The Dynamics Of Tri-Trophic Food Web Model With Mixed Selection Of Functional Responses

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Abstract: In this paper, a tri-trophic food web model with mixed selection of functional responses is proposed and analyzed. It is assumed that, the food web system consisting of one prey and two predators, in which there is an explicit inter-specific competition between the two predators. Dynamical behavior of all possible equilibrium points has been investigated locally as well as globally. Sufficient conditions for the system to be uniformly persistent and / or extinction have been derived.

1. Introduction

An important and ubiquitous problem in predator-prey theory and related topics in mathematical ecology concerns the concepts persistence and extinction of species. The persistence and extinction of interacting species in a food chain and food web models have been studied extensively in the literatures see [2, 3, 7, 8, 9, 12]. Most of these studies have been focused on the permanent and global stability of a model of living resources supporting two competing predators. It may be pointed out that all the above studies are based on the traditional prey dependent models.

Recently, Cantrell et al 2004 [1] proposed and analyzed a mathematical model of two consumer one resource with one of the consumer species exhibits intra-specific feeding interference but there is no inter-specific competition between the two consumer species. It is assumed that one consumer species exhibits Holling type-II functional response while the other consumer species exhibits Beddington-DeAngelis functional response. They shown that the two consumer species can coexist upon the single limiting resource in the sense of uniform persistence and the system has a globally stable positive equilibrium. Maiti et al 2006 [11], proposed and analyzed a tri-trophic food chain model composed of logistic prey, a classical Lotka-Volterra functional response for prey and predator, and a Holling type-II functional response for predator and top predator.

Keeping the above in view in this paper, the model of Cantrell et al [1], is modified so that, it contains inter-specific competition between the two predators. The stability analysis of the proposed model is investigated analytically. The uniform persistence and the extinction conditions are obtained.

2. A tri-trophic food web model

Consider a tri-trophic food web model consisting of two predators competing for a single prey in which the prey species grows logistically in the absence of predator species. Furthermore, the functional and numerical responses of the first predator are taken to be of Holling type-II form while those associated with the other predator species are taken of Beddington-DeAngils form. Let $u(T)$ represent the density of prey species at time T and

$v(T)$, $w(T)$ be the density of predator species that compete with each other for the prey. Therefore, the dynamics of such tri-trophic food web may be governed by the following system of autonomous differential equations.

$$\begin{aligned}
\frac{du}{dT} &= ru\left(1-\frac{u}{k}\right)-\frac{a_1uv}{1+b_1u}-\frac{a_2uw}{1+b_2u+cw}; u(0)\geq 0 \\
\frac{dv}{dT} &= v\left(-d_1-\alpha w+\frac{e_1u}{1+b_1u}\right); v(0)\geq 0 \\
\frac{dw}{dT} &= w\left(-d_2-\beta v+\frac{e_2u}{1+b_2u+cw}\right); w(0)\geq 0
\end{aligned} \tag{1}$$

Here all the parameters of the system (1), which denoted by $r, k, a_i, b_i, c, d_i, e_i, \alpha, \beta \ (i=1,2)$, are assumed to be positive constants. Now, to reduce the number of parameters, we are nondimensionalize system (1) with the following nondimensional variables and parameters.

$$\begin{aligned}
&t = rT,\ x=\frac{u}{k},\ y=\frac{a_1v}{r},\ z=\frac{a_2w}{r}, w_1=b_1k,\ w_2=b_2k, w_3=\frac{cr}{a_2}, \\
&w_4=\frac{d_1}{r},\ w_5=\frac{\alpha}{a_2}, w_6=\frac{e_1k}{r},\ w_7=\frac{d_2}{r},\ w_8=\frac{\beta}{a_1},\ w_9=\frac{e_2k}{r}
\end{aligned} \tag{2}$$

