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Mathematical Analysis in a Model of Obligate Mutualism with Food Chain Populations

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Abstract: This paper is concerned with a three-species food chain whose populations interact with a mutualist. The mutualism is obligate for one of the predators, and is modeled by a system of autonomous ordinary differential equations. Persistence and extinction criteria are developed in the cases of trivial, periodic and almost periodic dynamics.

Keywords: *Food chain; obligate mutualism; persistence; extinction; stability; periodic solutions; almost periodic solutions.*

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1 Introduction

The main thrust of this paper is to model obligate mutualism with the middle and top predators of a three-species food chain. The cases of facultative mutualism with the prey and middle predator populations have been considered in [24].

Previously, models of mutualism with predator-prey systems have been considered in [2, 12, 16, 24, 27, 34]. Models of obligate mutualism have been discussed in [7, 12, 13, 14]. For general discussions of mutualism the reader is referred to [1, 7, 11, 32].

Most models of mutualism are two dimensional. There has been a fair amount of work recently on three dimensional models, where the mutualism occurs between prey

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(see eg. [2, 15, 27]); predators (see [2, 13, 14, 15, 27]), perhaps both [30], or competitors (see [2, 9, 27, 29, 33]), etc. However, to date the only results dealing with mutualism in food chains are contained in [24].

Our main concern in this paper will be to develop criteria for the persistence or extinction of populations considered in our model. Persistence and extinction criteria for food chains and/or mutualism models have been discussed in [13, 15, 16, 17, 18, 21, 24].

At this time we give definitions of extinction, persistence and nonpersistence. First we define extinction. We say that $N(t) > 0$ exhibits *extinction* if $\lim_{t\to\infty} N(t) = 0$. We note that nonpersistence (defined below) does not necessarily imply extinction for all initial values $N(0)$. If $\lim_{t\to\infty} N(t) = 0$ for all $N(0) > 0$, we say that our system exhibits *total extinction* with respect to the $N(t)$ population. We will employ the notation R_v^+ to denote the positive v-axis and $\bar{R}_v^+$ for its closure, for any variable v. R_{vw}^+ denotes the positive $v-w$ plane and $\bar{R}_{vw}^+$ its closure etc.

Further if populations $N_1, \ldots, N_k$ exhibit total extinction in the space $R^+_{v_1,\ldots,v_\ell}$, we denote this by $\mathcal{E}_{N_1,\ldots,N_k} \to 0$. Here $N_1, \ldots, N_k$ and $v_1, \ldots, v_\ell$ are subsets of the set $\{u, x, y, z\}$.

We now define persistence with respect to the positive orthant in R^n (see [4, 5] for more general definitions). We say that $N(t)$, $N(0) > 0$, *persists* if $N(t) > 0$ for all $t > 0$ and $\liminf_{t\to\infty} N(t) > 0$. We say that $N(t)$ *uniformly persists* if, further, $\liminf_{t\to\infty} N(t) \geq \delta > 0$ for all $N(0) \in \overset{\circ}{R}_+$, where $\overset{\circ}{R}_+$ is the interior of R^n_+. Finally, we say that a vector $(N_1(t), \ldots, N_n(t)) \in R^n_+$ (uniformly) persists if each component (uniformly) persists. If any component fails to persist, we say that *nonpersistence* occurs.

In Section 2, we discuss our model. Section 3 contains an equilibrium analysis and a review of known persistence criteria. Section 4, gives persistence and extinction criteria for the total model including reversal of outcome. In particular, criteria are developed for the first time to the best of our knowledge for the case of almost periodic dynamics. Included in this are examples to illustrate our results. Section 5 contains a brief discussion.

2 The Models

In this section we describe a general model of interactions between a mutualist population and populations of a food chain. The mathematical formulation of obligate relationships between the mutualist and two different trophic levels of the food chain are also described. Finally, we estimate the region of attraction in each case, showing that the models are well-behaved.

We consider the autonomous system,

$$\begin{aligned}
\frac{du}{dt} &= uh(u, x, y, z), \\
\frac{dx}{dt} &= \alpha x g(u, x) - y p_1(u, x) - z p_2(u, x), \\
\frac{dy}{dt} &= y[-s_1(u, y) + c_1(u) p_1(u, x)] - z q(u, y), \\
\frac{dz}{dt} &= z[-s_2(u, z) + c_2(u) p_2(u, x) + c_3(u) q(u, y)], \\
u(0) &= u_0 \geq 0, \quad x(0) = x_0 \geq 0, \quad y(0) = y_0 \geq 0, \quad z(0) = z_0 \geq 0,
\end{aligned} \tag{2.1}$$

as a model of a mutualist-food chain interaction with continuous birth and death processes. The variable $u(t)$ represents the density of the mutualist at time t and $x(t)$, $y(t)$, $z(t)$ denote the prey, predator, and superpredator densities respectively.

The function $h(u,x,y,z)$ represents the specific growth rate of the mutualist population. We assume that $h(u,x,y,z)$ possesses the following properties.

(H1) $h(0,x,y,z) > 0$, $\frac{\partial h}{\partial u}(u,x,y,z) \le 0$.
(H2) There exists a unique function $L(x,y,z) > 0$, such that $h(L(x,y,z),x,y,z) = 0$.

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

(G1) $g(u,0) > 0$, $\frac{\partial g}{\partial x}(u,x) \le 0$.
(G2) There exists a unique $K(u) > 0$ such that $g(u,K(u)) = 0$.
(G3) $\frac{\partial g}{\partial u}(u,x) \ge 0$.

Next, the functions $p_i(u,x)$, $i = 1,2$ and $q(u,y)$ denote the predator's functional response to the prey and mutualist densities. We assume that,

(P1) $p_i(u,0) = 0$, $\frac{\partial p_i}{\partial x}(u,x) > 0$, $i = 1,2$, $q(u,0) = 0$, $\frac{\partial q}{\partial y}(u,y) > 0$.

The functions $s_1(u,y)$ and $s_2(u,z)$ are the specific death rates of the predators y and z, in the absence of predation. We assume that

(S1) $\frac{\partial s_1(u,y)}{\partial y} > 0$, $\frac{\partial s_2(u,z)}{\partial z} > 0$.
(S2) $\frac{\partial s_1(u,y)}{\partial u} \le 0$, $\frac{\partial s_2(u,z)}{\partial u} \ge 0$, $c_1'(u) \ge 0$, $c_i'(u) \le 0$, $i = 2,3$.

The non-negative functions $c_i(u)$, $i = 1,2,3$ are the conversion rates of prey biomass to the predator biomass. The implications of the above conditions are described in detail in [24]. Finally, we assume that all the functions are smooth enough so that existence and uniqueness of initial value problems hold and any required analysis can be carried out.

In model (2.1), we will think of α as a bifurcation parameter.

2.1 Obligate mutualism with the bottom-predator

In this section we consider the case of obligate mutualism between the mutualist u and the predator y. In addition to H(1-2), we assume the following for the specific growth rate $h(u,x,y,z)$ of the mutualist:

(H3) $\frac{\partial h}{\partial x}(u,x,y,z) \le 0$, $\frac{\partial h}{\partial y}(u,x,y,z) > 0$, $\frac{\partial h}{\partial z}(u,x,y,z) \le 0$.
(H4) $\lim\limits_{y\to\infty} L(0,y,0) = \widetilde{L} < \infty$.

The condition (H3) implies that u derives benefit from the predator population and that there might be a cost to the mutualist due to its interactions with the predators. The condition (H4) implies that u has a finite carrying capacity, no matter how much benefit it derives.

Further we assume

(P2) $\frac{\partial p_1(u,x)}{\partial u} \ge 0$, $\frac{\partial p_2(u,x)}{\partial u} \le 0$, $\frac{\partial q(u,y)}{\partial u} \le 0$.

