Persistence in Three-Species Food Chain Models with Group Defense

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ABSTRACT

Gause-type models of a three-species food web with group defense are analyzed. Persistence criteria are derived for both the case of no mutual interference and the case when there is mutual interference of predators.

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1. INTRODUCTION

Group defense in a predator–prey interaction is a term used to describe a phenomenom whereby predation is decreased or even prevented altogether by the ability of the prey population to better defend or disguise themselves when their numbers are large. A classical example is described by Tener [25]. A lone musk-ox or pairs of musk-oxen can be successfully attacked by wolves, but groups of six or more are rarely if ever successfully attacked. Many other examples can be found in Holmes and Bethel [19], Yang and Humphrey [27], and May and Robinson [21].

In [14], Freedman and Wolkowicz considered a predator–prey system in which the prey population exhibited group defense. They claimed that in the case of no mutual interference among predators, if the carrying capacity of the prey population is sufficiently large, the predator population is almost always driven to extinction. Biologically, this is intuitive, because the environment is such that the prey population can increase to the point where group defense prevents the predator population from increasing at any level. This is also related to the paradox of enrichment as described in Rosenzweig [24]. Freedman and Wolkowicz [14] proposed a mechanism

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that prevents the predator from becoming extinct when the prey exhibits group defense, namely, mutual interference among the predators. Subsequently, Freedman and Quan [10] considered another way in which the predator is prevented from heading to extinction, which is through interactions of the predator–prey system with a third population. For other work related to models of predator–prey systems with group defense, see [22] and [26].

Hassell [17] and Rogers and Hassell [23] introduced the notion of mutual interference of predators searching for prey (also see [1]). A predator–prey model with mutual interference was analyzed in [8]. Further analyses extending the results to food chains with mutual interference were carried out in [4] and [5]. However, the case of food chains with mutual interference and group defense has not previously been considered.

In general, three (or higher)-dimensional models are difficult to analyze as far as the detailed behavior of their solutions is concerned. Consequently, the notion of persistence has been used to describe the situation when all interacting populations in a given system survive. Persistence of various types (weak, strong, uniform, etc.) can be defined in an abstract manner for abstract metric spaces [2, 3, 6, 9, 15]. However, for our purposes we may define persistence with respect to R^n and the coordinate planes as follows. A population $N(t)$ is said to be (strongly) persistent if $N(t_0) > 0$ implies that $N(t) > 0$ and $\lim_{t\to\infty} \inf N(t) > 0$. A system is said to (strongly) persist if each component population persists. Clearly, persistence is equivalent to population survival in deterministic population models. For papers on persistence in this setting, see [10]–[13], [16], [18], and [20].

In the present paper, we consider models of three-species food chains with group defense that are of the Gause-type. Gause-type predator–prey models have been discussed in [7] and [8] and food chains in [11]. We first consider the case of no mutual interference and derive utilizable criteria for persistence. We then consider the case when the predators at both levels exhibit mutual interference. In [4], a technique was developed to transform such a system into a dynamical system for mutual interference parameters greater than or equal to 1/2. In this paper we extend these results to the model with group defense. We conclude with a brief discussion.

2. THE MODELS

We consider two models of a three-species food chain with group defense by the prey. The first model is of the form (where the dot represents the derivative with respect to time)

$$\begin{aligned} \dot{x} &= xg(x,K) - yp(x) - zh(x), & x(0) &= x_0 \geqslant 0, \\ \dot{y} &= y[-r + cp(x)] - zq(y), & y(0) &= y_0 \geqslant 0, \\ \dot{z} &= z[-s + dq(y) + eh(x)], & z(0) &= z_0 \geqslant 0, \end{aligned} \tag{1}$$

where at time $t \geqslant 0$, $x(t)$ represents the prey population; $y(t)$ the intermediate population, which feeds upon x and is in turn fed upon by z; and $z(t)$ the top predator population, which feeds upon y and may also feed upon x. We assume that the functions g, p, q, and h are continuously differentiable and that r, c, d, K, and e are positive constants. Then solutions of system (1) exist and are unique and continuable for all $t \geqslant 0$.

In the following, a prime denotes the derivative with respect to the argument, that is, $f'(x) = df(x)/dx$.

