)$ is unstable then $E_{31} = (0, \bar{y}_2, \bar{y}_3)$ is also unstable. However, for a suitable choice of parametric values E_{31} may be unstable even when E_{12} is a stable point.

(4) The point $E_{33} = (\hat{y}_1, \hat{y}_2, 0)$, where:

$$\hat{y}_1 = (1 - w_1)/(1 - w_1w_6), \quad \hat{y}_2 = (1 - w_6)/(1 - w_1w_6), \tag{23}$$

exists for system (5) in the positive plane (y_1, y_2) provided

$$w_i > 1, \quad \text{or} \quad w_i < 1, \quad i = 1, 6. \tag{24}$$

The coefficients of the variational matrix are:

$$\begin{aligned}
&a_{11} = -\hat{y}_1, \quad a_{12} = -w_1\hat{y}_1, \quad a_{13} = -w_2\hat{y}_1/(1 + w_3\hat{y}_1 + w_4\hat{y}_2),\\
&a_{21} = -w_5w_6\hat{y}_2, \quad a_{22} = -w_5\hat{y}_2, \quad a_{23} = -w_7\hat{y}_2/(1 + w_3\hat{y}_1 + w_4\hat{y}_2),\\
&a_{31} = 0, \quad a_{32} = 0, \quad a_{33} = \frac{w_8\hat{y}_1}{1 + w_3\hat{y}_1 + w_4\hat{y}_2} + \frac{w_9\hat{y}_2}{1 + w_3\hat{y}_1 + w_4\hat{y}_2} - w_{10}.
\end{aligned}$$

The coefficients of the characteristic equation are

$$\begin{aligned}
&A_1 = -(a_{11} + a_{22} + a_{33}),\\
&A_2 = a_{11}a_{33} + a_{22}a_{33} + a_{11}a_{22} - a_{21}a_{12},\\
&A_3 = a_{11}a_{22}a_{33} - a_{21}a_{12}a_{33}.
\end{aligned}$$

Therefore,

$$A_4 = -(a_{11})^2(a_{22} + a_{33}) - (a_{22})^2(a_{11} + a_{33}) - (a_{33})^2(a_{11} + a_{22}) - 4a_{11}a_{22}a_{33} + (a_{11} + a_{22} + 2a_{33})a_{21}a_{12}.$$

Hence, according to Routh–Hurwitz criterion, E_{33} is locally asymptotically stable if the following conditions are satisfied:

$$\begin{aligned}
&a_{33} < 0; \quad w_i > 1, \quad i = 1, 6;\\
&(a_{11} + a_{22} + 2a_{33})a_{21}a_{12} > (a_{11})^2(a_{22} + a_{33}) + (a_{22})^2(a_{11} + a_{33}) + (a_{33})^2(a_{11} + a_{22}) + 4a_{11}a_{22}a_{33}.
\end{aligned} \tag{25}$$

Observe that, for Kolmogorov systems the coefficient a_{33}, at the equilibrium point E_{33}, is always positive. Hence E_{33} is unstable point whenever it exists.

(5) The positive equilibrium point $E^* = (y_1^*, y_2^*, y_3^*)$ exists if and only if there is a positive solution to the following set of nonlinear equations:

$$\begin{aligned}
&(1 - y_1 - w_1y_2) - \frac{w_2y_3}{1 + w_3y_1 + w_4y_2} = 0,\\
&w_5(1 - y_2 - w_6y_1) - \frac{w_7y_3}{1 + w_3y_1 + w_4y_2} = 0,\\
&\frac{w_8y_1}{1 + w_3y_1 + w_4y_2} + \frac{w_9y_2}{1 + w_3y_1 + w_4y_2} - w_{10} = 0.
\end{aligned} \tag{26}$$

The existence and uniqueness of the positive equilibrium point E^* is established in the following theorem.

Theorem 2. *The positive equilibrium point $E^* = (y_1^*, y_2^*, y_3^*)$ exists and is unique for system* (5) *if and only if one of the following sets of conditions is satisfied.*

$$m_{11}m_{22} > m_{21}m_{12}, \quad m_{22}b_{11} > m_{12}b_{21}, \quad \text{and} \quad m_{11}b_{21} > m_{21}b_{11}, \tag{27}$$

$$m_{11}m_{22} < m_{21}m_{12}, \quad m_{22}b_{11} < m_{12}b_{21}, \quad \text{and} \quad m_{11}b_{21} < m_{21}b_{11}, \tag{28}$$

where, $m_{11} = w_2w_5w_6 - w_7$, $m_{12} = w_2w_5 - w_1w_7$, $b_{11} = w_2w_5 - w_7$, $m_{21} = w_8 - w_3w_{10}$, $m_{22} = w_9 - w_4w_{10}$, $b_{21} = w_{10}$.