This condition implies that the mutualist can benefit the bottom-predator by increasing its predator's response and/or by decreasing the response of the superpredator.

In order for system (2.1) to exhibit obligate mutualism between u and y, the food chain must collapse in the absence of the mutualist and the predator y must become extinct. Thus we require that the subsystem:

$$\begin{aligned}\frac{dx}{dt} &= \alpha x g(0,x) - y p_1(0,x) - z p_2(0,x),\\ \frac{dy}{dt} &= y[-s_1(0,y) + c_1(0)p_1(0,x)] - z q(0,y),\\ \frac{dz}{dt} &= z[-s_2(0,z) + c_2(0)p_2(0,x) + c_3(0)q(0,y)],\end{aligned} \tag{2.2}$$

with $x(0) > 0$, $y(0) > 0$ and $z(0) > 0$, exhibits extinction and $\lim_{t\to\infty} y(t) = 0$. As observed in [11] this happens when either

(S3a) $\lim_{x\to\infty} p_1(0,x) \le \frac{s_1(0,0)}{c_1(0)}$

or

(S3b) $p_1(0,\hat{x}) = \frac{s_1(0,0)}{c_1(0)}$ and $\hat{x} \ge K(0)$.

In conclusion whenever hypotheses H(1-4), G(1-3), P(1,2) and S(1-3) hold, mutualism occurs between u and y and is obligate for the predator y.

The following result establishes that under the above hypotheses, system (2.1) possesses a region of attraction. The proof is similar to one given in [24].

Theorem 2.1 *Let the hypotheses* H(1-4), G(1-3), P(1,2), S(1-3) *hold. Then the set*

$$\begin{aligned}\mathcal{C} = \{(u,x,y,z)\colon & 0 \le u \le \widetilde{L},\ \ 0 \le x \le \widetilde{K},\ \ 0 \le \widetilde{c}_1 x + y \le \widetilde{M},\\ & 0 \le c_2(\widetilde{L})x + c_3(\widetilde{L})y + z \le \widetilde{N},\ \ 0 \le c_2(0)x + c_3(0)y + z \le \widetilde{N}\},\end{aligned} \tag{2.3}$$

where

$$\begin{aligned}\widetilde{K} &= \max_{0\le u\le \widetilde{L}} K(u), \qquad \widetilde{c}_1 = \max_{0\le u\le \widetilde{L}} c_1(u),\\ \widetilde{M} &= \frac{c_1(\widetilde{L})\widetilde{K}}{s_1(\widetilde{L},0)}\,[\alpha g(\widetilde{L},0) + s_1(\widetilde{L},0)],\end{aligned} \tag{2.4}$$

$$\widetilde{N} = \frac{1}{s_2(0,0)}\left[c_2(0)\widetilde{K}\big(\alpha g(\widetilde{L},0) + s_2(0,0) + c_3(0)\widetilde{M}\left(\frac{c_1(\widetilde{L})}{\widetilde{L}\,\widetilde{K} + s_2(0,0)}\right)\right]$$

and

$$\widetilde{p}_1 = \max_{0\le u\le \widetilde{L}} p_1(u,\widetilde{K}),$$

is positively invariant and attracts all solutions starting with nonnegative initial-values.

2.2 Obligate mutualism with the top-predator

The system (2.1) exhibits mutualism between u and z, which is obligate for the top-predator z, whenever in addition to H(1-2), G(1-3), P1, S(1,3), the following assumptions hold:

(H3*) $\frac{\partial h(u,x,y,z)}{\partial x} \le 0,\ \frac{\partial h(u,x,y,z)}{\partial y} \le 0,\ \frac{\partial h(u,x,y,z)}{\partial z} > 0.$

(H4*) $\lim_{z\to\infty} L(0,0,z) = \widetilde{L} < \infty.$

(P2*) $\frac{\partial p_2(u,x)}{\partial u} \ge 0,\ \frac{\partial q(u,y)}{\partial u} \ge 0.$

(S2*) $\frac{\partial s_2(u,y)}{\partial u} \le 0,\ c_2'(u) \ge 0,\ c_3'(u) \ge 0.$

The following condition ensures that in the absence of u, z will become extinct.

(S4*a) $c_2(0) \lim_{x\to\infty} p_2(0,x) + c_3(0) \lim_{y\to\infty} q(0,y) \le s_2(0,0)$.

or

(S4*b) $c_2(0)p_2(0,\underline{x}) + c_3(0)q(0,\underline{y}) = s_2(0,0)$, for some $\underline{x}$ and $\underline{y}$, where $\underline{x} \ge K(0)$.

Finally the mutualist can indirectly benefit the predator z, by affecting the death rate, the predator response function or the conversion rate of prey biomass to the predator biomass of the predator y.

Under the above stated hypotheses by similar arguments as for Theorem 2.1, we can prove the following by using standard techniques (see e.g. [17]).

Theorem 2.2 *Let the hypotheses* H(1,2,3*, 4*), G(1-3), P(1,2*), S(1,2*,4*) *hold. Then the set*

$$\begin{aligned}\mathcal{D} = \{(u,x,y,z)\colon 0 \le u \le \widetilde{L},\ \ 0 \le x \le \widetilde{K},\ \ 0 \le \widetilde{c}_1 x + y \le \widetilde{M},\\ 0 \le c_2(\widetilde{L})x + c_3(\widetilde{L})y + z \le \widetilde{N}\},\end{aligned} \tag{2.5}$$

where the constants are given in (2.4), and

$$\widetilde{p}_1 = \max_{0\le u\le \widetilde{L}} p_1(u,\widetilde{K}),$$

is positively invariant and attracts all solutions starting with nonnegative initial-values.

3 The Equilibria

The question of existence and non-existence of various equilibria of system (2.1) and their stabilities are discussed in detail in [24]. Below we describe the information needed to study the question of reversal of outcome in our system for the two cases under consideration.

Case I: Obligate mutualism between u and y

The system (2.1) possesses the equilibrium $E_0(0,0,0,0)$ and one dimensional equilibria $E_1(L_0,0,0,0)$, $E_2(0,K_0,0,0)$, where $L_0 = L(0,0,0)$ and $K_0 = K(0)$. The two dimensional equilibrium $E_3(\widetilde{u},\widetilde{x},0,0)$ always exists. The equilibrium $E_5(0,x_2,0,z_2)$ in the $x-z$ plane may or may not exist. The three dimensional equilibria, if they exist are of the form $E_6(u_3,x_3,y_3,0)$ and $E_7(u_4,x_4,0,z_4)$. We note that a three dimensional submodel has an equilibrium if it is uniformly persistent (see [4]).

Case II: Obligate mutualism between u and z

In this case the equilibria $E_0(0,0,0,0)$, $E_1(L_0,0,0,0)$, $E_2(0,K_0,0,0)$, $E_3(\widetilde{u},\widetilde{x},0,0)$ always exist. The equilibrium $E_4(0,x_1,y_1,0)$ in the $x-y$ plane may or may not exist. The three dimensional equilibria if they exist are of the form $E_6(u_3,x_3,y_3,0)$ and $E_7(u_4,x_4,0,z_4)$.

Next, we list information regarding the eigenvalues of the variational matrix, computed at the various equilibria so that their stabilities may be discussed.

The eigenvalues of E_2 in the y and z-directions are

$$\alpha_i \triangleq -s_i(0,0) + c_i(0)p_i(0,K_0), \quad i = 1,2. \tag{3.1}$$

The eigenvalues of E_3 in the y and z directions are

$$\beta_i \triangleq -s_i(\widetilde{u},0) + c_i(\widetilde{u})p_i(\widetilde{u},\widetilde{x}), \quad i = 1,2. \tag{3.2}$$

The eigenvalues of E_4 in the z-direction and of E_5 in the y-direction are

$$\gamma \triangleq -s_2(0,0) + c_2 p_2(0,x_1) + c_3(0)q(0,y_1), \tag{3.3}$$

and

$$\delta \triangleq -s_1(0,0) + c_1(0)p_1(0,x_2) - z_2 q_y(0,0), \tag{3.4}$$

respectively.

