RELAXATION OSCILLATIONS IN A CLASS OF PREDATOR-PREY SYSTEMS

Weishi Liu[1]

Department of Mathematics

University of Kansas, Lawrence, KS 66045

E-mail: wliu@math.ukans.edu

Dongmei Xiao [2]

Department of Mathematics

Central China Normal University, Wuhan 430079, P.R. China

E-mail: dmxiao@ccnu-1.ccnu.edu.cn

Yingfei Yi [3]

School of Mathematics

Georgia Institute of Technology, Atlanta, GA 33032

E-mail: yi@math.gatech.edu

[1]Partially supported by NSF Grant DMS-0071931.

[2]Partially supported by NSF-China Grant 10071027.

[3]Partially supported by NSF Grant DMS-9803581.

Abstract. We consider a class of three dimensional, singularly perturbed predator-prey systems having two predators competing exploitatively for the same prey in a constant environment. By using dynamical systems techniques and the geometric singular perturbation theory, we give precise conditions which guarantee the existence of stable relaxation oscillations for systems within the class. Such result shows the coexistence of the predators and the prey with quite diversified time response which typically happens when the prey population grows much faster than those of predators. As an application, a well-known model will be discussed in detail by showing the existence of stable relaxation oscillations for a wide range of parameters values of the model.

AMS Subject Classifications: Primary 34C25, 92D25; Secondary 58F14.

Keywords: Predator-prey system, singular perturbation, relaxation oscillation, stability.

1. Introduction

The study of predator-prey dynamics was originated in the 1920s in the works of Lotka [9] and Volterra [16] who showed for a one-predator-one-prey model (known as the standard Lotka-Volterra model) that the predator and prey permanently oscillate for any positive initial conditions. In the same work, Volterra also argued that the coexistence of two or more predators competing for fewer prey resources is impossible, which was later known as the principle of competitive exclusion. The principle of competitive exclusion was re-examined by Koch ([7]) in 1974 who found via numerical simulation that the coexistence of two predators competing exploitatively for a single prey species in a constant and uniform environment was in fact possible when the predator functional response to the prey density was assumed according to the Michaelis-Menten kinetics or Holling's "nonlearning" function (in particular, nonlinear), and such coexistence occurred along what appeared to be a periodic orbit in the positive octant of $\mathbb{R}^3$ rather than an equilibrium. The similar themes were discussed and showed possible in [10] by McGehee and Armstrong for n competing species and fewer than n resources. In [4, 5], Hsu, Hubbell and Waltman further studied the competition problem of two predators for a single prey in a constant and uniform environment. By combining rigorous analysis with numerical simulations, not only was the parameter range of the validity of the principle of competitive exclusion identified, but also the coexistence was confirmed numerically for a wide range of parameter values, and it was further conjectured that the coexistence was only possible if the prey was not regenerated at a constant rate and the predators were not continually consuming the resource. The model considered in [4, 5, 7] is a system of ordinary differential equations of the form

$$\begin{aligned} \dot{S} &= \gamma S(1 - \frac{S}{K}) - \frac{m_1}{y_1}\frac{x_1 S}{a_1 + S} - \frac{m_2}{y_2}\frac{x_2 S}{a_2 + S}, \\ \dot{x}_1 &= \frac{m_1 x_1 S}{a_1 + S} - d_1 x_1, \\ \dot{x}_2 &= \frac{m_2 x_2 S}{a_2 + S} - d_2 x_2, \end{aligned} \tag{1.1}$$

where, for $i = 1, 2$, x_i represents the time-varying population density of the ith predator; S represents the time-varying population density of the prey; $m_i > 0$ is the maximal growth or birth rate of the ith predator; $d_i > 0$ is the death rate of the ith predator; y_i is the yield factor for the ith predator feeding on the prey, a_i is the half-saturation constant for the ith predator, i.e., the prey density at which the functional response of the predator is half maximal; and $\gamma > 0$, $K > 0$ are the intrinsic rate of growth of the prey and the carrying capacity of the prey, respectively. The term $(m_i/y_i)S/(a_i+S)$ is the functional response of the per capita rate at which the predator x_i captures prey S, for $i = 1, 2$.

Following the numerical observations, there have been several important theoretical developments in justifying the coexistence for systems like (1.1) along the line of the Hsu-Hubbell-Waltman conjecture. Bifurcation techniques were applied to (1.1) by Butler and Waltman ([1]), Smith ([15]), and Keener ([6]) to obtain a stable periodic cycle in the positive octant which was bifurcated from a two dimensional predator-prey cycle in the x_1S or x_2S planes that was shown to exist in [1] and [14]. But due to the use of local bifurcation arguments, the range of parameter values for the coexistence was restricted and not able to be given explicitly. To overcome the limitation, Muratori and Rinaldi considered (1.1) in [12] by assuming that the prey population has fast dynamics. By using a formal singular perturbation argument to one of the two dimensional predator-prey cycles in the x_1S or x_2S planes, they were able to give a precise parameter range in which stable relaxation oscillations exist in the positive octant of $\mathbb{R}^3$ sufficiently near either the x_1S or the x_2S plane.

This paper is devoted to the rigorous study of the existence of relaxation oscillations for a class of predator-prey models having two predators competing exploitatively for the same prey in a constant environment, which particularly include (1.1) as a special case. As in [12], we will assume that the prey population in our model has fast dynamics, i.e., the prey population grows much faster than those of the predators. Hence, the general models to be considered will have the following form:

$$\begin{aligned} \dot{x} &= xf(x, y, z; \epsilon), \\ \dot{y} &= yg(x, y, z; \epsilon), \\ \epsilon\dot{z} &= zh(x, y, z; \epsilon), \end{aligned} \tag{1.2}$$

where $0 < \epsilon \ll 1$, x, y are the populations of the two predators, z is the population of the prey, and f, g and h are sufficiently smooth functions in x, y, z and ϵ. We will restrict our attention to system (1.2) in the closed first octant of $\mathbb{R}^3$, and impose biological meaningful conditions on the functions f, g and h. In particular, we will show under these conditions that

(i) there exists an invariant cylinder which attracts all but the equilibria solutions and their possible connections;
(ii) the two end circles of the cylinder are the relaxation cycles of the subsystems on the invariant xz and yz-planes, respectively;
(iii) the two end circles of the cylinder are unstable along the interior of the cylinder, and hence there exists at least one stable relaxation oscillation (not necessary one cycle) in the interior of the cylinder.

As pointed out in [12], the existence of such relaxation oscillations implies that the coexistence of predators and prey occurs through a simple periodically alternated two-season behavior: a poor season, characterized by an almost endemic presence of the prey, alternates with a rich season, during which prey are abundant and predators are regenerated.

