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 therein).

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:

\[
\begin{align*}
\frac{d x_1}{dt} &= x_1 g_1(x_1) - y_1 p_1(x_1, y_2) - y_2 q_1(x_1, y_1), \\
\frac{d x_2}{dt} &= x_2 g_2(x_2) - y_1 p_2(x_2, y_2) - y_2 q_2(x_2, y_1), \\
\frac{d y_1}{dt} &= y_1 [-s_1(y_1) + c_1 p_1(x_1, y_2) + \tilde{c}_1 q_2(x_2, y_1)], \\
\frac{d y_2}{dt} &= y_2 [-s_2(y_2) + c_2 q_1(x_1, y_1) + \tilde{c}_2 q_2(x_2, y_1)],
\end{align*}
\]

(1)

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.

\( (H_2) \) \( g_i(x_i) : [0, \infty) \rightarrow \mathbb{R}, g_i(0) > 0, g_i'< 0; \) 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

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

The positive constants rate of conversion \( c_i \) and \( \tilde{c}_i \) denote the rate of conversion of
prey biomass to predator biomass.

\((H_3)\) 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,

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

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

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

Further let,

\[
\mathcal{A} = \{(x_1,x_2,y_1,y_2) : 0 \leq x_1 \leq K_1, 0 \leq x_1 \leq K_2, 0 \leq c_1 x_1 + \bar{c}_1 x_2 + y_1 \leq \frac{c_1 \bar{g}_1 + \bar{c}_1 \bar{g}_2}{s_1(0)}, 0 \leq c_2 x_1 + \bar{c}_2 x_2 + y_2 \leq \frac{c_2 \bar{g}_1 + \bar{c}_2 \bar{g}_2}{s_2(0)}\}.
\]

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

Similarly

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

Next,

\[
(c_1 x_1 + \bar{c}_1 x_2 + y_1') \leq c_1 x_1 g_1(x_1) + x_2 \bar{c}_1 g_2(x_2) - s_1(0) y_1 - c_1 x_1 s_1(0) - x_2 \bar{c}_1 s_1(0) + c_1 x_1 s_1(0) + \bar{c}_1 x_2 s_1(0).
\]
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Set \( u = c_1 x_1 + \bar{c}_1 x_2 + y_1 \) to get,

\[
u' + s_1(0)u \leq c_1 x_1 (s_1(0) + g_1(x_1)) + \bar{c}_1 x_2 (s_1(0) + g_2(x_2)) \leq c_1 G_1 + \bar{c}_1 G_2
\]

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

\[
\left( u e^{s_1(0)t} - u(0) \right) \leq \frac{(c_1 G_1 + \bar{c}_1 G_2)(e^{s_1(0)t} - 1)}{s_1(0)}.
\]

Or \( u(t) \leq u(0)e^{-s_1(0)t} + \frac{(c_1 G_1 + \bar{c}_1 G_2)(1-e^{-s_1(0)t})}{s_1(0)}. \)

\[
u(t) \leq e^{-s_1(0)t} \left( u(0) - \frac{c_1 G_1 + \bar{c}_1 G_2}{s_1(0)} \right) + \frac{c_1 G_1 + \bar{c}_1 G_2}{s_1(0)}.
\]

So, \( c_1 x_1(0) + \bar{c}_1 x_2(0) + y_1(0) \leq \frac{c_1 G_1 + \bar{c}_1 G_2}{s_1(0)} \)

Implies, \( c_1 x_1 + \bar{c}_1 x_2 + y_1 \leq \frac{c_1 G_1 + \bar{c}_1 G_2}{s_1(0)}. \)

In general,

\[
c_1 x_1(t) + \bar{c}_1 x_2(t) + y_1(t) \leq \frac{c_1 G_1 + \bar{c}_1 G_2}{s_1(0)} + \epsilon, \text{ as } t \to \infty.
\]

Similar argument holds for \( c_2 x_1 + \bar{c}_2 x_2 + y_2 \).

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, \( \exists \bar{x}_i^* \) such that,

\[
\begin{align*}
-s_1(0) + c_1 p_1(\bar{x}_1^*, 0) &= 0, \\
-s_1(0) + \bar{c}_1 p_2(\bar{x}_2^*, 0) &= 0, \\
\bar{x}_i^* &< K_i, \quad i = 1, 2.
\end{align*}
\]

(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
We conclude, that there exist equilibria 

\[ E_0 (0,0,0,0), E_1 (K_1, 0,0,0), E_2 (0,K_2, 0,0), E_3 (x_1, 0, \bar{y}_1, 0), E_4 (0, x_2, \bar{y}_2, 0), \]

\[ E_5 (x_1, 0,\bar{y}_2), E_6 (0, x_2, 0, \bar{y}_2), E_7 (x_{31}, x_{32}, y_{31}, 0), E_8 (x_{41}, x_{42}, 0, y_{42}), E_9 (x_{51}, 0, y_{51}, y_{52}) \]

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

\[ -s_1 (0) + c_1 p_2 (K_1, 0) + \bar{c}_1 q_2 (K_2, 0) < 0 \]  \hspace{1cm} (5.1) \]

It will be obligate for \( y_2 \), when

\[ -s_2 (0) + c_2 q_1 (K_1, 0) + \bar{c}_2 q_2 (K_2, 0) < 0 \]  \hspace{1cm} (5.2) \]

