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Models of Prey-Predator Systems with Two Mutualistic Predators

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Abstract

Models of population's interaction among one or two preys and two predator mutualists are studied. Sufficient conditions for local and global stability of the equilibria and uniform persistence are presented.

1. Introduction

In this paper we study models involving one or two preys and two mutualistic predators. We study both facultative and obligate mutualism. An example of this type of mutualism occurs in Red Sea [3,8], where the effect of mutualism is to increase the predator functional response. There, Yellow saddle goatfish, P. cyclostouces, and bird wrasse, Gomphosus caeruleus, tackle coral reefs from both sides so that the prey may be driven toward each other and thereby caught and eaten. Without the cooperation between these two fish species, such prey would be available only minimally and with great difficulty. Hence, the effect of each predator population on the other is to increase hunting efficiency. In earlier studies such three species models are analyzed in [3,6]. Specifically sufficient conditions for uniform persistence are obtained. Other models involving mutualism are studied in ([7,9,10] and references theirin).

In the next section we describe our model. We show that the model is meaningful, i.e. solutions with positive initial conditions stay positive and are bounded in forward time. In section 3 we consider existence of equilibria in case of facultative and obligate mutualism and study their local stability. In section 4 we derive conditions for global asymptotic stability of interior equilibria of three/four dimensional subsystems/system. In section 5 we obtain sufficient conditions for uniform persistence. In the section 6 we study a special case of our model and present numerical examples to illustrate our results.

2. The Model

The model is:

$$\frac{dx_1}{dt} = x_1 g_1(x_1) - y_1 p_1(x_1, y_2) - y_2 q_1(x_1, y_1),$$

$$\frac{dx_2}{dt} = x_2 g_2(x_2) - y_1 p_2(x_2, y_2) - y_2 q_2(x_2, y_1),$$

$$\frac{dy_1}{dt} = y_1[-s_1(y_1) + c_1 p_1(x_1, y_2) + \widetilde{c_1} p_2(x_2, y_2)], \qquad (1)$$

$$\frac{dy_2}{dt} = y_2[-s_2(y_2) + c_2 q_1(x_1, y_1) + \widetilde{c_2} q_2(x_2, y_1)],$$

$$x_i(0) = x_{i0} \geq 0\,,\ y_i(0) = y_{i0} \geq 0\,,\ i = 1,2,$$

where the variables x_1, x_2 denote prey densities and y_1, y_2 that of predators.

We assume the following hypotheses on the given functions,

(H_1) all functions are continuously differentiable so that solution to I.V.P. (1) exist, are unique and can be continued for all positive time.

$(H_2) g_i(x_i) : [0, \infty) \to R, g_i(0) > 0, g_i' < 0$; There exist K_i's such that $g_i(K_i) = 0, i = 1,2$. The constants K_1 and K_2 are the carrying capacities of x_1 and x_2 respectively.

The functions $p_i(x_i, y_2),\ i = 1,2$ are predator response functions of the predator y_1. We assume

$(H_3)\ p_i(0, y_2) = 0, \frac{\partial p_i}{\partial x_i} \geq 0, \frac{\partial p_i}{\partial y_2} \geq 0, i = 1,2.$

These conditions imply that there is no predation in absence of prey and that the predator response function $p_i(x_i, y_2)$ is an increasing function of density x_i. This hypothesis implies that y_2 increases the predation by y_1.

We also assume

$$(H_4)\ \ q_i(0, y_1) = 0\,, \qquad \frac{\partial q_i}{\partial x_i} \geq 0, \qquad and\, \frac{\partial q_i}{\partial y_1} \geq 0\,, \qquad i = 1,2.$$

The positive constants rate of conversion c_i and $\widetilde{c_i}$ denote the rate of conversion of prey biomass to predator biomass.

(H_5)Finally $s_i(y_i)$ denotes the death rate of the predator y_i and $\frac{\partial s_i}{\partial y_i} > 0\ ,\ i = 1,2.$

The first result is:

Theorem 1: The solutions to IVP (1) with positive initial conditions stay positive for $t > 0.$

Proof – We rewrite first equation in (1) as,

$$\int_0^t \frac{dx_1}{x_1} = \int_0^t \left\{ g_1\big(x_1(s)\big) - y_1(s)\frac{p_1\big(x_1(s), y_2(s)\big)}{x_1(s)} - y_2(s)\frac{q_1\big(x_1(s), y_1(s)\big)}{x_1(s)} \right\} ds,$$

where, $\lim_{x_1\to 0} \frac{p_1(x_1,y_2)}{x_1} = \frac{\partial p_1(0,y_2)}{\partial x_1} > 0$, and $\lim_{x_1\to 0} \frac{q_1(x_1,y_1)}{x_1} = \frac{\partial q_1(0,y_1)}{\partial x_1} > 0$.

Thus, $x_1(t) = x_{10} e^{\int_0^t \left(g_1 - \frac{y_1 p_1}{x_1} - \frac{y_2 q_1}{x_1}\right) ds} > 0$

Proceeding similarly we can show $x_2(t) > 0, y_1(t) > 0$ and $y_2(t) > 0\ for\ all\ t > 0.$

Theorem 2: Let $G_i = \max_{[0,K_i]}\big(s_1(0) + g_i(x)\big)\, x,\ \ i = 1,2,$ $L_i = \max_{[0,K_i]}\big(s_2(0) + g_i(x)\big)\, x,$ $i = 1,2.$

Further let,

$$\mathcal{A} = \Big\{(x_1, x_2, y_1, y_2) : 0 \le x_1 \le K_1, 0 \le x_1 \le K_2, 0 \le c_1 x_1 + \widetilde{c_1} x_2 + y_1 \le \frac{c_1 G_1 + \widetilde{c_1} G_2}{s_1(0)}, 0 \le c_2 x_1 + \widetilde{c_2} x_2 + y_2 \le \frac{c_2 L_1 + \widetilde{c_2} L_2}{s_2(0)}\Big\}. \qquad (2)$$

Then

(i) $\mathcal{A}$ is positively invariant.

(ii) $(x_1, x_2, y_1, y_2) \to \mathcal{A}\ as\ t \to \infty$

Proof – Let $0 \le x_1(0) \le K_1$. Then $u' = u g_1(u)\ , u(0) = x_1(0)$, has solution $u(t) \le K_1$. Thus by comparison Theorem [5], $x_1(t) \le K_1$. In general, $\lim sup_{t\to\infty} x_1(t) \le K_1$.

Similarly

$0 \le x_2(0) \le K_2\ implies, x_2(t) \le K_2$. In general, $\lim sup_{t\to\infty} x_2(t) \le K_2$.

Next ,

$$\begin{aligned}(c_1 x_1 + \widetilde{c_1} x_2 + y_1)' &\\ \le c_1 x_1 g_1(x_1) + x_2 \widetilde{c_1} g_2(x_2) - s_1(0) y_1 - c_1 x_1 s_1(0) - x_2 \widetilde{c_1} s_1(0) &\\ + c_1 x_1 s_1(0) + \widetilde{c_1} x_2 s_1(0).&\end{aligned}$$

Set $u = c_1x_1 + \widetilde{c_1}x_2 + y_1$ to get,

$$u' + s_1(0)u \leq c_1x_1\big(s_1(0) + g_1(x_1)\big) + \widetilde{c_1}x_2\big(s_1(0) + g_2(x_2)\big)$$

$$\leq c_1G_1 + \widetilde{c_1}G_2$$

Solving for $u(t)$ and using comparison theorem,

$$\left(ue^{s_1(0)t} - u(0)\right) \leq \frac{(c_1G_1+\widetilde{c_1}G_2)(e^{s_1(0)t}-1)}{s_1(0)},$$

Or $\mathrm{u}(t) \leq u(0)e^{-s_1(0)t} + \frac{(C_1G_1+\widetilde{c_1}G_2)(1-e^{s_1(0)t})}{s_1(0)}$,

$$u(t) \leq e^{-s_1}(0)t\left(u(0) - \frac{c_1G_1+\widetilde{c_1}G_2}{s_1(0)}\right) + \frac{c_1G_1+\widetilde{c_1}G_2}{s_1(0)}.$$

So, $c_1x_1(0) + \widetilde{c_1}x_2(0) + y_1(0) \leq \frac{c_1G_1+\widetilde{c_1}G_2}{s_1(0)}$

Implies, $c_1x_1 + \widetilde{c_1}x_2 + y_1 \leq \frac{c_1G_1+\widetilde{c_1}G_2}{s_1(0)}$.

In general,

$$c_1x_1(t) + \widetilde{c_1}x_2(t) + y_1(t) \leq \frac{c_1G_1 + \widetilde{c_1}G_2}{s_1(0)} + \epsilon, as\ t \to \infty\ .$$

Similar argument holds for $c_2x_1 + \widetilde{c_2}x_2 + y_2$.

3. Equilibria and their local stability

In this section we study existence of equilibria depending on the form of mutualism.

3.1.1 The Facultative Mutualism

In this section we consider the case when predators exhibit facultative mutualism, i.e. when both predator populations are capable of surviving on their own, but are able to sustain higher population numbers due to mutualism. Thus we require, $\exists\ \overline{x_i}^*$ such that,

$$\left.\begin{array}{ll} -s_1(0) + c_1p_1(\overline{x_1}^*, 0) = 0, & (3.1) \\ -s_1(0) + \widetilde{c_1}p_2(\overline{x_2}^*, 0) = 0, & (3.2) \\ \quad \overline{x_i}^* < K_i\ , \qquad i = 1,2. & \end{array}\right\} (3)$$

If (3.1) does not hold, there exists no equilibrium in positive $x_1 - y_1$quadrant and hence has no periodic solution in it. Hence by Poincare Bendixson Theorem, equilibrium $(K_1, 0,0,0)$is globally asymptotically stable in the positive $x_1 - y_1$ quadrant. Similar conclusion follows when (3.2) does not hold.