The work uses the geometric singular perturbation theory and dynamical systems techniques. We first examine the global dynamics of the limiting systems in Section 2 and show that the limiting system admits a relaxation cylinder formed by orbits of limiting slow and fast systems. To show the persistence of this cylinder for $\epsilon > 0$, we will construct a global Poincaré map of system (1.2) in Section 3 along the limiting cylinder and show the existence of an invariant curve of the Poincaré map which corresponds to an invariant cylinder for the flow. Explicit conditions will then be imposed on the vector field (1.2) to ensure the instability of the two end relaxation cycles of the cylinder and hence the existence of a stable relaxation oscillation in the interior of the cylinder. As an application, we will discuss the model (1.1) in Section 4 and give an explicit range of parameters for the existence of stable relaxation oscillations in the positive octant of $\mathbb{R}^3$.

Acknowledgment. The work is partially done when the second and third authors were visiting the National University of Singapore. The authors would also like to thank the referee for valuable comments and suggestions.

2. Dynamics of the limiting systems

In this section, we will examine the limiting systems obtained from the slow system (1.2) and its corresponding fast system.

Setting $\epsilon = 0$ in (1.2) results in the so-called *limiting slow system*:

$$\begin{aligned} \dot{x} &= xf(x,y,z), \\ \dot{y} &= yg(x,y,z), \\ 0 &= zh(x,y,z), \end{aligned} \tag{2.1}$$

which is generally defined on the *slow manifold*

$$S_0 = \{(x,y,z): \ zh(x,y,z) = 0, \ x \geq 0, \ y \geq 0, \ z \geq 0\}.$$

Orbits or parts of orbits of system (2.1) on S_0 are called the *slow orbits* of system (1.2), and the variables x and y are called the *slow variables*. For system (2.1), the slow manifold S_0 consists of two portions S_1 and S_2 where

$$S_1 = \{(x,y,z) \in S_0 : \ z = 0\} \ \text{ and } \ S_2 = \{(x,y,z) \in S_0 : \ h(x,y,z) = 0\}.$$

In terms of the fast time scale $\tau = t/\epsilon$, system (1.2) becomes:

$$\begin{aligned} \frac{dx}{d\tau} &= \epsilon x f(x,y,z), \\ \frac{dy}{d\tau} &= \epsilon y g(x,y,z), \\ \frac{dz}{d\tau} &= z h(x,y,z). \end{aligned} \tag{2.2}$$

This system is referred to as the *fast system*. Its limit, *the limiting fast system*, is obtained by setting $\epsilon = 0$:

$$\begin{aligned} \frac{dx}{d\tau} &= 0, \\ \frac{dy}{d\tau} &= 0, \\ \frac{dz}{d\tau} &= z h(x,y,z). \end{aligned} \tag{2.3}$$

The orbits of system (2.3) are parallel to the z-axis and their directions are characterized by the signs of $zh(x,y,z)$. We refer to these orbits as *fast orbits* of system (1.2) and refer to the variable z as the *fast variable*.

A continuous and piecewise smooth curve is said to be a *limiting orbit* of system (1.2) if it is the union of a finitely many fast and slow orbits with compatible orientations.

A limiting orbit is called *a limiting periodic orbit* if it is a simple closed curve and contains no equilibrium of system (1.2).

A periodic orbit of system (1.2) is called a *relaxation oscillation* if its limit as $\epsilon \to 0$ is a limiting periodic orbit consisting of both fast and slow orbits.

2.1. **Behavior of equilibria.** We assume that the equilibrium $(0,0,0)$ of (1.2) is a saddle which is attracting in the invariant xy plane and repelling in the invariant z-axis. Corresponding to the absence of the predators when the prey population reaches its carrying capacity, we also assume that $(0,0,1)$ is a saddle equilibrium point which is attracting along the invariant z-axis and repelling along the xy directions. With respect to the vector field, these assumptions are summarized as the following.

Condition 1. *System* (1.2) *has* (0,0,0) *and* (0,0,1) *as equilibrium points for any* ϵ. *Moreover,* $f(0,0,0) < 0$*,* $g(0,0,0) < 0$*,* $h(0,0,0) > 0$*;* $h(0,0,1) = 0$*,* $f(0,0,1) > 0$*,* $g(0,0,1) > 0$ *and* $\dfrac{\partial h}{\partial z}(0,0,1) < 0$.

In fact, as implied by other conditions in this section, (1.2) admits at least two other equilibria which lie in the first quadrant of the invariant xz and yz-planes, respectively.

2.2. **Dynamics in the vicinity of S_1.** We first impose some conditions relative to S_1 and describe both the fast dynamic in the vicinity of S_1 and the slow dynamic on S_1.

Condition 2. *The equation $h(x, y, 0) = 0$ defines a smooth curve S_1^0 in the first quadrant of the xy-plane, connecting the x-axis to the y-axis, which divides the slow manifold S_1 into two subdomains*

$$S_1^+ = \{(x, y, 0) \in S_1 : \ h(x, y, 0) > 0\}, \ \ S_1^- = \{(x, y, 0) \in S_1 : \ h(x, y, 0) < 0\},$$

among which S_1^+ is the bounded portion enclosed by S_1^0, the x-axis, and the y-axis.

The limiting fast dynamic is governed by system (2.3) having S_1 as a set of equilibria. It is obvious that S_1^- is normally stable with vertical stable fibers and S_1^+ is normally unstable with vertical unstable fibers, i.e., all solutions of (2.3) in the vicinity of S_1^- (S_1^+ resp.) move vertically toward S_1^- (away from S_1^+, resp.). The normal hyperbolicity of S_1 is lost along the turning point curve S_1^0.

For the slow dynamic on S_1, the limiting slow system (2.1) is reduced to

$$\begin{aligned} \dot{x} &= xf(x, y, 0), \\ \dot{y} &= yg(x, y, 0), \\ z &= 0. \end{aligned} \tag{2.4}$$

We assume the following.

Condition 3. *The origin is the global attractor of system* (2.4), *and the vector field $(xf(x, y, 0), yg(x, y, 0))$ is transversal to S_1^0.*

As a consequence, we have

Lemma 2.1. *For any $(x_0, y_0) \in S_1^-$, there exists a unique $t_0 = t_0(x_0, y_0)$ and a unique $t_1 = t_1(x_0, y_0)$ with $t_1 > t_0 > 0$ such that $(x(t_0), y(t_0)) \in S_1^0$ and*

$$\int_0^{t_1} h(x(s), y(s), 0)\, ds = 0,$$

where $(x(t), y(t))$ is the solution of (2.4) *with the initial value (x_0, y_0).*

As we will see in the next section, the time map t_1 above characterizes a phenomenon of the singularly perturbed system, known as the *delay of stability loss.*

We will call the map $\mathcal{P}^0 : S_1^- \to S_1^+$: $\mathcal{P}^0(x_0, y_0) = ((x(t_1(x_0, y_0)), y(t_1(x_0, y_0))$ the *delay map*, where $(x(t), y(t))$ and t_1 are as in Lemma 2.1.

2.3. **Dynamics in the vicinity of S_2.** We now discuss the other portion S_2 of the slow manifold.

