



A MATHEMATICAL MODEL OF STABILITY AND PERSISTENCE IN AN INTERACTING MUTUALISM

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ABSTRACT

The aim of this paper is to investigate a mathematical model of stability and persistence in an interacting mutualism. Four interacting population where one of them a mutualist, interact with the other three species lead to mutualism between them.

The models represent two species predator-prey or competition system in which a third species acts as a mutualist with either the predator, the prey, or one of the competitors. Stability and persistence are investigated.

Key words: Facultative mutualism, prey-predator, population interacting in a food chain.

A. M. S. C.: 92D25, 34D20, 92D40.

1. INTRODUCTION:

In this paper we investigate a model of four interacting populations where one of them, a mutualist, interacts with the other three so as to benefit, and receive benefit, from one of those three. We are interested in establishing persistence and stability criteria, which can be interpreted as the survival of all biological populations. There are now many papers in the literature dealing with mutualistic system. Most of these papers deal with two-dimensional systems modeling direct mutualism between two populations and ignore all other populations interactions, see ([1], [3], [4], [6]). Recently, some papers have been appeared which deal with cases where the mutualism is due to or influenced by the interacting with a third population, see ([4], [7], [8], [9], [10], [13], [14]).

The persistence in biological system in a context related to this paper has been discussed in [5], [7], [8], [9], [10], [11]. We utilize the definition of persistence developed in [5], [12].

Definition: Let $N(t)$ be such that $N(0) > 0$. Then we say that $N(t)$ persists if $\liminf N(t) > 0$ as $t \rightarrow \infty$. Further, we say that $N(t)$ persists uniformly if there exists $\delta > 0$ such that $\liminf N(t) \geq \delta$ as $t \rightarrow \infty$. Finally, a system in R^n persists (uniformly) if all components persist (uniformly).

2. MODEL:

We describe a general system that models a mutualist interacting with populations in a food chain. The mathematical formulation of facultative relationships between the mutualist and two different trophic levels of the food chain are also described.

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We consider the autonomous system

$$\begin{aligned}\dot{u} &= uh(u, x, y, z), \quad . = d/dt \\ \dot{x} &= \alpha x g(u, x) - yp_1(u, x, y) - z p_2(u, x, z), \\ \dot{y} &= y[-s_1(u, y) + c_1(u)p_1(u, x, y)] - z q(u, y, z), \\ \dot{z} &= z[-s_2(u, z) + c_2(u)p_2(u, x, z) + c_3(u)q(u, y, z)], \\ u(o) &= u_o \geq 0, \quad x(o) = x_o \geq 0, \quad y(o) = y_o \geq 0, \quad z(o) = z_o \geq 0,\end{aligned}\tag{2.1}$$

as a model of a mutualist-food chain interaction with continuous birth and death process. $u(t)$ represents the density of the mutualist at time t , $x(t), y(t), z(t)$ denote the prey and predator densities respectively. If $u \equiv 0$ system (2.1) reduces to food chain model. The functions $h, g, p_1, p_2, s_1, s_2, c_1, c_2, c_3$ are sufficiently smooth so that the solutions of (2.1) exist uniquely and are continuable for all positive time. The function h represents the specific growth rate of the mutualist.

We assume that h has the following properties, see ([6], [13], [16]):

- (H_1) $h(0, x, y, z) > 0$, $\frac{\partial h}{\partial u}(u, x, y, z) \leq 0$.
- (H_2) There exists a unique function $L(u, y, z) > 0$, such that $h(L(x, y, z), x, y, z) = 0$.
- (H_3) $h_x(u, x, y, z) > 0$, $h_y(u, x, y, z) \leq 0$, $h_z(u, x, y, z) \leq 0$,

(H_1) implies that, independent of x, y, z populations, u is capable of growing even when rare. Also, the growth rate is assumed to be density-dependent and decreases as the population increases. (H_2) implies that $L(x, y, z)$ is the mutualist carrying capacity and in part specifies in what way the prey and predator become part of the mutualist's environment. (H_3) implies that u derives benefit from the prey population and that there might be a cost to the mutualist due its interactions with the predators.

Also, (H_1) implies

(H_4) As $t \rightarrow \infty, 0 < \lim L(x, 0, 0) = \bar{L} < \infty, L_x(x, y, z) > 0, L_y(x, y, z) \leq 0, L_z(x, y, z) \leq 0$, which implies that the mutualist has a finite carrying capacity.