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,

\[
V = \begin{bmatrix}
g_1 + x_1 g'_1 - y_1 p_{1x_1} - y_1 q_{1x_1} & 0 & -p_1 - y_2 q_{1y_1} & -y_1 p_{2y_1} - q_1 \\
0 & g_2 + x_2 g'_2 - y_1 p_{2x_2} - y_2 q_{2x_2} & -p_2 - y_2 q_{2y_2} & -y_2 p_{2y_2} - q_2 \\
y_1 c_1 p_{1x_1} & y_1 c_1 p_{2x_2} & -s_1 + c_1 p_1 + \bar{c}_1 q_1 - y_1 s_1 & c_1 y_1 p_{1y_1} + \bar{c}_1 q_{1y_1} \\
c_1 y_2 q_{1x_1} & \bar{c}_1 y_2 q_{1x_2} & c_1 y_2 q_{1y_1} + \bar{c}_1 q_{1y_2} y_1 & -s_1 + c_1 q_1 + \bar{c}_1 q_1 - y_2 s_2
\end{bmatrix}
\]

\( V(E_0) = \text{diag}(g_1(0), g_2(0), -s_1(0), -s_2(0)) \)

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

\[
V(E_1) = \begin{bmatrix}
K_1 g_1(K_1) & 0 & -p_1(K_1, 0) & -q_1(K_1, 0) \\
0 & g_2(0) & 0 & 0 \\
0 & 0 & -s_1(0) + c_1 p_1(K_1, 0) & 0 \\
0 & 0 & 0 & -s_2(0) + c_2 q_2(K_1, 0)
\end{bmatrix}
\]

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.
Next, where, eigenvalues will be given by, \( -\sigma \)

Proceeding same way where, eigenvalues will be given by, \( -\sigma \) and \( -s_2(0) + \bar{c}_2 q_2(K_2,0) \) respectively. Also,

So \( V(E_3) \) has eigenvalue \( g_2(0) - \bar{y}_1^2 p_{x_2}(0,0) \) in \( x_2 \) direction. The eigenvalue in \( y_2 \) direction is \( -s_2(0) + c_2 q_1(\bar{x}_1, \bar{y}_1) \). The other two eigenvalues are roots of \( \lambda^2 + (\alpha_1 + \bar{y}_1 s_1(\bar{y}_1) \lambda + \alpha_1 \bar{y}_1 s_1(\bar{y}_1) + \bar{c}_1 \bar{y}_1 p_1(\bar{x}_1,0)p_{1x_1}(\bar{x}_1,0) = 0 \), where, \( \alpha_1 = g_1(\bar{x}_1) + \bar{x}_1 g_1'(\bar{x}_1) - \bar{y}_1 p_{1x_1}(\bar{x}_1,0) \).

Proceeding same way \( V(E_4(0, \bar{x}_2, \bar{y}_1, 0)) \) has eigenvalues \( g_1(0) - \bar{y}_1^2 p_{x_2}(0,0) \) and \( -s_2(0) + \bar{c}_2 q_2(\bar{x}_2, \bar{y}_1) \) in \( x_2 \) and \( y_1 \) directions respectively. The other two eigenvalues are the roots of \( \lambda^2 + (\alpha_2 + \bar{y}_1 s_1(\bar{y}_1)) \lambda + \alpha_2 \bar{y}_1 s_1(\bar{y}_1) + \bar{c}_1 \bar{y}_1 p_1(\bar{x}_2,0)p_{2x_2}(\bar{x}_2,0) = 0 \), where, \( \alpha_2 = g_2(\bar{x}_2) + \bar{x}_2 g_2'(\bar{x}_2) - \bar{y}_1 p_{2x_2}(\bar{x}_2,0) \).

Also, \( V(E_5(\bar{x}_1,0,0,\bar{y}_2)) \) has eigenvalues \( g_2(0) - \bar{y}_2 q_{2x_2}(0,0) \) and \( -s_1(0) + c_2 p_1(\bar{x}_1, \bar{y}_2) \) in \( x_2 \) and \( y_1 \) directions respectively. The other two eigenvalues are the roots of \( \lambda^2 + (\alpha_3 + \bar{y}_2 s_1(\bar{y}_2)) \lambda + \alpha_3 \bar{y}_2 s_1(\bar{y}_2) + \bar{c}_2 \bar{y}_2 q_1(\bar{x}_1,0)q_{1x_1}(\bar{x}_1,0) = 0 \), where, \( \alpha_3 = g_1(\bar{x}_1) + \bar{x}_1 g_1'(\bar{x}_1) - \bar{y}_2 q_{1x_1}(\bar{x}_1,0) \).

Next, \( \lambda^2 + (\alpha_4 + \bar{y}_2 s_1(\bar{y}_2)) \lambda + \alpha_4 \bar{y}_2 s_1(\bar{y}_2) + \bar{c}_2 \bar{y}_2 q_2(\bar{x}_2,0)q_{2x_2}(\bar{x}_2,0) = 0 \), where, \( \alpha_4 = g_2(\bar{x}_2) + \bar{x}_2 g_2'(\bar{x}_2) - \bar{y}_2 q_{2x_2}(\bar{x}_2,0) \).

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

\[
\xi_1 = -s_2(0) + c_2 q_1(x_{31}, y_{31}) + \bar{c}_2 q_2(x_{32}, y_{31}).
\]
Other eigenvalues are the roots of
\[ \lambda^3 + \mu_1 \lambda^2 + \mu_2 \lambda + \mu_3 = 0 \]
where, \( \mu_1 = -(y_{31} s'_1(y_{31}) + a_1 + a_2) \),
\[ \mu_2 = a_3 + a_1 \left( a_2 + y_{31} s'_1(y_{31}) + c_1 y_{31} p_{1x_1}(x_{31}, 0)p_1(x_{31}, 0) \right), \]
\[ \mu_3 = -a_1 a_3 - a_2 c_1 y_{31} p_{1x_1}(x_{31}, 0)p_1(x_{31}, 0) \],
\[ a_i = g_i(x_{3i}) + x_{3i} g'_i(x_{3i}) - y_{3i} p_{ix_1}(x_{3i}, 0), i = 1,2, \]
and
\[ a_3 = \tilde{c}_1 y_{31} p_2(x_{32}, 0)p_{2x_2}(x_{32}, 0) - y_{31} s'_1(y_{31}) a_2 . \]
Similarly, the eigenvalue of \( V \left( E_8(x_{41}, x_{42}, 0, y_{42}) \right) \) in \( y_1 \) - direction is \( \xi_2 = -s_1(0) + c_1 p_1(x_{41}, y_{42}) + \tilde{c}_2 p_2(x_{42}, y_{42}) \).