Similarly, we require

$$\left.\begin{array}{ll}-s_2(0) + c_2 q_1(\widetilde{x_1}^*, 0) = 0, & (4.1)\\ -s_2(0) + \widetilde{c_2} q_2(\widetilde{x_2}^*, 0) = 0, & (4.2)\\ for\ some\ \widetilde{x_i}^* < K_i\ , i = 1,2. & \end{array}\right\} (4)$$

We conclude, that there exist equilibria

$E_0(0,0,0,0), E_1(K_1, 0,0,0), E_2(0, K_2, 0,0), E_3(\overline{x_1}, 0, \overline{y_1}, 0), E_4(0, \overline{x_2}, \overline{y_{11}}, 0),$
$E_5(\widetilde{x_1}, 0,0, \widetilde{y_2}), E_6(0, \widetilde{x_2}, 0, \widetilde{y_{22}}), E_7(x_{31}, x_{32}, y_{31}, 0), E_8(x_{41}, x_{42}, 0, y_{42}), E_9(x_{51}, 0, y_{51}, y_{52})$ and $E_{10}(0, x_{62}, y_{61}, y_{62})$. Also interior equilibrium $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ may exist. One sufficient condition for existence of E^* is that system (1) be uniformly persistent (see[2]).

3.1.2 Facultative – Obligate mutualism

Next we consider the case when mutualism is obligate for one predator and facultative for the other. The mutualism will be obligate for y_1, when

$$\left.\begin{array}{ll}-s_1(0) + c_1 p_1(K_1, 0) + \widetilde{c_1} p_2(K_2, 0) < 0 & (5.1)\\ \text{It will be obligate for } y_2, \text{when} & \\ -s_2(0) + c_2 q_1(K_1, 0) + \widetilde{c_2} q_2(K_2, 0) < 0 & (5.2)\end{array}\right\} (5)$$

When (5.1) holds then boundary equilibria E_3, E_4 and E_7 do not exist.

When (5.2) holds then equilibria E_5, E_6 and E_8 do not exist.

3.1.3 Obligate Mutualism

When (5.1) and (5.2) both hold then mutualism is obligate for both y_1 and y_2. In this case equilibria E_3, E_4, E_5, E_6, E_7 and E_8 do not exist.

3.2 Stability of Equilibria

Jacobian matrix V of system (1) is,

$$V = \begin{bmatrix} g_1 + x_1 g_1' - y_1 p_{1x_1} - y_2 q_{1x_1} & 0 & -p_1 - y_2 q_{1y_1} & -y_1 p_{1y_2} - q_1 \\ 0 & g_2 + x_2 g_2' - y_1 p_{2x_2} - y_2 q_{2x_2} & -p_2 - y_2 q_{2y_1} & -y_1 p_{2y_2} - q_2 \\ y_1 c_1 p_{1x_1} & y_1 \widetilde{c_1} p_{2x_2} & -s_1 + c_1 p_1 + \widetilde{c_1} p_2 - y_1 s_1' & c_1 y_1 p_{1y_2} + \widetilde{c_1} p_{2y_2} \\ c_2 y_2 q_{1x_1} & \widetilde{c_2} y_2 q_{2x_2} & c_2 y_2 q_{1y_1} + \widetilde{c_2} q_{2y_1} y_2 & -s_2 + c_2 q_1 + \widetilde{c_2} q_2 - y_2 s_2' \end{bmatrix}$$

$$V(E_0) = diag\big(g_1(0), g_2(0), -s_1(0), -s_2(0)\big)$$

So E_0 is unstable in x_1 and x_2 directions and stable in y_1 and y_2 directions. Next,

$$V(E_1) = \begin{bmatrix} K_1 g_1'(K_1) & 0 & -p_1(K_1, 0) & -q_1(K_1, 0) \\ 0 & g_2(0) & 0 & 0 \\ 0 & 0 & -s_1(0) + c_1 p_1(K_1, 0) & 0 \\ 0 & 0 & 0 & -s_2(0) + c_2 q_1(K_1, 0) \end{bmatrix}$$

The equilibrium $E_1(K_1, 0,0,0)$ is unstable in x_2 direction. In y_1 and y_2 directions the eigenvalues are

$-s_1(0) + c_1 p_1(K_1, 0)$ and $-s_2(0) + c_2 q_1(K_1, 0) > 0$, respectively.

Same way $E_2(0, K_2, 0,0)$ is unstable in x_1 direction. The eigenvalues of $V(E_2)$ in y_1 and y_2 direction are $-s_1(0) + \widetilde{c_1} p_2(K_2, 0)$ and $-s_2(0) + \widetilde{c_2} q_2(K_2, 0)$. respectively. Also,

$$V[E_3(\overline{x_1}, 0, \overline{y_1}, 0)] = \begin{bmatrix} g_1(\overline{x_1}) + \overline{x_1} g_1'(\overline{x_1}) - \overline{y_1} p_{1x_1}(\overline{x_1}, 0) & 0 & -p_1(\overline{x_1}, 0) & -\overline{y_1} p_{1y_2}(\overline{x_1}, 0) - q_1(\overline{x_1}, \overline{y_1}) \\ 0 & g_2(0) - \overline{y_1} p_{2x_2}(0,0) & 0 & 0 \\ c_1 \overline{y_1} p_{1x_1}(\overline{x_1}, 0) & 0 & -s_1'(\overline{y_1}) \overline{y_1} & c_1 \overline{y_1} p_{1y_2}(\overline{x_1}, 0) \\ 0 & 0 & 0 & -s_2(0) + c_2 q_1(\overline{x_1}, \overline{y_1}) \end{bmatrix}$$

So $V(E_3)$ has eigenvalue $g_2(0) - \overline{y_1} p_{2x_2}(0,0)$ in x_2 – direction. The eigenvalue in y_2 – direction is $-s_2(0) + c_2 q_1(\overline{x_1}, \overline{y_1})$. The other two eigenvalues are roots of

$$\lambda^2 + \left(\alpha_1 + \overline{y_1} s_1'(\overline{y_1})\right)\lambda + \alpha_1 \overline{y_1} s_1'(\overline{y_1}) + c_1 \overline{y_1} p_1(\overline{x_1}, 0) p_{1x_1}(\overline{x_1}, 0) = 0,$$

where, $\alpha_1 = g_1(\overline{x_1}) + \overline{x_1} g_1'(\overline{x_1}) - \overline{y_1} p_{1x_1}(\overline{x_1}, 0)$.

Proceeding same way $V\left(E_4(0, \overline{x_2}, \overline{y_{11}}, 0)\right)$has eigenvalues $g_1(0) - \overline{y_{11}} p_{1x_1}(0,0)$ and $-s_2(0) + \widetilde{c_2} q_2(\overline{x_2}, \overline{y_{11}})$ in x_1 and y_2 directions, respectively. The other two eigenvalues will be given by,

$$\lambda^2 + \left(\alpha_2 + \overline{y_{11}} s_2'(\overline{y_{11}})\right)\lambda + \alpha_2 \overline{y_{11}} s_1'(\overline{y_{11}}) + \widetilde{c_1} \overline{y_{11}} p_2(\overline{x_2}, 0) p_{2x_2}(\overline{x_2}, 0) = 0,$$

where, $\alpha_2 = g_2(\overline{x_2}) + \overline{x_2} g_2'(\overline{x_2}) - \overline{y_{11}} p_{2x_2}(\overline{x_2}, 0)$.

Also, $V\left(E_5(\widetilde{x_1}, 0,0, \widetilde{y_2})\right)$ has eigenvalues $g_2(0) - \widetilde{y_2} q_{2x_2}(0,0)$ and $-s_1(0) + c_2 p_1(\widetilde{x_1}, \widetilde{y_2})$ in x_2 and $y_1$directions. The other two eigenvalues are the roots of

$$\lambda^2 + \left(\alpha_3 + \widetilde{y_2} s_2'(\widetilde{y_2})\right)\lambda + \alpha_3 \widetilde{y_2} s_2'(\widetilde{y_2}) + \widetilde{y_2} c_2 q_1(\widetilde{x_1}, 0) q_{1x_1}(\widetilde{x_1}, 0) = 0,$$

where, $\alpha_3 = g_1(\widetilde{x_1}) + \widetilde{x_1} g_1'(\widetilde{x_1}) - \widetilde{y_2} q_{1x_1}(\widetilde{x_1}, 0)$.

$V\left(E_6(0, \widetilde{x_2}, 0, \widetilde{y_{22}})\right)$has eigenvalues $g_1(0) - \widetilde{y_{22}} q_{1x_1}(0,0)$ and $-s_1(0) + \widetilde{c_1} p_2(\widetilde{x_2}, \widetilde{y_{22}})$ in x_1 and $y_1$directions. The other two eigenvalues are roots of

$$\lambda^2 + \left(\alpha_4 + \widetilde{y_{22}} s_2'(\widetilde{y_{22}})\right)\lambda + \alpha_4 \widetilde{y_{22}} s_2'(\widetilde{y_{22}}) + \widetilde{c_2} \widetilde{y_{22}} q_2(\widetilde{x_2}, 0) q_{2x_2}(\widetilde{x_2}, 0) = 0,$$

where, $\alpha_4 = g_2(\widetilde{x_2}) + \widetilde{x_2} g_2'(\widetilde{x_2}) - \widetilde{y_{22}} q_{2x_2}(\widetilde{x_2}, 0)$.