The function $g(x, K)$ represents the specific growth rate of the prey in the absence of predation and is assumed to satisfy [8, 14]

$$\begin{gathered} g(0,K) > 0, \qquad g(K,K) = 0, \qquad g_x(K,K) < 0, \\ g_x(x,K) \leqslant 0 \quad \text{and} \quad g_K(x,K) > 0 \quad \text{for any } x > 0. \end{gathered} \tag{2}$$

The function $p(x)$ denotes the predator response function and is assumed to satisfy [8]

$$\begin{gathered} p(0) = 0, \qquad p(x) > 0 \quad \text{for } x > 0 \\ \text{and there exists} \quad M > 0, \quad \text{such that } p(M) > r/c. \end{gathered} \tag{3}$$

In order to model group defense, it is assumed as well [14] that for the above $M > 0$,

$$p'(x) > 0 \quad \text{for } 0 \leqslant x < M \qquad \text{and} \qquad p'(x) < 0 \quad \text{for } x > M. \tag{4}$$

The function $h(x)$ denotes the fact that the predator z feeds upon x directly and has properties similar to those of $p(x)$; that is,

$$\begin{gathered} h(0) = 0, \qquad h(x) > 0 \quad \text{for } x > 0 \\ \text{and there exists} \quad M > 0 \quad \text{such that } h(M) > s/e \end{gathered} \tag{5}$$

and

$$h'(x) > 0 \quad \text{for } 0 \leqslant x < M \qquad \text{and} \qquad h'(x) < 0 \quad \text{for } x > M. \tag{6}$$

The function $q(y)$ is interpreted as a predator functional response of z on y. Therefore we assume that

$$q(0) = 0, \quad q(y) > 0 \quad \text{and} \quad q'(y) > 0 \quad \text{for } y > 0. \tag{7}$$

The existence of $M > 0$ is precisely the assumption that models group defense, and we assume that the same M holds for both $p(x)$ and $h(x)$, which means that the prey population x has the same group defense ability with respect to both of the predator populations y and z. We assume that $p(M) > r/c$ because otherwise the predator y could not survive on the prey at any density in the absence of the predator z. Therefore, there exists $\lambda_1 < M$ such that $p(\lambda_1) = r/c$, and we assume that $\lambda_1 < K$, or again the predator y cannot survive on the prey in the absence of z. Similarly, we assume $h(M) > s/e$ and there exists $\mu_1 < M$ (and $\mu_1 < K$) such that $h(\mu_1) = s/e$.

We note from techniques used in [11] that there exists a region $\mathscr{A}$ of the form

$$\mathscr{A} = \{x, y, z : 0 \leqslant x \leqslant a, 0 \leqslant x + y \leqslant b, 0 \leqslant x + y + z \leqslant c\}$$

such that $\mathscr{A}$ is an attractor, that is, there exists $T(x_0, y_0, z_0)$ such that $(x(t), y(t), z(t)) \in \mathscr{A}$ for $t \geqslant T$, where $[x(t), y(t), z(t)]^T$ is a solution of system (1).

The second model is a modification of the first so as to incorporate mutual interference among the predators in their search for and handling of prey. It takes the form

$$\begin{aligned} \dot{x} &= xg(x,K) - y^m p(x) - z^k h(x), && x(0) = x_0 \geqslant 0, \\ \dot{y} &= -ry + cy^m p(x) - z^k q(y), && y(0) = y_0 \geqslant 0, \\ \dot{z} &= -sz + dz^k q(y) + ez^k h(x), && z(0) = z_0 \geqslant 0. \end{aligned} \tag{8}$$

The functions g, p, q, h have the same meanings and properties as for system (1). m and k are the mutual interference parameters and satisfy $0 < m < 1$, $0 < k < 1$.

Under the above assumptions, solutions to system (8) exist and are continuable for all $t \geqslant 0$. However, uniqueness of the solutions is no longer guaranteed. This will be dealt with in Section 4.

The existence of an $\mathscr{A}$ for system (8) follows by considerations similar to those for system (1).

3. ANALYSIS OF SYSTEM (1)

In this section, we proceed to analyze system (1). We first recall the subsystem analyses. We then determine the equilibria and their stabilities. Finally, we derive utilizable persistence criteria.

Clearly, the subsystem of system (1) restricted to the yz plane has completely trivial dynamics; that is, if $x_0 = 0$, then $\lim_{t\to\infty} y(t) = \lim_{t\to\infty} z(t) = 0$.