The eigenvalues of E_6 and E_7 in the z and y directions are

$$\xi \triangleq -s_2(u_3,0) + c_2(u_3)p_2(u_3,x_3) + c_3(u_3)q(u_3,y_3) \tag{3.5}$$

and

$$\eta \triangleq -s_1(u_4,0) + c_1(u_4)p_1(u_4,x_4) - z_4 q_y(u_4,0), \tag{3.6}$$

respectively.

The above values are computed in a straightforward manner using standard techniques of ordinary differential equations.

4 Reversal of Outcome

Case I: Obligate mutualism between u and y

Suppose that for the system (2.1) the hypotheses H(1-4), G(1-3), P(1-2), S(1-3) hold. The obligate relationship between u and y implies that $\mathcal{E}_{y\to 0}$ in R^+_{xy} and R^+_{xyz}, that is, in the absence of mutualism, the predator y becomes extinct. However, we will show that with mutualism present, system (2.1) can exhibit uniform persistence resulting in a reversal of the outcome exhibited by the food chain submodel. The following result specifies a set of conditions leading to such a reversal. The proof follows using techniques similar to those used in [24] and is thus omitted. First we assume the following additional hypotheses for technical mathematical reasons.

- (H5) Let E_5 (if it exists) be globally asymptotically stable with respect to solutions initiating in $\overset{\circ}{R}{}^+_{xz}$.
- (H6) Let the equilibria E_6 and E_7 be globally asymptotically stable in $\overset{\circ}{R}{}^+_{uxy}$ and $\overset{\circ}{R}{}^+_{uxz}$, respectively.

Theorem 4.1 *Let the hypotheses* H(1-6), G(1-3), P(1,2) *and* S(1-3) *hold. Then the system (2.1) is uniformly persistent whenever* $\xi > 0$ *and* $\eta > 0$*, where* ξ *and* η *are given by (3.5) and (3.6), respectively.*

The above theorem can be interpreted as follows. If the predator y is unable to survive on its own, then the mutualist could help the predator population to survive. As observed in [13], the mutualist can benefit the mutualist predator in several ways: by increasing the prey growth rate, by increasing the rate of predation of its prey x, by providing an alternate food source for the mutualist-predator and by enhancing the efficiency of utilization of the prey by the mutualist-predator. Below we illustrate each of these cases with an example. All examples considered are of the form

$$\begin{aligned}
\frac{du}{dt} &= u\left(1-\frac{u}{L+\ell y}\right),\\
\frac{dx}{dt} &= \alpha x\left(1-\frac{x}{K+ku}\right)-(\gamma_0+\gamma_1 u)xy-\frac{\delta_0}{1+\delta_1 u}\,xz,\\
\frac{dy}{dt} &= y\big[-s_{10}+s_{11}u-s_{12}y+(c_{10}+c_{11}u)(\gamma_0+\gamma_1 u)x-\xi_0 z\big],\\
\frac{dz}{dt} &= z\left[-s_{20}-s_{21}u-s_{22}z+\frac{c_{20}}{1+c_{21}u}\frac{\delta_0}{1+\delta_1 u}x+\frac{c_{30}\xi_0}{1+c_{31}u}y\right],
\end{aligned}\tag{4.1}$$

where all the constants are assumed to be nonnegative.

In the absence of the mutualist u, there will be an equilibrium in R^+_{xy},

$$(x,y)=\left(\frac{K(s_{10}\gamma_0+\alpha s_{12})}{\alpha s_{12}+Kc_{10}\gamma_0^2},\frac{\alpha(Kc_{10}\gamma_0-s_{10})}{\alpha s_{12}+Kc_{10}\gamma_0^2}\right),$$

unless $Kc_{10}\gamma_0 \le s_{10}$. Thus for obligate mutualism we require

$$Kc_{10}\gamma_0 \le s_{10}. \tag{4.2}$$

Example 4.1 When $\gamma_1=\delta_1=s_{11}=c_{11}=s_{21}=c_{21}=c_{31}=0$ and $k>0$, mutualism occurs by means of the mutualist enhancing the prey growth rate.

The region of attraction for the system is contained in the set

$$\begin{aligned}
\mathcal{B}=\{(u,x,y,z)\colon 0\le u\le L+\ell\widetilde{M},\ \ 0\le x\le K+k(L+\ell\widetilde{M}),\\
0\le y\le \widetilde{M},\ \ 0\le z\le \widetilde{N}\},
\end{aligned}\tag{4.3}$$

where

$$\widetilde{M}=\frac{-s_{10}+c_{10}\gamma_0(K+kL)}{s_{12}-c_{10}\gamma_0 k\ell},$$

$$\widetilde{N}=\frac{1}{s_{22}}\big(-s_{20}+Kc_{20}\delta_0+K(L+\ell\widetilde{M})+c_{30}\xi_0\widetilde{M}\big).$$

We assume that $\widetilde{M}$ and $\widetilde{N}$ are positive, otherwise the system will always exhibit extinction. The equilibria in $\overline{R}^+_{ux}$ are $E_0(0,0,0,0)$, $E_1(L,0,0,0)$, $E_2(0,K,0,0)$, $E_3(L,K+kL,0,0,0)$. The equilibrium $E_5\left(0,\frac{K(\delta_0 s_{20}+\alpha s_{22})}{\alpha s_{22}+Kc_{20}\delta_0^2},0,\frac{\alpha(-s_{20}+Kc_{20}\delta_0)}{\alpha s_{22}+Kc_{20}\delta_0^2}\right)$ exists provided $Kc_{20}\delta_0>s_{20}$.

The subsystem in R^+_{uxy} is uniformly persistent whenever

$$\beta_1=-s_{10}+c_{10}\gamma_0(K+kL)>0, \tag{4.4}$$

in which case the equilibrium in R^+_{uxy} is given by

$$E_6(u_3,x_3,y_3,0)=(L+\ell y_3,\frac{s_{10}+s_{12}y_3}{c_{10}\gamma_0},y_3,0),$$

where

$$y_3 = \frac{b + \sqrt{b^2 + 4k\ell c_{10}\gamma_0^2\beta_1}}{2k\ell c_{10}\gamma_0^2}$$

and

$$b = \alpha k\ell c_{10}\gamma_0 - \alpha s_{12} - c_{10}\gamma_0^2(K + kL).$$

The subsystem in R^+_{uxz} is uniformly persistent provided

$$\beta_2 = -s_{20} + c_{20}\delta_0(K + kL) > 0, \tag{4.5}$$

and then the equilibrium in R^+_{uxz} is given by

$$E_7(u_4, x_4, 0, z_4) = \left(L, \frac{(\alpha s_{22} + \delta_0 s_{20})(K + kL)}{\alpha s_{22} + (K + kL)c_{20}\delta_0^2}, 0, \frac{\alpha\beta_2}{\alpha s_{22} + (K + kL)c_{20}\delta_0^2}\right).$$