The function $g(u, x)$ is the specific growth rate of the prey in the absence of any predation. We assume that g satisfies:

- (G_1) $g(u, 0) > 0, g_x(u, x) < 0$.
- (G_2) There exists a unique $k(u) > 0$ such that $g(u, k(u)) > 0, k(u) < \bar{k} < \infty$, where $\bar{k} = \max_{0 \leq u \leq L} k(u)$.

(G_1) implies that the prey population is capable of surviving in the presence or absence of the mutualist and the growth rate in the absence of predation is density-dependent. (G_2) implies that $k(u)$ is the carrying capacity of the prey in the absence of predation.

In the case that $g_u(u, x) > 0$, then, even in the absence of predation, u acts as a mutualist with respect to x . If $g_u < 0$, then there is a cost to x for associating with u , and u can be mutualist of x only by its effect upon predator. If $g_u(u, x) \equiv 0$, the relationship between u and x without predation is commensal.

The functions $p_1(u, x, y), p_2(u, x, z)$ and $q(u, y, z)$ denote the predator's functional response to the prey and mutualist densities.

We assume

$$(P_1) \quad p_i(u, 0, 0) = 0, i = 1, 2$$

$$p_{1x}(u, x, y) > 0, \quad p_{1y}(u, x, y) > 0,$$

$$p_{2x}(u, x, y) \geq 0, \quad p_{2z}(u, x, z) \geq 0.$$

$$(P_2) \quad p_{1u} \leq 0, \quad p_{2u} \geq 0.$$

The functions p_1, p_2 are the competition functions and condition (P_1) states that competition between x and y , and x and z occurs when both populations are presented, and is an increasing function of their population. (P_2) implies the fact that the mutualism may decrease the competitive effect of y on x or may increase the competitive of x on z .

Also, we assume

$$(Q_1) \quad q(u, 0, 0) = 0, \quad q_u(u, y, z) \leq 0, \quad q_y(u, y, z) \geq 0, \quad q_z(u, y, z) > 0.$$

$$(Q_2) \quad \text{When } y \equiv 0, \quad zq_z + q = 0, \quad q \neq 0.$$

Also, we assume

$$(S_1) \quad s_{1y}(u, y) \geq 0, \quad s_{2z}(u, z) \geq 0.$$

$$(S_2) \quad s_{1u}(u, y) \geq 0, \quad c_{iu}(u) \leq 0, i = 1, 2, 3.$$

The non-negative functions $c_i(u)$, $i = 1, 2, 3$ are the rates of conversion of prey biomass to predator biomass, α is a bifurcation parameter. The functions $s_1(u, y)$, $s_2(u, z)$ are the specific death rate of the predators y and z in the absence of predation. We make the standard assumption that (S_1) , (S_2) , the death rates are increasing functions of population. Also, in order to have a viable system we must have that

$$(S_3) \quad \text{There exists } x_1, y_1 \text{ such that } s_1(0, 0) = c_1(0)p_1(0, x_1, 0), x_1 < k_1(0), \text{ and}$$

$$s_1(0, 0) = c_1(0)p_1(0, 0, y_1), y_1 < k_2(0).$$

$$(S_4) \quad \text{There exists } x_2, z_1 \text{ such that } s_2(0, 0) = c_2(0)p_2(0, x_2, 0), 0 < x_2 < \bar{k}_1(0), \text{ and}$$

$$s_2(0, 0) = c_2(0)p_2(0, 0, z_2), 0 < z_2 < \bar{k}_2(0).$$

We will make use of the following theorem.

Theorem 2.1: Under the above assumptions, the set

$$A = \{(u, x, y, z) : 0 \leq u \leq \bar{L}, 0 \leq x \leq \bar{k}, 0 \leq c_1(u)x + y \leq \bar{M}, 0 \leq c_2(u)x + \bar{c}_3y + z \leq \bar{N}\}, \quad (2.1)$$

Where

$$\bar{L} = \lim_{x \rightarrow \infty} L(x, 0, 0), \quad \bar{k} = \max_{0 \leq u \leq \bar{L}} k(u), \quad \bar{g} = \max_{0 \leq u \leq \bar{L}} g(u, 0),$$

$$\bar{M} = c_1(0)\bar{k}[(\alpha \bar{g} + s_1(0, 0)) / s_1(0, 0)],$$

$$\bar{s}_2 = \min_{0 \leq u \leq \bar{L}} s_2(u, 0), \quad \bar{c}_3 = \max_{0 \leq u \leq \bar{L}} c_3(u),$$

and

$$\bar{N} = \{c_2(0)\bar{k}(\bar{s}_2 + \alpha \bar{g}) + \bar{c}_3\bar{M}[\bar{s}_2 + c_1(0)p_1(0, \bar{k})]\},$$

is positively invariant and attracts all solutions initiating with non-negative initial conditions.