The subsystem in the xy plane has the form

$$\begin{aligned} \dot{x} &= xg(x,K) - yp(x), & x(0) &= x_0 \geqslant 0, \\ \dot{y} &= y(-r + cp(x)), & y(0) &= y_0 \geqslant 0. \end{aligned} \tag{9}$$

This is a special case of a model considered in [14]. Given our assumptions, there is always an equilibrium of the form $F_1(\lambda_1, cr^{-1}\lambda_1 g(\lambda_1, K))$, where $p(\lambda_1) = rc^{-1}$ and $p'(\lambda_1) > 0$. F_1 may be stable or unstable, and there may be one or more limit cycles surrounding it.

There may also be an equilibrium of the form $F_2(\lambda_2, cr^{-1}\lambda_2 g(\lambda_2, K))$, where $p(\lambda_2) = rc^{-1}$ and $p'(\lambda_2) < 0$. In this case, it follows that $\lambda_2 > \lambda_1$. If it is also the case that $\lambda_2 < K$, then F_2 is a saddle point, and extinction of the predator population may occur in conjunction with statements in [24].

The subsystem in the xz plane is of the form

$$\begin{aligned} \dot{x} &= xg(x,K) - zh(x), & x(0) &= x_0 > 0, \\ \dot{z} &= z[-s + eh(x)], & z(0) &= z_0 \geqslant 0. \end{aligned} \tag{10}$$

Similar statements may be made about system (10) with respect to equilibria $G_i(\mu_i, es^{-1}\mu_i g(\mu_i, K)$, $i = 1,2$.

We now examine the equilibria for the full system (1) under assumptions (2)–(7). Clearly, $E_0(0,0,0)$ and $E_K(K,0,0)$ always exist. By the above, we have established the existence of one or two equilibria in the interior of each of the xy and xz coordinate planes, $E_{\lambda_i}(\lambda_i, cr^{-1}\lambda_i g(\lambda_i, K), 0)$ in the xy plane, and $E_{\mu_i}(\mu_i, 0, es^{-1}\mu_i g(\mu_i, K))$ in the xz plane.

For an equilibrium point $E^*(x^*, y^*, z^*)$ in the interior of the first octant, we need to solve the algebraic equations

$$xg(x,K) - yp(x) - zh(x) = 0, \tag{11}$$

$$y[-r + cp(x)] - zq(y) = 0, \tag{12}$$

$$-s + dq(y) + eh(x) = 0. \tag{13}$$

From Equation (13), we have

$$q(y^*) = d^{-1}[s - eh(x^*)].$$

Substituting into Equation (12), we get

$$z^* = \frac{dy^*[-r + cp(x^*)]}{s - eh(x^*)},$$

and then, substituting in Equation (11), we get

$$y^* = \frac{x^* g(x^*, K)[s - eh(x^*)]}{[s - eh(x^*)]p(x^*) + d[-r + cp(x^*)]h(x^*)}, \tag{14}$$

yielding

$$z^* = \frac{dx^* g(x^*, K)[-r + cp(x^*)]}{[s - eh(x^*)]p(x^*) + d[-r + cp(x^*)]h(x^*)}. \tag{15}$$

For $y^* > 0$ and $z^* > 0$, it follows that $g(x^*, K) > 0$, $s - eh(x^*) > 0$, and $-r + cp(x^*) > 0$, which imply that $x^* < K$, $x^* < \mu_1$, and $x^* > \lambda_1$, respectively, or $\mu_2 < x^* < K$ and $x^* < \lambda_2$. Thus, if $E^*(x^*, y^*, z^*)$ exists, it follows that

$$\lambda_1 < x^* < \mu_1 < M < K, \tag{16a}$$

or

$$M < \mu_2 < x^* < \lambda_2 < K. \tag{16b}$$

The above analysis shows that if E^* exists, then inequality (16) must hold for x^*, and then y^* and z^* are given by (14) and (15), respectively. However, we have not yet given criteria that guarantee that E^* exists. This will be done following our persistence analysis.