The symmetric matrix $\mathcal{B}(u, x, y)$ corresponding to E_6 is given by

$$b_{11} = \frac{1}{(L + \ell y_3)},$$

$$b_{12} = \frac{-\alpha k c_{10} x}{2(K + ku)(K + k(L + \ell y_3))},$$

$$b_{13} = -\frac{\ell u}{2(L + \ell y)(L + \ell y_3)},$$

$$b_{22} = \frac{\beta c_{10}}{K + k(L + \ell y_3)},$$

$$b_{23} = 0 \quad \text{and} \quad b_{33} = s_{12}.$$

It is positive definite in the region of attraction of the subsystem in R^+_{uxy}, whenever

$$s_{12}\left(\frac{\alpha c_{10}}{L + \ell y_3} - \frac{\alpha^2 k^2 c_{10}^2 (K + k(L + \ell\widetilde{M}))^2}{4K^2(K + k(L + \ell y_3))}\right) - \frac{\alpha c_{10}\ell^2(L + \ell\widetilde{M})^2}{4L^2(L + \ell y_3)^2} > 0. \tag{4.6}$$

The matrix $\mathcal{D}(u, x, z)$ corresponding to E_7 is given by

$$d_{11} = \frac{1}{L}, \quad d_{12} = \frac{\alpha k c_{20} x}{2(K + kL)(K + ku)}, \quad d_{13} = 0,$$

$$d_{22} = \frac{\alpha c_{20}}{K + kL}, \quad d_{23} = 0, \quad d_{33} = s_{22}.$$

It is positive definite whenever

$$\frac{1}{L} - \frac{\alpha k^2 c_{20}(K + kL)^2}{4(K + kL)K^2} > 0. \tag{4.7}$$

Thus the system (4.1) will be uniformly persistent whenever (4.4)–(4.7) hold and

$$\xi = -s_{20} + c_{20}\delta_0 x_3 + c_{30}\xi_0 y_3 > 0, \tag{4.8}$$

and

$$\eta = -s_{10} + c_{10}\gamma_0 x_4 - \xi_0 z_4 > 0. \tag{4.9}$$

Example 4.2 When $k = \delta_1 = s_{11} = c_{11} = s_{21} = c_{21} = c_{31} = 0$ and $\gamma_1 > 0$, the mutualist enhances the rate of predation of the mutualist-predator y. Here the region of attraction is contained in the set

$$\begin{aligned}\mathcal{B} = \{(u,x,y,z)\colon 0 \le u \le L + \ell\widetilde{M},\ \ 0 \le x \le K,\ \ 0 \le y \le \widetilde{M},\\ 0 \le z \le \frac{1}{s_{22}}\,(-s_{20} + Kc_{20}\delta_0 + c_{30}\xi_0\widetilde{M})\},\end{aligned} \tag{4.10}$$

where

$$\widetilde{M} = -\frac{s_{10} + Kc_{10}(\gamma_0 + \gamma_1 L)}{s_{12} - Kc_{10}\gamma_1\ell}.$$

The equilibria in $\overline{R}^+_{ux}$ are given by $E_0(0,0,0,0)$, $E_1(L,0,0,0)$, $E_2(0,K,0,0)$, $E_3(L,K,0,0)$.

The subsystem in R^+_{uxy} is uniformly persistent whenever

$$\beta_1 = -s_{10} + Kc_{10}(\gamma_0 + \gamma_1 L) > 0, \tag{4.11}$$

in which case the equilibrium $E_6(u_3,x_3,y_3,0) = (L+\ell y_3, \frac{1}{\alpha}[\alpha-(\gamma_0+\gamma_1(L+\ell y_3))y_3], y_3, 0)$, where from Descartes' rule of signs y_3 is the unique positive root of the equation

$$y^3 + \frac{2}{\gamma_1\ell}\,(\gamma_0 + \gamma_1 L)y^2 + \big(Kc_{10}(\gamma_0 + \gamma_1 L)^2 + \alpha s_{12} - \alpha K c_{10}\gamma_1\ell\big)y - \alpha\beta_1 = 0. \tag{4.12}$$

The subsystem in R^+_{uxz} is uniformly persistent provided

$$\beta_2 = -s_{20} + c_{20}\delta_0 K > 0, \tag{4.13}$$

in which case $E_7(u_4,x_4,0,z_4) = \Big(L, \frac{K(\alpha s_{22}+\delta_0 s_{20})}{\alpha s_{22}+Kc_{20}\delta_0^2}, 0, \frac{\alpha\beta_2}{\alpha s_{22}+Kc_{20}\delta_0^2}\Big)$. Now we consider the global asymptotic stability of E_6 and E_7 in R^+_{uxy} and R^+_{uxz}, respectively.

The symmetric matrix $\mathcal{B}(u,x,y)$ corresponding to $E_6(u_3,x_3,y_3,0)$ is given by

$$b_{11} = \frac{1}{u_3}, \quad b_{12} = \frac{\gamma_1 y}{2}, \quad b_{13} = -\frac{1}{2}\bigg(\frac{\ell u}{u_3(L+\ell y)} + c_{10}\gamma_1 x - s_{11}\bigg),$$

$$b_{22} = \frac{c_{10}}{K}, \quad b_{23} = 0, \quad b_{33} = s_{12}.$$

It is positive definite in its region of attraction whenever

$$\frac{4}{s_{12}}\left(\frac{1}{Ku_3} - \frac{\gamma_1^2 c_{10}\widetilde{M}^2}{4}\right) - \frac{1}{K}\bigg(\frac{\ell(L+\ell\widetilde{M})}{u_3 L} + Kc_{10}\gamma_1 - s_{11}\bigg) > 0, \tag{4.14}$$

where $\widetilde{M}$ is given by (4.10). The symmetric matrix $\mathcal{D}(u,x,z)$ corresponding to E_7 is given by

$$d_{11} = \frac{1}{u_4}, \quad d_{12} = 0, \quad d_{13} = \frac{1}{2}s_{21},$$

$$d_{22} = \frac{\alpha c_{20}}{K}, \quad d_{23} = 0, \quad d_{33} = s_{22}.$$

It is positive definite in its region of attraction whenever

$$4s_{22} - Ls_{21}^2 > 0. \tag{4.15}$$

Thus whenever (4.11), (4.13) – (4.15) hold and

$$\xi = -s_{20} + c_{20}\delta_0 x_3 + c_3\xi_0 y_3 > 0, \tag{4.16}$$

and

$$\eta = -s_{10} + c_{10}(\gamma_0 + \gamma_1 u_4)x_4 - \xi_0 z_4 > 0, \tag{4.17}$$

the system (4.1) is uniformly persistent.

Example 4.3 When $k = \gamma_1 = \delta_1 = c_{11} = s_{21} = c_{21} = c_{31} = 0$ and $s_{11} > 0$, the mutualist provides the mutualist-predator with an alternate food source.

The region of attraction is contained in the set

$$\mathcal{B} = \{(u,x,y,z)\colon 0 \le u \le L + \ell\widetilde{M},\ \ 0 \le x \le K,\ \ 0 \le y \le \widetilde{M},\ \ 0 \le z \le \widetilde{N}\}, \tag{4.18}$$

where

$$\begin{aligned} \widetilde{M} &= -\frac{s_{10} + s_{11}L + c_{10}\gamma_0 K}{s_{12} - s_{11}\ell}, \\ \widetilde{N} &= \frac{1}{s_{22}}(-s_{20} + Kc_{20}\delta_0 + c_3\xi_0\widetilde{M}). \end{aligned} \tag{4.19}$$

The equilibria in $\overline{R}^+_{ux}$ are $E_0(0,0,0,0)$, $E_1(L,0,0,0)$, $E_2(0,K,0,0)$ and $E_3(L,K,0,0)$. The subsystem in R^+_{uxy} is uniformly persistent whenever

$$\beta_1 = -s_{10} + s_{11}L + Kc_{10}\gamma_0 > 0. \tag{4.20}$$

The subsystem in R^+_{uxz} is uniformly persistent whenever

$$\beta_2 = -s_{20} + Kc_{20}\delta_0 > 0. \tag{4.21}$$

Whenever the inequalities (4.20) and (4.21) hold the equilibria in R^+_{uxy} and R^+_{uxz} are given by

$$E_6(u_3,x_3,y_3,0) = \left(L + \ell y_3, \frac{K(s_{10}\gamma_0 + \alpha s_{12} - \alpha s_{11}\ell + s_{11}L\gamma_0)}{Kc_{10}\gamma_0^2 - \alpha s_{11}\ell + \alpha s_{12}}, \frac{\alpha\beta_1}{Kc_{10}\gamma_0^2 - \alpha s_{11}\ell + \alpha s_{12}}, 0\right)$$

and

$$E_7(u_4,x_4,0,z_4) = \left(L, \frac{s_{20} + s_{22}z_4}{c_{20}\delta_0}, 0, \frac{\alpha\beta_2}{Kc_{20}\delta_0^2 + \alpha s_{22}}\right).$$