Other eigenvalues are given by the roots of
\[ \lambda^3 + y_1 \lambda^2 + y_2 \lambda + y_3 = 0 \]
\[ y_1 = -(y_{42} s'_2(y_{42}) + a_4 + a_5) \]
\[ y_2 = a_6 + a_4 \left( a_5 + y_{42} s'_2(y_{42}) + c_2 y_{42} q_{1x_1}(x_{41}, 0)q_1(x_{41}, 0) \right) \]
\[ y_3 = -a_4 a_6 - a_5 c_2 y_{42} q_{1x_1}(x_{41}, 0)q_1(x_{41}, 0) \]
\[ a_{i+3} = g_i(x_{4i}) + x_{4i} g'_i(x_{4i}) - y_{42} p_{ix_1}(x_{4i}, 0), i = 1,2, \]
and
\[ a_6 = \tilde{c}_2 y_{42} q_2(x_{42}, 0)q_{2x_2}(x_{42}, 0) - y_{42} s'_2(y_{42}) a_5 \]
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
\[ \lambda^3 + (y_{51} s'_1 + y_{52} s'_2) \lambda^2 \]
\[ - \left[ e_1(y_{51} s'_1 + y_{52} s'_2) + \left( y_{51} c_1 p_{1x_1}(p_1 + y_{52} q_{1y_1}) + c_2 y_{52} q_{1x_1}(y_{51} p_{1y_2} + q_1) \right) \right] \lambda \]
\[ + \left[ y_{51} c_1 p_{1x_1}(p_1 + y_{52} q_{1y_1}) y_{52} s'_2 + c_2 y_{52} q_{1x_1}(y_{51} p_{1y_2} + q_1) \right] \lambda \]
\[ + c_2 y_{52} q_{1x_1}(p_1 + y_{52} q_{1y_1}) c_1 y_{51} p_{1y_2} + y_{51} s'_1(y_{51} p_{1y_2} + q_1) = 0 \]
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.
Eigenvale of $V(E_{10}(0, x_{62}, y_{61}, y_{62}))$ 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

$$\lambda^2 + (y_{61}s'_1 + y_{62}s'_2 - e_2)\lambda$$

$$- \left[ e_2(y_{61}s'_1 + y_{62}s'_2) + (y_{61}\tilde{c}_1p_{2x_2}(p_2 + y_{62}q_{2y_1}) + \tilde{c}_2y_{62}q_{2x_2}(y_{61}p_{2y_2} + q_2)) - y_{61}y_{62}s'_1s'_2 + \tilde{c}_2y_{61}y_{62}q_{2y_1}\tilde{c}_1p_{2y_2} \right] \lambda$$

$$+ y_{61}\tilde{c}_1p_{2x_2}\{(p_2 + y_{62}q_{2y_1})y_{62}s'_2 + \tilde{c}_2y_{62}q_{2y_1}(y_{61}p_{2y_2} + q_2)\}$$

$$+ \tilde{c}_2y_{62}q_{2x_2}\{(p_2 + y_{62}q_{2y_1})\tilde{c}_1y_{61}p_{2y_2} + y_{61}s'_1(p_2 + y_{62}q_{2y_1} + q_2)\} = 0,$$

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 $E^*$:

$$F(\lambda) = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0,$$

where,

$$a_1 = -\Sigma^4 a_{ii},$$

$$a_2 = m_1 - m_2 + (a_{11} + a_{22})(a_{33} + a_{44}) + a_{11}a_{22} + \beta_1,$$

$$a_3 = -(a_{11} + a_{22})m_1 - a_{11}a_{22}(a_{33} + a_{44}) + y_1 + y_2,$$

$$a_4 = m_1a_{11}a_{22} + \delta_1 + \delta_2 + \delta_3 + \beta_1 = -(a_{11}a_{31} + a_{14}a_{41}),$$

$$y_1 = (a_{13}a_{22} + m_5)a_{31} - a_{41}(m_6 - a_{14}a_{22}).$$

$$\delta_1 = m_6a_{22}a_{41} - m_5a_{22}a_{31},$$

$$y_2 = a_{11}m_2 + a_{32}m_3 - a_{42}m_4, \quad \delta_2 = a_{11}(a_{42}m_4 - a_{32}m_3),$$

$$\delta_3 = m_7(a_{31}a_{42} - a_{41}a_{32}).$$

$$m_1 = a_{33}a_{44} - a_{14}a_{43}, m_2 = a_{23}a_{32} + a_{24}a_{42}.$$

$$m_3 = a_{23}a_{44} - a_{24}a_{43}, m_4 = a_{23}a_{34} - a_{24}a_{33}.$$

$$m_5 = a_{13}a_{44} - a_{14}a_{43}, m_6 = a_{13}a_{34} - a_{14}a_{33},$$

and $m_7 = a_{13}a_{24} - a_{14}a_{23}.$

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
\[
\alpha_i > 0, \quad 1 \leq i \leq 4, \alpha_1\alpha_2 - \alpha_3^2 - \alpha_4^2 > 0.
\]