Proof. The first two equations in system (26) yield:

$$\frac{y_3}{1 + w_3y_1 + w_4y_2} = \frac{1}{w_2}(1 - y_1 - w_1y_2) = \frac{w_5}{w_7}(1 - y_2 - w_6y_1). \tag{29}$$

Then system (26) reduced to the following 2×2 linear system, for $y_3 \neq 0$

$$\begin{aligned}
&m_{11}y_1 + m_{12}y_2 = b_{11},\\
&m_{21}y_1 + m_{22}y_2 = b_{21}.
\end{aligned} \tag{30}$$

Clearly, system (30) has a unique solution if and only if

$$m_{11}m_{22} \neq m_{12}m_{21}.$$

And, the solution is

$$y_1^* = (m_{22}b_{11} - m_{12}b_{21})/(m_{11}m_{22} - m_{12}m_{21}),$$
$$y_2^* = (m_{11}b_{21} - m_{21}b_{11})/(m_{11}m_{22} - m_{12}m_{21}). \quad (31)$$

Substituting (31) into (29) yields the value of y_3^*. Moreover, y_1^* and y_2^* are positive if and only if one of the conditions (27) and (28) is satisfied, and y_3^* is positive due to the positivity of logistic terms in (29). Hence the proof is complete. □

Although the coefficients of variational matrix and then the coefficients of characteristic equation, for the equilibrium point E^* have been obtained similarly, but applications of Routh–Hurwitz criterion give rise to complex set of mathematical conditions for stability. No biologically meaningful conclusion could be drawn from these. Therefore, in the following section, numerical simulations are used to study the dynamic behavior of the system in positive octant. The analytical results obtained in this section are used to fix the parameters in biologically feasible range. Thus, if the parameters satisfy conditions (13) and (17) then all the boundary equilibrium points of 3D system will be unstable. If the interior equilibrium point is also linearly unstable, then the system may have a limit cycle or chaos.

5. Numerical simulation

Numerical integration of system (5) was used to investigate the global dynamic behavior of the system. The objective was to explore the possibility of chaotic behavior. Extensive numerical simulations were carried out for various parameter values and for different sets of initial conditions. Our choice of parameters was guided by two factors: First, the system had to be biologically feasible, and second, the two subsystems had to have limit cycles. One such set of parameter values that led to cycling in each of subsystems (6) and (7), is presented here:

$$w_1 = 1.0, \quad w_2 = 6.001, \quad w_3 = 4.0, \quad w_4 = 4.0, \quad w_5 = 1.0001, \quad w_6 = 1.004, \quad w_7 = 6.0,$$
$$w_8 = 3.0005, \quad w_9 = 3.0, \quad w_{10} = 0.2. \quad (32)$$

We observed that all possible equilibrium states except the nontrivial positive state E^* were saddle points/unstable for the above set of values.

The Fig. 3 shows the dynamic behavior of the three species after eliminating the transient effect. The figure clearly suggests the irregular chaotic behavior. The 3D phase plot in Fig. 4, obtained after letting system (5) run for 100,000 time steps and examining only the last 50,000 time steps to eliminate the transient effect, also suggests the presence of a chaotic attractor.

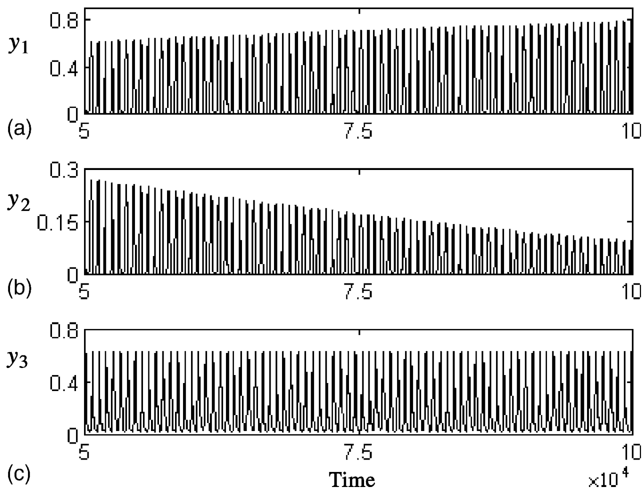

Fig. 3. (a) y_1 vs. time; (b) y_2 vs. time; (c) y_3 vs. time.