Proof: The proof can be carried out by following the same steps of proof of theorem 2.1 in [13] and so will be omitted.

3. EXISTENCE OF EQUILIBRIA:

In this section we shall establish criteria for the existence and nonexistence of equilibria of the system (2.1). It is clear that the origin $E_o(0,0,0,0)$ is an equilibrium point for the system (2.1).

From $(H_1), (H_2)$ and Freedman [6], we have the following theorem:

Theorem 3.1: The system (2.1) has exactly two one-dimensional equilibria $E_1(L_o, 0, 0, 0)$ and $E_2(0, k_o, 0, 0)$.

Remark 3.1: The subsystem in R_y^+ and R_z^+ have no equilibria since all of their solutions tend to zero exponentially. Also, it follows that E_o is locally stable in the y and z directions and locally unstable in the u and x directions.

As shown in [10], the following result holds in R_{ux}^+ .

Theorem 3.2: The subsystem in R_{ux}^+ has an equilibrium $E_3(\bar{u}, \bar{x}, 0, 0)$ provided E_1 and E_2 are unstable in R_{ux}^+ .

Remark 3.2: Under hypotheses $(H_1), (G_1), E_3$ exists.

It is easy to prove the following theorems (see [6], [13]).

Theorem 3.3: A necessary and sufficient conditions for an equilibrium of the form $E_4(0, x_1, y_1, 0)$ to exist in R_{xy}^+ is that hypotheses (S_3) be satisfied.

Theorem 3.4: A necessary and sufficient conditions for equilibrium $E_5(0, x_2, 0, z_2)$ to exist is that the hypotheses (S_4) be satisfied.

The following result for the existence of an interior equilibrium of the system (2.1) follows from [4], [13].

Theorem 3.5: Let the following hypotheses hold for the system (2.1):

- (a) All solutions with non-negative initial conditions are bounded in forward time.
- (b) The system (2.1) is persistent.
- (c) The subsystems of (2.1) are isolated and a cyclic.

Then, an interior equilibrium $E^*(u^*, x^*, y^*, z^*)$ exists for system (2.1).

4. STABILITY OF EQUILIBRIA:

To determine the stability of the above equilibria, we need to compute variational matrix of system (2.1). The signs of the real part of the eigenvalues of this matrix evaluated at these equilibrium determine its stability.

$$V(u, x, y, z) = \begin{bmatrix} uh_u + h & uh_x & uh_y & uh_z \\ -yp_{1u} - zp_{2u} + \alpha xg_u & \vartheta & -p_1 - y_1p_{1y} & -p_2 - zp_{2z} \\ \phi & yc_1p_{1x} & \phi & -zq_z - q \\ \tau & zc_2p_{2x} & zc_3q_y & \chi \end{bmatrix}, \quad (4.1)$$

where

$$\begin{aligned} \vartheta &= \alpha g + \alpha xg_x - yp_{1x} - zp_{2x}, \\ \phi &= y(-s_{1u} + c_{1u}p_1 + c_1p_{1u}) - zq_u, \end{aligned}$$

$$\begin{aligned}\phi &= -s_1 + c_1 p_1 + y(-s_{1y} + c_1 p_{1y}) - z q_y, \\ \tau &= z(-s_{2u} + c_{2u} p_2 + c_2 p_{2u} + c_{3u} q + c_3 q_u), \\ \chi &= -s_2 + c_2 p_2 + c_3 q + z(-s_{2z} + c_2 p_{2z} + c_3 q_z),\end{aligned}$$

also, all functions are evaluated at (u, x, y, z) and we have used the notation F_x to represent $\partial F / \partial x$, etc.

The variational matrix V_o i.e. evaluating V at $E_o(0,0,0,0)$ is diagonal and for which the eigenvalues in u and x directions are positive and hence the equilibrium point E_o is locally unstable in u and x directions. The eigenvalues in the y and z directions are negative and hence E_o is stable in the y and z directions. Thus, E_o has non-empty stable and unstable manifolds.