4. Global Stability

In this section we obtain conditions of global asymptotic stability of four, boundary equilibria 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 \( R_{xyz}^{++} \) 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,
\[
\begin{align*}
\dot{x}_1 &= \alpha x_1 g_1(x_1) - y_1 p_1(x_1, 0), \\
\dot{x}_2 &= x_2 g_2(x_2) - y_1 p_2(x_2, 0), \\
\dot{y}_1 &= y_1 [-s_1(y_1) + c_1 p_1(x_1, 0) + \tilde{c}_1 p_2(x_2, 0)] \\
x_1(t_0) &= x_{10} \geq 0, x_2(t_0) = x_{20} \geq 0, y_1(t_0) = y_{10} \geq 0.
\end{align*}
\]

We will find sufficient 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
\[
\frac{dV}{dt} = (x_1 - x_{31}) \left[ \alpha g_1(x_1) - y_1 \frac{p_1(x_1, 0)}{x_1} \right] + (x_2 - x_{32}) \left[ g_2(x_2) - y_1 \frac{p_2(x_2, 0)}{x_2} \right] + (y_1 - y_{31}) \{-s_1(y_1) + c_1 p_1(x_1, 0) + \tilde{c}_1 p_2(x_2, 0)\}
\]
\[
= \sum_{i,j=1}^{2} l_{ij},
\]
where,
\[ l_{11} = (x_1 - x_{31}) \left\{ \alpha [g_1(x_1) - g_1(x_{31})] + y_1 \left[ \frac{p_1(x_{31},0)}{x_{31}} - \frac{p_1(x_1,0)}{x_1} \right] \right\}, \]
\[ l_{12} = 0, \; l_{13} = -\frac{(x_1 - x_{31})}{x_{31}} (y_1 - y_{31})p_1(x_{31},0), \]
\[ l_{21} = 0, \; l_{22} = (x_2 - x_{32}) \left\{ g_2(x_2) - g_2(x_{32}) + y_1 \left[ \frac{p_2(x_{32},0)}{x_{32}} - \frac{p_2(x_2,0)}{x_2} \right] \right\}, \]
\[ l_{23} = -\frac{1}{x_{32}} (x_2 - x_{32})(y_1 - y_{31})p_2(x_{32},0), \; l_{31} = c_1 (y_1 - y_{31}) \left[ p_1(x_1,0) - p_1(x_{31},0) \right], \]
\[ l_{32} = \tilde{c}_1 (y_1 - y_{31}) \left[ p_2(x_2,0) - p_2(x_{32},0) \right], \; l_{33} = -(y_1 - y_{31}) [s_1(y_1) - s_1(y_{31})]. \]

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
\[ m_{ij} = m_{ji}, \; i > j. \]

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 \( \mathcal{A}_1 = \{ (x_1, x_2, y_1) | 0 \leq x_1 \leq K_1, 0 \leq x_2 \leq K_2, c_1 x_1 + \tilde{c}_1 x_2 + y_1 \leq \frac{c_1 G_1 + \tilde{c}_1 G_2}{s_1(0)} \} \) is an attracting set for the subsystem in \( R_{x_1 x_2 y_1}^+ \).

**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 \( R_{x_1 x_2 y_1}^+ \).

**Proof:** The solutions are bounded and the largest invariant set of \( \{ x \in R_{x_1 x_2 y_1}^+ | \dot{V} = 0 \} = \{ E_7 \} \). Hence \( E_7 \) is globally asymptotically stable in \( R_{x_1 x_2 y_1}^+ \). [11].

Next we consider the question of global asymptotically stability of \( E_8(x_{41}, x_{42}, 0, y_{42}) \)
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for the system
\[
\begin{align*}
    x_1' &= \alpha x_1 g_1(x_1) - y_2 q_1(x_1, 0), \\
    x_2' &= x_2 g_2(x_2) - y_2 q_2(x_2, 0), \\
    y_2' &= y_2 \left[ -s_2(y_2) + c_2 q_1(x_1, 0) + \tilde{c}_2 q_2(x_2, 0) \right]
\end{align*}
\]

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

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,

\[
    \frac{dV}{dt} = (x_1 - x_{41}) \left\{ \alpha g_1(x_1) - \frac{y_2}{x_1} q_1(x_1, 0) \right\} + (x_2 - x_{42}) \left\{ g_2(x_2) - \frac{y_2}{x_2} q_2(x_2, 0) \right\}
\]

\[
    + (y_2 - y_{42}) \left\{ -s_2(y_2) + c_2 q_1(x_1, 0) + \tilde{c}_2 q_2(x_2, 0) \right\}
\]

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

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

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

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

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

\[
l_{31} = c_2 (y_2 - y_{42}) [q_1(x_1, 0) - q_1(x_{41}, 0)], \quad l_{32} = \tilde{c}_2 (y_2 - y_{42}) [q_2(x_2, 0) - q_2(x_{42}, 0)],
\]

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

Next, we define \(n_{ij}\)'s, such that

\[
l_{11} = (x_1 - x_{41})^2 n_{11}(x_1, y_2), \quad n_{12} = 0, \quad l_{13} = 2(x_1 - x_{41})(y_2 - y_{42}) n_{13}(x_1),
\]

\[
l_{22} = (x_2 - x_{42})^2 n_{22}(x_2, y_2), \quad l_{23} = 2(x_2 - x_{42})(y_2 - y_{42}) n_{23}(x_2),
\]

\[
l_{33} = (y_2 - y_{42})^2 n_{33}(y_2),
\]

and
\[ n_{ij} = n_{ji}, \quad i > j. \]

Thus
\[
\frac{dv}{dt} = x^T N x,
\]