Condition 4. *The equation* $\dfrac{\partial h}{\partial z}(x, y, z) = 0$ *defines a smooth curve* S_2^0 *on* S_2, *which divides* S_2 *into two smooth surfaces*

$$S_2^- = \{(x, y, z) \in S_2 : \frac{\partial h}{\partial z}(x, y, z) < 0\}, \quad S_2^+ = \{(x, y, z) \in S_2 : \frac{\partial h}{\partial z}(x, y, z) > 0\}.$$

The projection J^0 *of* S_2^0 *onto the xy-plane is a smooth curve in* S_1^-, *and there are smooth functions* $q : \bar{D}_1 \to R_+$ *and* $r : \bar{D}_2 \to R_+$ *such that* $S_2^- = \{(x, y, q(x, y)) : (x, y) \in D_1\}$ *and* $S_2^+ = \{(x, y, r(x, y)) : (x, y) \in D_2\}$, *where* D_1 *is the domain in the xy-plane bounded by the x-axis, the y-axis, and* J^0, *and* D_2 *is the domain in the xy-plane bounded by* S_1^0, *the x-axis, the y-axis, and* J^0. *Moreover,* q *and* r *agree on* J^0, *and* $S_2^0 = \{(x, y, q(x, y)) = (x, y, r(x, y)) : (x, y) \in J^0\}$.

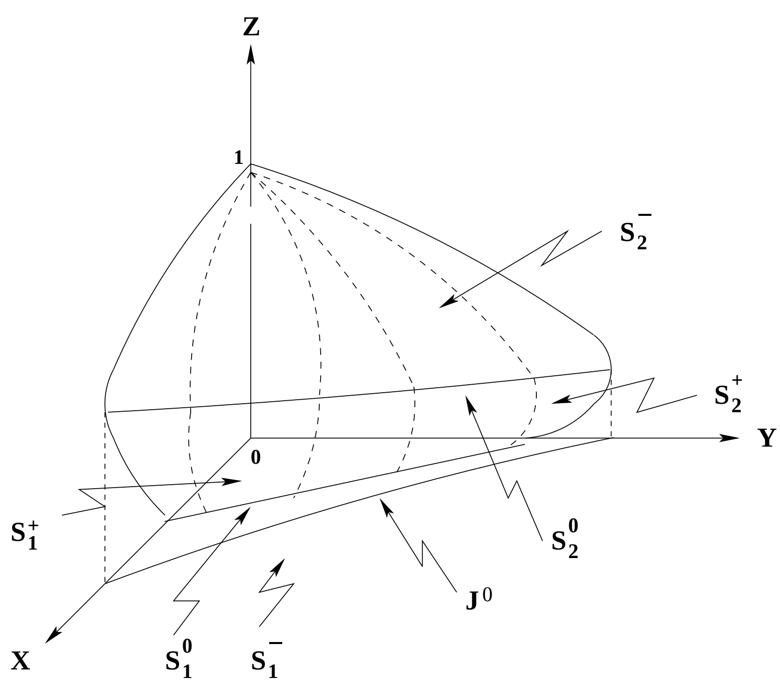

FIGURE 2.1. *The slow manifold and its portions.*

For the limiting fast dynamic, it is clear that all solutions of system (2.3) in the vicinity of S_2^- will move vertically toward S_2^- and those in the vicinity of S_2^+ will move vertically away from S_2^+.

The slow manifold S_2 losses normal hyperbolicity at the turning points curve S_2^0 with respect to the fast system, and hence it does not persist for $\epsilon > 0$ in general. Difficulty also arises due to the fact that the limiting slow system (2.1) is not defined on S_2^0 and the slow orbits on S_2 can reach S_2^0 in finite time from both side. For the purpose of this work, we are mainly interested in the slow dynamic on S_2^-. With the parameterization $q : D_1 \to \mathbb{R}_+$ of S_2^-, the limiting slow flow on S_2^- is simply described by

$$\begin{aligned} \dot{x} &= xf(x, y, q(x, y)), \\ \dot{y} &= yg(x, y, q(x, y)), \\ z &= q(x, y). \end{aligned} \tag{2.5}$$

where $(x, y) \in D_1$.

Condition 5. *The equilibrium* $(0, 0, 1)$ *is a global repellor of system* (2.5) *on* S_2^-*, and the vector field* (xf, yg) *is transversal to* J^0.

Biologically, the first part of the condition means that the predator populations must grow near the capacity population of the prey. This condition together with the Poincaré-Bendixon theorem implies that the flow (2.5) on S_2^- is negatively invariant with $(0, 0, 1)$ as the α-limit set of all solutions with initial values on S_2^-. The second part of the condition allows one to control the breakup of the surface S_2 as $\epsilon > 0$ and the behavior of solutions of (2.2) after reaching the vicinity of S_2^0. The precise consequence of such controlling effect will be stated in the next section.

Lemma 2.2. *For any* $(x_1, y_1) \in D_1$*, there exists a unique* $t_2 = t_2(x_1, y_1) > 0$ *such that* $(x(t_2), y(t_2), q(x(t_2), y(t_2))) \in S_2^0$*, where* $(x(t), y(t))$ *is the solution of system* (2.5) *with the initial value* (x_1, y_1).

2.4. **Limiting Poincaré map.** We will construct a limiting Poincaré map to illustrate the global limiting dynamics. First, we choose two Poincaré sections Σ_0 and Σ_1 in the first octant as follows. Let $0 < z_0 < \min\{q(x, y) : (x, y) \in D_1\}$. If z_0 is sufficiently small, then, by Condition 4, the plane $\{z = z_0\}$ intersects S_2^+ along a curve and, in the first octant, the curve separates the plane into a bounded portion and an unbounded one. Now let Σ_1 be the bounded portion and Σ_0 be a bounded region of the unbounded portion of the plane so that its projection to the xy-plane contains J^0 (see Figure 2.2).

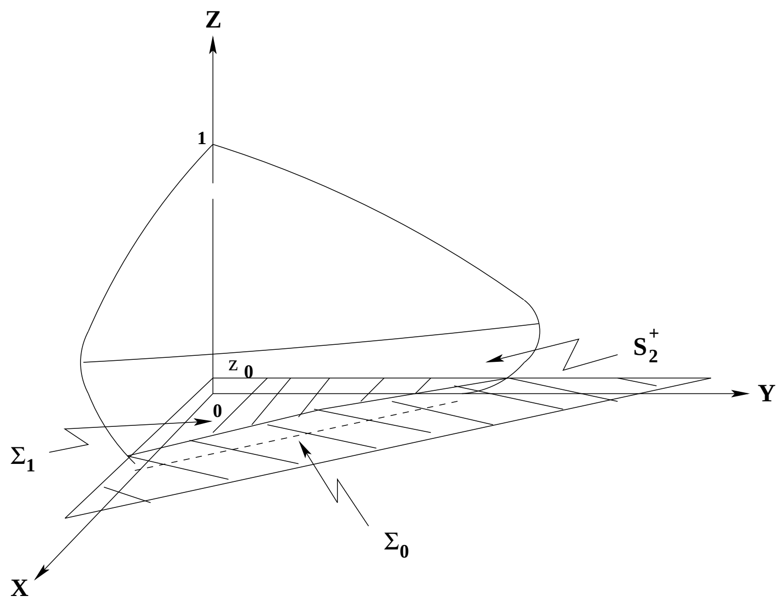

FIGURE 2.2. *The Poincaré sections* Σ_0 *and* Σ_1.