The symmetric matrix $\mathcal{B}(u,x,y)$ corresponding to E_6 is given by

$$\begin{aligned} b_{11} &= \frac{1}{u_3}, \quad b_{12} = 0, \quad b_{13} = -\frac{\ell u}{2u_3}, \\ b_{22} &= \frac{\alpha c_{10}}{K}, \quad b_{23} = 0, \quad b_{33} = s_{12}. \end{aligned}$$

It is positive definite in the region of attraction whenever

$$s_{12} - \frac{\ell^2}{4u_3}(L + \ell\widetilde{M})^2 > 0. \tag{4.22}$$

The matrix corresponding to E_7, $\mathcal{D}(u,x,z) = \operatorname{diag}\left(\frac{1}{u_4}, \frac{\alpha c_{20}}{K}, s_{22}\right)$ is always positive definite.

Thus the system (4.1) will be uniformly persistent whenever inequalities (4.20) – (4.22) hold and

$$\xi = -s_{20} + c_{20}\delta_0 x_3 + c_{30}\xi_0 y_3 > 0, \tag{4.23}$$

and

$$\eta = -s_{10} + s_{11}u_4 + c_{10}\gamma_0 x_4 - \xi_0 z_4 > 0. \tag{4.24}$$

Example 4.4 When $k = \gamma_1 = \delta_1 = s_{11} = s_{21} = c_{21} = c_{31} = 0$ and $c_{11} > 0$, the mutualist enhances the efficiency of the utilization of the prey by the mutualist-predator. Here the region of attraction is contained in the set

$$\mathcal{B} = \{(u,x,y,z)\colon 0 \le u \le L + \ell\widetilde{M},\ \ 0 \le x \le K,\ \ 0 \le y \le \widetilde{M},\ \ 0 \le z \le \widetilde{N}\}, \tag{4.25}$$

where

$$\widetilde{M} = \frac{-s_{10} + K\gamma_0(c_{10} + c_{11}L)}{s_{12} - K\gamma_0 c_{11}\ell},$$

$$\widetilde{N} = \frac{-s_{20} + Kc_{20}\delta_0 + c_{30}\xi_0\widetilde{M}}{s_{22}}.$$

The equilibrium in R^+_{ux} is $E_3(L,K,0,0)$. The subsystems in R^+_{uxy} and R^+_{uxz} are uniformly persistent provided

$$\beta_1 = -s_{10} + (c_{10} + c_{11}L)\gamma_0 K > 0, \tag{4.26}$$

and

$$\beta_2 = -s_{20} + Kc_{20}\delta_0 > 0. \tag{4.27}$$

The equilibrium

$$E_6(u_3,x_3,y_3,0) = \left(L + \ell y_3, \frac{K}{\alpha}(\alpha - \gamma_0 y_3), \frac{b + \sqrt{b^2 + 4\alpha\beta_1}}{2Kc_{11}\gamma_0^2\ell}, 0\right),$$

where

$$b = \alpha(\ell K c_{11}\gamma_0 - s_{12}) - K\gamma_0^2(c_{10} + c_{11}L).$$

The equilibrium

$$E_7(u_4,x_4,0,z_4) = \left(L, \frac{K(\alpha s_{22} + \delta_0 s_{21})}{\alpha s_{22} + Kc_{20}\delta_0^2}, 0, \alpha\beta_2\right).$$

The symmetric matrix $\mathcal{B}(u,x,y)$ corresponding to E_6 is given by

$$b_{11} = \frac{1}{u_3}, \quad b_{12} = 0, \quad b_{13} = -\frac{\ell u}{2u_3(L + \ell y)} - \frac{1}{2}c_{11}\gamma_0 x,$$

$$b_{22} = \frac{\alpha}{K}(c_{10} + c_{11}u_3), \quad b_{23} = 0, \quad b_{33} = s_{12}.$$

It is positive definite in its region of attraction whenever

$$\frac{4s_{12}}{u_3} - \left(\frac{\ell(L + \ell\widetilde{M})}{u_3 L} + Kc_{11}\gamma_0\right)^2 > 0. \tag{4.28}$$

The symmetric matrix corresponding to E_7 is given by

$$\mathcal{D}(u,x,z) = \operatorname{diag}\left(\frac{1}{L},\ \frac{\alpha c_{20}}{K},\ s_{22}\right).$$

Thus whenever inequalities (4.26) – (4.28) hold and

$$\xi = -s_{20} - s_{21}u_3 + c_{20}\delta_0 x_3 + c_{30}\xi_0 y_3 > 0, \tag{4.29}$$

and

$$\eta = -s_{10} + (c_{10} + c_{11}u_4)\gamma_0 x_4 - \xi_0 z_4 > 0, \tag{4.30}$$

the given system is uniformly persistent.

In the above examples, all boundary equilibria of predator-prey type were globally asymptotically stable in their respective predator-prey planes, i.e. we assumed that hypotheses (H5) and (H6) hold.

We now allow for the possibility that (H5) and/or (H6) be violated, in which case there could be periodic solutions in $\overset{\circ}{R}{}^{+}_{xz}$ and periodic, almost periodic, or recurrent motions in $\overset{\circ}{R}{}^{+}_{uxz}$ and $\overset{\circ}{R}{}^{+}_{uxy}$.

Persistence criteria have been obtained in three dimensional systems when periodic solutions occur in the predator-prey planes. To the best of our knowledge the almost periodic case for four dimensions has not yet been considered.

Hence we next demonstrate that uniform persistence can occur even when one or more of the three-dimensional subsystems have almost periodic solutions. We note that the closure Σ of an almost periodic orbit is a compact, minimal set and every solution in Σ is almost periodic (see [26]).

We state and prove a theorem for persistence in the case where almost periodic solutions occur in R^{+}_{uxy}, but that E_7 is globally stable with respect to $\overset{\circ}{R}{}^{+}_{uxz}$. Let there be k nontrivial almost periodic solutions in R^{+}_{uxy}, denoted $(\phi_i(t), \psi_i(t), \xi_i(t), 0)$, with disjoint closures $\sum_i$, $i = 1, \ldots, k$.

Theorem 4.2 *Let the hypotheses* H(1-5), G(1-3), P(1,2) *and* S(1-3) *hold, and* E_7 *be globally stable with respect to* $\overset{\circ}{R}_{+uxz}$. *Also let the omega limit sets of all solutions initiating in* R^{+}_{uxy} *lie in the acyclic set* $\left\{ \bigcup_{i=1}^{k} \Sigma_i \cup E_6 \right\}$. *Then the system (2.1) is uniformly persistent whenever* $\xi > 0$, $\eta > 0$ *and*

$$\lim_{t\to\infty} \frac{1}{t} \int_0^t [-s_2(\phi_i(r), 0) + c_2(\phi_i(r)) p_2(\phi_i(r), \psi_i(r)) + c_3(\phi_i(r)) q(\phi_i(r), \xi_i(r))]\, dr > 0, \quad i = 1, \ldots, k. \tag{4.31}$$

Proof First we observe that the limit in the inequality (4.31) exists. Also as each Σ_i is a compact minimal set, it lies in R^{+}_{uxy} and the subsystem in R^{+}_{uxy} is uniformly persistent. The uniform persistence of (2.1) will follow (see [5]) if we can show that the stable sets, $W^s(\Sigma_i)$ and $W^s(E_j)$ do not intersect R^{+}_{uxyz} and each of them is isolated in $\overline{R}{}^{+}_{uxyz}$.