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

Also from Theorem 2 we have: \( \mathcal{A}_2 = \left\{ (x_1, x_2, y_2) \mid 0 \leq x_1 \leq K_1, 0 \leq x_2 \leq K_2, c_2 x_2 + \tilde{c}_2 x_2 + y_2 \leq \frac{c_2 k_1 + \tilde{c}_2 k_2}{s_2(0)} \right\} \) 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,

\[
\frac{dv}{dt} = (x_1 - x_{51}) \left\{ a g_1(x_1) - y_1 \frac{p_1(x_1, y_2)}{x_1} - y_2 \frac{q_1(x_1, y_1)}{x_1} \right\} \\
+ (y_1 - y_{52}) \left\{ -s_1(y_1) + c_1 p_1(x_1, y_2) \right\} \\
+ (y_2 - y_{52}) \left\{ -s_2(y_2) + c_2 q_1(x_1, y_1) \right\}
\]

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

where,

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

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

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

\[
l_{21} = c_1 (y_1 - y_{51}) \left\{ p_1(x_1, y_2) - p_1(x_{51}, y_2) \right\}.
\]
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\[ l_{22} = -(y_1 - y_{51})[s_1(y_1) - s_1(y_{51})]. \]
\[ l_{23} = c_1(y_1 - y_{51})[p_1(x_{51}, y_2) - p_1(x_{51}, y_{52})]. \]
\[ l_{31} = (y_2 - y_{52})c_2[q_1(x_1, y_1) - q_1(x_{51}, y_1)]. \]
\[ l_{32} = c_2(y_2 - y_{52})[-q_1(x_{51}, y_{51}) + q_1(x_{51}, y_1)]. \]
\[ l_{33} = -(y_2 - y_{52})[s_2(y_2) - s_2(y_{52})]. \]

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, \[ \mathcal{A}_3 = \{ (x_1, y_1, y_2) \mid 0 \leq x_1 \leq K_1, 0 \leq c_1 x_1 + y_1 \leq \frac{c_1 \delta_1}{s_1(0)}, c_2 x_1 + y_2 \leq \frac{c_2 \delta_2}{s_2(0)} \} \]
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
\[
\frac{dV}{dt} = (x_2 - x_{62}) \left\{ g_2(x_2) - y_1 \frac{p_2(x_2, y_2)}{x_2} - y_2 \frac{q_2(x_2, y_1)}{x_2} \right\} \\
+ (y_1 - y_{62}) \{-s_1(y_1) + c_1p_1(x_2, y_2)\} \\
+ (y_2 - y_{62}) \{-s_2(y_2) + c_2q_1(x_2, y_4)\} \\
= \sum_{i,j=1}^{3} l_{ij},
\]

where,

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

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

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

\[
l_{21} = \tilde{c}_1(y_1 - y_{61}) \left[ p_2(x_2, y_2) - p_2(x_{62}, y_{62}) \right],
\]

\[
l_{22} = (y_1 - y_{61}) \left[ s_1(y_1) - s_1(y_{61}) \right],
\]

\[
l_{23} = (y_1 - y_{61}) \tilde{c}_2 \left[ p_2(x_{62}, y_2) - p_2(x_2, y_2) \right],
\]

\[
l_{31} = (y_2 - y_{62}) \tilde{c}_2 \left[ q_2(x_2, y_1) - q_2(x_{62}, y_1) \right],
\]

\[
l_{32} = \tilde{c}_2 (y_2 - y_{62}) \left[ -q_2(x_{62}, y_{61}) + q_2(x_{62}, y_{1}) \right],
\]

\[
l_{33} = (y_2 - y_{62}) \left[ s_2(y_2) - s_2(y_{62}) \right].
\]

We set

\[
l_{11} = (x_2 - x_{62})^2 t_{11}(x_2, y_1, y_2),
\]

\[
l_{12} + l_{21} = 2(x_2 - x_{62})(y_1 - y_{61}) t_{12}(x_2, y_1, y_2),
\]

\[
l_{13} + l_{31} = 2(x_2 - x_{62})(y_2 - y_{62}) t_{13}(x_2, y_1, y_2),
\]

\[
l_{23} + l_{32} = 2(y_1 - y_{61}) t_{23}(y_2) (y_2 - y_{62}),
\]

\[
l_{33} = (y_2 - y_{62})^2 t_{33}(y_2).
\]

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, \(\mathcal{A}_4 = \{(x_2, y_1, y_2) | 0 \leq x_2 \leq K_2, 0 \leq \tilde{c}_1 x_2 + y_1 \leq \frac{c_1 G_2}{s_1(0)}, 0 \leq \tilde{c}_2 x_2 + y_2 \leq \frac{c_2 L_2}{s_2(0)}\}\) is an attracting set for the subsystem in \(R_{x_2 y_1 y_2}^+\). Thus we have:
Theorem 7: Whenever the symmetric matrix T is negative definite in the region $A_4$, the equilibrium $E_{10}(0, x_{62}, y_{51}, y_{52})$ is globally asymptotically stable in $R^+_2 y_1 y_2$.