Hence we now assume that E^* exists, and we analyze the local stability of all possible equilibria. We do this by computing the variational matrices about these equilibria. The general variational matrix is given by

$$V(x, y, z) = \begin{bmatrix} g(x, K) + xg_x(x, K) - yp'(x) - zh'(x) & -p(x) & -h(x) \\ cyp'(x) & -r + cp(x) - zq'(y) & -q(y) \\ ezh'(x) & dzq'(y) & -s + dq(y) + eh(x) \end{bmatrix}.$$

Let V_l denote $V(x, y, z)$ at E_l ($l = 0$, K, λ_i, μ_i, and $*$), $i = 1, 2$, respectively.

$$V_0=\begin{bmatrix} g(0,K) & 0 & 0 \\ 0 & -r & 0 \\ 0 & 0 & -s \end{bmatrix},$$

$$V_K=\begin{bmatrix} Kg_x(K,K) & -p(K) & -h(K) \\ 0 & -r+cp(K) & 0 \\ 0 & 0 & -s+eh(K) \end{bmatrix},$$

$$V_{\lambda_i}=\begin{bmatrix} \begin{matrix} g(\lambda_i,K)+\lambda_i g_x(\lambda_i,K) \\ -r^{-1}c\lambda_i g(\lambda_i,K)p'(\lambda_i) \end{matrix} & -p(\lambda_i) & -h(\lambda_i) \\ r^{-1}c^2\lambda_i g(\lambda_i,K)p'(\lambda_i) & 0 & -q\left(r^{-1}c\lambda_i g(\lambda_i,K)\right) \\ 0 & 0 & \begin{matrix} -s+dq\left(r^{-1}c\lambda_i g(\lambda_i,K)\right) \\ +eh(\lambda_i) \end{matrix} \end{bmatrix},$$

$$V_{\mu_i}=\begin{bmatrix} \begin{matrix} g(\mu_i,K)+\mu_i g_x(\mu_i,K) \\ -s^{-1}e\mu_i g(\mu_i,K)h'(\mu_i) \end{matrix} & -p(\mu_i) & -h(\mu_i) \\ 0 & \begin{matrix} -r+cp(\mu_i) \\ -s^{-1}e\mu_i g(\mu_i,K)q'(0) \end{matrix} & 0 \\ s^{-1}e^2\mu_i g(\mu_i,K)h'(\mu_i) & s^{-1}de\mu_i g(\mu_i,K)q'(0) & 0 \end{bmatrix},$$

$$V_*=\begin{bmatrix} \begin{matrix} g(x^*,K)+x^*g_x(x^*,K) \\ -y^*p'(x^*)-z^*h'(x^*) \end{matrix} & -p(x^*) & -h(x^*) \\ cy^*p'(x^*) & \begin{matrix} -r+cp(x^*) \\ -z^*q'(y^*) \end{matrix} & -q(y^*) \\ ez^*h'(x^*) & dz^*q'(y^*) & 0 \end{bmatrix}$$

From the hypotheses of our model, E_0 is a saddle point because $g(0,K)>0$. Since $g_x(K,K)<0$, E_K is locally stable in the x direction and locally unstable in the y and z directions. Hence E_K is a hyperbolic saddle point.

At any rate, because of the hyperbolic nature of both equilibria and because $\dot{x}>0$ if y and z are sufficiently small and $\dot{y}>0$ if x is sufficiently close to K and z is sufficiently small, neither E_0 nor E_K can be the limit of a trajectory initiating in the interior of the first octant.

If E_{λ_1} or E_{μ_2} exists under the assumptions that $\lambda_2<K$ or $\mu_2<K$, respectively, then they are hyperbolic saddle points, because F_2 and G_2 are.

We can now state and prove our main results of this section, which give criteria for the persistence of system (1).

THEOREM 1

Let system (1) *be such that there are no nontrivial periodic or homoclinic solutions in the xy and xz planes. If*

$$-s+dq\left(r^{-1}c\lambda_i g(\lambda_i,K)\right)+eh(\lambda_i)>0, \qquad i=1,2, \tag{17}$$

and

$$-r+cp(\mu_i)-s^{-1}e\mu_i g(\mu_i,K)q'(0)>0, \qquad i=1,2, \tag{18}$$

with the understanding that the case $i=2$ *in* (17) *and* (18) *holds if the appropriate equilibrium exists, then the system* (1) *exhibits persistence.*