Next,

$$V[E_7(x_{31}, x_{32}, y_{31}, 0)] = \begin{bmatrix} g_1(x_{31}) + x_{31} g_1'(x_{31}) - y_{31} p_{1x_1}(x_{31}, 0) & 0 & -p_1(x_{31}, 0) & -\overline{y_{31}} p_{1y_2}(x_{31}, 0) \\ 0 & g_2(x_{32}) + x_{32} g_1'(x_{32}) - y_{31} p_{2x_2}(x_{32}, 0) & -p_2(x_{32}, 0) & -y_{31} p_{2y_2}(x_{32}, 0) - q_2(x_{32}, y_{31}) \\ c_1 y_{31} p_{1x_1}(x_{31}, 0) & \widetilde{c_1} y_{31} p_{2x_2}(x_{32}, 0) & -y_{31} s_1'(y_{31}) & c_1 y_{31} p_{1y_2}(x_{31}, 0) + \widetilde{c_1} p_{2y_2}(x_{32}, 0) \\ 0 & 0 & 0 & -s_2(0) + c_2 q_1(x_{31}, y_{31}) + \widetilde{c_2} q_2(x_{32}, y_{31}) \end{bmatrix}$$

Eigenvalue of $V\left(E_7(x_{31}, x_{32}, y_{31}, 0)\right)$ in y_2– direction is

$$\xi_1 = -s_2(0) + c_2 q_1(x_{31}, y_{31}) + \widetilde{c_2} q_2(x_{32}, y_{31}).$$

Other eigenvalues are the roots of

$\lambda^3 + \mu_1\lambda^2 + \mu_2\lambda + \mu_3 = 0$

where, $\mu_1 = -(y_{31}s_1'(y_{31}) + a_1 + a_2)$,

$\mu_2 = a_3 + a_1\left(a_2 + y_{31}s_1'(y_{31}) + c_1 y_{31} p_{1x_1}(x_{31}, 0)p_1(x_{31}, 0)\right)$,

$\mu_3 = -a_1 a_3 - a_2 c_1 y_{31} p_{1x_1}(x_{31}, 0)p_1(x_{31}, 0)$,

$a_i = g_i(x_{3i}) + x_{3i}g_i'(x_{3i}) - y_{31}p_{ix_i}(x_{3i}, 0), i = 1,2.$

and $a_3 = \widetilde{c_1} y_{31} p_2(x_{32}, 0)p_{2x_2}(x_{32}, 0) - y_{31}s_1'(y_{31})a_2$.

Similarly, the eigenvalue of $V\left(E_8(x_{41}, x_{42}, 0, y_{42})\right)$ in y_1– direction is $\xi_2 = -s_1(0) + c_1 p_1(x_{41}, y_{42}) + \widetilde{c_1} p_2(x_{42}, y_{42})$.

Other eigenvalues are given by the roots of

$\lambda^3 + \gamma_1\lambda^2 + \gamma_2\lambda + \gamma_3 = 0$

$\gamma_1 = -(y_{42}s_2'(y_{42}) + a_4 + a_5)$

$\gamma_2 = a_6 + a_4\left(a_5 + y_{42}s_2'(y_{42}) + c_2 y_{42} q_{1x_1}(x_{41}.0)q_1(x_{41}, 0)\right)$

$\gamma_3 = -a_4 a_6 - a_5 c_2 y_{42} q_{1x_1}(x_{41}, 0)q_1(x_{41}, 0)$

$a_{i+3} = g_i(x_{4i}) + x_{4i}g_i'(x_{4i}) - y_{42}q_{ix_i}(x_{4i}, 0), i = 1,2,$

and $a_6 = \widetilde{c_2} y_{42} q_2(x_{42}, 0)q_{2x_2}(x_{42}, 0) - y_{42}s_2'(y_{42})a_5$

Eigenvalue of $V\left(E_9(x_{51}, 0, y_{51}, y_{52})\right)$ in x_2 - direction is

$\xi_3 = g_2(0) - y_{51}p_{2x_2}(0, y_{52}) - y_{52}q_{2x_2}(0, y_{51})$.

Other eigenvalues are given by the roots of

$$\begin{aligned}
\lambda^3 &+ (y_{51}s_1' + y_{52}s_2')\lambda^2 \\
&- \Big[e_1(y_{51}s_1' + y_{52}s_2') \\
&+ \left(y_{51}c_1 p_{1x_1}(p_1 + y_{52}q_{1y_1}) + c_2 y_{52} q_{1x_1}(y_{51}p_{1y_2} + q_1)\right) \\
&- \left(y_{51}y_{52}s_1's_2' - c_2 y_{52} q_{1y_1} c_1 y_{51} p_{1y_2}\right)\Big]\lambda \\
&+ y_{51}c_1 p_{1x_1}\left\{(p_1 + y_{52}q_{1y_1})y_{52}s_2' + c_2 y_{52} q_{1y_1}(y_{51}p_{1y_2} + q_1)\right\} \\
&+ c_2 y_{52} q_{1x_1}\left\{(p_1 + y_{52}q_{1y_1})c_1 y_{51} p_{1y_2} + y_{51}s_1'(y_{51}p_{1y_2} + q_1)\right\} = 0
\end{aligned}$$

where, $e_1 = g_1 + x_1 g_1' - y_1 p_{1x_1} - y_2 q_{1x_1}$.

Above as well as below all functions are evaluated at the equilibrium under consideration.

Eigenvalue of $V\big(E_{10}(0, x_{62}, y_{61}, y_{62})\big)$ in x_1 - direction is

$\xi_4 = g_1(0) - y_{61}p_{1x_1}(0, y_{62}) - y_{62}q_{1x_1}(0, y_{61})$. Other eigenvalues are the roots of

$$\begin{aligned}\lambda^3 + (y_{61}s_1' + y_{62}s_2' - e_2)\lambda^2 \\ &- \Big[e_2(y_{61}s_1' + y_{62}s_2') \\ &+ \Big(y_{61}\tilde{c_1}p_{2x_2}\big(p_2 + y_{62}q_{2y_1}\big) + \tilde{c_2}y_{62}q_{2x_2}\big(y_{61}p_{2y_2} + q_2\big)\Big) - y_{61}y_{62}s_1's_2' \\ &+ \tilde{c_2}y_{61}y_{62}q_{2y_1}\tilde{c_1}p_{2y_2}\Big]\lambda \\ &+ y_{61}\tilde{c_1}p_{2x_2}\big\{\big(p_2 + y_{62}q_{2y_1}\big)y_{62}s_2' + \tilde{c_2}y_{62}q_{2y_1}\big(y_{61}p_{2y_2} + q_2\big)\big\} \\ &+ \tilde{c_2}y_{62}q_{2x_2}\big\{\big(p_2 + y_{62}q_{2y_1}\big)\tilde{c_1}y_{61}p_{2y_2} + y_{61}s_2'\big(y_{61}p_{2y_2} + q_2\big)\big\} = 0,\end{aligned}$$

where, $e_2 = g_1 + x_2g_2' - y_1p_{2x_2} - y_2q_{2x_2}$.

We now obtain conditions of asymptotic stability of interior equilibrium E^* :

$$A = \big(a_{ij}\big) = \begin{bmatrix} g_1 + x_1g_1' - y_1p_{1_{x_1}} - y_2q_{1_{x_1}} & 0 & -p_1 - y_2q_{1_{y_1}} & -y_1p_{1_{y_2}} - q_1 \\ 0 & g_2 + x_2g_2' - y_1p_{2_{x_2}} - y_2q_{2_{x_2}} & -p_2 - y_2q_{2_{y_1}} & -y_1p_{2_{y_2}} - q_2 \\ c_1y_1p_{1_{x_1}} & \tilde{c_1}y_1p_{2_{x_2}} & -y_1s_1' & c_1y_1p_{1_{y_2}} + \tilde{c_1}y_1p_{2_{y_2}} \\ c_2y_2q_{1_{x_1}} & \tilde{c_2}y_2q_{2_{x_2}} & c_2y_2q_{1_{y_1}} + \tilde{c_2}y_2q_{2_{y_1}} & -y_2s_2' \end{bmatrix}$$

Computing $det(\,A - \lambda\, I\,)\ =\ 0$ we get

$F(\lambda) = \lambda^4 + \alpha_1\lambda^3 + \alpha_2\lambda^2 + \alpha_3\lambda + \alpha_4 = 0,$

where,

$\alpha_1 = -\sum_1^4 a_{ii}$,

$\alpha_2 = m1 - m2 + (a_{11} + a_{22})(a_{33} + a_{44}) + a_{11}a_{22} + \beta_1$,

$\alpha_3 = -(a_{11} + a_{22})\ m1 - a_{11}a_{22}(a_{33} + a_{44}) + \gamma_1 + \gamma_2,$

$\alpha_4 = m1\ a_{11}a_{22} + \delta_1 + \delta_2 + \delta_3, \beta_1 = -(a_{13}a_{31} + a_{14}a_{41}),$

$\gamma_1 = (a_{13}a_{22} + m5)a_{31} - a_{41}(m6 - a_{14}a_{22}),$

$\delta_1 = m6\ a_{22}a_{41} - m5\ a_{22}a_{31},$

$\gamma_2 = a_{11}\ m2 + a_{32}\ m3 - a_{42}\ m4,\ \delta_2 = a_{11}\ (a_{42}\ m4 - a_{32}\ m3)$

$\delta_3 = m7\ (a_{31}a_{42} - a_{41}a_{32}).$

$m1 = a_{33}a_{44} - a_{34}a_{43}, m2 = a_{23}a_{32} + a_{24}a_{42}$,

$m3 = a_{23}a_{44} - a_{24}a_{43}, m4 = a_{23}a_{34} - a_{24}a_{33},$

$m5 = a_{13}a_{44} - a_{14}a_{43},\ \ m6 = a_{13}a_{34} - a_{14}a_{33},$

and $m7 = a_{13}a_{24} - a_{14}a_{23}.$

All the entries of matrix A above are assumed to be computed at $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$.