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 derive of $V$ along the solutions of (1) we get,

$$\frac{dV}{dt} = (x_1 - x_1^*) \left\{ \alpha g_1(x_1) - y_1 \frac{p_1(x_1, y_2)}{x_1} - y_2 \frac{q_1(x_1, y_1)}{x_1} \right\}$$

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

$$+ (y_1 - y_1^*) \left( -s_1(y_1) + c_1 p_1(x_1, y_2) + \tilde{c}_1 p_2(x_2, y_2) \right)$$

$$+ (y_2 - y_2^*) \left( -s_2(y_2) + c_2 q_1(x_1, y_1) + \tilde{c}_2 q_2(x_2, y_1) \right)$$

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

where,

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

$$l_{12} = 0,$$

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

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

$$l_{21} = 0,$$

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

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

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

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

$$l_{32} = \tilde{c}_1(y_1 - y_1^*) \left( p_2(x_2, y_2) - p_2(x_2^*, y_2) \right),$$
We set
\[ l_{11} = (x_1 - x_1^*)^2 u_{11}(x_1, y_1, y_2), \]
\[ l_{12} = 0, l_{13} + l_{31} = 2(x_1 - x_1^*)(y_1 - y_1^*)u_{13}(x_1, y_1, y_2), \]
\[ l_{14} + l_{41} = 2(x_1 - x_1^*)(y_2 - y_2^*)u_{14}(x_1, y_1, y_2), l_{21} = 0, \]
\[ l_{22} = (x_2 - x_2^*)^2 u_{22}(x_2, y_1, y_2), l_{23} + l_{32} = 2(x_2 - x_2^*)(y_1 - y_1^*)u_{23}(x_2, y_1, y_2), \]
\[ l_{24} = 2(x_2 - x_2^*)(y_2 - y_2^*)u_{24}(x_2, y_1, y_2), l_{33} = (y_1 - y_1^*)^2 u_{33}(y_1), \]
\[ l_{34} + l_{43} = 2(y_1 - y_1^*)u_{34}(y_2)(y_2 - y_2^*), l_{44} = (y_2 - y_2^*)^2 u_{44}(y_2). \]

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
\[ P(x) = x_1^{y_1} x_2^{y_2} y_1^\delta y_2^\mu (x_1 + x_2)^\epsilon \]
\[ \ln P = y_1 \ln x_1 + y_2 \ln x_2 + \delta \ln y_1 + \mu \ln y_2 + \epsilon \ln (x_1 + x_2) \]
\[ \psi = \frac{d \ln P}{dt} = \frac{1}{P} \dot{P} \]

\[ = y_1\left( g_1(x_1) - y_1 \frac{p_1(x_1,y_2)}{x_1} - y_2 \frac{q_1(x_1,y_1)}{x_1} \right) + y_2\left( g_2(x_2) - y_1 \frac{p_2(x_2,y_2)}{x_2} - y_2 \frac{q_2(x_2,y_1)}{x_2} \right) + \delta(-s_1(y_1) + c_1p_1(x_1,y_2) + \bar{c}_1p_2(x_2,y_2)) + \mu(-s_2(y_2) + c_2q_1(x_1,y_1) + \bar{c}_2q_2(x_2,y_1)) + \frac{\epsilon}{x_1 + x_2} [(x_1g_1 - y_1p_1 - y_2q_1) + x_2g_2 - y_1p_2 - y_2q_2] \]

It is sufficient to show (6), that there exist positive constants \( y_1, y_2, \delta, \mu \) and \( \epsilon \) such that \( \psi > 0 \) at all boundary equilibria. That is we require,

\[
\begin{align*}
\gamma_1g_1(0) + y_2g_2(0) - s_1(0)\delta - s_2(0)\mu + \epsilon \min(g_1(0), g_2(0)) &> 0 \quad (6.1) \\
y_2g_2(0) + \delta(-s_1(0) + c_1p_1(K_1,0)) + \mu(-s_2(0) + c_2q_1(K_1,0)) &> 0 \quad (6.2) \\
g_1(0)y_1 + \delta(-s_1(0) + \bar{c}_1p_2(K_2,0)) + \mu(-s_2(0) + \bar{c}_2q_2(K_2,0)) &> 0 \quad (6.3) \\
y_2\left(g_2(0) - y_2p_2(x_2,0,0)\right) + \mu(-s_2(0) + c_2q_1(x_1,0)) &> 0 \quad (6.4) \\
y_1\left(g_1(0) - y_1p_1(x_1,0)\right) + \mu(-s_2(0) + \bar{c}_2q_2(x_2,0)) &> 0 \quad (6.5) \\
y_2\left(g_2(0) - y_2q_2(x_2,0)\right) + \delta(-s_1(0) + c_1p_1(x_1,0)) &> 0 \quad (6.6) \\
y_1\left(g_1(0) - y_1q_1(x_1,0)\right) + \delta(-s_1(0) + \bar{c}_1p_2(x_2,0)) &> 0 \quad (6.7) \\
\mu(-s_2(0) + c_2q_1(x_3,0) + \bar{c}_2q_2(x_3,0)) &> 0 \quad (6.8) \\
\delta(-s_1(0) + c_1p_1(x_3,0) + \bar{c}_1p_2(x_3,0)) &> 0 \quad (6.9) \\
y_2\left(g_2(0) - y_2p_2(x_2,0,0)\right) - y_2q_2(x_2,0) &> 0 \quad (6.10) \\
y_1\left(g_1(0) - y_1p_1(x_1,0)\right) - y_2q_2(x_2,0) &> 0 \quad (6.11)
\end{align*}
\]

Let boundary equilibria \( E_i \), \( 3 \leq i \leq 10 \) be globally asymptotically stable in their respective subsystems. Then

\[
\begin{align*}
g_1(0) - y_1p_1(x_1,0) &> 0, & g_1(0) - y_2q_1(x_1,0) &> 0, \\
g_2(0) - y_2q_2(x_2,0) &> 0, & g_2(0) - y_1p_2(x_2,0) &> 0, \\
-s_2(0) + c_2q_1(x_1,0) &> 0, & -s_2(0) + \bar{c}_2q_2(x_2,0) &> 0, \\
-s_1(0) + c_1p_1(x_1,0) &> 0, & -s_1(0) + \bar{c}_1p_2(x_2,0) &> 0.
\end{align*}
\]

Recall from section 3.2

\[
\begin{align*}
\xi_1 &= -s_2(0) + c_2q_1(x_3,0) + \bar{c}_2q_2(x_3,0), \\
\xi_2 &= -s_1(0) + c_1p_1(x_4,0) + \bar{c}_1p_2(x_4,0), \\
\xi_3 &= g_2(0) - y_2p_2(x_2,0) - y_2q_2(x_2,0), \\
\text{and} & \\
\xi_4 &= g_1(0) - y_1p_2(x_1,0) - y_2q_1(x_1,0).
\end{align*}
\]
For positive small $\delta$ and $\mu$ (6.1) holds.