Proof. We use Theorem 5.1 of Freedman and Waltman [13] to prove our result. Let

$$F(x,y,z)=\begin{cases} g(x,K)-y\dfrac{p(x)}{x}-z\dfrac{h(x)}{x}, & x\neq 0 \\ g(0,K)-yp'(0)-zh'(0), & x=0, \end{cases}$$

$$G(x,y,z)=\begin{cases} -r+cp(x)-z\dfrac{q(y)}{y}, & y\neq 0 \\ -r+cp(x)-zq'(0), & y=0, \end{cases}$$

$$H(x,y,z)=-s+dq(y)+eh(x).$$

Conditions (C1)–(C4) of the theorem in [13] are satisfied, where (C1)

$$\frac{\partial F}{\partial y}=-\frac{p(x)}{x}<0, \qquad \frac{\partial F}{\partial z}=-\frac{h(x)}{x}<0,$$

$$\frac{\partial G}{\partial x}=cp'(x)>0 \qquad \text{for } 0\leqslant x<M,$$

$$\frac{\partial H}{\partial x}=eh'(x)>0 \qquad \text{for } 0\leqslant x<M,$$

$$\frac{\partial H}{\partial y}=dq'(y)>0,$$

$$G(0,y,z)=\begin{cases} -r-\dfrac{zq(y)}{y}, & y\neq 0 \\ -r-zq'(0), & y=0, \end{cases}$$

and hence

$$G(0,y,z)<0, \qquad H(0,0,z)=-s<0.$$

(C2)

$$F(0,0,0)=g(0,K)>0, \qquad F(K,0,0)=g(K,K)=0,$$

$$\frac{\partial F}{\partial x}(x,0,0)=g_x(x,K)\leqslant 0.$$

(C3) There are no equilibria in the yz plane.

(C4) For the equilibria

$$E_{\lambda_i}\big(\lambda_i,r^{-1}c\lambda_i g(\lambda_i,K),0\big) \text{ and } E_{\mu_i}\big(\mu_i,0,s^{-1}e\mu_i g(\mu_i,K)\big),$$

we have

$$H\big(\lambda_i,r^{-1}c\lambda_i g(\lambda_i,K),0\big)=-s+dq\big(r^{-1}c\lambda_i g(\lambda_i,K)\big)+eh(\lambda_i)$$

and

$$G\big(\mu_i,0,s^{-1}e\mu_i g(\mu_i,K)\big)=-r+cp(\mu_i)-s^{-1}e\mu_i g(\mu_i,K)q'(0).$$

Hence by (17) and (18), all conditions of Theorem 5.1 of [13] are satisfied, and so system (1) persists. ■

THEOREM 2

Suppose conditions (17) *and* (18) *hold and there are a finite number of limit cycles or homoclinic orbits in the xy plane or in the xz plane. For each limit cycle or homoclinic orbit* $(\varphi(t),\psi(t))$ *in the xy plane, let*

$$-s+\frac{d}{T}\int_0^T q(\psi(t))\,dt+\frac{e}{T}\int_0^T h(\varphi(t))\,dt>0, \tag{19}$$

and for each limit cycle or homoclinic orbit $(\bar\varphi(t),\bar\psi(t))$ *in the xz plane, let*

$$-r+\frac{c}{T}\int_0^T p(\bar\varphi(t))\,dt-\frac{q'(0)}{T}\int_0^T\bar\psi(t)\,dt>0, \tag{20}$$

where T is the appropriate period in the case of a limit cycle and where $\lim_{T\to\infty}$ *is taken in the case of a homoclinic orbit. Then system* (1) *persists.*

Proof. We give the proof in the case of a periodic orbit. Let $V_p(t)=V_p(\varphi(t),\psi(t),0)$ be the variational matrix about $(\varphi(t),\psi(t),0)$. Then

$$V_p(t)$$

$$=\begin{bmatrix} g(\varphi(t),K)+\varphi(t)g_x(\varphi(t),K) & -p(\varphi(t)) & -h(\varphi(t)) \\ -\psi(t)p'(\varphi(t)) & & \\ c\psi(t)p'(\varphi(t)) & -r+cp(\varphi(t)) & -q(\psi(t)) \\ 0 & 0 & -s+dq(\psi(t)) \\ & & +eh(\varphi(t)) \end{bmatrix}$$

is the variational matrix of the system (1) about the limit cycle $(\varphi(t), \psi(t))$ in the xy plane.