Then, the nondimensionalized form of system (1) can be written as follows:

$$\begin{aligned}
\frac{dx}{dt} &= x\left[1-x-\frac{y}{1+w_1x}-\frac{z}{1+w_2x+w_3z}\right]=xf_1(x,y,z)=F_1(x,y,z) \\
\frac{dy}{dt} &= y\left[-w_4-w_5z+\frac{w_6x}{1+w_1x}\right]=yf_2(x,y,z)=F_2(x,y,z) \\
\frac{dz}{dt} &= z\left[-w_7-w_8y+\frac{w_9x}{1+w_2x+w_3z}\right]=zf_3(x,y,z)=F_3(x,y,z)
\end{aligned} \tag{3}$$

Observe that, the interaction functions F_1, F_2 and F_3 of the system (3) are continuous on R_+^3, where $R_+^3=\{(x,y,z): x\geq 0,\ y\geq 0,\ z\geq 0\}$ and have a continuous partial derivations, therefore these functions are Lipschitzian on R_+^3. Hence, solution of system (3) with nonnegative initial condition exists and is unique. Further, it is easy to prove the following theorem, which establishes the uniform boundedness of the system (3).

Theorem 1. All the solutions of the system (3), which start in the interior of R_+^3 (i.e. $Int.R_+^3$), are uniformly bounded.

It is well known that, the ecological system is said to be dissipative if the solution of the system, which initiate in the R_+^3 is uniformly bounded as $t\to\infty$ [5]. Therefore, system (3) is dissipative.

3. ***A tri-trophic food web analysis with persistence***

The tri-trophic food web system (3) have at most four non negative boundary equilibrium points, say $E_0 = (0,0,0)$, $E_1 = (1,0,0)$, $E_2 = (\bar{x}, \bar{y}, 0)$, $E_3 = (\tilde{x}, 0, \tilde{z})$ and one positive equilibrium point $E^* = (x^*, y^*, z^*)$ belongs to $Int.R_+^3$.

- The equilibrium points E_0 and E_1 are always exist.
- The equilibrium point $E_2 = (\bar{x}, \bar{y}, 0)$ where

$$\bar{x} = \frac{w_4}{w_6 - w_1 w_4}; \quad \bar{y} = (1-\bar{x})(1+w_1\bar{x}) \tag{4}$$

is a planer equilibrium point, which exists in the interior of positive quadrant of $x - y$ plane under the following condition.

$$w_4 < w_6/(1+w_1) \tag{5}$$

- The equilibrium point $E_3 = (\tilde{x}, 0, \tilde{z})$ where

$$\tilde{x} = \frac{1}{2}\left[\left(1 - \frac{w_9 - w_2 w_7}{w_3 w_9}\right) + M\right]; \; \tilde{z} = \frac{(w_9 - w_2 w_7)\tilde{x} - w_7}{w_3 w_7} \tag{6}$$

with $M = \left[\left(\frac{w_9 - w_2 w_7}{w_3 w_9} - 1\right)^2 + 4\frac{w_7}{w_3 w_9}\right]^{1/2}$

Is a planer equilibrium point, which exists in the interior of positive quadrant of $x - z$ plane under the following condition.

$$0 < \frac{w_7}{w_9 - w_2 w_7} < \tilde{x} < 1 \tag{7}$$

- The positive equilibrium point $E^* = (x^*, y^*, z^*)$, exists in the $Int.R_+^3$ if and only if

$$0 < \frac{w_4}{w_6 - w_1 w_4} = \bar{x} < x^* \tag{8a}$$

$$0 < \frac{(w_6 - w_1 w_4)x^* - w_4}{(w_9 - w_2 w_7)x^* - w_7} < \frac{w_5 B_1}{w_3 w_7} \tag{8b}$$

with

$$y^* = \frac{1}{w_5 w_8 B_1 B_2}\Big[w_5 B_1\big((w_9 - w_2 w_7)x^* - w_7\big) - w_3 w_7\big((w_6 - w_1 w_4)x^* - w_4\big)\Big] \tag{9a}$$

$$z^* = \frac{(w_6 - w_1 w_4)x^* - w_4}{w_5 B_1}; \text{ and } B_1 = 1 + w_1 x^*; \; B_2 = 1 + w_2 x^* + w_3 z^* \tag{9b}$$

Now the local dynamical behavior of system (3) near the above equilibrium points is investigated, and then the following results are obtained.