First, we show that $W^s(\Sigma_i) \cap R^{+}_{uxyz} = \phi$, $1 \le i \le k$. Let $\Phi(t) = (\phi(t), \psi(t), \xi(t), 0)^T$ be any almost periodic solution in Σ_{i_0} and $X(t) = (u(t), x(t), y(t), z(t))^T$, $X(0) = X_0 \in$

R^+_{uxyz} be any solution starting sufficiently close to $\Phi(t)$. Linearizing $X(t)$ about $\Phi(t)$ we obtain

$$Y'(t) = A(t)Y(t), \tag{4.32}$$

where $Y(t) = (u_1(t), x_1(t), y_1(t), z_1(t))^T$ is the linearized vector variable, and

$$A(t) = \begin{pmatrix} \phi h_u + h & \phi h_x & \phi h_y & \phi h_z \\ \alpha\psi g - \psi p_1 & \alpha g + \alpha g_x - \xi p_{1_x} & -p_1 & -p_2 \\ -\psi(-s_{1u} + c_1' p_{1u}) & \psi c_1 p_{1x} & -s_1 + c_1 p_1 - \xi s_{1y} & -q \\ 0 & 0 & 0 & -s_2 + c_2 p_2 + c_3 q \end{pmatrix},$$

where all the functions are evaluated at $\Phi(t)$. Solving the last equation in (4.32) we obtain

$$z_1(t) = z_1(0) \exp \int_0^t [-s_2(\phi(r), 0) + c_2(\phi(r)) p_2(\phi(r), \psi(r)) + c_3(\phi(r)) q(\phi(r), \xi(r))]\, dr.$$

Now since $\Phi(t)$ lies in Σ_{i_0} and the solutions through Σ_{i_0} are uniformly stable in both directions in Σ_{i_0}, the inequality (4.31) (with $i = i_0$) implies that $z_1(t) > 0$ for $t \ge 0$ and is an increasing function for sufficiently large t. Thus any solution in R^+_{uxyz}, starting sufficiently close to Σ_{i_0} eventually gets away from it.

Hence, $\Omega(X_0) \not\subset \Sigma_{i_0}$. Thus $W^s(\Sigma_{i_0}) \cap R^+_{uxyz} = \phi$, $1 \le i \le k$.

Since all boundary equilibria are hyperbolic we conclude as in [24] that $W^s(E_i) \cap R^+_{uxyz} = \emptyset$, $1 \le i \le 7$.

Now suppose that for some i_0, Σ_{i_0} is not an isolated invariant set in R^+_{uxyz}. Then there must exist closed invariant sets in arbitrarily close neighbourhoods of Σ_{i_0}. Let $M \supset \Sigma_{i_0}$ be such a closed invariant set. Then by repeating the arguments, given above we conclude that Σ_{i_0} repels the solutions starting in M/Σ_{i_0} and hence they must leave M. However this contradicts the fact that M is invariant. Hence the proof.

Remark 4.3 The acyclic condition of the above theorem is always satisfied when each Σ_i is either asymptotically stable or completely unstable in R^+_{uxy} and there do not exist any homoclinic orbits in R^+_{uxy}.

Remark 4.4 In the event that almost periodic solutions exist for the subsystems in R^+_{uxz} a criterion similar to the one given by the above theorem can be obtained.

Case II: Obligate mutualism between u and z

The system (2.1) exhibits obligate mutualism between the mutualist u and the top-predator z, whenever the hypotheses H(1,2,3*,4*), G(1-3), P(1,2*) and S(1,2*,4*) hold.

Also from the hypothesis S(4*) the mutualism is obligate for the predator. Hence $\mathcal{E}_{z\to 0}$ in R^+_{xz} and R^+_{xyz} and the equilibrium E_5 does not exist. To obtain the persistence criteria in this case, we need to introduce the following additional hypothesis:

(H5*) Let the equilibrium E_4 (if it exists) be globally asymptotically stable with respect to solutions initiating in $\overset{\circ}{R}{}^+_{xy}$.

The following result holds for system (2.1).

Theorem 4.3 *Let the hypotheses* H(1,2,3*,4*,5*,6), G(1-3), P(1,2*), S(1,2*,4*) *hold. Then system (2.1) is uniformly persistent whenever* $\xi > 0$ *and* $\eta > 0$.

Persistence in system (2.1) can result in any of the following ways.

The mutualist u can directly benefit the mutualist-predator z, by enhancing the growth rate of the prey x, by providing an alternate food supply, by increasing its rate of predation or by enhancing the efficiency of utilization of the prey(s). Below we illustrate each of these cases with an example. We also note that the mutualist's interaction with the predator y can also lead to a beneficial effect for the top-predator.

Consider the system

$$\begin{aligned} u' &= u\left(1 - \frac{u}{L+\ell z}\right), \\ x' &= \alpha x\left(1 - \frac{x}{K+ku}\right) - \frac{\gamma_0}{1+\gamma_1 u}xy - (\delta_0+\delta_1 u)xz, \\ y' &= y\left[-s_{10} + s_{12}y + \frac{c_1\gamma_0}{1+\gamma_1 u}xy\right] - (\xi_0+\xi_1 u)yz, \\ z' &= z[-s_{20} - s_{21}u - s_{22}z + (c_{20}+c_{21}u)(\delta_0+\delta_1 u)x + c_3(\xi_0+\xi_1 u)y], \end{aligned} \tag{4.33}$$

where all the constants are assumed to be nonnegative.

It is easily seen that in the absence of the mutualist, $y(t) \le \frac{-s_{10}+Kc_1\gamma_0}{s_{12}}$. Hence assume that

$$s_{10} < Kc_1\gamma_0, \tag{4.34}$$

otherwise $\mathcal{E}_{y\to 0}$ in R^+_{uxyz}. Furthermore for obligate mutualism to occur we require that

$$Kc_{20}\delta_0 + c_3\xi_0\frac{(-s_{10}+Kc_1\gamma_0)}{s_{12}} \le s_{20}. \tag{4.35}$$

Example 4.5 When $\gamma_1 = \delta_1 = \xi_1 = s_{21} = c_{21} = 0$ and $k > 0$, mutualism occurs by means of mutualist enhancing the rate of growth of the prey x.