Consider now a solution of (1) with positive initial conditions $(\alpha_1, \alpha_2, \alpha_3)$ sufficiently close to the limit cycle. From $V_p(t)$, $\partial z/\partial\alpha_3$ is a solution of the system

$$\begin{cases} z' = [-s + dq(\psi(t)) + eh(\varphi(t))]z \\ z(0) = 1 \end{cases}.$$

That is,

$$\frac{\partial z}{\partial \alpha_3}(t, \alpha_1, \alpha_2, \alpha_3) = \exp\left[-st + d\int_0^t q(\psi(t))\, dt + e\int_0^t h(\varphi(t))\, dt\right].$$

Hence, by Taylor's expansion theorem, we have

$$\begin{aligned} z(t, \alpha_1, \alpha_2, \alpha_3) &= z(t, \alpha_1, \alpha_2, 0) + \frac{\partial z}{\partial \alpha_3}(t, \alpha_1, \alpha_2, 0)\alpha_3 + O(\alpha_3^2) \\ &= \frac{\partial z}{\partial \alpha_3}(t, \alpha_1, \alpha_2, 0)\alpha_3 + O(\alpha_3^2). \end{aligned}$$

Then z increases or decreases according as

$$-s + \frac{d}{T}\int_0^T q(\psi(t))\, dt + \frac{e}{T}\int_0^T h(\psi(t))\, dt$$

is positive or negative. Since E_{λ_1} and these limit cycles are the only possible limits in the xy plane of trajectories with positive initial conditions, these trajectories go away from the xy plane if (17) and (19) hold, and a similar argument applies for (18) and (20). This completes the proof. ■

Before proceeding with the analysis, we illustrate the above theorem with a numerical example. Consider the system

$$\begin{aligned} \dot{x} &= x(1.3 - x - 2e^{-x}y), \\ \dot{y} &= y(-0.36 + xe^{-x} - 8ze^{-y}), \\ \dot{z} &= z(-1 + 5e^{-y}). \end{aligned} \tag{21}$$

Boundary equilibria are $E_0(0, 0, 0)$, $E_K(1.3, 0, 0)$, $E_1(0.81, 0.55, 0)$, and $E_2(1.22, 0.135, 0)$, correct to two decimal places. The variation matrix about

E_i, $i=1,2$, is given by

$$M_i = \begin{bmatrix} x_i(2e^{-x_i}y_i - 1) & -2x_i e^{-x_i} & 0 \\ y_i e^{-x_i}(1-x_i) & 0 & -8y_i e^{-y_i} \\ 0 & 0 & -1+5e^{-y_i} \end{bmatrix}.$$

Letting $f(y_i) = -1+5e^{-y_i}$, one gets that $f(0.55) \approx 1.885 > 0$ and $f(0.135) = 3.37 > 0$. Hence if time averages along any and all periodic or homoclinic orbits, if they exist in the xy plane, are positive, Theorem 2 will give that persistence occurs.

To show that this is the case, consider the submodel in the xy plane given by

$$\begin{aligned} \dot{x} &= x(1.3 - x - 2e^{-x}y) \\ \dot{y} &= y(-0.36 + xe^{-x}). \end{aligned} \tag{22}$$

From the first of these by standard comparison, $\lim_{t\to\infty} x(t) \leqslant 1.3$. Consider now

$$\begin{aligned} \frac{d}{dt}\left(\tfrac{1}{2}x + y\right) &= -0.36\left(\tfrac{1}{2}x + y\right) + \tfrac{1}{2}x(1.66 - x) \\ &\leqslant -0.36\left(\tfrac{1}{2}x + y\right) + 0.42. \end{aligned}$$

Then $\lim_{t\to\infty}(\frac{1}{2}x + y) \leqslant 1.2$. Hence any closed-path solution, should one occur, must lie in the box given by $\mathscr{A} = \{(x,y)\colon 0 \leqslant x \leqslant 1.3,\ 0 \leqslant \frac{1}{2}x + y \leqslant 1.2\}$. But if $(x,y) \in \mathscr{A}$, then $-1+5e^{-y} \geqslant 0.5 > 0$. Hence all time averages are positive.

We now are able to state criteria that guarantee the existence of E^*. This is given in the following theorem, the result of which is valid from the corollary in [2].