The Jacobean matrix at the equilibrium points E_0, E_1, E_2, E_3, and E^* can be written, respectively, as the following

$$J(E_0)=\begin{bmatrix}1 & 0 & 0\\ 0 & -w_4 & 0\\ 0 & 0 & -w_7\end{bmatrix};\ J(E_1)=\begin{bmatrix}-1 & -\dfrac{1}{1+w_1} & -\dfrac{1}{1+w_2}\\ 0 & -w_4+\dfrac{w_6}{1+w_1} & 0\\ 0 & 0 & -w_7+\dfrac{w_9}{1+w_2}\end{bmatrix};$$

$$J(E_2)=\begin{bmatrix}\bar{x}\left[-1+\dfrac{w_1(1-\bar{x})}{1+w_1\bar{x}}\right] & -\dfrac{\bar{x}}{1+w_1\bar{x}} & -\dfrac{\bar{x}}{1+w_2\bar{x}}\\ \dfrac{w_6(1-\bar{x})}{1+w_1\bar{x}} & 0 & -w_5\bar{y}\\ 0 & 0 & -w_7-w_8\bar{y}+\dfrac{w_9\bar{x}}{1+w_2\bar{x}}\end{bmatrix};$$

$$J(E_3)=\begin{bmatrix}\tilde{x}\left[-1+\dfrac{w_2\tilde{z}}{\gamma^2}\right] & -\dfrac{\tilde{x}}{1+w_1\tilde{x}} & -\dfrac{(1+w_2\tilde{x})\tilde{x}}{\gamma^2}\\ 0 & -w_4-w_5\tilde{z}+\dfrac{w_6\tilde{x}}{1+w_1\tilde{x}} & 0\\ \dfrac{w_9\tilde{z}(1+w_3\tilde{z})}{\gamma^2} & -w_8\tilde{z} & -\dfrac{w_3w_9\tilde{x}\tilde{z}}{\gamma^2}\end{bmatrix};$$

with $\gamma=(1+w_2\tilde{x}+w_3\tilde{z})$. Finally we have

$$J(E^*)=\begin{bmatrix}a_{11} & a_{12} & a_{13}\\ a_{21} & a_{22} & a_{23}\\ a_{31} & a_{32} & a_{33}\end{bmatrix}$$

with

$$a_{11}=x^*\left[-1+\frac{w_1y^*}{B_1^2}+\frac{w_2z^*}{B_2^2}\right],\ a_{12}=-\frac{x^*}{B_1}<0,\ a_{13}=-\frac{(1+w_2x^*)x^*}{B_2^2}<0$$

$$a_{21}=\frac{w_6y^*}{B_1^2}>0,\ a_{22}=0,\ a_{23}=-w_5y^*<0,$$

$$a_{31}=\frac{w_9(1+w_3z^*)z^*}{B_2^2}>0,\ a_{32}=-w_8z^*<0,\ a_{33}=-\frac{w_3w_9x^*z^*}{B_2^2}<0.$$

Here B_1 and B_2 are given by (9b).

Obviously, the eigenvalues of $J(E_0)$ are given by $\lambda_{01}=1>0, \lambda_{02}=-w_4<0,$ and $\lambda_{03}=-w_7<0$. Hence, $E_0=(0,0,0)$ is unstable saddle point with locally stable manifold in the $y-z$ plane and with locally unstable manifold in the x-direction.