Define

$$\mathcal{P}^0 : \Sigma_0 \to \Sigma_1 : \quad \mathcal{P}^0(x_0, y_0, z_0) = (x(t_1), y(t_1), z_0),$$

where $(x(t), y(t), 0)$ is the solution of system (2.4) with the initial value (x_0, y_0) and $t_1 = t_1(x_0, y_0)$ is as in Lemma 2.1. Note that the restriction of $\mathcal{P}^0$ to the xy-plane is nothing but the delay map defined after Lemma 2.1. Also define

$$\mathcal{Q}^0 : \mathcal{P}^0(\Sigma_0) \to \Sigma_0 : \quad \mathcal{Q}^0(x_1, y_1, z_0) = (x(t_2), y(t_2), z_0),$$

where $(x(t), y(t))$ is the solution of system (2.5) with the initial value (x_1, y_1) and $t_2 = t_2(x_1, y_1)$ is as in Lemma 2.2. We refer to the composition

$$F^0 = \mathcal{Q}^0 \circ \mathcal{P}^0 : \Sigma_0 \to \Sigma_0$$

as the *limiting Poincaré map.*

The existence of an invariant cylinder of the perturbed system will be based on a limiting cylinder, consisting of four portions as illustrated in Figure 2.3. The first portion is the set of fast orbits from S_2^0 to J^0 (the front vertical piece in Figure 2.3).

The next portion is formed by the slow orbits from J^0 to $J^1 = \mathcal{P}^0(J^0)$ (the piece on the xy-plane). Let T be the image of the curve J^1 under the map q. Then the third portion consists of J^1, T and the fast orbits in between (the vertical piece on the back). The last portion is the set of slow orbits from T to S_2^0 on S_2^- (the piece on the top). To avoid collapse of orbits during the above construction, we need the following condition.

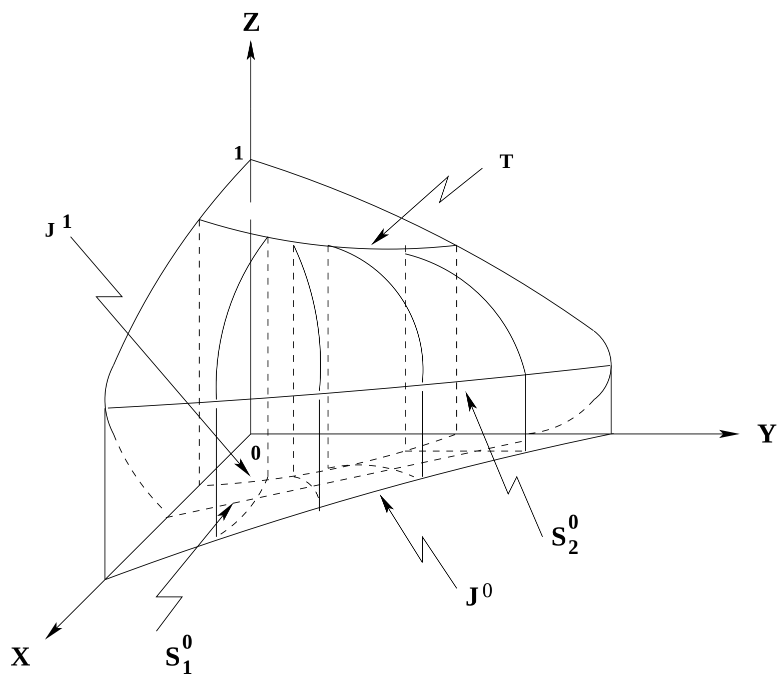

FIGURE 2.3. *The limiting cylinder.*

Condition 6. *The curve J^0 is transversal to the vector field $(xf, yg, 0)$ on S_1^- and the curve T is transversal to the vector field $(xf, yg, 0)$ on S_2^-.*

3. DYNAMICS OF SYSTEM (1.2) FOR $\epsilon > 0$

3.1. **Poincaré map.** We now consider a Poincaré map for $\epsilon > 0$ which will be a perturbation of the limiting one along the limiting cylinder. To do so, we restrict the Poincaré sections Σ_0, Σ_1 defined above to a small neighborhood of the limiting cylinder. With Conditions 1-3, it has been shown in [8, 11, 13] that the map

$$\mathcal{P}^\epsilon : \Sigma_0 \to \Sigma_1 : \quad \mathcal{P}^\epsilon(x_0, y_0, z_0) = (x(t_1(\epsilon); \epsilon), y(t_1(\epsilon); \epsilon), z(t_1(\epsilon); \epsilon))$$

is a well defined diffeomorphism, where $(x(t;\epsilon), y(t;\epsilon), z(t;\epsilon))$ is the solution of system (1.2) with the initial value (x_0, y_0, z_0) and $t_1(\epsilon) = t_1(x_0, y_0, z_0; \epsilon) > 0$ is the first time at which the solution reaches Σ_1, i.e, $z(t_1(\epsilon);\epsilon) = z_0$, and moreover,

$$\mathcal{P}^\epsilon \to \mathcal{P}^0 \text{ smoothly as } \epsilon \to 0.$$

With the Conditions 4, 5 and 6, it has been also shown (see [2] and the references therein) that the map

$$\mathcal{Q}^\epsilon : \mathcal{P}^\epsilon(\Sigma_0) \to \Sigma_0 : \mathcal{Q}^\epsilon(x_1, y_1, z_0) = (x(t_2(\epsilon);\epsilon), y(t_2(\epsilon);\epsilon), z(t_2(\epsilon);\epsilon))$$

is a well defined diffeomorphism, where $(x(t;\epsilon), y(t;\epsilon), z(t;\epsilon))$ is the solution of system (1.2) with the initial value $(x_1, y_1, z_0) \in \Sigma_1$ and $t_2(\epsilon) = t_2(x_1, y_1, z_0; \epsilon) > 0$ is the first time at which the solution reaches Σ_0, i.e., $z(t_2(\epsilon);\epsilon) = z_0$, and moreover,

$$\mathcal{Q}^\epsilon \to \mathcal{Q}^0 \text{ smoothly as } \epsilon \to 0.$$

We refer to the map

$$F^\epsilon = \mathcal{Q}^\epsilon \circ \mathcal{P}^\epsilon : \Sigma_0 \to \Sigma_0$$

as the *Poincaré map*. Hence, the following holds.