The region of attraction is contained in the set

$$\begin{aligned} \mathcal{C} = \{(u,x,y,z)\colon 0 \le u \le L+\ell\widetilde{N},\ 0 \le x \le K + k(L+\ell\widetilde{N}), \\ 0 \le y \le \widetilde{M},\ 0 \le z \le \widetilde{N}\}, \end{aligned} \tag{4.36}$$

where

$$\widetilde{M} = \frac{-s_{10} + c_1\gamma_0(K+k(L+\ell\widetilde{N}))}{s_{11}}$$

and

$$\widetilde{N} = \frac{-s_{20} + c_{20}\delta_0(K+kL) + c_3\xi_0\widetilde{M}}{s_{22} - c_{20}\delta_0 + K\ell}.$$

The equilibrium in R^+_{ux} is $(L, K+kL)$. The subsystems in R^+_{uxy} and R^+_{uxz} are uniformly persistent whenever

$$\beta_1 = -s_{10} + c_1\gamma_0(K+kL) > 0, \tag{4.37}$$

and

$$\beta_2 = -s_{20} + c_{20}\delta_0(K + kL) > 0. \tag{4.38}$$

The equilibrium

$$E_6(u_3, x_3, y_3, 0) = \left(L, \frac{(K+kL)(\gamma_0 s_{10} + \alpha s_{11})}{\alpha s_{11} + (K+kL)\gamma_0^2 c_1}, \frac{\alpha\beta_1}{\alpha s_{11} + (K+kL)\gamma_0^2 c_1}, 0\right),$$
$$E_7(u_4, x_4, 0, z_4) = (L + \ell z_4, x_4, 0, z_4),$$

where

$$x_4 = \frac{1}{\alpha}(\alpha - \delta_0 z_4)(K + kL + k\ell z_4),$$
$$z_4 = \frac{b_4 + \sqrt{b_0^2 + 4c_{20}\delta_0^2\alpha k\ell\beta_2}}{2c_{20}\delta_0^2 k\ell},$$

and $b_0 = \alpha(-s_{22} + c_{20}\delta_0 k\ell) - c_{20}\delta_0^2(K + kL)$. The symmetric matrix $\mathcal{B}(u,x,y)$ corresponding to E_8 is given by

$$b_{11} = \frac{1}{u_3}, \quad b_{12} = \frac{-c_1\alpha kx}{2(K+ku_3)(K+ku)}, \quad b_{13} = 0,$$
$$b_{22} = \frac{\alpha c_1}{K + ku_3}, \quad b_{23} = 0, \quad b_{33} = s_{11}.$$

Thus $\mathcal{B}(u,x,y)$ is positive definite in its region of attraction whenever

$$4K^2(K + ku_3) - \alpha u_3 c_1 k^2 (K + kL)^2 > 0. \tag{4.39}$$

The symmetric matrix $\mathcal{D}(u,x,z)$ corresponding to E_7 is given by

$$d_{11} = \frac{1}{u_4}, \quad d_{12} = \frac{-\alpha k c_{20} x}{2(K+ku_4)(K+ku)}, \quad d_{13} = -\frac{1}{2}\frac{\ell u}{u_4(L+\ell z)},$$
$$d_{22} = \frac{\alpha c_{20}}{(K + ku_4)}, \quad d_{23} = 0, \quad b_{33} = s_{22}.$$

The region of attraction of the subsystem in R^+_{uxz} is contained in the set

$$\mathcal{C}_1 = \{(u,x,z)\colon 0 \le u \le L + \ell N_1,\ \ 0 \le x \le K + k(L + \ell N_1),\ \ 0 \le z \le N_1\},$$

where $N_1 = \frac{\beta_2}{s_{22} - c_{20}\delta_0 k\ell}$. The matrix $\mathcal{D}(u,x,z)$ is positive definite in $\mathcal{B}_1$ whenever

$$4c_{20}s_{22} - \frac{\alpha u_4 c_{20}^2 s_{22} k^2}{(K + ku_4)K^2}(K + kL + k\ell N_1)^2 - \frac{\ell^2}{L^2 u_4}(L + \ell N_1)^2 > 0. \tag{4.40}$$

Thus the system (4.31) is uniformly persistent whenever the inequalities (4.35)–(4.38) hold and

$$\xi = -s_{20} + c_{20}\delta_0 x_3 + c_3\xi_0 y_3 > 0 \tag{4.41}$$

and

$$\eta = -s_{10} + c_1\gamma_0 x_4 - \xi_0 z_4 > 0. \tag{4.42}$$

Example 4.6 When $k = \gamma_1 = \delta_1 = \xi_1 = c_{21} = 0$ and $s_{21} > 0$, mutualism occurs by means of providing an alternate food source to the top-predator. The region of attraction is contained in the set

$$\mathcal{C} = \{(u,x,z)\colon 0 \le u \le L + \ell\widetilde{N},\ \ 0 \le x \le K,\ \ 0 \le y \le \widetilde{M},\ \ 0 \le z \le \widetilde{N}\}, \tag{4.43}$$

where

$$\widetilde{M} = \frac{-s_{10} + Kc_1\gamma_0}{s_{11}} \quad \text{and} \quad \widetilde{N} = \frac{-s_{20} + s_{21}L + Kc_{20}\delta_0 + c_3\xi_0\widetilde{M}}{s_{22} - \ell s_{21}}.$$

The equilibrium in R^+_{ux} is $(L, K, 0, 0)$. The subsystems in R^+_{uxy} and R^+_{uxz} are uniformly persistent whenever

$$\beta_1 = -s_{10} + c_1\gamma_0 K > 0, \tag{4.44}$$

and

$$\beta_2 = -s_{20} + s_{21}L + c_{20}\delta_0 K > 0, \tag{4.45}$$

respectively, in which case the equilibria are

$$E_6(u_3,x_3,y_3,0) = \left(L,\ \frac{K(\gamma_0 s_{10} + \alpha s_{12})}{Kc_1\gamma_0^2 + \alpha s_{12}},\ \frac{\alpha(-s_{10} + Kc_1\gamma_0)}{Kc_1\gamma_0^2 + \alpha s_{12}},\ 0\right)$$

and

$$E_7(u_4,x_4,0,z_4) = \left(L + \ell z_4,\ \frac{K((s_{20} - s_{21}L)\delta_0 + (s_{22} - s_{21}\ell)\alpha)}{Kc_{20}\delta_0^2 + \alpha(s_{22} - s_{21}\ell)},\ 0,\ \frac{\alpha\beta_2}{Kc_{20}\delta_0^2 + \alpha(s_{22} - s_{21}\ell)}\right).$$

The symmetric matrix corresponding to E_6 is $\mathcal{B}(u,x,y) = \operatorname{diag}\left(\frac{1}{u_3}, \frac{\alpha c_1}{K}, s_{12}\right)$. The symmetric matrix $\mathcal{D}(u,x,z)$, corresponding to E_7 is given by

$$b_{11} = \frac{1}{u_4}, \quad b_{12} = 0, \quad b_{13} = \left(\frac{\ell u}{u_4(L + \ell z)} + s_{21}\right),$$

$$b_{22} = \frac{\alpha c_{20}}{K}, \quad b_{23} = 0, \quad b_{33} = s_{22}.$$

The region of attraction of the subsystem in R^+_{uxz} is contained in the set

$$\mathcal{C}_1 = \left\{(u,x,z)\colon 0 \le u \le L + \frac{\ell\beta_2}{s_{22} - s_{21}\ell},\ \ 0 \le x \le K,\ \ 0 \le z \le \frac{\beta_2}{s_{22} - s_{21}\ell}\right\}.$$

The matrix $\mathcal{D}(u,x,z)$ is positive definite in $\mathcal{C}_1$ whenever

$$s_{22} - u_4\left(s_{21} + \frac{\ell}{Lu_4}\left(L + \frac{\ell\beta_2}{s_{22} - s_{21}\ell}\right)\right)^2 > 0. \tag{4.46}$$

Therefore the system (4.31) will be uniformly persistent whenever inequalities (4.42)–(4.44) hold and

$$\xi = -s_{20} + s_{21}u_3 + c_{20}\delta_0 x_3 + c_3\xi_0 y_3 > 0, \tag{4.47}$$

and

$$\eta = -s_{10} + c_1\gamma_0 x_4 - \xi_0 z_4 > 0. \tag{4.48}$$

Example 4.7 When $k = \gamma_1 = \delta_1 = \xi_1 = s_{21} = 0$ and $c_{21} > 0$, mutualism occurs by mutualist enhancing the utilization of the prey by the top-predator. Here the region of attraction is contained in

$$\mathcal{C} = \{(u,x,y,z)\colon 0 \le u \le L + \ell\widetilde{N},\ 0 \le x \le K,\ 0 \le y \le \widetilde{M},\ 0 \le z \le \widetilde{N}\}, \tag{4.49}$$

where

$$\widetilde{M} = \frac{-s_{10} + Kc_1\gamma_0}{s_{11}} \quad \text{and} \quad \widetilde{N} = \frac{-s_{20} + (c_{20} + c_{21}L)\delta_0 K + c_3\xi_0\widetilde{M}}{s_{22} - Kc_{21}\ell\delta_0}.$$