The result below follows from Hurwitz's theorem [1]:

Theorem 3: The interior equilibrium $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ is asymptotically stable if

$$\alpha_i > 0, \qquad 1 \le i \le 4, \alpha_1\alpha_2\ \alpha_3 - \alpha_3^2 - \alpha_1^2\alpha_4 > 0.$$

4. Global Stability

In this section we obtain conditions of global asymptotic stability of four, boundary equlibria that are interior to three dimensional subsystems and the interior equilibrium of (1).

The results of boundary equilibria will be used to obtain conditions for uniform persistence in the next section.

We set $R_{xyz}^+ = \{(x, y, z) | x > 0, y > 0, z > 0\}$, and define $\overline{R_{xyz}^+}$ to be the closure of R_{xyz}^+ and, so on.

We consider the question of global asymptotically stability of $E_7(x_{31}, x_{32}, y_{31}, 0)$ for the system,

$$x_1' = \alpha x_1 g_1(x_1) - y_1 p_1(x_1, 0),$$

$$x_2' = x_2 g_2(x_2) - y_1 p_2(x_2, 0),$$

$$y_1' = y_1[-s_1(y_1) + c_1 p_1(x_1, 0) + \tilde{c_1} p_2(x_2, 0)]$$

$$x_1(t_0) = x_{10} \ge 0, x_2(t_0) = x_{20} \ge 0, y_1(t_0) = y_{10} \ge 0.$$

We will find sufficent conditions, such that $E_7(x_{31}, x_{32}, y_{31}, 0)$ is globally asymptotically stable in $R_{x_1x_2y_1}^+$.

We define $V(x_1, x_2, y_1)$[4]:

$$V(x_1, x_2, y_1) = \sum_{i=1}^{2}\left(x_i - x_{3i} - x_{3i}\log\frac{x_i}{x_{3i}}\right) + y_1 - y_{31} - y_{31}\log\frac{y_1}{y_{31}}.$$

V is positive definite about $E_7(x_{31}, x_{32}, y_{31}, 0)$. Also $V(x_1, x_2, y_1) \to +\infty$, as x_1, x_2 and/or $y_1$tend to zero.

Computing $\frac{dV}{dt}$ along the solutions, we get

$$\frac{dV}{dt} = (x_1 - x_{31})\left[\alpha g_1(x_1) - y_1\frac{p_1(x_1, 0)}{x_1}\right] + (x_2 - x_{32})\left[g_2(x_2) - y_1\frac{p_2(x_2, 0)}{x_2}\right]$$
$$+ (y_1 - y_{31})\{-s_1(y_1) + c_1 p_1(x_1, 0) + \tilde{c_1} p_2(x_2, 0)\}$$

$$=\sum_{i,j=1}^{3} l_{ij},$$

where,

$l_{11} = (x_1 - x_{31})\left\{\alpha[g_1(x_1) - g_1(x_{31})] + y_1\left[\frac{p_1(x_{31},0)}{x_{31}} - \frac{p_1(x_1,0)}{x_1}\right]\right\}$,

$l_{12} = 0,\, l_{13} = -\frac{(x_1-x_{31})}{x_{31}}(y_1 - y_{31})p_1(x_{31},0)$,

$l_{21} = 0,\, l_{22} = (x_2 - x_{32})\left\{g_2(x_2) - g_2(x_{32}) + y_1\left[\frac{p_2(x_{32},0)}{x_{32}} - \frac{p_2(x_2,0)}{x_2}\right]\right\}$,

$l_{23} = -\frac{1}{x_{32}}(x_2 - x_{32})(y_1 - y_{31})p_2(x_{32},0),\, l_{31} = c_1(y_1 - y_{31})[p_1(x_1,0) - p_1(x_{31},0)]$,

$l_{32} = \widetilde{c_1}(y_1 - y_{31})[p_2(x_2,0) - p_2(x_{32},0)],\ l_{33} = -(y_1 - y_{31})[s_1(y_1) - s_1(y_{31})]$.

We set

$l_{11} = (x_1 - x_{31})^2 m_{11}(x_1, y_1), m_{12} = 0$,

$l_{13} + l_{31} = 2(x_1 - x_{31})(y_1 - y_{31})m_{13}(x_1)$,

$l_{22} = (x_2 - x_{32})^2 m_{22}(x_2)$,

$l_{23} + l_{32} = 2(x_2 - x_{32})(y_1 - y_{31})m_{23}(x_2)$,

$l_{33} = (y_1 - y_{31})^2 m_{33}(y_1)$,

and

$m_{ij} = m_{ji}, \qquad i > j.$

Thus

$\frac{dV}{dt} = x^T M x$,

where, M $=(m_{ij}), x = \begin{pmatrix} x_1 - x_{31} \\ x_2 - x_{32} \\ y_1 - y_{31} \end{pmatrix}$.

Also from Theorem 2 we have that $\mathcal{A}_1 = \left\{(x_1, x_2, y_1)\middle| 0 \le x_1 \le K_1, 0 \le x_2 \le K_2, c_1x_1 + \widetilde{c_1}x_2 + y_1 \le \frac{c_1G_1 + \widetilde{c_1}G_2}{s_1(0)}\right\}$ is an attracting set for the subsystem in $R^+_{x_1x_2y_1}$.

Theorem 4: Let the symmetric matrix M be negative definite in $\mathcal{A}_1$. Then $E_7(x_{31}, x_{32}, y_{31}, 0)$ is globally asymptotically stable in $R^+_{x_1x_2y_1}$.

Proof : The solutions are bounded and the largest invariant set of $\left\{x \in R^+_{x_1x_2y_1}\middle|\dot{V} = 0\right\} = \{E_7\}$. Hence E_7 is globally asymptotically stable in $R^+_{x_1x_2y_1}$[11].

Next we consider the question of global asymptotically stability of $E_8(x_{41}, x_{42}, 0, y_{42})$

for the system

$x_1' = \alpha x_1 g_1(x_1) - y_2 q_1(x_1, 0),$

$x_2' = x_2 g_2(x_2) - y_2 q_2(x_2, 0),$

$y_2' = y_2[-s_2(y_2) + c_2 q_1(x_1, 0) + \widetilde{c_2} q_2(x_2, 0)]$

$x_1(t_0) = x_{10} \geq 0, x_2(t_0) = x_{20} \geq 0, y_2(t_0) = y_{20} \geq 0.$

We define a Lyapunov function V((x_1, x_2, y_2),

$$V(x_1, x_2, y_2) = \sum_{i=1}^{2}\left(x_i - x_{4i} - x_{4i}\log\frac{x_i}{x_{4i}}\right) + y_2 - y_{42} - y_{42}\log\frac{y_2}{y_{42}}.$$

V is positive definite about $E_8(x_{41}, x_{42}, 0, y_{42})$. Also $V(x_1, x_2, y_2) \to +\infty$, as x_i and/or $y_2$tend to zero, $i = 1,2$. Computing time derivative of V along the solutions, we get,

$$\frac{dV}{dt} = (x_1 - x_{41})\left\{\alpha\, g_1(x_1) - \frac{y_2}{x_1} q_1(x_1, 0)\right\} + (x_2 - x_{42})\left\{g_2(x_2) - \frac{y_2}{x_2} q_2(x_2, 0)\right\}$$
$$+ (y_2 - y_{42})\{-s_2(y_2) + c_2 q_1(x_1, 0) + \widetilde{c_2} q_2(x_2, 0)\}$$

$=\sum_{i,j=1}^{3} l_{ij},$

$l_{11} = (x_1 - x_{41})\left\{\alpha[g_1(x_1) - g_1(x_{41})] + y_2\left[\frac{q_1(x_{41},0)}{x_{41}} - \frac{q_1(x_1,0)}{x_1}\right]\right\},$

$l_{12} = 0, l_{13} = -\frac{(x_1 - x_{41})}{x_{41}}(y_2 - y_{42}) q_1(x_{41}, 0)$,

$l_{21} = 0, l_{22} = (x_2 - x_{42})\left\{g_2(x_2) - g_2(x_{42}) + y_2\left[\frac{q_2(x_{42},0)}{x_{42}} - \frac{q_2(x_2,0)}{x_2}\right]\right\}$,

$l_{23} = -\frac{1}{x_{42}}(x_2 - x_{42})(y_2 - y_{42}) q_2(x_{42}, 0)$,

$l_{31} = c_2(y_2 - y_{42})[q_1(x_1, 0) - q_1(x_{41}, 0)], l_{32}$
$= \widetilde{c_2}(y_2 - y_{42})[q_2(x_2, 0) - q_2(x_{42}, 0)],$

$l_{33} = -(y_2 - y_{42})[s_2(y_2) - s_2(y_{42})].$

Next, we define $n_{ij}'s$, such that

$l_{11} = (x_1 - x_{41})^2 n_{11}(x_1, y_2), \qquad n_{12} = 0, l_{13} + l_{31} = 2(x_1 - x_{41})(y_2 - y_{42}) n_{13}(x_1),$

$l_{22} = (x_2 - x_{42})^2 n_{22}(x_2, y_2)$, $l_{23} + l_{32} = 2(x_2 - x_{42})(y_2 - y_{42}) n_{23}(x_2),$

$l_{33} = (y_2 - y_{42})^2 n_{33}(y_2),$

and

$n_{ij} = n_{ji}, \qquad i > j.$

Thus

$\frac{dV}{dt} = x^T N x,$

$N = (n_{ij}), \qquad x = \begin{pmatrix} x_1 - x_{41} \\ x_2 - x_{42} \\ y_2 - y_{42} \end{pmatrix}$

Also from Theorem 2 we have: $\mathcal{A}_2 = \left\{(x_1, x_2, y_2) \middle| 0 \le x_1 \le K_1, 0 \le x_2 \le K_2, c_2 x_2 + \widetilde{c_2} x_2 + y_2 \le \frac{c_2 L_1 + \widetilde{c_2} L_2}{s_2(0)}\right\}$ is an attracting set for the subsystem in $R^+_{x_1 x_2 y_2}$. Proceeding as in Theorem 4, we get:

Theorem 5: Let the symmetric matrix N be negative definite in $\mathcal{A}_2$. Then $E_8(x_{41}, x_{42}, 0, y_{42})$ is globally asymptotically stable in $R^+_{x_1 x_2 y_2}$.