THEOREM 3

Suppose the hypotheses of Theorem 1 *or Theorem* 2 *hold but that homoclinic orbits do not exist. Then E^* exists.*

Note that from the theorem of [2], we obtain uniform persistence for our system. The characteristic equation of the variational matrix V^* is

$$\begin{vmatrix} m_{11}-\lambda & m_{12} & m_{13} \\ m_{21} & m_{22}-\lambda & m_{23} \\ m_{31} & m_{32} & -\lambda \end{vmatrix} = 0, \tag{23}$$

where

$$\begin{aligned}
&m_{11} = g(x^*, K) + x^* g_x(x^*, K) - y^* p'(x^*) - z^* h'(x^*),\\
&m_{12} = -p(x^*) < 0, \qquad m_{13} = -h(x^*) < 0,\\
&m_{21} = c y^* p'(x^*), \qquad m_{22} = c p(x^*) - [r + z^* q'(y^*)],\\
&m_{23} = -q(y^*) < 0, \qquad m_{31} = e z^* h'(x^*), \qquad m_{32} = d z^* q'(y^*) > 0.
\end{aligned}$$

Then (23) has the form

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

where

$$\begin{aligned}
&a_1 = -(m_{11} + m_{22}),\\
&a_2 = m_{11} m_{22} - (m_{12} m_{21} + m_{13} m_{31} + m_{23} m_{32}),\\
&a_3 = (m_{11} m_{23} m_{32} + m_{22} m_{13} m_{31}) - (m_{12} m_{23} m_{31} + m_{13} m_{32} m_{21}).
\end{aligned}$$

Hence

$$\begin{aligned}
a_1 a_2 - a_3 = &-[(m_{11} + m_{22})(m_{11} m_{22} - m_{12} m_{21}) + m_{11} m_{13} m_{31} + m_{22} m_{23} m_{32}]\\
&+ (m_{12} m_{23} m_{31} + m_{13} m_{32} m_{21}).
\end{aligned}$$

Let $m_{11} < 0$, $m_{22} \leqslant 0$. If inequality (16a) holds, then $m_{21} > 0$, $m_{31} > 0$, hence $a_1 > 0$, $a_2 > 0$, and the terms in the first parentheses of a_3 and the first square brackets of $a_1 a_2 - a_3$ are positive. If inequality (16b) holds, then $m_{21} < 0$, $m_{31} < 0$. Using the Routh–Hurwitz criteria, we have the following theorem.

THEOREM 4

Suppose $E^*(x^*, y^*, z^*)$ *exists, and let* $m_{11} < 0$, $m_{22} \leqslant 0$.

(a) *Let* (16a) *hold and any one of the following conditions be satisfied.*

(i) $0 < m_{12} m_{23} m_{31} + m_{13} m_{32} m_{21} < m_{11} m_{23} m_{32} + m_{22} m_{13} m_{31}$, or
(ii) $m_{12} m_{23} m_{31} + m_{13} m_{32} m_{21} = 0$, or
(iii) $0 < -m_{12} m_{23} m_{32} - m_{13} m_{32} m_{21}$
$< [-(m_{11} + m_{22})(m_{12} m_{22} - m_{12} m_{21}) + m_{11} m_{13} m_{31}$
$+ m_{22} m_{23} m_{32}]$;

then E^* *is asymptotically stable.*

(b) *Let* (16b) *hold and the following conditions be satisfied*:

(iv) $m_{11} m_{23} m_{32} - m_{13} m_{23} m_{31} > m_{13} m_{32} m_{21} - m_{22} m_{13} m_{31}$,
(v) $m_{22} m_{23} m_{32} + m_{13} m_{32} m_{21} - (m_{11} + m_{22}) m_{11} m_{22} > -m_{11} m_{13} m_{31}$
$- m_{12} m_{23} m_{31} - (m_{11} + m_{22}) m_{12} m_{21}$.

Then E^* *is asymptotically stable.*

4. ANALYSIS OF SYSTEM (8)

As mentioned previously, uniqueness of solutions for system (8) does not necessarily hold. The reason for this is that $0 < m,\ k < 1$, making the system sublinear.

System (8) without group defense was considered in [5]. By the change of coordinates $u = x$, $v = y^{1-m}$, $w = z^{1-k}$, system (8) was transformed into a dynamical system for which uniqueness of solutions held. However, this is valid only in the case $\frac{1}{2} \leqslant m,\ k < 1$. For $0 < m,\ k < \frac{1}{2}$, such a transformation is unavailable at this time.