The eigenvalues of $J(E_1)$ are $\lambda_{11}=-1<0, \lambda_{12}=-w_4+\frac{w_6}{1+w_1}$, $\lambda_{13}=-w_7+\frac{w_9}{1+w_2}$. This implies that $E_1=(1,0,0)$ is locally asymptotically stable in the R_+^3 if and only if

$w_4 > \frac{w_6}{1+w_1}$ and $w_7 > \frac{w_9}{1+w_2}$, or equivalently the planer equilibrium points E_2 and E_3 do not exist. However, E_1 is unstable saddle point with non-empty stable and unstable manifolds if and only if $w_4 < \frac{w_6}{1+w_1}$ and / or $w_7 < \frac{w_9}{1+w_2}$ (i.e. at least one of planer equilibrium points exist). Further, the dynamical behavior near the planer equilibrium points E_2 and E_3 is given in the following two theorems respectively.

Theorem 2. Suppose that the planer equilibrium point $E_2 = (\bar{x}, \bar{y}, 0)$ of system (3) exists, and let

$$w_4 > \frac{w_6(w_1-1)}{w_1(w_1+1)} \tag{10}$$

Then

1. E_2 is locally asymptotically stable in the R_+^3 if and only if $\lambda_{23} < 0$.
2. E_2 is unstable saddle point in the R_+^3, with locally stable manifolds in the $x-y$ plane and with unstable manifold in the $z-$direction, if and only if $\lambda_{23} > 0$.

Proof: According to the $J(E_2)$, it is easy to verify that, the eigenvalues satisfy the following relations:

$$\lambda_{21} + \lambda_{22} = \bar{x}\left[-1 + \frac{w_1(1-\bar{x})}{1+w_1\bar{x}}\right] \tag{11a}$$

$$\lambda_{21}\lambda_{22} = \frac{w_6\bar{x}(1-\bar{x})}{1+w_1\bar{x}} > 0 \tag{11b}$$

$$\lambda_{23} = -w_7 - w_8\bar{y} + \frac{w_9\bar{x}}{1+w_2\bar{x}} \tag{11c}$$

Where λ_{2j} $(j=1,2,3)$ represents the eigenvalue in the $x-, y-$ and $z-$direction respectively. Now, substituting the value of $\bar{x}$ in equation (11a) and then simplify the result yields

$$\lambda_{21} + \lambda_{22} = \frac{w_4}{w_6(w_6 - w_1w_4)}\left[w_6(w_1-1) - w_1w_4(w_1+1)\right] \tag{11d}$$

Clearly, under the given condition (10) we get $\lambda_{21} + \lambda_{22} < 0$. So according to (11b) the eigenvalues λ_{21} and λ_{22} have negative sign, and hence E_2 is locally asymptotically stable in the interior of positive quadrant of $x-y$ plane.

Now, since the eigenvalue λ_{23} describes the dynamics in the $z-$direction orthogonal on the $x-y$ plane. Hence, if $\lambda_{23} < 0$ holds, then E_2 is locally asymptotically stable in R_+^3 and the proof of (1) follows. Further, if $\lambda_{23} > 0$ holds, then E_2 is unstable saddle point in the R_+^3 with locally stable manifolds in the $x-y$ plane (due to the negativity of λ_{21} and λ_{22}) and with unstable manifold in the $z-$direction. ■

Theorem 3. Suppose that the planer equilibrium point $E_3 = (\tilde{x}, 0, \tilde{z})$ of the system (3) exists and let one of the following conditions holds.

$$w_2 \le w_3 w_9 \tag{12a}$$

$$w_3 w_9 < w_2 \text{ and } \delta_1^2 - 4\delta_2 \le 0 \tag{12b}$$

$$w_3 w_9 < w_2,\ \delta_1^2 - 4\delta_2 > 0 \text{ with } 0 < \tilde{x} \le r_1 \text{ or } r_2 \le \tilde{x} < 1 \tag{12c}$$

Then

(1) E_3 is locally asymptotically stable in the R_+^3 if and only if $\lambda_{32} < 0$.

(2) E_3 is unstable saddle point in the R_+^3, with locally stable manifolds in the $x-z$ plane and with unstable manifold in the $y-$direction, if and only if $\lambda_{32} > 0$.