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

When $\xi_i > 0$, $1 \leq i \leq 4$, 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 $E_i, 3 \leq i \leq 10$ exist and be globally stable in their respective octants. When $\xi_i > 0$, $1 \leq i \leq 4$, 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 $E_5, E_6, E_i, 8 \leq i \leq 10$ be globally stable in their respective octants. When $\xi_i > 0, 2 \leq i \leq 4$, 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 $E_i, 3 \leq i \leq 8$ 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 $R^+_{x_1y_1y_2}$ and $R^+_{x_2y_1y_2}$, 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

\[
\begin{align*}
\frac{dx_1}{dt} &= a_1 \left(1 - \frac{x_1}{K_1}\right)x_1 - p_1(x_1, y_2)y_1 - q_1(x_1, y_1)y_2 \\
\frac{dx_2}{dt} &= a_2 \left(1 - \frac{x_2}{K_2}\right)x_2 - p_2(x_2, y_2)y_1 - q_2(x_2, y_1)y_2 \\
\frac{dy_1}{dt} &= y_1\left(-s_{11} - s_{12}y_1 + c_1p_1(x_1, y_2) + \xi_1p_2(x_2, y_2)\right) \\
\frac{dy_2}{dt} &= y_2\left(-s_{21} - s_{22}y_2 + c_2q_1(x_1, y_1) + \xi_2q_2(x_2, y_1)\right)
\end{align*}
\]

(9)

For global stability of all equilibria, below (except $E_{10}(x_{41}, x_{42}, 0, y_{42})$) we take

\[p_i(x_i, y_2) = p_{i1}x_i, \quad q_i(x_i, y_1) = q_{i1}x_iy_1, \quad i = 1, 2.\]

(10)
For $E_8$, we set:

\[ p_i(x_i, y_2) = p_{i1}x_i y_2, \quad q_i(x_i, y_1) = q_{i1}x_i, \quad i = 1, 2. \quad (11) \]

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 \[.\] The constants $L_i, G_i, i = 1, 2$, are as in Theorem 2. Computing matrix $M$ as in Theorem 4, we get

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

**Corollary 1:** $E_7$ will be globally stable in $R_{x_1, x_2, y_1}^+$, whenever $M$ is negative definite.

For $E_8$, we get

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

By Theorem 5, we have:

**Corollary 2:** When $N$ is negative definite, $E_8$ is globally stable in $R_{x_1, x_2, y_2}^+$.

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

Computing symmetric matrix $R$ as in Theorem 6,

\[ R = (r_{ij}), \text{ is given by } \]

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

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

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

Now, proceeding as in Theorem 2 of section 2,

\[ y_1 \leq \delta_{19} = \frac{c_1G_1}{s_{1}(0)} + \epsilon, \text{ for large } t, \quad y_2 \leq \delta_{29} = \frac{c_2L_1}{s_{2}(0)} + \epsilon, \text{ for large } t. \]
Thus,

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

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

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

\[ \frac{a_1}{K_1} > r_{12}\max + r_{13}\max, s_{12} > r_{12}\max + r_{23}, s_{22} > r_{13}\max + r_{23}. \]  \( (12) \)

Then \( E_9 \) is globally stable in \( R^+_x \).

**Proof:**

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

\[ \lambda \leq r_{ii} + \sum_{j \neq i} |r_{ij}| \]

Also \( |r_{ii}| > \sum_{k \neq i} |r_{ik}| \) and \( r_{ii} < 0, \quad j = 1,2,3 \). Thus, \( r_{ii} + \sum_{j \neq i} |r_{ij}| < 0 \)

i.e. eigenvalues of \( R \) in \( \mathcal{A}_3 \) are negative and by Theorem 6 \( E_9 \) is globally stable in \( R^+_x y_1 y_2 \).

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

where,

\[ \delta_{110} = \frac{c_1 g_2}{s_{11}} + \epsilon, \quad \delta_{210} = \frac{c_2 l_2}{s_{21}} + \epsilon, \]

Computing symmetric matrix \( T \), as in Theorem 7, then

\[ T = (t_{ij})_{3x3} \]

where,

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

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

and

\[ t_{ij} = t_{ji}, i > j. \]
Define,
\[ t_{12} \max = \frac{1}{2} \max \{|t_{12}(0)|, t_{12}(\delta_{210})\}, \quad t_{13} \max = \frac{1}{2} \max \{q_{21} y_{61}, q_{21}(\delta_{10} - y_{61})\} \]

We require
\[ \frac{a_2}{K_2} > t_{12} \max + t_{13} \max, \quad s_{12} > t_{12} \max + t_{23}, \quad s_{22} > t_{13} \max + t_{23}. \] (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 \( R^{+}_{x_{1} x_{2} y_{1} y_{2}} \).

For global stability of \( E^{*} \), we computing \( L \), as in Theorem 8,
\[ u_{11} = -\frac{a_1}{K_1} u_{12} = 0, \quad u_{13} = \frac{1}{2} \{(c_1 - 1)p_{11} - q_{11} y_2\}, \quad u_{14} = \frac{1}{2} q_{11}(y_1 - y_1^{*}) \],
\[ u_{22} = -\frac{a_2}{K_2} u_{23} = \frac{1}{2} \{\tilde{c}_1 - 1\} p_{21} - q_{21} y_2\}, \quad u_{24} = \frac{1}{2} q_{21}(\tilde{c}_2 y_1 - y_1^{*}) \],
\[ u_{33} = -s_{12}, \quad u_{34} = \frac{1}{2} (c_{2} x_1^{*} q_{11} + \tilde{c}_2 x_2^{*} q_{21}), \quad u_{44} = -s_{22} \].
\[ u_{ij} = u_{ji}, \quad i > j, \quad 1 \leq i, j \leq 4. \]

Set \( U = (u_{ij}) \).