The transformed system takes the form

$$\begin{aligned}
\dot{u} &= ug(u,K) - v^{m/(1-m)}p(u) - w^{k/(1-k)}h(u), && u(0) = x_0 \geqslant 0\\
\dot{v} &= (1-m)\big[-rv + cp(u)\\
&\qquad - v^{-m/(1-m)}w^{k/(1-k)}q\big(v^{1/(1-m)}\big)\big], && v(0) = y_0^{1-m} \geqslant 0\\
\dot{w} &= (1-k)\big[-sw + dq\big(v^{1/(1-m)}\big) + eh(u)\big], && w(0) = z_0^{1-k} \geqslant 0.
\end{aligned} \tag{24}$$

System (24) defines a dynamical system under our hypotheses, and the boundedness of solutions of system (8) implies boundedness of solutions of system (24) as $t \to +\infty$.

The only boundary equilibrium of system (24) is $E_0(0,0,0)$. The vw plane is easily seen to be invariant, and if $u = 0$, then $v \to 0$, $w \to 0$. For initial conditions in the uv plane or the uw plane, the vector field points into the positive octant. Hence, we have the following theorem.

THEOREM 5

System (8) *exhibits persistence for solutions initiating in the interior of the positive cone.*

In the language of dynamical systems, a solution with initial conditions in the positive cone will persist if there are no ω limit points on the boundary of the positive cone (i.e., on the coordinate axes and planes). We use the technique developed by Freedman and Waltman [13], that is, the Butler–McGehee lemma, to prove Theorem 5.

Proof. Let $O(X)$ denote the orbit through a point X, and let $\Omega(X)$ denote the ω limit set of an orbit. If P is a hyperbolic equilibrium, then $M^+(P)$ and $M^-(P)$ denote the stable and unstable manifolds of P. The Butler–McGehee lemma states that if P is an isolated hyperbolic equilibrium in the ω limit set $\Omega(X)$ of an orbit $O(X)$, then either $\Omega(X) = P$ or there exist points Q^+, Q^- in $\Omega(X)$ with $Q^+ \in M^+(P)$ and $Q^- \in M^-(P)$.

Since all solutions of system (8) with positive initial conditions are bounded in positive time, all solutions of system (24) with positive initial conditions are bounded in positive time. As a consequence, the ω limit set of such solutions is a bounded, closed, connected, and nonempty set. Suppose (u_0, v_0, w_0) is a point in the positive octant and Ω is the ω limit set of the orbit through (u_0, v_0, w_0). We will have proved the theorem if we can show that Ω does not intersect any of the coordinate planes.

If $E_0 = (0,0,0) \in \Omega$ then, since $E_0 \neq \Omega$ and E_0 is a saddle point, E_0 cannot be the only point in Ω. Hence by the Butler–McGehee lemma, there is an orbit in the stable manifold of E_0, say $Q \in M^+(E_0) \subset vw$ plane, that belongs to Ω, that is, $O(Q) \subset \Omega$. Since $M^+(E_0)$ is a one-dimensional manifold and E_0 is asymptotically stable in the direction of the u axis, $M^+(E_0)$ contains an orbit along the u axis that comes from positive infinity of the u axis. If $Q \in M^+(E_0)$, since the entire orbit through Q is contained in Ω and the orbit $M^+(E_0)$ is unbounded, we have a contradiction. Hence $E_0 \notin \Omega$.

If E_1 is any other point in the coordinate planes such that $E_1 \in \Omega$, similarly $O(E_1)$ is unbounded, again giving a contradiction. Since there are no other closed orbits in the planes, there are no planar equilibria in the ω limit set Ω; hence the orbit through (u_0, v_0, w_0) persists, which, translating back to x, y, z coordinates, implies that system (8) persists. ∎

5. DISCUSSION

In [14], a predator–prey model with group defense was considered. It was shown that sufficient enrichment could cause predator extinction in the absence of mutual interference. In [10] it was shown that extinction could be averted through competition or through additional predation.

In this paper, we tie these results together for Gause food chain models and give criteria for persistence of such food chains with prey group defense and for predators that may or may not exhibit mutual interference.

We believe that our results in the case of mutual interference can be extended to n-dimensional food chains and to food webs. However, we leave this to a future work.

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