Next we consider global stability of E_9 for the submodel in $R^+_{x_1 y_1 y_2}$: we define a Lyapunov function $V(x_1,\, y_1,\, y_2)$:

$V(x_1,\, y_1,\, y_2) = \left(x_1 - x_{51} - x_{51} \log \frac{x_1}{x_{51}}\right) + \sum_{i=1}^{2} \left(y_i - y_{5i} - y_{5i} \log \frac{y_i}{y_{5i}}\right).$

V is positive definite about $E_9(x_{51}, 0, y_{51}, y_{52})$. Also as x_i and/or $y_i \to 0$, $V \to +\infty$, $i = 1,2$.

Computing the time derivative of V along the solutions of we get,

$$\begin{aligned} \frac{dV}{dt} = (x_1 - x_{51}) &\left\{\alpha g_1(x_1) - y_1 \frac{p_1(x_1, y_2)}{x_1} - y_2 \frac{q_1(x_1, y_1)}{x_1}\right\} \\ &+ (y_1 - y_{52})\{-s_1(y_1) + c_1 p_1(x_1, y_2)\} \\ &+ (y_2 - y_{52})\{-s_2(y_2) + c_2 q_1(x_1, y_1)\} \end{aligned}$$

$= \sum_{i,j=1}^{3} l_{ij},$

where,

$l_{11} = (x_1 - x_{51})\left\{\alpha[g_1(x_1) - g_1(x_{51})] + y_1\left(\frac{p_1(x_{51}, y_{52})}{x_{51}} - \frac{p_1(x_1, y_{52})}{x_1}\right) + y_2\left(\frac{q_1(x_{51}, y_{51})}{x_{51}} - \frac{q_1(x_{51}, y_{51})}{x_1}\right)\right\},$

$l_{12} = -\frac{(x_1 - x_{51})}{x_{51}}\left\{(y_1 - y_{51}) p_1(x_{51}, y_{52}) + \frac{y_2}{x_1}[q_1(x_1, y_1) - q_1(x_1, y_{51})]\right\},$

$$l_{13} = -(x_1 - x_{51})\left\{\frac{y_1}{x_{51}}[p_1(x_1, y_2) - p_1(x_1, y_{52})] + \frac{(y_2 - y_{52})}{x_{51}} q_1(x_{51}, y_{51})\right\},$$

$l_{21} = c_1(y_1 - y_{51})\{p_1(x_1, y_2) - p_1(x_{51}, y_2)\},$

$l_{22} = -(y_1 - y_{51})[s_1(y_1) - s_1(y_{51})]$,

$l_{23} = c_1(y_1 - y_{51})[p_1(x_{51}, y_2) - p_1(x_{51}, y_{52})]$,

$l_{31} = (y_2 - y_{52})c_2\{q_1(x_1, y_1) - q_1(x_{51}, y_1)\}$,

$l_{32} = c_2(y_2 - y_{52})[-q_1(x_{51}, y_{51}) + q_1(x_{51}, y_1)]$,

$l_{33} = -(y_2 - y_{52})[s_2(y_2) - s_2(y_{52})]$.

We set

$l_{11} = (x_1 - x_1^*)^2 r_{11}(x_1, y_1, y_2)$, $l_{12} + l_{21} = 2(x_1 - x_{51})(y_1 - y_{51}) r_{12}(x_1, y_1, y_2)$,

$l_{13} + l_{31} = 2(x_1 - x_{51})(y_2 - y_{52}) r_{13}(x_1, y_1, y_2)$, $l_{22} = (y_1 - y_{51})^2 r_{22}(y_1)$,

$l_{23} + l_{32} = 2(y_1 - y_{51}) r_{23}(y_2)(y_2 - y_{52})$, $l_{33} = (y_2 - y_{52})^2 r_{33}(y_2)$.

Define

$r_{ij} = r_{ji}, i > j, R = (r_{ij})$,

So, $\dot{V} = x^T R\, x$,

Also from Theorem 2, $\mathcal{A}_3 = \left\{(x_1, y_1, y_2) \middle| 0 \le x_1 \le K_1, 0 \le c_1 x_1 + y_1 \le \frac{c_1 G_1}{s_1(0)}, c_2 x_1 + y_2 \le \frac{c_2 L_1}{s_2(0)}\right\}$ is an attracting set for the subsystem in $R^+_{x_1 y_1 y_2}$.

where, $R = (r_{ij})$ *and* $x = \begin{pmatrix} x_1 - x_{51} \\ y_1 - y_{51} \\ y_2 - y_{52} \end{pmatrix}$.

We obtain the following result:

Theorem 6: Whenever the symmetric matrix R is negative definite on $\mathcal{A}_3$, the equilibrium $E_9(x_{51}, 0, y_{51}, y_{52})$ is globally asymptotically stable in $R^+_{x_1 y_1 y_2}$.

In order to obtain global asymptotic criteria for the equilibrium $E_{10}(0, x_{62}, y_{61}, y_{62})$ in $R^+_{x_2 y_1 y_2}$, We define a Lyapunov function $V(x_2, y_1, y_2)$,

$$V(x_2, y_1, y_2) = \left(x_2 - x_{62} - x_{62}\log\frac{x_2}{x_{62}}\right) + \sum_{i=1}^{2}\left(y_i - y_{6i} - y_{6i}\log\frac{y_i}{y_{6i}}\right).$$

V is positive definite about $E_{10}(0, x_{62}, y_{61}, y_{62})$. Also $V \to +\infty$ as x_2 or y_i tend to $0+$, $i = 1,2$.

Computing the time derivative of V along the solutions, we get

$$\frac{dV}{dt} = (x_2 - x_{62})\left\{g_2(x_2) - y_1\frac{p_2(x_2,y_2)}{x_2} - y_2\frac{q_2(x_2,y_1)}{x_2}\right\}$$
$$+ (y_1 - y_{62})\{-s_1(y_1) + c_1p_1(x_2,y_2)\}$$
$$+ (y_2 - y_{62})\{-s_2(y_2) + c_2q_1(x_2,y_1)\}$$
$$=\textstyle\sum_{i,j=1}^{3} l_{ij},$$

where,

$l_{11} = (x_2 - x_{62})\left\{g_2(x_2) - g_2(x_{62}) + y_1\left(\frac{p_2(x_{62},y_{62})}{x_{62}} - \frac{p_2(x_2,y_{62})}{x_2}\right) + y_2\left(\frac{q_2(x_{62},y_{61})}{x_{62}} - \frac{q_2(x_2,y_{61})}{x_2}\right)\right\}$,

$l_{12} = -(x_2 - x_{62})\left\{\frac{1}{x_{62}}(y_1 - y_{61})p_2(x_{62},y_{62}) + \frac{y_2}{x_2}[q_2(x_2,y_1) - q_2(x_2,y_{61})]\right\}$,

$l_{13} = -(x_2 - x_{62})\left\{\frac{y_1}{x_{62}}[p_2(x_2,y_2) - p_2(x_2,y_{62})] + \frac{(y_2-y_{62})}{x_{62}}q_2(x_{62},y_{61})\right\}$,

$l_{21} = \widetilde{c_1}(y_1 - y_{61})\{p_2(x_2,y_2) - p_2(x_{62},y_2)\}$, $l_{22} = (y_1 - y_{61})[s_1(y_1) - s_1(y_{61})]$,

$l_{23} = (y_1 - y_{61})\widetilde{c_1}[p_2(x_{62},y_2) - p_2(x_{62},y_{62})]$, $l_{31} = (y_2 - y_{62})\widetilde{c_2}\{q_2(x_2,y_1) - q_2(x_{62},y_1)\}$,

$l_{32} = \widetilde{c_2}(y_2 - y_{62})[-q_2(x_{62},y_{61}) + q_2(x_{62},y_1)]$, $l_{33} = (y_2 - y_{62})[s_2(y_2) - s_2(y_{62})]$.

We set

$l_{11} = (x_2 - x_{62})^2 t_{11}(x_2,y_1,y_2)$, $l_{12} + l_{21} = 2(x_2 - x_{62})(y_1 - y_{61})t_{12}(x_2,y_1,y_2)$,

$l_{13} + l_{31} = 2(x_2 - x_{62})(y_2 - y_{62})t_{13}(x_2,y_1,y_2)$, $l_{22} = (y_1 - y_{61})^2 t_{22}(y_1)$,

$l_{23} + l_{32} = 2(y_1 - y_{61})t_{23}(y_2)(y_2 - y_{62})$, $l_{33} = (y_2 - y_{62})^2 t_{33}(y_2)$,

Define

$t_{ij} = t_{ji}, i > j, T = (t_{ij})$.

So

$\dot{V} = x^T T x$,

Where, $= \begin{pmatrix} x_2 - x_{62} \\ y_1 - y_{61} \\ y_2 - y_{62} \end{pmatrix}$.

Also from Theorem 2, $\mathcal{A}_4 = \left\{(x_2,y_1,y_2)\middle| 0 \le x_2 \le K_2, 0 \le \widetilde{c_1}x_2 + y_1 \le \frac{\widetilde{c_1}G_2}{s_1(0)}, 0 \le \widetilde{c_2}x_2 + y_2 \le \frac{\widetilde{c_2}L_2}{s_2(0)}\right\}$ is an attracting set for the subsystem in $R^+_{x_2y_1y_2}$. Thus we have:

Theorem 7: Whenever the symmetric matrix T is negative definite in the region $\mathcal{A}_4$, the equilibrium $E_{10}(0, x_{62}, y_{51}, y_{52})$ is globally asymptotically stable in $R^+_{x_2 y_1 y_2}$.