Next, for the equilibrium $E_1(L_o, 0, 0, 0)$ $L(0, 0, 0) = L_o$, the variational matrix V_1 has a positive eigenvalue $\alpha g(L_o, 0)$ in x -direction and a negative eigenvalues $L_o h_u(L_o, 0, 0, 0)$ in the other directions. Thus, E_1 is unstable in the x -direction and stable in the u, y and z -directions. Hence, E_1 has non-empty stable and unstable manifolds.

The variational matrix V_2 for $E_2(0, k_o, 0, 0)$, $k_o = k(o)$ has the form:

$$V_2(0, k_o, 0, 0) = \begin{bmatrix} h(0, k_o, 0, 0) & 0 & 0 & 0 \\ \alpha k_o g_u(0, k_o) & \alpha g(0, k_o) + \alpha k_o g_x(0, k_o) & -p_1(0, k_o, 0) & -p_2(0, k_o, 0) \\ 0 & 0 & -s_1(0, 0) + c_1(o) p_1(0, k_o, 0) & -q(0, 0, 0) \\ 0 & 0 & 0 & \zeta \end{bmatrix},$$

where

$$\zeta = -s_2(0, 0) + c_2(o) p_2(0, k_o, 0) + c_3(o) q(0, 0, 0).$$

The equilibrium E_2 yield that its eigenvalue $h(0, k_o, 0, 0)$ which is positive in u -direction and negative eigenvalue $\alpha k_o g_x(0, k_o)$ in x -direction. The eigenvalues in y and z directions are

$$\alpha_i = -s_i(0, 0) + c_i(o) p_i(0, k_o, 0), \quad i = 1, 2.$$

From theorem 3.3, the eigenvalues in y -direction are positive but the eigenvalues in z -direction may be positive or negative.

Remark 4.1: From the above analysis, it follows that E_1 and E_2 are unstable R_{ux}^+ . A similar analysis for equilibrium $E_3(\bar{u}, \bar{x}, 0, 0)$ yields its eigenvalue

$B_1^* = -s_2(\bar{u}, 0) + c_2(\bar{u}) p_2(\bar{u}, \bar{x}, 0)$ in z -direction which is positive or negative, but the eigenvalue in y -direction is $B_2^* = -s_1(\bar{u}, 0) + c_1(\bar{u}) p_1(\bar{u}, \bar{x}, 0)$, which by Theorem 3.3 is positive and thus E_3 is unstable in y -direction. The other eigenvalues in u and x directions are:

$$B_{1,2} = \frac{1}{2}(\alpha \bar{x} g_x + \bar{u} h_u) \pm \frac{1}{2} \sqrt{(\alpha \bar{x} g_x + \bar{u} h_u)^2 - 4 \bar{u} \bar{x} (h_u g_x - g_u h_x)}.$$

Thus, whenever $h_u g_x - g_u h_x > 0$, eigenvalues $B_{1,2}$ have negative real parts where $\alpha \bar{x} g_x + \bar{u} h_u < 0$. Thus, E_3 has nonempty stable and unstable manifolds.

Similarly, we analyze $E_4(0, x_1, y_1, 0)$, the eigenvalue of $V_4(0, x_1, y_1, 0)$ in the u -direction has the value $h(0, x_1, y_1, 0)$ which is positive and hence E_4 is unstable in u -direction. The eigenvalue in z -direction is given by

$$\gamma_1 = -s_2(0, 0) + c_2(0)p_2(0, x_1, 0) + c_3(0)q(0, y_1, 0),$$

and the other two eigenvalues are the roots of

$$\gamma^2 - (\alpha x_1 g_x + \alpha g - y_1 p_{1x} - y_1 s_{1y} + c_1 y_1 p_{1y}) \gamma + (y_1 s_{1y} + c_1 y_1 p_{1y}) \times \\ (\alpha g + \alpha x_1 g_x - y_1 p_{1x}) + y_1 p_{1x} c_1 (p_1 + y_1 p_{1y}) = 0.$$