Lemma 3.1. *Assume the Conditions 1-6. Then*

$$F^\epsilon \to F^0 \text{ smoothly as } \epsilon \to 0.$$

3.2. **Invariant cylinder.**

Theorem 3.2. *Assume the Conditions 1-6. Let L_0 be the intersection of the limiting cylinder with the section Σ_0. Then, for $\epsilon > 0$ small, the Poincaré map $F^\epsilon : \Sigma_0 \to \Sigma_0$ admits an asymptotically stable smooth invariant curves L_ϵ which is also smoothly varying in ϵ and satisfying that $L_\epsilon \to L_0$ smoothly as $\epsilon \to 0$. Such an invariant curve corresponds to an invariant, normally asymptotically stable cylinder of* (1.2) *with the two ends being the relaxation cycles in the invariant xz and yz planes.*

Proof. For simplicity, we identify Σ_0 with a rectangle $\mathcal{R} = \{(u, v) : u \in [-1, 1], v \in [-1, 1]\}$ and L_0 with $\{(u, v) \in \mathcal{R} : v = 0\}$, and use F^ϵ again as the (identified) Poincaré map. Let L_ϵ be the ω-limit set of $\mathcal{R}$ under F^ϵ. Since F^0 maps $\mathcal{R}$ to L_0, $\mathcal{R}$ is positively invariant with respect to F^ϵ for small ϵ, and thus, L_ϵ is simply connected, and converges to L_0 smoothly as $\epsilon \to 0$. We claim that L_ϵ must be a curve. For otherwise, L_ϵ would have non-empty interior and hence non-zero area, which, by its invariance under F^ϵ, is given by the integral of $|\det(DF^\epsilon)|$ over L_ϵ. It follows that $|\det(DF^\epsilon(u_0,v_0))| = 1$ for some $(u_0,v_0)\in L_\epsilon$, which contradicts to the fact that $DF^\epsilon \to DF^0$ as $\epsilon\to 0$ since, for the latter, $|\det(DF^0)| = 0$.

Thus, each F^ϵ admits an asymptotically stable smooth invariant curve which is close to L_0 smoothly. This invariant curve corresponds to a normally asymptotically stable invariant cylinder in the first octant of $\mathbb{R}^3$ with the two boundaries being the relaxation cycles in the invariant xz and yz planes. □

3.3. **Relaxation oscillations.** For the existence of stable relaxation oscillations in the interior of the invariant cylinder, we now derive a condition under which the two relaxation cycles are unstable within the cylinder. Let $\Gamma_\epsilon^1 = \{(x_\epsilon^{(1)}(t), 0, z_\epsilon^{(1)}(t))\}$ and $\Gamma_\epsilon^2 = \{(0, y_\epsilon^{(2)}(t), z_\epsilon^{(2)}(t))\}$ be the relaxation cycles on the xz-plane and yz-plane respectively with $(x_\epsilon^{(1)}(0), 0, z_\epsilon^{(1)}(0)) \to (x_0,0,0)$ and $(0, y_\epsilon^{(2)}(0), z_\epsilon^{(2)}(0)) \to (0,y_0,0)$ as $\epsilon\to 0$. Then the limits of Γ_ϵ^i as $\epsilon \to 0$ are $\Gamma_0^i = \gamma_1^i\cup\gamma_2^i\cup\gamma_3^i\cup\gamma_4^i$, for $i=1,2$, respectively (see Figure 3.1), with

$$\begin{aligned}\gamma_1^1 &= \{(x,0,0):\ x\in[x_1,x_0]\}, & \gamma_2^1 &= \{(x_1,0,z):\ z\in[0,q(x_1,0)]\},\\ \gamma_3^1 &= \{(x,0,q(x,0)):\ x\in[x_1,x_0]\}, & \gamma_4^1 &= \{(x_0,0,z):\ z\in[0,q(x_0,0)]\}\end{aligned} \tag{3.1}$$

and

$$\begin{aligned}\gamma_1^2 &= \{(0,y,0):\ y\in[y_1,y_0]\}, & \gamma_2^2 &= \{(0,y_1,z):\ z\in[0,q(0,y_1)]\},\\ \gamma_3^2 &= \{(0,y,q(0,y)):\ y\in[y_1,y_0]\}, & \gamma_4^2 &= \{(0,y_0,z):\ z\in[0,q(0,y_0)]\},\end{aligned} \tag{3.2}$$

where $q(x,y)$ is defined as in the Condition 4, x_1 and y_1 are defined via the delay map $\mathcal{P}^0$ at the end of Section 2.2 as $(x_1,0) = \mathcal{P}^0(x_0,0)$ and $(0,y_1) = \mathcal{P}^0(0,y_0)$.

Lemma 3.3. *For $\epsilon > 0$ small, the relaxation cycle Γ_ϵ^1 is stable (unstable) along the invariant cylinder if the following integral is negative (positive)*

$$I_1 = \int_{x_0}^{x_1} \frac{g(x,0,0)}{xf(x,0,0)}dx + \int_{x_1}^{x_0} \frac{g(x,0,q(x,0))}{xf(x,0,q(x,0))}dx; \tag{3.3}$$

and, the relaxation cycle Γ_ϵ^2 is stable (unstable) along the cylinder if the following integral is negative (positive)

$$I_2 = \int_{y_0}^{y_1} \frac{f(0,y,0)}{yg(0,y,0)}dy + \int_{y_1}^{y_0} \frac{f(0,y,q(0,y))}{yg(0,y,q(0,y))}dy. \tag{3.4}$$

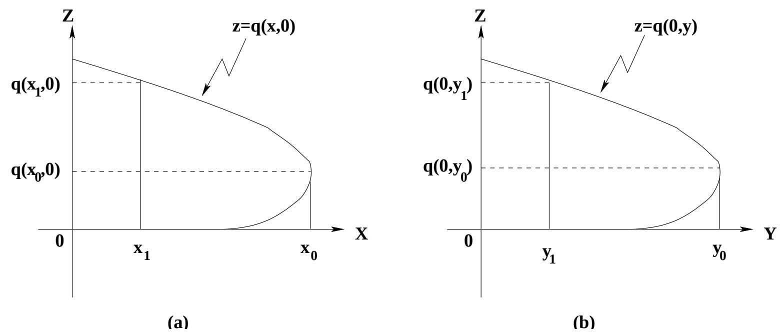

FIGURE 3.1. *(a) The limiting relaxation Γ_0^1 on the xz-plane; (b) The limiting relaxation Γ_0^2 on the yz-plane.*

Proof. We only show the first statement. From the linearization along the relaxation cycle $\Gamma_\epsilon^1 = \left(x_\epsilon^{(1)}(t), 0, z_\epsilon^{(1)}(t)\right)$, one sees that its stability within the cylinder is determined by the sign of

$$\int_0^p g\left(x_\epsilon^{(1)}(t), 0, z_\epsilon^{(1)}(t)\right) dt,$$

where p is the period of Γ_ϵ^1. Since Γ_ϵ^1 limits to the union of γ_i, $i = 1, 2, 3, 4$, with both γ_2 and γ_4 being fast orbits, the limit of the above integral is

$$\lim_{\epsilon\to 0} \int_0^p g\left(x_\epsilon^{(1)}(t), 0, z_\epsilon^{(1)}(t)\right) dt = \int_0^{t_1} g\left(x_0^{(1)}(t), 0, 0\right) dt + \int_{t_1}^{t_2} g\left(x_0^{(1)}(t), 0, q(x_0^{(1)}(t), 0)\right) dt,$$

where $\left(x_0^{(1)}(t), 0, 0\right)$ for $t \in [0, t_1]$ is the limiting slow orbit on the x-axis from x_0 to x_1, and $\left(x_0^{(1)}(t), 0, q(x_0^{(1)}(t), 0)\right)$ for $t \in [t_1, t_2]$ is the one on the slow manifold S_2^- from $(x_1, 0, q(x_1, 0))$ to $(x_0, 0, z_0)$. Substituting $x = x_0^{(1)}(t)$, one has that

$$\lim_{\epsilon\to 0} \int_0^p g\left(x_\epsilon^{(1)}(t), 0, z_\epsilon^{(1)}(t)\right) dt = \int_{x_0}^{x_1} \frac{g(x, 0, 0)}{xf(x, 0, 0)} dx + \int_{x_1}^{x_0} \frac{g(x, 0, q(x, 0))}{xf(x, 0, q(x, 0))} dx,$$

from which the statement of the lemma follows. □

We now state our main results on the existence of stable relaxation oscillations of (1.2) in the positive octant of $\mathbb{R}^3$.