Proof:- From $J(E_3)$ the eigenvalues satisfy the following relations:

$$\lambda_{31} + \lambda_{33} = -\tilde{x} + \frac{\tilde{x}\tilde{z}}{\gamma^2}(w_2 - w_3 w_9) \tag{13a}$$

$$\lambda_{31}\lambda_{33} = \frac{w_3 w_9 \tilde{x}\tilde{z}}{\gamma^2} + \frac{w_9 \tilde{x}\tilde{z}}{\gamma^3} > 0 \tag{13b}$$

$$\lambda_{32} = -w_4 - w_5 \tilde{z} + \frac{w_6 \tilde{x}}{1 + w_1 \tilde{x}} \tag{13c}$$

Now, clearly if the given condition (12a) holds then $\lambda_{31} + \lambda_{33} < 0$ and hence both the eigenvalues λ_{31} and λ_{33} are negative.

While, if the condition (12b) holds, then by substituting the values of $\tilde{x}$ and $\tilde{z}$ in equation (13a) and simplifying the resulting term we obtain

$$\lambda_{31} + \lambda_{33} = -\left(\frac{w_9}{w_7}\right)^2 \frac{\tilde{x}}{\gamma^2}\left[\tilde{x}^2 + \delta_1 \tilde{x} + \delta_2\right] = -\left(\frac{w_9}{w_7}\right)^2 \frac{\tilde{x}}{\gamma^2} p(\tilde{x}) \tag{13d}$$

Where $\delta_1 = w_7\left(1 - \frac{w_2}{w_3 w_9}\right)\left(1 - \frac{w_2 w_7}{w_9}\right) < 0$; and $\delta_2 = \frac{(w_7)^2}{w_9}\left(\frac{w_2}{w_3 w_9} - 1\right) > 0$. Obviously, the sign of $\lambda_{31} + \lambda_{33}$ is depends on the sign of quadratic function $p(\tilde{x})$. Since $\delta_1^2 - 4\delta_2 \le 0$ [due to condition (12b)], then $p(\tilde{x}) > 0$ for all values of $\tilde{x}$ and hence $\lambda_{31} + \lambda_{33} < 0$. Therefore, both the eigenvalues λ_{31} and λ_{33} are negative.

Finally, if the condition (12c) holds, then the quadratic function $p(\tilde{x})$ has two positive roots, say $r_1 = \frac{1}{2}\left[-\delta_1 - (\delta_1^2 - 4\delta_2)^{1/2}\right]$; and $r_2 = \frac{1}{2}\left[-\delta_1 + (\delta_1^2 - 4\delta_2)^{1/2}\right]$ with $r_1 < r_2$. Accordingly, $p(\tilde{x})$ can be written as $p(\tilde{x}) = (\tilde{x} - r_1)(\tilde{x} - r_2)$, and hence $p(\tilde{x}) \ge 0$ under condition (12c). Therefore, $\lambda_{31} + \lambda_{33} < 0$ or both the eigenvalues λ_{31} and λ_{33} are negative. Consequently, if the condition (12a) or (12b) or (12c) holds, then E_3 is locally asymptotically stable in the interior of positive quadrant of the $x-z$ plane.

Now since the eigenvalue λ_{32} describes the dynamics in the $y-$direction orthogonal on the $x-z$ plane. Hence, for $\lambda_{32} < 0$ we get E_3 is locally asymptotically stable in the R_+^3 and the proof of (1) is done. However, for $\lambda_{32} > 0$ we obtain E_3 is unstable saddle point in R_+^3 with locally stable manifold in the $x-z$ plane and with unstable manifold in the $y-$direction. Therefore, the proof of theorem is complete. ■

Now, according to the above two theorems the following results can be easily proved.