From the Routh-Hurwitz criteria, the roots have negative real parts iff

$$\alpha x_1 g_x(0, x_1) + \alpha g(0, x_1) - y_1 p_{1x}(0, x_1, y_1) - y_1 s_{1y}(0, y_1) + c_1(0) y_1 p_{1y}(0, x_1, y_1) < 0,$$

and

$$\{y_1 s_{1y}(0, y_1) + c_1 y_1 p_{1y}(0, x_1, y_1)\} \{\alpha g(0, x_1) + \alpha x_1 g_x(0, x_1) - y_1 p_{1x}(0, x_1, y_1)\} + \\ y_1 p_{1x}(0, x_1, y_1) c_1 (p_1(0, x_1, y_1) + y_1 p_{1y}(0, x_1, y_1)) > 0.$$

Under these conditions we notice that E_4 is stable in R_{xy}^+ . For $E_5(0, x_2, 0, z_2)$, the variational matrix has the form

$$V_5(0, x_2, 0, z_2) = \begin{bmatrix} h(0, x_2, 0, z_2) & 0 & 0 & 0 \\ G & L & -p_1(0, x_2, 0) & -p_2(0, x_2, z_2) - z_2 p_{2z}(0, x_2, z_2) \\ -z_2 q_u(0, 0, z_2) & 0 & \eta & -z_2 q_z(0, 0, z_2) - q(0, 0, z_2) \\ H & z_2 c_2(0) p_{2x}(0, x_2, z_2) & z_2 c_3(0) q_y(0, 0, z_2) & \xi \end{bmatrix},$$

where

$$G = -z p_{2u}(0, x_2, z_2) + \alpha x_2 g_u(0, x_2),$$

$$H = z_2 [-s_{2u}(0, z_2) + c_{2u}(0) p_2(0, x_2, z_2) + c_2(0) p_{2u}(0, x_2, z_2) + c_{3u}(0) q(0, 0, z_2) \\ + c_3(0) q_u(0, 0, z_2)], \quad L = \alpha g(0, x_2) + \alpha x_2 g_x(0, x_2) - z_2 p_{2x}(0, x_2, z_2),$$

$$\eta = -s_1(0, 0) + c_1(0) p_1(0, x_2, 0) - z_2 q_y(0, 0, z_2),$$

$$\xi = -s_2(0, z_2) + c_2(0) p_2(0, x_2, z_2) + c_3(0) q(0, 0, z_2) \\ + z_2 [-s_{2z}(0, z_2) + c_2(0) p_{2z}(0, x_2, z_2) + c_3(0) q_z(0, 0, z_2)].$$

The eigenvalue of V_5 in u -direction is $h(0, x_2, 0, z_2)$ which is positive and thus E_5 is unstable in u -direction. The eigenvalue in y -direction is given by:

$$\delta_1 = s_1(0, 0) + c_1(0) p_1(0, x_2, 0) - z_2 q_y(0, 0, z_2),$$

and the other eigenvalues in x and z directions are obtained from the equation

$$\delta^2 - (\xi + L)\delta + L\xi + z_2 c_2 p_2 p_{2x} = 0.$$

The eigenvalues $\delta_{1,2}$ have negative real parts iff $L + \xi < 0$, and

$$L\xi - z_2 c_2(0) p_2(0, x_2, z_2) p_{2x}(0, x_2, z_2) > 0.$$

Similarly for $E_6(u_3, x_3, y_3, 0)$, the variational matrix has the form

$$V_6(u_3, x_3, y_3, 0) = \begin{bmatrix} u_3 h_u + h & u_3 h_x & u_3 h_y & u_3 h_z \\ A & B & C & -p_2 \\ D & y_3 c_1 p_{1x} & F & -q \\ 0 & 0 & 0 & K \end{bmatrix},$$

where

$$\begin{aligned} A &= y_3 p_{1u} + \alpha x_3 g_u, \\ B &= \alpha g + \alpha x_3 g_x - y_3 p_{1x}, \\ C &= -p_1 - y_3 p_{1y}, \\ D &= y_3 (-s_{1u} + c_{1u} p_1 + c_1 p_{1u}), \\ F &= -s_1 + c_1 p_1 + y_3 (-s_{1y} + c_1 p_{1y}), \\ K &= -s_2 + c_2 p_2 + c_3 q, \end{aligned}$$

and all the above functions are evaluated at $(u_3, x_3, y_3, 0)$. The eigenvalue of E_6 in z -direction is K . The other eigenvalues are the roots of the polynomial

$$\xi^3 + a_1 \xi^2 + a_2 \xi + a_3 = 0,$$

where

$$\begin{aligned} a_1 &= u_3 h_u + B + F, \\ a_2 &= y_3 BF - u_3 h_x A - y_3 u_3 h_y D + y_3 c_1 p_{1x} C + u_3 h_u B + y_3 F, \\ a_3 &= y_3 u_3 h_u (BF + c_1 p_1 x_3 C) - u_3 h_x y_3 (AF - CD) + u_3 y_3 h_y (c_1 p_{1x} A - FB). \end{aligned}$$