Theorem 3.4. *Assume the Conditions 1-6 for* (1.2)*. Then, for $\epsilon > 0$ small, the following holds.*

(i) *The normally asymptotically stable invariant cylinder consists of relaxation periodic solutions along with connecting orbits.*

(ii) *Either at least one of the end relaxation cycles is stable along the invariant cylinder or there is a stable relaxation oscillation in the interior of the invariant cylinder.*

(iii) *If both the integrals defined in* (3.3) *and* (3.4) *are positive, then there is at least one stable relaxation oscillation in the positive octant of* $\mathbb{R}^3$.

Proof. Since there are no equilibria on the cylinder, (i) and (ii) follow from the Poincaré-Bendixon theorem. The statement (iii) follows from (ii) and Lemma 3.3, i.e., the instability of the two end cycles Γ_ϵ^1, Γ_ϵ^2 along the cylinder. □

4. Application to the model system (1.1)

We will apply Theorem 3.4 to study the existence of relaxation oscillations for the model system (1.1). By assuming that the prey population S has a very large intrinsic growth rate γ, we will identify a range of parameters in (1.1) so that all conditions in Theorem 3.4 are satisfied.

4.1. **Stable relaxation oscillations.** Using the rescaling

$$\epsilon = \frac{1}{\gamma}, \quad \beta_1 = \frac{a_1}{K}, \quad \beta_2 = \frac{a_2}{K}, \quad x = \frac{x_1}{\gamma y_1 K}, \quad y = \frac{x_2}{\gamma y_2 K}, \quad z = \frac{S}{K},$$

it is easy to see that the model (1.1) becomes

$$\begin{aligned} \dot{x} &= x\left(\frac{m_1 z}{\beta_1 + z} - d_1\right) =: xf(z), \\ \dot{y} &= y\left(\frac{m_2 z}{\beta_2 + z} - d_2\right) =: yg(z), \\ \epsilon\dot{z} &= z\left(1 - z - \frac{m_1 x}{\beta_1 + z} - \frac{m_2 y}{\beta_2 + z}\right) =: zh(x, y, z). \end{aligned} \tag{4.1}$$

We remark that the above rescaling has the advantage of keeping the competitive symmetry between the two predators, although specific co-existence conditions often identify environmental factors that are in favor of one predator over the other. In a food chain model with three species, the rescaling introduced in [3] should however be used to reflect different role played by each specie.

Let $\lambda_i = \beta_i d_i/(m_i - d_i)$ for $i = 1, 2$. We first assume that

(H1). $0 < \beta_1 < \beta_2 < 1$, $d_1 < m_1$, $d_2 < m_2$, *and* $(1 - \beta_2)/2 > \max\{\lambda_1, \lambda_2\}$.

With this assumption, it is easy to see that the Condition 1 is satisfied with the equilibria $E_0 = (0, 0, 0)$ and $E_\infty = (0, 0, 1)$ of system (4.1). System (4.1) also admits at least two other equilibria

$$E_1 = \left(\frac{\beta_1(1-\lambda_1)}{m_1 - d_1}, 0, \lambda_1\right),\ E_2 = \left(0, \frac{\beta_2(1-\lambda_2)}{m_2 - d_2}, \lambda_2\right)$$

which all lie in the first octant of $\mathbb{R}^3$, and, if $\lambda_1 = \lambda_2$, then the line segment joining E_1 and E_2 consists of equilibria.

For the portion $S_1 = \{(x, y, z) :\ z = 0\}$ of the slow manifold, the Condition 2 is fulfilled with

$$S_1^0 = \left\{(x, y, 0) :\ 1 - \frac{m_1}{\beta_1}x - \frac{m_2}{\beta_2}y = 0\right\},$$
$$S_1^+ = \left\{(x, y, 0) :\ 1 - \frac{m_1}{\beta_1}x - \frac{m_2}{\beta_2}y > 0\right\},$$
$$S_1^- = \left\{(x, y, 0) :\ 1 - \frac{m_1}{\beta_1}x - \frac{m_2}{\beta_2}y < 0\right\}.$$

Since the limiting slow system of (4.1) on S_1 (corresponding to system (2.4)) is simply

$$\dot{x} = -d_1 x,$$
$$\dot{y} = -d_2 y.$$

Condition 3 is clearly satisfied.

We note that

$$S_2 = \{(x, y, z) :\ h(x, y, z) = 0\} = \left\{(x, y, z) :\ 1 - z - \frac{m_1 x}{\beta_1 + z} - \frac{m_2 y}{\beta_2 + z} = 0\right\}.$$

The three parts

$$S_2^0 = \left\{(x, y, z) \in S_2 :\ \frac{\partial h}{\partial z}(x, y, z) = 0\right\},$$
$$S_2^- = \left\{(x, y, z) \in S_2 :\ \frac{\partial h}{\partial z}(x, y, z) < 0\right\},$$
$$S_2^+ = \left\{(x, y, z) \in S_2 :\ \frac{\partial h}{\partial z}(x, y, z) > 0\right\}$$

of S_2 can be characterized as follows. First of all, it is not hard to see that S_2^0 has the parameterization:

$$S_2^0 = \left\{(x, y, z) : x = \frac{(2z - 1 + \beta_2)(\beta_1 + z)^2}{m_1(\beta_2 - \beta_1)},\ y = \frac{(2z - 1 + \beta_1)(\beta_2 + z)^2}{m_2(\beta_1 - \beta_2)}\right\} \tag{4.2}$$

for $z \in [(1-\beta_2)/2, (1-\beta_1)/2]$. Secondly, let D_1, D_2, J^0 be as in the Condition 4 for the particular system (4.1). Then there are two non-negative solutions $z = q(x,y)$ and $z = r(x,y)$ of

$$1 - z - \frac{m_1 x}{\beta_1 + z} - \frac{m_2 y}{\beta_2 + z} = 0$$

defined on D_1, D_2 respectively with $q(x,y) > r(x,y)$ if $(x,y) \in D_2$ and $q(x,y) = r(x,y)$ if $(x,y) \in J^0$, such that

$$S_2^- = \{(x,y,z) : \, z = q(x,y), \, (x,y) \in D_1\},$$
$$S_2^+ = \{(x,y,z) : \, z = r(x,y), \, (x,y) \in D_2\}.$$

Thus, the Condition 4 holds.