Corollary 4. (1) Assume that the planer equilibrium point $E_2 = (\bar{x}, \bar{y}, 0)$ of the system (3) is a locally asymptotically stable in the interior of positive quadrant of $x-y$ plane, then it is a globally asymptotically stable in the interior of positive quadrant of $x-y$ plane.
(2) Assume that the planer equilibrium point $E_3 = (\tilde{x}, 0, \tilde{z})$ of the system (3) is a locally asymptotically stable in the interior of positive quadrant of $x-z$ plane with $w_2 < w_3 w_9$, then it is a globally asymptotically stable in the interior of positive quadrant of $x-z$ plane.
Proof: - Follow directly from the above theorems with the Bendixson-Dulac criterion and Poincare-Bendixson theorem. ■

In the following we show that the tri-trophic food web system (3) is uniform persistent. Biologically, persistence of a system means the survival of all populations of the system in future time. However, from mathematical point of view, persistence of a system means that strictly positive solutions do not have omega limit points on the boundary of the non-negative cone.

Theorem 5. Suppose that the planer equilibrium points E_2 and E_3 are globally asymptotically stable in the interior of positive boundary planes $x-y$ and $x-z$ respectively. In addition, if the following set of conditions hold.

$$\lambda_{23} > 0 \text{ and } \lambda_{32} > 0 \tag{14}$$

Then system (3) is uniformly persistent.
Proof: - Consider the following function $\sigma(x, y, z) = x^{s_1} y^{s_2} z^{s_3}$, where $s_i; i = 1,2,3$ is an undetermined positive constant. Obviously, $\sigma(x, y, z)$ is C^1 positive function defined in R_+^3, and $\sigma(x, y, z) \to 0$ if $x \to 0$ or $y \to 0$ or $z \to 0$. Now, since

$$\psi(x, y, z) = \frac{\sigma'(x, y, z)}{\sigma(x, y, z)} = s_1 \frac{x'}{x} + s_2 \frac{y'}{y} + s_3 \frac{z'}{z}$$

Therefore,

$$\begin{aligned}\psi(x, y, z) = s_1 &\left(1 - x - \frac{y}{1 + w_1 x} - \frac{z}{1 + w_2 x + w_3 z}\right) \\ &+ s_2 \left(-w_4 - w_5 z + \frac{w_6 x}{1 + w_1 x}\right) \\ &+ s_3 \left(-w_7 - w_8 y + \frac{w_9 x}{1 + w_2 x + w_3 z}\right)\end{aligned}$$

Recall that, according to the given hypotheses, we have E_2 and E_3 are globally asymptotically stable in the interior of positive boundary planes $x-y$ and $x-z$ respectively. Therefore, there are no periodic orbits in these boundary planes.
So, to prove that σ is a persistence function and hence system (3) is uniform persistence [10], it is enough to show that the following conditions should be satisfied [4, 6, 13].

$$\psi(E_0) = s_1 - w_4 s_2 - w_7 s_3 > 0 \tag{15a}$$

$$\psi(E_1) = \left(-w_4 + \frac{w_6}{1+w_1}\right)s_2 + \left(-w_7 + \frac{w_9}{1+w_2}\right)s_3 > 0 \tag{15b}$$

$$\psi(E_2) = s_3\left(-w_7 - w_8\bar{y} + \frac{w_9\bar{x}}{1+w_2\bar{x}}\right) = s_3\lambda_{23} > 0 \tag{15c}$$

$$\psi(E_3) = s_2\left(-w_4 - w_5\tilde{z} + \frac{w_6\tilde{x}}{1+w_1\tilde{x}}\right) = s_2\lambda_{32} > 0 \tag{15d}$$

Note that by choosing $s_1 > 0$ sufficiently large value and keeping s_2 and s_3 fixed at small positive values then condition (17a) holds. Also, due to the existence of E_2 and E_3, the inequality (15b) holds for any positive values of s_2 and s_3. Further, the inequalities (15c) and (15d) are satisfied under the given condition (14) for any positive values of s_2 and s_3. Hence σ represents persistence function and system (3) is uniform persistent. ■

In the next corollary, sufficient conditions at which the predators species of system (3) facing extinction, and hence system (3) is not persistent (or equivalently the system faces extinction), are obtained.