Thus, from the Routh-Hurwitz criteria, the necessary and sufficient conditions for E_6 to be asymptotically stable in

R_{uxy}^+ are that:

$$K < 0, \quad a_1 > 0, \quad a_3 > 0, \quad \text{and} \quad a_1 a_2 - a_3 > 0.$$

Also, for $E_7(u_4, x_4, 0, z_4)$, the eigenvalue of V_7 in y -direction is given by:

$$\eta = -s_1(u_4, 0) + c_1(u_4) p_1(u_4, x_4, 0) - z_4 q_y(u_4, 0, z_4).$$

The other eigenvalues are the roots of the polynomial

$$\eta^3 + b_1 \eta^2 + b_2 \eta + b_3 = 0,$$

where

$$\begin{aligned} b_1 &= -(u_4 h_u + J + N), \\ b_2 &= u_4 h_u (J + N) + NJ - I z_4 c_2 p_{2x} - u_4 h_x M - u_4 Q h_z, \\ b_3 &= u_4 h_4 I z_4 c_2 p_{2x} + u_4 M J h_x - u_4 N J h_u - u_4 I Q h_x - u_4 h_z M z_4 c_2 p_{2x} + u_4 Q N h_z, \\ J &= z_4 c_2 p_{2z} - z_4 s_{2z}, \\ N &= \alpha g + \alpha x_4 g_x - z_4 p_{2x}, \\ I &= -(p_2 + z_4 p_{2z}), \\ M &= \alpha x_4 g_u - z_4 p_{2u}, \\ Q &= z_4 (-s_{2u} + c_{2u} p_2 + c_2 p_{2u} + c_{3u} q). \end{aligned}$$

All the above functions are evaluated at $(u_4, x_4, 0, z_4)$.

E_7 will be asymptotically stable in R_{uxz}^+ iff:

$$\eta^* < 0, \quad b_1 > 0, \quad b_3 > 0, \quad b_1 b_2 - b_3 > 0.$$

Similarly, since for $E_8(0, x_5, y_5, z_5)$, the eigenvalue of V_8 in the u -direction is $h(0, x_5, y_5, z_5) > 0$, and hence E_8 is unstable in u -direction. The other eigenvalues are the zeros of the polynomial

$$\lambda^3 + d_1 \lambda^2 + d_2 \lambda + d_3 = 0$$

i.e. $\lambda^3 + (M - N - L)\lambda^2 + \{M(N + L) + NL + y c_1 p_{1x}(p_1 + y p_{1y}) + z c_2 p_{2x}(p_2 + z p_{2z})\} +$

$(p_2 + z p_{2z})(y + c_1 p_{1x} z c_3 q_y - z c_2 p_{2x} N) + L y c_1 p_{1x}(p_1 + y p_{1y}) - z c_3 q(z q_z + z)M - MNL = 0$, where

$$M = d_1 g + \alpha x g_x - y p_{1x} - z p_{2x},$$

$$N = (-s_1 + c_1 p_1) + y(-s_{1y} + c_1 p_{1y}) - z q_y,$$

$$L = (-s_2 + c_2 p_2 + c_3 q) + z(-s_{2z} + c_2 p_{2z} + c_3 q_z).$$

The equilibrium E_8 will be asymptotically stable in R_{xyz}^+ iff

$$d_1 > 0, \quad d_3 > 0 \quad \text{and} \quad d_1 d_2 - d_3 > 0.$$

Now, we will consider the stability of the interior equilibrium $E^*(u^*, x^*, y^*, z^*)$. In what follows all functions are assumed to be evaluated at (u^*, x^*, y^*, z^*) . The variational matrix at E^* is given by (4.1) evaluated at E^* .