Lastly we derive conditions for global stability of interior equilibrium E^*

Define a Lyapunov function $V(x_1, x_2, y_1, y_2)$.

$$V(x_1,\ x_2,\ y_1,\ y_2) = \sum_{i=1}^{2}\left(x_i - x_i^* - x_i^* \log\frac{x_i}{x_i^*}\right) + \sum_{i=1}^{2}\left(y_i - y_i^* - y_i^* \log\frac{y_i}{y_i^*}\right)$$

V is positive definite about $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$.Also as x_i and/or $y_i \to 0$, $V \to +\infty$, $i = 1,2$.

Computing the time derivate of V along the solutions of (1) we get,

$$\begin{aligned}\frac{dV}{dt} = (x_1 - x_1^*)&\left\{\alpha g_1(x_1) - y_1\frac{p_1(x_1, y_2)}{x_1} - y_2\frac{q_1(x_1, y_1)}{x_1}\right\}\\ &+ (x_2 - x_2^*)\left\{g_2(x_2) - y_1\frac{p_2(x_2, y_2)}{x_2} - y_2\frac{q_2(x_2, y_1)}{x_2}\right\}\\ &+ (y_1 - y_1^*)\{-s_1(y_1) + c_1 p_1(x_1, y_2) + \widetilde{c_1} p_2(x_2, y_2)\}\\ &+ (y_2 - y_2^*)\{-s_2(y_2) + c_2 q_1(x_1, y_1) + \widetilde{c_2} q_2(x_2, y_1)\}\end{aligned}$$

$=\sum_{i,j=1}^{4} l_{ij}$,

where,

$l_{11} = (x_1 - x_1^*)\left\{\alpha[g_1(x_1) - g_1(x_1^*)] + y_1\left(\frac{p_1(x_1^*, y_2^*)}{x_1^*} - \frac{p_1(x_1, y_2^*)}{x_1}\right) + y_2\left(\frac{q_1(x_1^*, y_1^*)}{x_1^*} - \frac{q_1(x_1, y_1^*)}{x_1}\right)\right\}$,

$l_{12} = 0$,

$l_{13} = -\,(x_1 -\ x_1^*)\left\{(y_1 - y_1^*)\frac{p_1(x_1^*, y_2^*)}{x_1^*} + \frac{y_2}{x_1}[q_1(x_1, y_1) - q_1(x_1, y_1^*)]\right\}$,

$l_{14} = -(x_1 - x_1^*)\left\{\frac{y_1}{x_1}[p_1(x_1, y_2) - p_1(x_1, y_2^*)] + \frac{(y_2 - y_2^*)}{x_1^*} q_1(x_1^*, y_1^*)\right\}$,

$l_{21} = 0$,

$l_{22} = (x_2 - x_2^*)\left\{g_2(x_2) - g_2(x_2^*) + y_1\left[\frac{p_2(x_2^*, y_2^*)}{x_2^*} - \frac{p_2(x_2, y_2^*)}{x_2}\right] + y_2\left[\frac{q_2(x_2^*, y_1^*)}{x_2^*} - \frac{q_2(x_2, y_1^*)}{x_2}\right]\right\}$,

$l_{23} = -(x_2 - x_2^*)\{\frac{y_2}{x_2}[q_2(x_2, y_1) - q_2(x_2, y_1^*)] + \frac{1}{x_2^*}[(y_1 - y_1^*)p_2(x_2^*, y_2^*)]\}$,

$l_{24} = -(x_2 - x_2^*)\left\{\frac{y_1}{x_2}[p_2(x_2, y_2) - p_2(x_2, y_2^*)] + \frac{q_2(x_2^*, y_1^*)}{x_2^*}(y_2 - y_2^*)\right\}$,

$l_{31} = c_1(y_1 - y_1^*)\{p_1(x_1, y_2) - p_1(x_1^*, y_2)\}$,

$l_{32} = \widetilde{c_1}(y_1 - y_1^*)\{p_2(x_2, y_2) - p_2(x_2^*, y_2)\}$,

$l_{33} = -(y_1 - y_1^*)[s_1(y_1) - s_1(y_1^*)]$,

$l_{34} = (y_1 - y_1^*)\{[p_1(x_1^*, y_2) - p_1(x_1^*, y_2^*)]c_1 + [p_2(x_2^*, y_2) - p_2(x_2^*, y_2^*)]\widetilde{c_1}\}$,

$l_{41} = (y_2 - y_2^*)c_2\{q_1(x_1, y_1) - q_1(x_1^*, y_1)\}$,

$l_{42} = (y_2 - y_2^*)\widetilde{c_2}\{q_2(x_2, y_1) - q_2(x_2^*, y_1)\}$,

$l_{43} = (y_2 - y_2^*)\{c_2[-q_1(x_1^*, y_1^*) + q_1(x_1^*, y_1)] + \widetilde{c_2}[q_2(x_2^*, y_1) - q_2(x_2^*, y_1^*)]\}$,

$l_{44} = -(y_2 - y_2^*)[s_2(y_2) - s_2(y_2^*)]$.

We set

$l_{11} = (x_1 - x_1^*)^2 u_{11}(x_1, y_1, y_2),$

$l_{12} = 0, l_{13} + l_{31} = 2(x_1 - x_1^*)(y_1 - y_1^*)u_{13}(x_1, y_1, y_2),$

$l_{14} + l_{41} = 2(x_1 - x_1^*)(y_2 - y_2^*)u_{14}(x_1, y_1, y_2), l_{21} = 0,$

$l_{22} = (x_2 - x_2^*)^2 u_{22}(x_2, y_1, y_2), l_{23} + l_{32} = 2(x_2 - x_2^*)(y_1 - y_1^*)u_{23}(x_2, y_1, y_2),$

$l_{24} + l_{42} = 2(x_2 - x_2^*)(y_2 - y_2^*)u_{24}(x_2, y_1, y_2), l_{33} = (y_1 - y_1^*)^2 u_{33}(y_1),$

$l_{34} + l_{43} = 2(y_1 - y_1^*)u_{34}(y_2)(y_2 - y_2^*), l_{44} = (y_2 - y_2^*)^2 u_{44}(y_2),$

Define

$u_{ij} = u_{ji}, i > j.$

So, $\dot{V} = x^T U x,$

where, $U = (u_{ij})$ *and* $x = \begin{pmatrix} x_1 - x_1^* \\ x_2 - x_2^* \\ y_1 - y_1^* \\ y_2 - y_2^* \end{pmatrix}.$

Theorem 8: When matrix U is negative definite on $\mathcal{A}$, the equilibrium $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ is globally asymptotically stable in $R^+_{x_1 x_2 y_1 y_2}$.

Proof : The solutions are bounded and the largest invariant set of $\{x \in R^+_{x_1 x_2 y_1 y_2} | \dot{V} = 0\} = \{E^*\}$. Hence the result follows from [11].

5. Uniform Persistence

We study the question of uniform persistence [2] of system (1) in this section.

Define

$P(x) = x_1^{\gamma_1} x_2^{\gamma_2} y_1^{\delta} y_2^{\mu} (x_1 + x_2)^{\epsilon}$

$\ln P = \gamma_1 \ln x_1 + \gamma_2 \ln x_2 + \delta \ln y_1 + \mu \ln y_2 + \epsilon \ln(x_1 + x_2)$

$$
\begin{aligned}
\psi &= \frac{d \ln P}{dt} = \frac{1}{P}\dot{P} \\
&= \gamma_1\left(g_1(x_1) - y_1\frac{p_1(x_1,y_2)}{x_1} - y_2\frac{q_1(x_1,y_1)}{x_1}\right) \\
&\qquad + \gamma_2\left(g_2(x_2) - y_1\frac{p_2(x_2,y_2)}{x_2} - y_2\frac{q_2(x_2,y_1)}{x_2}\right) \\
&\qquad + \delta\big(-s_1(y_1) + c_1p_1(x_1,y_2) + \widetilde{c_1}p_2(x_2,y_2)\big) \\
&\qquad + \mu\big(-s_2(y_2) + c_2q_1(x_1,y_1) + \widetilde{c_2}q_2(x_2,y_1)\big) \\
&\qquad + \frac{\epsilon}{x_1+x_2}[(x_1g_1 - y_1p_1 - y_2q_1) + x_2g_2 - y_1p_2 - y_2q_2]
\end{aligned}
$$