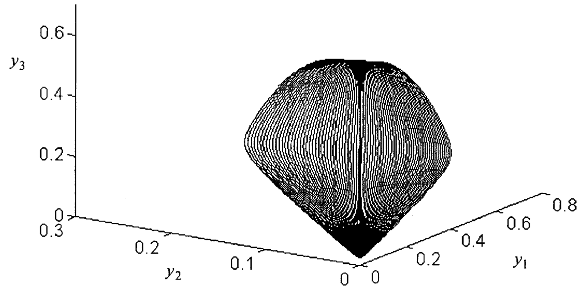

Fig. 4. Three-dimensional phase plot for system (5) at the parametric values given by (32).

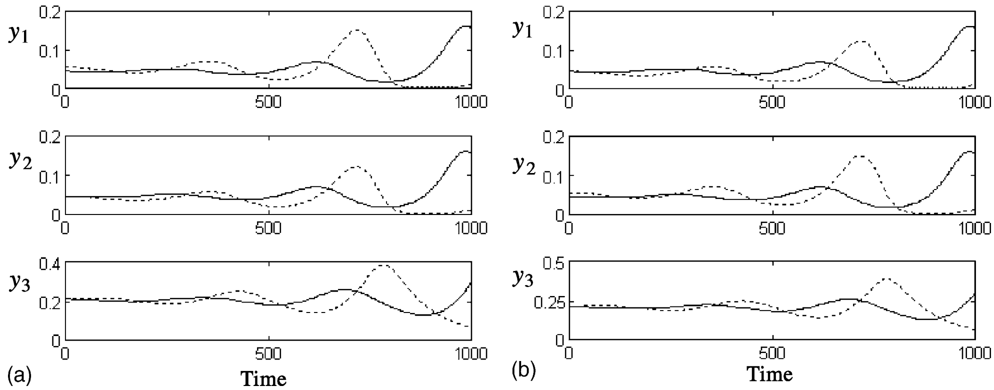

Fig. 5. Sensitive dependence on initial conditions. —: Initial conditions same as attractor in Fig. 4. (a) $\cdots$: Initial y_1 is increased by 0.01, y_2, y_3 unchanged. (b) $\cdots$: Initial y_2 is increased by 0.01, y_1, y_3 unchanged.

The unique character of chaotic dynamics may be seen most clearly by sensitivity to initial conditions. That is, a small change in initial conditions may lead to different dynamic behavior. We have illustrated this behavior by comparing the trajectories generated by changing the initial conditions slightly for the set of parameter values that led to the chaotic dynamics illustrated previously in Fig. 4. One set of initial conditions was on the attractor, and in the other set y_1 was increased by 0.01, keeping y_2 and y_3 fixed. The trajectories are shown in Fig. 5(a), which demonstrates the sensitive dependence of the trajectories on initial condition. A similar result is obtained for y_2 Fig. 5(b) (keeping y_1 and y_3 fixed).

Another set of parametric values that led to cycling in each of subsystems (6) and (7) is chosen as:

$$\begin{aligned} &w_1 = 1.001, \quad w_2 = 3.0, \quad w_3 = 1.5, \quad w_4 = 2.0, \quad w_5 = 1.167, \quad w_6 = 1.006, \quad w_7 = 3.5, \quad w_8 = 1.35, \\ &w_9 = 1.925, \quad w_{10} = 0.06. \end{aligned} \tag{33}$$

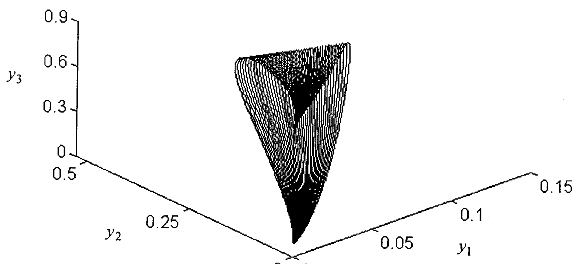

Fig. 6. Three-dimensional phase plot for system (5) at the parametric values given by (33).

Clearly, the parametric values for subsystem (6) are completely different than those for subsystem (7). Moreover, all the nonnegative equilibrium states of system (5) were saddle point/unstable for this set of values. The presence of chaotic attractor is shown in Fig. 6, for the above set of parametric values, after eliminating the transient effect. Sensitivity to initial values was observed for the trajectories given in Fig. 6.

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