The equilibrium in R^+_{ux} is $E_3(L,K,0,0)$. The subsystems in R^+_{uxy} and R^+_{uxz} are uniformly persistent whenever

$$\beta_1 = -s_{20} + Kc_1\gamma_0 > 0, \tag{4.50}$$

and

$$\beta_2 = -s_{20} + (c_{20} + c_{21}L)K\delta_0 > 0. \tag{4.51}$$

The equilibrium $E_6(u_3,x_3,y_3,0)$ in R^+_{uxy} is the same as in Example 4.6 and the corresponding matrix $\mathcal{B}(u,x,y) = \operatorname{diag}\Big(\frac{1}{u_3}, \frac{\alpha c_1}{K}, s_{12}\Big)$. The equilibrium

$$E_7(u_4,x_4,0,z_4) = \left(L + \ell z_4, \frac{s_{20} + s_{22}z_4}{\delta_0(c_{20} + c_{21}u_4)}, 0, \frac{-b_0 + \sqrt{b_0^2 + 4K\ell\alpha\beta_2\delta_0^2 c_{21}}}{2\delta_0^2 K\ell c_{21}}\right),$$

where $b_0 = \alpha s_{22} - K\ell\alpha\delta_0 c_{21} + K\delta_0^2(c_{20} + c_{21}L)$. The symmetric matrix $\mathcal{D}(u,x,z)$ corresponding to E_7 is given by

$$d_{11} = \frac{1}{u_4}, \quad d_{12} = 0, \quad d_{13} = -\frac{1}{2}\left(\frac{\ell u}{(L + \ell z)u_4} + c_{21}\delta_0 x\right),$$
$$d_{22} = \frac{\alpha}{K}(c_{20} + c_{21}u_4), \quad d_{23} = 0, \quad d_{33} = s_{22}.$$

The region of attraction for the subsystem in R^+_{uxz} is contained in the set

$$\mathcal{C}_1 = \left\{(u,x,z)\colon 0 \le u \le L + \ell N_1,\ 0 \le x \le K,\ 0 \le z \le \frac{\beta_2}{s_{22} - K\ell\delta_0 c_{21}} = N_1\right\}.$$

The matrix $\mathcal{D}(u,x,z)$ is positive definite in $\mathcal{A}_1$ whenever

$$4s_{22} - u_4\left(\frac{\ell(L + \ell N_1)}{Lu_4} + c_{21}\delta_0 K\right)^2 > 0. \tag{4.52}$$

Thus if inequalities (4.48)–(4.50) hold and

$$\xi = -s_{20} + (c_{20} + c_{21}u_3)\delta_0 x_3 + c_3\xi_0 y_3 > 0 \tag{4.53}$$

and

$$\eta = -s_{10} + c_1\gamma_0 x_4 - \xi_0 z_4 > 0, \tag{4.54}$$

then the system will be uniformly persistent.

Example 4.8 When $k = \gamma_1 = \xi_1 = s_{21} = c_{21} = 0$ and $\delta_1 > 0$, mutualism occurs by means of the mutualist increasing the rate of predation by the predator z on the prey x.

$$\mathcal{C} = \{(u,x,y,z)\colon 0 \le u \le L + \ell\widetilde{N},\ 0 \le x \le K,\ 0 \le y \le \widetilde{M},\ 0 \le z \le \widetilde{N}\}, \tag{4.55}$$

where

$$\widetilde{M} = \frac{-s_{10} + Kc_1\gamma_0}{s_{11}} \quad \text{and} \quad \widetilde{N} = \frac{-s_{20} + c_{20}(\delta_0 + \delta_1 L)K + c_3\xi_0\widetilde{M}}{s_{22} - Kc_{20}\ell\delta_1}.$$

The equilibrium in R^+_{ux} is $E_3(L, K, 0, 0)$. The subsystem in R^+_{uxy} is uniformly persistent if

$$\beta_1 = -s_{10} + c_1\gamma_0 K > 0. \tag{4.56}$$

The equilibrium E_6 in R^+_{uxy} is the same as in Example 4.7 and is always globally asymptotically stable with respect to solutions initiating in R^+_{uxy}.

The subsystem in R^+_{uxz} will be uniformly persistent whenever

$$\beta_2 = -s_{20} + c_{20}(\delta_0 + \delta_1 L)K > 0. \tag{4.57}$$

The equilibrium in R^+_{uxz} is

$$E_7(u_4, x_4, 0, z_4) = \left(L + \ell z_4,\ \frac{K}{\alpha}(\alpha - (\delta_0 + \delta_1 u_4)z_4), 0, z_4\right),$$

where z_4 is the unique positive root of the cubic equation

$$k\ell^2c_{20}\delta_1^2z^3 + 2K\ell c_{20}\delta_1(\delta_0 + \delta_1 L)z^2 + (\alpha s_{22} - \alpha K\ell c_{21}\delta_1 + Kc_{20}(\delta_0 + \delta_1 L)^2)z - \alpha\beta_2 = 0.$$

The symmetric matrix $\mathcal{D}(u,x,z)$ corresponding to E_7 is given by

$$d_{11} = \frac{1}{u_4}, \quad d_{12} = \frac{1}{2}c_{20}\delta_1 z, \quad d_{13} = -\frac{1}{2}\left(\frac{\ell u}{u_4(L + \ell z)} + c_{20}\delta_1 x\right),$$
$$d_{22} = \frac{\alpha}{K}c_{20}, \quad d_{23} = 0, \quad d_{33} = s_{22}.$$

The region of attraction for the subsystem in R^+_{uxz} is contained in

$$\mathcal{C}_1 = \left\{(u,x,z)\colon 0 \le u \le L + \ell N_1,\ 0 \le x \le K,\ 0 \le z \le \frac{\beta_2}{s_{22} - K\ell c_{20}\delta_1} = N_1\right\}.$$

The matrix $\mathcal{D}(u,x,z)$ is positive definite in $\mathcal{A}_1$ provided

$$s_{22}\left(\frac{4\alpha}{u_4} - Kc_{20}\delta_1^2N_1\right) - \alpha\left(\frac{\ell}{u_4L}(L + \ell N_1) + Kc_{20}\delta_1\right)^2 > 0. \tag{4.58}$$

Thus whenever the inequalities (4.54) − (4.56) hold and

$$\xi = -s_{20} + c_{20}(\delta_0 + \delta_1 u_3)x_3 + c_3\xi_0 y_3 > 0, \tag{4.59}$$

and

$$\eta = -s_{10} + c_1\gamma_0 x_4 - \xi_0 z_4 > 0, \tag{4.60}$$

the given system is uniformly persistent.

5 Discussion

The main focus in this paper is to examine the possible effects of an obligate mutualist on the middle and top predator in a food chain. In particular, it was shown how a mutualist could reverse the outcome of extinction in the case of no mutualism to persistence in the case of mutualism.

Such mutualisms occur in nature. Examples are cleaner mutualists. The large iguanas of the Galapagos Islands may be thought of as either middle predators or top predators depending on whether or not their eggs are subject to predation [10]. Similarly for the giant tortoises [8]. Both have evolved a mutualism with finches which act as cleaner mutualists by removing ticks and other pests from the iguanas and tortoises. Such cleaner mutualism has been shown to be obligate in the Carribean [28]. in that if the cleaning is not performed, the individuals (in this case certain fish) will soon die.

A remaining problem to be analyzed is the case where the mutualism is obligate on both mutualists. This is left to future work.

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