It is sufficient to show ([6]), that there exist positive constants $\gamma_1, \gamma_2, \delta, \mu \; and \; \epsilon$ such that $\psi > 0$ at all boundary equilibria. That is we require,

$$
\left.
\begin{array}{lr}
\gamma_1g_1(0) + \gamma_2g_2(0) - s_1(0)\delta - s_2(0)\mu + \epsilon\, min\big(g_1(0), g_2(0)\big) > 0 & (6.1)\\
\gamma_2g_2(0) + \delta\big(-s_1(0) + c_1p_1(K_1,0)\big) + \mu\big(-s_2(0) + c_2q_1(K_1,0)\big) > 0 & (6.2)\\
g_1(0)\gamma_1 + \delta\big(-s_1(0) + \widetilde{c_1}p_2(K_2,0)\big) + \mu\big(-s_2(0) + \widetilde{c_2}q_2(K_2,0)\big) > 0 & (6.3)\\
\gamma_2\left(g_2(0) - \overline{y_1}p_{2_{x_2}}(0,0)\right) + \mu\big(-s_2(0) + c_2q_1(\overline{x_1},\overline{y_1})\big) > 0 & (6.4)\\
\gamma_1\left(g_1(0) - \overline{y_{11}}p_{1_{x_1}}(0,0)\right) + \mu\big(-s_2(0) + \widetilde{c_2}q_2(\overline{x_2},\overline{y_{11}})\big) > 0 & (6.5)\\
\gamma_2\left(g_2(0) - \widetilde{y_2}q_{2_{x_2}}(0,0)\right) + \delta\big(-s_1(0) + c_1p_1(\widetilde{x_1},\widetilde{y_2})\big) > 0 & (6.6)\\
\gamma_1\left(g_1(0) - \widetilde{y_{22}}q_{1_{x_1}}(0,0)\right) + \delta\big(-s_1(0) + \widetilde{c_1}p_2(\widetilde{x_2},\widetilde{y_{22}})\big) > 0 & (6.7)\\
\mu\big(-s_2(0) + c_2q_1(x_{31},y_{31}) + \widetilde{c_2}q_2(x_{32},y_{31})\big) > 0 & (6.8)\\
\delta\big(-s_1(0) + c_1p_1(x_{41},y_{42}) + \widetilde{c_1}p_2(x_{42},y_{42})\big) > 0 & (6.9)\\
\gamma_2\left(g_2(0) - y_{51}p_{2_{x_2}}(0,y_{52}) - y_{52}q_{2_{x_2}}(0,y_{51})\right) > 0 & (6.10)\\
\gamma_1\left(g_1(0) - y_{61}p_{1_{x_1}}(0,y_{62}) - y_{62}q_{1_{x_1}}(0,y_{61})\right) > 0 & (6.11)
\end{array}
\right\} (6)
$$

Let boundary equilibria E_i, $3 \le i \le 10$ be globally asymptotically stable in their respective subsystems. Then

$$
\left.
\begin{array}{ll}
g_1(0) - \overline{y_{11}}p_{1_{x_1}}(0,0) > 0, & g_1(0) - \widetilde{y_{22}}q_{1_{x_1}}(0,0) > 0,\\
g_2(0) - \widetilde{y_2}q_{2_{x_2}}(0,0) > 0, & g_2(0) - \overline{y_1}p_{2_{x_2}}(0,0) > 0,\\
-s_2(0) + c_2q_1(\overline{x_1},\overline{y_1}) > 0, & -s_2(0) + \widetilde{c_2}q_2(\overline{x_2},\overline{y_{11}}) > 0,\\
-s_1(0) + c_1p_1(\widetilde{x_1},\widetilde{y_2}) > 0, & -s_1(0) + \widetilde{c_1}p_2(\widetilde{x_2},\widetilde{y_{22}}) > 0,
\end{array}
\right\} (7)
$$

Recall from section 3.2

$$
\left.
\begin{array}{l}
\xi_1 = -s_2(0) + c_2q_1(x_{31},y_{31}) + \widetilde{c_2}q_2(x_{32},y_{31}),\\
\xi_2 = -s_1(0) + c_1p_1(x_{41},y_{42}) + \widetilde{c_1}p_2(x_{42},y_{42}),\\
\xi_3 = g_2(0) - y_{51}p_{2_{x_2}}(0,y_{52}) - y_{52}q_{2_{x_2}}(0,y_{51}),\\
and\\
\xi_4 = g_1(0) - y_{61}p_{1_{x_1}}(0,y_{62}) - y_{62}q_{1_{x_1}}(0,y_{61}).
\end{array}
\right\} (8)
$$

For positive small δ and μ (6.1) holds.

From conditions (3) and (4) equalities (6.2) and (6.3) above hold.

When $\xi_i > 0,\ 1 \le i \le 4$, using (7), inequalities $(6.4) - (6.11)$ hold.

We thus have the following results:

Theorem 9: Let hypotheses $(H_1) - (H_5)$ hold and condition of facultative mutualism hold. Further $E_i, 3 \le i \le 10$ exist and be globally stable in their respective octants. When $\xi_i > 0,\ 1 \le i \le 4$, system (1) will be uniformly persistent.

Theorem 10: Let hypotheses $(H_1) - (H_5)$ hold and mutualism be obligate for y_1 (i.e. condition (5.1) holds). Furthermore let $E_5, E_6, E_i, 8 \le i \le 10$ be globally stable in their respective octants. When $\xi_i > 0, 2 \le i \le 4$, system (1) will be uniformly persistent.

In next result we give conditions for uniform persistence when mutualism is obligate for y_2.

Theorem 11: Let hypotheses $(H_1) - (H_5)$ hold and mutualism be obligate for y_2 (i.e. condition (5.2) holds). Further let $E_3,\ E_4,\ E_7,\ E_9$ and E_{10} be globally stable in their respective positive octants. When $\xi_1 > 0, \xi_3 > 0$ and $\xi_4 > 0$, system (1) is uniformly persistent.

When mutualism is obligate for both y_1 and y_2, equilibria $E_i, 3 \le i \le 8$ do not exist, and we have:

Theorem 12: Let hypotheses $(H_1) - (H_5)$ hold. Further let mutualism is obligate for both y_1 and y_2 (i.e. (5.1) and (5.2) hold). Let E_9 and E_{10} be globally stable in $R^+_{x_1 y_1 y_2}$ and $R^+_{x_2 y_1 y_2}$, respectively. If $\xi_3 > 0$ and $\xi_4 > 0$ then system is uniformly persistent.

6. Special case

Finally we present a special case of model (1):

We consider the system

$$\left.\begin{aligned}
\frac{dx_1}{dt} &= a_1\left(1-\frac{x_1}{K_1}\right)x_1 - p_1(x_1,y_2)y_1 - q_1(x_1,y_1)y_2\\
\frac{dx_2}{dt} &= a_2\left(1-\frac{x_2}{K_2}\right)x_2 - p_2(x_2,y_2)y_1 - q_2(x_2,y_1)y_2\\
\frac{dy_1}{dt} &= y_1\{-s_{11} - s_{12}y_1 + c_1p_1(x_1,y_2) + \widetilde{c_1}p_2(x_2,y_2)\}\\
\frac{dy_2}{dt} &= y_2\{-s_{21} - s_{22}y_2 + c_2q_1(x_1,y_1) + \widetilde{c_2}q_2(x_2,y_1)\}
\end{aligned}\right\} \quad (9)$$

For global stability of all equilibria, below$\big($except $E_8(x_{41}, x_{42}, 0, y_{42})\big)$ we take

$$p_i(x_i, y_2) = p_{i1}x_i,\ \ q_i(x_i, y_1) = q_{i1}x_i y_1, i = 1,2. \quad (10)$$

For E_8, we set:

$$p_i(x_i, y_2) = p_{i1}x_iy_2, \qquad q_i(x_i, y_1) = q_{i1}x_i, i = 1,2. \tag{11}$$

The model considered exhibits commensalism between y_1 and y_2.

A set of sufficient conditions for existence of E_i , $7 \leq i \leq 10$ is that the corresponding submodel be uniformly persistent [2]. The constants L_i, G_i , $i = 1,2$, are as in Theorem 2. Computing matrix M as in Theorem 4, we get

$$M = \begin{bmatrix} -\frac{a_1}{K_1} & 0 & \frac{(c_1-1)p_{11}}{2} \\ 0 & -\frac{a_2}{K_2} & \frac{(\widetilde{c_1}-1)p_{21}}{2} \\ \frac{(c_1-1)p_{11}}{2} & \frac{(\widetilde{c_1}-1)p_{21}}{2} & -s_{12} \end{bmatrix}$$

Corollary 1: E_7 will be globally stable in $R^+_{x_1x_2y_1}$, whenever M is negative definite.

For E_8 , we get

$$N = \begin{bmatrix} -\frac{a_1}{K_1} & 0 & \frac{q_{11}(c_2-1)}{2} \\ 0 & -\frac{a_2}{K_2} & \frac{q_{21}(\widetilde{c_2}-1)}{2} \\ \frac{q_{11}(c_2-1)}{2} & \frac{q_{21}(\widetilde{c_2}-1)}{2} & -s_{22} \end{bmatrix}$$

By Theorem 5, we have:

Corollary 2: When N is negative definite, E_8 is globally stable in $R^+_{x_1x_2y_2}$.

Next let $E_9(x_{51}, 0, y_{51}, y_{52})$ exist.

Computing symmetric matrix R as in Theorem 6,

$R = (r_{ij})$, is given by

$r_{11} = -\frac{a_1}{K_1}$, $r_{12}(y_2) = \frac{1}{2}\{(c_1-1)p_{11} - q_{11}y_2\}$,

$r_{13}(y_1) = \frac{1}{2}q_{11}(y_1 - y_{51})$, $r_{22} = -s_{12}$, $r_{23} = \frac{1}{2}q_{11}c_2x_{51}$,

$r_{33} = -s_{22}$, $|r_{12}(0)| = \frac{p_{11}}{2}|c_1 - 1|$,

Now, proceeding as in Theorem 2 of section 2,

$y_1 \leq \delta_{19} = \frac{c_1G_1}{s_1(0)} + \epsilon$, for large t, $y_2 \leq \delta_{29} = \frac{c_2L_1}{s_2(0)} + \epsilon$, for large t.

Thus,

$$|r_{12}(\delta_{29})| = \frac{1}{2}|p_{11}(c_1 - 1) - q_{11}\delta_{29}|, \qquad r_{12}max = max\{|r_{12}(0)|, |r_{12}(\delta_{29})|\}$$

$$|r_{13}(y_1)| \le \frac{q_{11}}{2} max\{y_{51}, |\delta_{19} - y_{51}|\} = r_{13}max$$

Corollary 3: Let $E_9(x_{51}, 0, y_{51}, y_{52})$ exists and

$$\frac{a_1}{K_1} > r_{12}max + r_{13}\,\mathrm{max}\,,\; s_{12} > r_{12}max + r_{23}, s_{22} > r_{13}max + r_{23}. \qquad (12)$$

Then E_9 is globally stable in $R^+_{x_1y_1y_2}$.