Since $(1-\beta_2)/2 > \max\{\lambda_1, \lambda_2\}$, the equilibria E_1 and E_2 are not on S_2^-. The Condition 5 is thus equivalent to that

$$x\left(\frac{m_1 z}{\beta_1 + z} - d_1\right)\left(-\frac{m_1 x}{\beta_1 + z}\right) + y\left(\frac{m_2 z}{\beta_2 + z} - d_2\right)\left(-\frac{m_2 y}{\beta_2 + z}\right) \neq 0$$

for all $(x,y,z) \in S_2^0$, i.e.,

$$I(z) = (m_1 - d_1)(z - \lambda_1)\frac{m_1 x^2}{(\beta_1 + z)^2} + (m_2 - d_2)(z - \lambda_2)\frac{m_2 y^2}{(\beta_2 + z)^2} \neq 0$$

for all $z \in [(1-\beta_2)/2, (1-\beta_1)/2]$, where $x = x(z), y = y(z)$ are as in (4.2). By **(H1)**, we actually have $I(z) > 0$ for z lying in the above range. This verifies the Condition 5.

Concerning the transversality Condition 6, we note that the curve J^0 has negative slope at each point, and hence, it is transversal to the vector field $(xf, yg, 0) = (-d_1 x, -d_2 y, 0)$ on S_1. It remains to check the transversality of T to the vector field $(xf, yg, 0)$ on S_2. Note that the limiting flow on S_2^- is given by $z = q(x,y)$ where (x,y) is determined by system (2.5) with respect to (4.1). Thus, this transversality is equivalent to that of $J^1 = \mathcal{P}^0(J^0)$ with (xf, yg). Since J^0 is the projection of S_2^0, (4.2) induces a parameterization on J^0 hence on J^1. If we denote such parameterization of J^1 by $(x(z), y(z))$, then the transversality is simply

$$(xf(x,y,q(x,y)), yg(x,y,q(x,y))) \times (\frac{\partial x}{\partial z}, \frac{\partial y}{\partial z}) \neq 0,$$

or equivalently,

$$-x\left(\frac{m_1 q(x,y)}{\beta_1 + q(x,y)} - d_1\right)\frac{\partial y}{\partial z} + y\left(\frac{m_2 q(x,y)}{\beta_2 + q(x,y)} - d_2\right)\frac{\partial x}{\partial z} \neq 0, \tag{4.3}$$

for $(x, y) = (x(z), y(z)) \in J^1$.

Lemma 4.1. *For any $(x, y) \in J^1$, the value $q(x, y)$ is independent of m_1 and m_2.*

Proof. We note that, from the parameterization of J^0, $m_1 x_0(z)$ and $m_2 y_0(z)$ are independent of m_1 and m_2, so is the time $t_1 = t_1(x_0(z), y_0(z))$ in the definition of the delay map $\mathcal{P}^0$. Thus, $m_1 x = m_1 x_0(z) e^{-d_1 t_1}$ and $m_2 y = m_2 y_0(z) e^{-d_2 t_1}$ are independent of m_1 and m_2. Since $q(x, y)$ is a solution of

$$1 - q - \frac{m_1 x}{\beta_1 + q} - \frac{m_2 y}{\beta_2 + q} = 0,$$

we conclude that $q(x, y)$ is independent of m_1 and m_2. □

Let $q^* = \min\{q(x, y) : (x, y) \in J^1\}$. Then q^* depends only on β_1, β_2, d_1 and d_2. We assume

(H2). $d_1 \le d_2$ *and* $\dfrac{m_2}{d_2} \ge \dfrac{\beta_2 + q^*}{\beta_1 + q^*} \dfrac{m_1}{d_1}$.

The second inequality above can certainly hold since q^* is independent of m_1 and m_2.

Lemma 4.2. *Under the hypotheses* **(H1)** *and* **(H2)***, the Condition 6 is satisfied.*

Proof. We need to verify (4.3). According to (4.2), J^0 has the parameterization

$$x_0(z) = \frac{(2z - 1 + \beta_2)(\beta_1 + z)^2}{m_1(\beta_2 - \beta_1)}, \; y_0(z) = \frac{(2z - 1 + \beta_1)(\beta_2 + z)^2}{m_2(\beta_1 - \beta_2)}$$

for $z \in [(1 - \beta_2)/2, (1 - \beta_1)/2]$. It follows that

$$\frac{dx_0}{dz} = \frac{2(\beta_1 + z)(3z - 1 + \beta_1 + \beta_2)}{m_1(\beta_2 - \beta_1)}, \; \frac{dy_0}{dz} = \frac{2(\beta_2 + z)(3z - 1 + \beta_1 + \beta_2)}{m_2(\beta_1 - \beta_2)}. \tag{4.4}$$

Moreover, any point $(x, y) \in J^1$ has the form $x = x_0(z) e^{-d_1 t}, y = y_0(z) e^{-d_2 t}$, where $t = t(z)$ satisfies

$$t + \frac{m_1 x_0(z)}{\beta_1 d_1} \left(e^{-d_1 t} - 1\right) + \frac{m_2 y_0(z)}{\beta_2 d_2} \left(e^{-d_2 t} - 1\right) = 0. \tag{4.5}$$

Differentiating (4.5) with respect to z yields that

$$\frac{dt}{dz} = \frac{1}{\Delta} \left(\frac{m_1}{\beta_1 d_1} (e^{-d_1 t} - 1) \frac{dx_0}{dz} + \frac{m_2}{\beta_2 d_2} (e^{-d_2 t} - 1) \frac{dy_0}{dz} \right),$$

where

$$\Delta = 1 - \frac{m_1 x_0}{\beta_1} e^{-d_1 t} - \frac{m_2 y_0}{\beta_2} e^{-d_2 t} > 0.$$

Let

$$\Lambda = y_0\left(\frac{m_2 q}{\beta_2+q}-d_2\right)\left(\frac{dx_0}{dz}-d_1x_0\frac{dt}{dz}\right)-x_0\left(\frac{m_1 q}{\beta_1+q}-d_1\right)\left(\frac{dy_0}{dz}-d_2y_0\frac{dt}{dz}\right),$$

where $q=q(x,y)$. Since

$$\frac{dx}{dz}=\frac{dx_0}{dz}e^{-d_1t}-d_1x_0e^{-d_1t}\frac{dt}{dz}\qquad\text{and}\qquad\frac{dy}{dz}=\frac{dy_0}{dz}e^{-d_2t}-d_2y_0e^{-d_2t}\frac{dt}{dz},$$

the inequality (4.3) will be satisfied if $\Lambda\neq 0$. We now show that **(H2)** implies that $\Lambda>0$.