Corollary 6. (1) If the conditions $w_4 > \frac{w_6}{1+w_1}$ and $w_7 > \frac{w_9}{1+w_2}$ hold then system (3) is not persistence and both the predators will go to extinction.
(2) Assume that E_2 and E_3 are globally asymptotically stable in the interior of positive quadrant of $x-y$ and $x-z$ respectively with $\lambda_{23} < 0$ and $\lambda_{32} < 0$. Then system (3) is not persistence and one of the predators y or z will goes to extinction.

Proof: - Follows directly from theorem (5). ■

Now, in order to investigate the local dynamical behavior of the positive equilibrium point $E^* = (x^*, y^*, z^*)$, the characteristic equation of the Jacobean matrix $J(E^*)$ is determined.

$$P_3(\lambda) = \lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0$$

where

$$A_1 = -(a_{11} + a_{33})$$
$$A_2 = a_{11}a_{33} - a_{13}a_{31} - a_{23}a_{32} - a_{12}a_{21}$$
$$A_3 = a_{11}a_{23}a_{32} + a_{33}a_{12}a_{21} - a_{12}a_{23}a_{31} - a_{13}a_{21}a_{32}$$

and

$$\Delta = A_1A_2 - A_3 = (a_{11} + a_{33})(a_{13}a_{31} - a_{11}a_{33}) + a_{12}(a_{11}a_{21} + a_{23}a_{31}) + a_{32}(a_{23}a_{33} + a_{13}a_{21})$$

Therefore, the local asymptotic stability conditions of E^* are established in the following theorem.

Theorem 7. Assume that the positive equilibrium point E^* exists and let the following set of conditions holds

$$\frac{w_1y^*}{B_1^2} + \frac{w_2z^*}{B_2^2} < 1 \tag{16a}$$

$$0 < w_5w_8B_2^2(B_1^2 - w_1y^*) + w_5w_9B_1 + w_6w_8 < H_1H_2 \tag{16b}$$

$$H_3 > 0 \tag{16c}$$

Where

$$H_1 = (w_2w_8B_1 - w_3w_9)\,,\ H_2 = \left(w_5B_1z^* - \frac{w_6x^*}{B_1}\right),$$

$$H_3 = \left(\frac{z^*}{{B_2}^2}a_{12} - \frac{x^*}{{B_2}^2}a_{32}\right)\left(\frac{w_2w_6x^*y^*}{{B_1}^2} - w_3w_5w_9y^*z^*\right).$$

With B_1 and B_2 are given by equation (9b) and a_{ij} are the elements of $J(E^*)$. Then E^* is locally asymptotically stable.

Proof: - According to the Routh-Hurwitz criterion, the necessary and sufficient conditions for E^* to be locally asymptotically stable are $A_1 > 0$, $A_3 > 0$ and $\Delta > 0$. Now, substituting the values of a_{ij} and then simplify the results we get

$$A_1 = -x^*\left[-1 + \frac{w_1y^*}{B_1^2} + \frac{w_2z^*}{B_2^2} - \frac{w_3w_9z^*}{B_2^2}\right]$$

$$A_3 = \frac{x^*y^*z^*}{B_1^2B_2^2}\left\{\left[w_5w_8B_2^2(w_1y^* - B_1^2) - w_5w_9B_1 - w_6w_8\right] + H_1H_2\right\}.$$

Also, we obtain

$$\Delta = -\frac{w_9x^*z^*}{B_2^3}(a_{11} + a_{33}) - \left(1 - \frac{w_1y^*}{B_1^2}\right)\left[\frac{w_3w_9(x^*)^2z^*}{B_2^2}(a_{11} + a_{33}) + \frac{w_6x^*y^*a_{12}}{B_1^2}\right] + H_3 - \frac{w_5w_9y^*z^*}{B_2^2}a_{12} - \frac{w_6x^*y^*}{B_1^2B_2^2}a_{32}$$

Thus, according to forms of A_1, A_3, Δ and the sign of a_{ij}, the Routh-Hurwitz criterion is satisfied under the conditions (16a)–(16c). ■

Let Ω be the region in the $Int.R_+^3$, where:

$$\Omega = \left\{(x, y, z) : x < 1 \text{ with } y^* < y,\ z^* < z \text{ or } y < y^*,\ z < z^*\right\}$$

Then the following theorem shows that the positive equilibrium point E^* is a global asymptotically stable in the region Ω, and hence Ω represents the basin of attraction for E^* in the $Int.R_+^3$.