Proof:

Under condition(12), R is a symmetric diagonally dominant matrix in $\mathcal{A}_3$. By Gersgorin theorem if λ is an eigenvalue then there exists $1 \le i \le 3$ such that

$$\lambda \le r_{ii} + \sum_{j \ne i} |r_{ij}|$$

Also $|r_{ii}| > \sum_{k \ne i} |r_{ik}|$ and $r_{ii} < 0,\;\; j = 1,2,3$. Thus, $r_{ii} + \sum_{j \ne i} |r_{ij}| < 0$

i.e. eigenvalues of R in $\mathcal{A}_3$ are negative and by Theorem 6 E_9 is globally stable in $R^+_{x_1y_1y_2}$.

Next, let $E_{10}(0, x_{62}, y_{61}, y_{62})$ exists. From Theorem 2, $y_i(t) \le \delta_{i10}$ for large t, $= 1,2$.

where,

$$\delta_{110} = \frac{\widetilde{c_1}G_2}{s_{11}} + \epsilon\,,\;\; \delta_{210} = \frac{\widetilde{c_2}L_2}{s_{21}} + \epsilon\,,$$

Computing symmetric matrix T, as in Theorem 7, then

$$T = \left(t_{ij}\right)_{3x3}$$

where,

$$t_{11} = -\frac{a_2}{K_2}\,, t_{12}(y_2) = \frac{1}{2}\{p_{21}(\widetilde{c_1} - 1) - q_{21}y_2\}\,, t_{13} = \frac{1}{2}q_{21}(y_1 - y_{61})\,, t_{22} = -s_{12}\,,$$

$$t_{23} = \frac{1}{2}[q_{21}\widetilde{c_2}x_{62}]\,, t_{33} = -s_{22}\,,$$

and

$$t_{ij} = t_{ji}\,, i > j\,.$$

Define,

$t_{12}max = \frac{1}{2}max\{|t_{12}(0)|, t_{12}(\delta_{210})\}$, $t_{13}max = \frac{1}{2}max\{q_{21}y_{61}, q_{21}(\delta_{10} - y_{61})\}$

We require

$\frac{a_2}{K_2} > t_{12}max + t_{13}$ max , $s_{12} > t_{12}max + t_{23}, s_{22} > t_{13}max + t_{23}$. (13)

Then we have the following result:

Corollary 4: Let $E_{10}(0, x_{62}, y_{61}, y_{62})$ exists and inequalities (13) hold. Then E_{10} is globally asymptotically stable in $R^{+}_{x_2y_1y_2}$.

For global stability of E^*, we computing L, as in Theorem 8,

$u_{11} = -\frac{a_1}{K_1}, u_{12} = 0, u_{13} = \frac{1}{2}\{(c_1 - 1)p_{11} - q_{11}y_2\}$, $u_{14} = \frac{1}{2}q_{11}(y_1 - y_1^*)$,

$u_{22} = -\frac{a_2}{K_2}$, $u_{23} = \frac{1}{2}\{(\widetilde{c_1} - 1)p_{21} - q_{21}y_2\}$, $u_{24} = \frac{1}{2}q_{21}(\widetilde{c_2}y_1 - y_1^*)$, $u_{33} = -s_{12}$,

$u_{34} = \frac{1}{2}(c_2x_1^*q_{11} + \widetilde{c_2}x_2^*q_{21}), u_{44} = -s_{22}$.

$u_{ij} = u_{ji}$, $i > j$, $1 \leq i, j \leq 4$.

Set U= (u_{ij}) .

Next, if $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ exists in interior of $R^{+}_{x_1x_2y_1y_2}$, Define

$l_{13}max = \frac{1}{2}max\{|(c_1 - 1)p_{11}|, |(c_1 - 1)p_{11} - q_{11}\delta_2|\}, l_{14}max = \frac{1}{2}q_{11}max\{(\delta_1 - y_1^*), y_1^*\}$,

$l_{23}max = \frac{1}{2}max\{|\widetilde{c_1} - 1|p_{21}, |(\widetilde{c_1} - 1)p_{21} - q_{21}\delta_2|\}$, $l_{24}max = \frac{1}{2}q_{21}(\widetilde{c_2}\delta_1 - y_1^*)$,

where, $\delta_1 = \frac{c_1G_1 + \widetilde{c_1}G_2}{s_{11}}$, and $\delta_2 = \frac{c_2L_1 + \widetilde{c_1}L_2}{s_{21}}$.

The next result is clear from Theorem 8.

Corollary 5: Let $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ exists and

$\frac{a_1}{K_1} > l_{13}max + l_{14}max$, $\frac{a_2}{K_2} > l_{23}max + l_{24}max$,

$s_{12} > l_{13}max + l_{23}max + l_{24}max$, and $s_{22} > l_{14}max + l_{24}max + l_{34}$.

Then E^* is globally stable.

Below we present specific examples:

With $a_1 = a_2 = 1$, $K_1 = 0.8, K_2 = 1, p_{11} = .4$, $p_{21} = .3$, $c_1 = 2.5$, $\widetilde{c_1} = 3.5$,

$s_{11} = .5, s_{12} = 1.5$, $E_7(x_{31}, x_{32}, y_{31}, 0) = (0.5977, 0.8103, 0.6323, 0)$ exists and the symmetric matrix

$$M = \begin{bmatrix} -1.25 & 0 & .3 \\ 0 & -1 & .375 \\ 0.3 & .375 & -1.5 \end{bmatrix}$$

is negative definite as its eigenvalues are $-1.8263, -1.1716, -.7521$. Hence by Theorem 4 E_7 is globally stable in $R^+_{x_1x_2y_1}$.

With $a_1 = a_2 = 1, K_1 = K_2 = 1, q_{11} = 0.4, c_2 = 2.5, \widetilde{c_2} = 3.5, q_{21} = 0.3,\ s_{21} = 0.5\ and\ s_{22} = 1.50$.

Equilibrium $E_8(x_{41}, x_{42}, 0, y_{41}) = (0.7201, 0.7901, 0, 0.6998)$ exists and symmetric matrix N in Theorem 5 is

$$N = \begin{bmatrix} -1 & 0 & .3 \\ 0 & -1 & .3750 \\ 0.3 & .375 & -1.5 \end{bmatrix}$$

and has eigenvalues $-1.7914, -1\ and -0.7086$. Thus E_8 is globally stable in $R^+_{x_1x_2y_2}$.

With $a_1 = 2.2,\ K_1 = 0.85,\ p_{11} = 0.45,\ q_{11} = .21,\ s_{11} = 0.5,\ s_{12} = 2.52,$ $s_{21} = 0.065, s_{22} = 1.75,\ c_1 = 2.4\ and\ c_2 = 3.47, E_9(x_{51}, 0, y_{51}, y_{52}) = (0.823, 0, 0.1543, 0.0157)$ exists and conditions (12) of Corollary 3 are satisfied. Thus E_9 is globally stable in $R^+_{x_1y_1y_2}$.

With $a_2 = 1.8,\ K_2 = 0.80,\ p_{11} = 0.4,\ p_{21} = .42,\ \ q_{21} = .25,\ s_{11} = 0.50,$ $s_{12} = 1.9, s_{21} = 0.1,\ s_{22} = 1,\ \widetilde{c_1} = 2.55\ and\ \widetilde{c_2} = 3.5,\ E_{10}(0, x_{62}, y_{61}, y_{62}) = (0, 0.768, 0.1698, 0.0141)$ exists. Also conditions of Corollary 4 are satisfied and E_{10} is globally stable in $R^+_{x_2y_1y_2}$.

With $a_2 = 1,\ K_1 = 2,\ a_2 = 1.05,\ K_2 = 1,\ p_{11} = 0.365,\ \ q_{11} = 0.25,\ p_{21} = .30,$ $q_{21} = 0.5,\ s_{11} = 0.4,\ s_{12} = 0.37,\ s_{21} = 0.4,\ s_{22} = 0.90,\ c_1 = 1,\ \widetilde{c_1} = 1.5,\ c_2 = 1.2,\ \ and\ \widetilde{c_2} = 2.5$, interior equilibrium $E^*(x_1^*, x_2^*, y_1^*, y_2^*) = (1.2352, 0.7106, 1.0017, 0.0669)$ exists. The conditions of Corollary 5 are also satisfied and E^* is globally stable.

Next we illustrate Theorem 11.

With $a_1 = 1.8, a_2 = 1.8,\ K_1 = 0.8,\ K_2 = 0.8,\ p_{11} = 0.4,\ p_{21} = .42, s_{11} = 0.5,$ $s_{12} = 1.9, s_{21} = 0.1,\ s_{22} = 1,\ \widetilde{c_1} = 2.55,\ c_2 = 3.5, \widetilde{c_2} = 3.5, c_2 = 3.5, \widetilde{c_2} = 3.5, q_{11} = 0.25\ and\ q_{21} = \ 0.25$, equilibria $E_0(0{,}0{,}0{,}0), E_1(0.8{,}0{,}0{,}0)$, $E_2(0{,}0.8{,}0{,}0), E_3(0.4902{,}0{,}3.3971{,}0)$, $E_4(0{,}0.3401{,}1.7847{,}0)$, $E_7(0.7086{,}0.7040{,}0.5140{,}0), E_9(0.7730{,}0{,}0.1518{,}0.0027)$ and

$E_{10}(0,0.7680,0.1698,0.0141)$ exist. Further E_3, E_4, E_7, E_9 and E_{10} are globally stable in their respective octants. Finally, $\xi_1 = 0.5355, \xi_3 = 1.7361, \xi_4 = 1.7315.$ are positive and by Theorem 11 system (9) with p_i, q_i as given by (10) is uniformly persistent.

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