In general [13], it is not possible to determine the stability of E^* . Thus, mutualist's interaction with food chain populations can result in either stabilization or destabilization of the system as has been noted in two- and three species models (see [2], [8]). Finally, it shows that the populations feeding on more than one trophic level do not necessarily cause an unstable system, the possibility of which has been pointed out by Pimm and Lawton [15], and that mutualistic interactions can have a significant effect on stability, even in the case of complex system.

5. PERSISTENCE AND UNIFORM PERSISTENCE:

In this section, we shall investigate the persistence of the populations given by the system (2.1). We shall derive criteria that ensure the uniform persistence of the system (2.1) in the cases of facultative mutualism between the mutualist and the prey x as well as between u and prey y .

(i) Facultative mutualism between u and x .

The system (2.1) exhibits facultative mutualism between mutualist u and the prey x , whenever the hypotheses $(H_1) - (H_4)$, (G_1) , (G_2) , (P_1) , (P_2) and (S_1) , (S_2) are satisfied. Also, we shall assume the following hypotheses:

(P₁') Let the equilibrium E_4 be globally asymptotic stable with respect to solutions initiating in R_{xy}^+ .

(P₂') Let E_5 (if it exists) be globally asymptotic stable with respect to solutions initiating in R_{xz}^+ .

(P₃') Let the equilibria E_6 , E_7 and E_8 be globally stable in R_{uxy}^+ , R_{uxz}^+ and R_{uyz}^+ respectively.

The following results hold for the food chain in R_{xyz}^+ (see [11], and [13]).

Theorem 5.1: Let the hypotheses $(H_1) - (H_4)$, (G_1) , (G_2) , (P_1) , (P_2) and $(S_1) - (S_3)$ hold. Then, the system (2.1) persists for $\alpha_1 > 0$.

Theorem 5.2: Let the hypotheses (G_1) , (G_2) , (P_1) , (P_2) , $(S_1) - (S_3)$, (P_1') , (P_2') hold. Then, the subsystem in R_{uyz}^+ is uniformly persistent whenever $\gamma_1 > 0$, $\delta_1 > 0$.

Theorem 5.3: Let the hypotheses $(H_1) - (H_4)$, $(P_1') - (P_3')$, $\setminus (P_{-1})$, (P_1) , (P_2) and $(S_1) - (S_3)$ hold. Then, the three-dimensional subsystem in R_{uxy}^+ is uniformly persistent whenever $B_2^* > 0$, and \mathfrak{R}_{uxy}^+ is uniformly persistent whenever $B_1^* > 0$.

It follows from [5] that whenever a subsystem of (2.1) is uniformly persistent, it has an interior equilibrium.

Theorem 5.4: Let the hypotheses $(H_1) - (H_4)$, (G_1) , (G_2) , (P_1) , (P_2) , $(S_1) - (S_3)$ and $(P_1') - (P_3')$ hold. Then, the system (2.1) is uniformly persistent whenever $\eta^* > 0$ and $K > 0$.

Proof: The proof is similar to that of Theorem 4.4 in [13], and will be omitted.

(ii) Facultative mutualism between u and y .

This case can be treated, as case (i) with some suitable conditions and so will be omitted.

6. EXAMPLE:

Consider the system

$$\begin{aligned}\dot{u} &= u \left(1 - \frac{u}{1+y} \right), \\ \dot{x} &= x(3-x) - xy - xz^2u, \\ \dot{y} &= y \left(-\frac{5}{18}(1+y) + \frac{5}{9}x \right) - uz^2y, \\ \dot{z} &= z \left(-\frac{11}{10} - \frac{1}{10}z + \frac{1}{2}zux + \frac{1}{2}uzy \right).\end{aligned}\tag{6.1}$$

The system (6.1) has the boundary equilibria

$$E_o(0,0,0,0), E_1(1,0,0,0), E_2(0,3,0,0), E_3(1,3,0,0), E_4\left(0, \frac{4}{3}, \frac{5}{3}, 0\right), E_5(0,3,0,1),$$

$$E_6\left(\frac{8}{3}, \frac{4}{3}, \frac{5}{3}, 0\right), E_7(1,2,0,1), E_8\left(0, \frac{4}{3}, \frac{5}{3}, \frac{33}{3}\right).$$

. After simple but long calculations, it is easy to see that E_4, E_5 is globally asymptotic stable in R_{xy}^+ and all the three-dimensional subsystems are uniformly persistent.

Using theorem 5.4, we can easily prove that the system (6.1) is uniform persistence.

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