Next, if \( E^{*}(x_1^{*}, x_2^{*}, y_1^{*}, y_2^{*}) \) exists in interior of \( R^{+}_{x_{1} x_{2} y_{1} y_{2}} \), Define
\[ l_{13} \max = \frac{1}{2} \max \{|(c_1 - 1)p_{11}|, |(c_1 - 1)p_{11} - q_{11} \delta_2|\}, \quad l_{14} \max = \frac{1}{2} q_{11} \max \{\delta_1 - y_1^{*}\}, \quad l_{23} \max = \frac{1}{2} \max \{|\tilde{c}_1 - 1| p_{21}, |(\tilde{c}_1 - 1) p_{21} - q_{21} \delta_2|\}, \quad l_{24} \max = \frac{1}{2} q_{21}(\tilde{c}_2 \delta_1 - y_1^{*}) \],
\[ \delta_1 = \frac{c_1 g_1 + \tilde{c}_2 g_2}{s_{11}}, \quad \text{and} \quad \delta_2 = \frac{c_2 L_1 + \tilde{c}_2 L_2}{s_{21}}. \]

The next result is clear from Theorem 8.

**Corollary 5:** Let \( E^{*}(x_1^{*}, x_2^{*}, y_1^{*}, y_2^{*}) \) exists and
\[ \frac{a_1}{K_1} > l_{13} \max + l_{14} \max, \quad \frac{a_2}{K_2} > l_{23} \max + l_{24} \max, \]
\[ s_{12} > l_{13} \max + l_{23} \max + l_{24} \max, \quad s_{22} > l_{14} \max + l_{24} \max + l_{34}. \]

Then \( E^{*} \) is globally stable.

Below we present specific examples:

With \( a_1 = a_2 = 1, \quad K_1 = 0.8, K_2 = 1, p_{11} = .4, p_{21} = .3, \quad c_1 = 2.5, \quad \tilde{c}_1 = 3.5, \)
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\[ s_{11} = .5, s_{12} = 1.5, E_7(x_{31}, x_{32}, y_{31}, 0) = (0.5977, 0.8103, 0.6323, 0) \] exists and the symmetric matrix

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

is negative definite as its eigenvalues are \(-1.8263, -1.1716, -0.7521\). Hence by Theorem 4 \( E_7 \) is globally stable in \( R_{x_1 x_2 y_1}^+ \).

With \( a_1 = a_2 = 1, K_1 = K_2 = 1, q_{11} = 0.4, c_2 = 2.5, \bar{c}_2 = 3.5, q_{21} = 0.3, s_{21} = 0.5 \) and \( s_{22} = 1.50 \).

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

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

and has eigenvalues \(-1.7914, -1\) and \(-0.7086\). Thus \( E_9 \) is globally stable in \( R_{x_2 y_1 y_2}^+ \).

With \( a_2 = 2.2, K_1 = 0.85, p_{11} = 0.45, q_{11} = .21, s_{11} = 0.5, s_{12} = 2.52, s_{21} = 0.065, s_{22} = 1.75 \) and \( c_1 = 2.4, \bar{c}_2 = 3.5, E_9(x_{51}, 0, y_{51}, y_{52}) = (0.823, 0.1543, 0.0157) \) exists and conditions (12) of Corollary 3 are satisfied. Thus \( E_9 \) is globally stable in \( R_{x_2 y_1 y_2}^+ \).

With \( a_2 = 1.8, K_2 = 0.80, p_{11} = 0.4, p_{21} = .42, q_{21} = .25, s_{11} = 0.50, s_{12} = 1.9, s_{21} = 0.1, s_{22} = 1, \bar{c}_1 = 2.55 \) and \( \bar{c}_2 = 3.5, E_{10}(0, x_{62}, y_{61}, y_{62}) = (0, 0.768, 0.1698, 0.0141) \) exists. Also conditions of Corollary 4 are satisfied and \( E_{10} \) is globally stable in \( R_{x_2 y_1 y_2}^+ \).

With \( a_2 = 1, K_1 = 1.05, K_2 = 1, p_{11} = 0.365, p_{21} = .30, q_{21} = 0.5, s_{11} = 0.4, s_{12} = 0.37, s_{21} = 0.4, s_{22} = 0.90, c_1 = 1, \bar{c}_1 = 1.5, c_2 = 1.2, \) and \( c_2 = 2.5, \) 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 \( a_1 = 1.8, a_2 = 1.8, K_1 = 0.8, K_2 = 0.8, p_{11} = 0.4, p_{21} = .42, s_{11} = 0.5, s_{12} = 1.9, s_{21} = 0.1, s_{22} = 1, \bar{c}_1 = 2.55, c_2 = 3.5, \bar{c}_2 = 3.5, c_2 = 1.2, \) and \( c_2 = 2.5, \) equilibria \( E_0(0, 0, 0, 0), E_1(0, 0.8, 0, 0), E_2(0, 0.8, 0, 0), E_3(0.4902, 0, 3.3971, 0), E_4(0, 0.3401, 1.7847, 0), E_7(0.7086, 0.7040, 0.5140, 0), E_9(0.7730, 0, 0.1518, 0.0027) \) and
$E_{10}(0.07680,0.1698,0.0141)$ 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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