Theorem 8. Assume that E^* is locally asymptotically stable with

$$\frac{w_1 y^*}{(1+w_1 x^*)} + \frac{w_2 z^*}{(1+w_2 x^* + w_3 z^*)} < 1 \tag{17}$$

Then the positive equilibrium point E^* is a globally asymptotically stable in Ω.
Proof: - Consider the following positive definite function

$$V(x,y,z) = c_1 \int_{x^*}^{x} \frac{(X-x^*)}{X} dX + c_2 \int_{y^*}^{y} \frac{(Y-y^*)}{Y} dY + c_3 \int_{z^*}^{z} \frac{Z-z^*}{Z} dZ$$

Where c_1, c_2 and c_3 are positive constants to be determined. Now, along any trajectory of system (3), we have

$$\begin{aligned}
\frac{dV}{dt} &= c_1 \frac{(x-x^*)}{x} x' + c_2 \frac{(y-y^*)}{y} y' + c_3 \frac{z-z^*}{z} z' \\
&= c_1 (x-x^*)\left[(1-x) - \frac{y}{1+w_1 x} - \frac{z}{1+w_2 x + w_3 z}\right] \\
&\quad + c_2 (y-y^*)\left[-w_4 - w_5 z + \frac{w_6 x}{1+w_1 x}\right] \\
&\quad + c_3 (z-z^*)\left[-w_7 - w_8 y + \frac{w_9 x}{1+w_2 x + w_3 z}\right]
\end{aligned}$$

Straightforward computations give that

$$\begin{aligned}
\frac{dV}{dt} &= c_1\left[-1 + \frac{w_1 y^*}{M_1} + \frac{w_2 z^*}{M_2}\right](x-x^*)^2 \\
&\quad + \left[\frac{-c_1}{M_1} - \frac{c_1 w_1 x^*}{M_1} + \frac{w_6 c_2}{M_1}\right](x-x^*)(y-y^*) \\
&\quad + \left[\frac{-c_1}{M_2} - \frac{c_1 w_2 x^*}{M_2} + \frac{c_3 w_9}{M_2} + \frac{c_3 w_9 w_3 z^*}{M_2}\right](x-x^*)(z-z^*) \\
&\quad + (-c_2 w_5 - c_3 w_8)(y-y^*)(z-z^*) - \frac{c_3 w_3 w_9}{M_2} x^* (z-z^*)^2
\end{aligned}$$

Here $M_1 = (1+w_1 x)(1+w_1 x^*)$; $M_2 = (1+w_2 x + w_3 z)(1+w_2 x^* + w_3 z^*)$. By choosing the positive constants as $c_1 = 1$; $c_2 = \frac{1+w_1 x^*}{w_6}$; $c_3 = \frac{1+w_2 x^*}{w_9(1+w_3 z^*)}$. Therefore, we obtain

$$\frac{dV}{dt} = -\left[1 - \frac{w_1 y^*}{M_1} - \frac{w_2 z^*}{M_2}\right](x - x^*)^2$$

$$+(-c_2 w_5 - c_3 w_8)(y - y^*)(z - z^*) - \frac{c_3 w_3 w_9 x^*}{M_2}(z - z^*)^2$$

Clearly, under the condition (17), we have dV/dt is negative definite in the region Ω. Thus V is a Lyapunov function with respect to all solutions in Ω, and hence E^* is a globally asymptotically stable in Ω. ■

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