First of all, due to the fact that $dx_0/dz>0$ and $dy_0/dz<0$, it is clear that if either $x_0=0$ or $y_0=0$, then $\Lambda>0$. Now let $x_0\neq 0$ and $y_0\neq 0$. Then

$$\begin{aligned}
\Delta\Lambda =& y_0\left(\frac{m_2q}{\beta_2+q}-d_2\right)\left(\Delta+\frac{m_1x_0}{\beta_1}(1-e^{-d_1t})\right)\frac{dx_0}{dz}\\
&-x_0\left(\frac{m_1q}{\beta_1+q}-d_1\right)\left(\Delta+\frac{m_2y_0}{\beta_2}(1-e^{-d_2t})\right)\frac{dy_0}{dz}\\
&+\left(\frac{m_2q}{\beta_2+q}-d_2\right)\frac{d_1x_0m_2y_0}{\beta_2d_2}(1-e^{-d_2t})\frac{dy_0}{dz}\\
&-\left(\frac{m_1q}{\beta_1+q}-d_1\right)\frac{m_1x_0d_2y_0}{\beta_1d_1}(1-e^{-d_1t})\frac{dx_0}{dz}\\
=&\Delta y_0\left(\frac{m_2q}{\beta_2+q}-d_2\right)\frac{dx_0}{dz}-\Delta x_0\left(\frac{m_1q}{\beta_1+q}-d_1\right)\frac{dy_0}{dz}\\
&+\left(\frac{m_1m_2x_0y_0q}{\beta_1(\beta_2+q)}-\frac{m_1^2d_2x_0y_0q}{\beta_1d_1(\beta_1+q)}\right)(1-e^{-d_1t})\frac{dx_0}{dz}\\
&-\left(\frac{m_1m_2x_0y_0q}{\beta_2(\beta_1+q)}-\frac{m_2^2d_1x_0y_0q}{\beta_2d_2(\beta_2+q)}\right)(1-e^{-d_2t})\frac{dy_0}{dz}\\
>&\left(\frac{m_1m_2x_0y_0q}{\beta_1(\beta_2+q)}-\frac{m_1^2d_2x_0y_0q}{\beta_1d_1(\beta_1+q)}\right)(1-e^{-d_1t})\frac{dx_0}{dz}\\
&-\left(\frac{m_1m_2x_0y_0q}{\beta_2(\beta_1+q)}-\frac{m_2^2d_1x_0y_0q}{\beta_2d_2(\beta_2+q)}\right)(1-e^{-d_2t})\frac{dy_0}{dz}.
\end{aligned}$$

Using (4.4), we further obtain that

$$\Lambda > K\left(\frac{m_1}{d_1}(\beta_2+q)-\frac{m_2}{d_2}(\beta_1+q)\right)\left(\frac{\beta_2+z}{\beta_2}\frac{1-e^{-d_2t}}{d_2}-\frac{\beta_1+z}{\beta_1}\frac{1-e^{-d_1t}}{d_1}\right),$$

where

$$K=\frac{2d_1d_2x_0y_0q(3z-1+\beta_1+\beta_2)}{\Delta(\beta_1+q)(\beta_2+q)}>0.$$

Now the condition $d_1\leq d_2$ implies that

$$\frac{1-e^{-d_1t}}{d_1}\geq\frac{1-e^{-d_2t}}{d_2},$$

and the condition

$$\frac{m_2}{d_2} \geq \frac{\beta_2 + q^*}{\beta_1 + q^*} \frac{m_1}{d_1}$$

implies that

$$\frac{m_1}{d_1}(\beta_2 + q) \leq \frac{m_2}{d_2}(\beta_1 + q)$$

since $q \geq q^*$. Hence $\Lambda > 0$. □

With the Conditions 1-6, the following theorem is an immediate consequence of Theorem 3.2 and Theorem 3.4 ii).

Theorem 4.3. *Assume* **(H1)** *and* **(H2)**. *Then, for* $\epsilon > 0$ *small, system* (4.1) *has at least one stable relaxation oscillation in the first octant of* $\mathbb{R}^3$. *More precisely, for* $\epsilon > 0$ *small, the following holds.*

- (i) *System* (4.1) *admits a normally asymptotically stable invariant cylinder in the first octant of* $\mathbb{R}^3$ *with the two ends being the relaxation cycles in the invariant* xz *and* yz *planes, which are asymptotically stable in the respective planes.*
- (ii) *Either at least one of the end relaxation cycles is stable along the invariant cylinder or there is a stable relaxation oscillation in the interior of the invariant cylinder.*

4.2. **Co-existence.** We now discuss the existence of relaxation oscillations for the model (1.1) in the positive octant of $\mathbb{R}^3$. To do so, we will characterize certain range of parameter values so that both integrals I_1 and I_2 in Lemma 3.3 are positive. As a consequence, system (4.1) will then have a stable relaxation oscillation on the invariant cylinder and in the interior of the first octant, which then justifies the co-existence of the two predators and the prey.

Recall from (3.1) that the limit Γ_0^1 of the relaxation cycle Γ_ϵ^1 of system (4.1) in the xz-plane is determined by the four corner points $(x_0, 0, 0)$, $(x_1, 0, 0)$, $(x_1, 0, q(x_1, 0))$ and $(x_0, 0, q(x_0, 0))$. The point $(x_0, 0, 0)$ is the projection of $(x_0, 0, q(x_0, 0)) \in S_2^0$ with $x_0 = (1+\beta_1)^2/(4m_1)$ and $q(x_0, 0) = (1-\beta_1)/2$ (see the parameterization (4.2) of S_2^0). The point $(x_1, 0, 0)$ is related to $(x_0, 0, 0)$ by the delay map $\mathcal{P}^0$; more precisely, $x_1 = x_0 e^{-d_1 t_1(x_0)}$, where $t_1 = t_1(x_0)$ satisfies

$$\int_0^{t_1} h(x_0 e^{-d_1 s}, 0, 0)\, ds = \int_0^{t_1} \left(1 - \frac{m_1 x_0}{\beta_1} e^{-d_1 s}\right) ds = 0.$$

Making the change of variable $x = x_0 e^{-d_1 s}$ in the above integral, we have that

$$\int_{x_0}^{x_1} \frac{1 - m_1 x/\beta_1}{x}\, dx = 0 \quad \text{or} \quad \ln\frac{x_1}{x_0} = \frac{m_1}{\beta_1}(x_1 - x_0).$$

We now have

$$\begin{aligned} I_1 &= \int_{x_0}^{x_1} \frac{g(x,0,0)}{xf(x,0,0)}dx + \int_{x_1}^{x_0} \frac{g(x,0,q(x,0))}{xf(x,0,q(x,0))}dx \\ &= \int_{x_0}^{x_1} \frac{d_2}{d_1 x}dx + \int_{x_1}^{x_0} \frac{g(q(x,0))}{xf(q(x,0))}dx \\ &= \frac{d_2}{d_1}\ln\frac{x_1}{x_0} + \int_{x_1}^{x_0} \frac{g(q(x,0))}{xf(q(x,0))}dx \\ &= \frac{d_2}{d_1}\frac{m_1}{\beta_1}(x_1 - x_0) + \int_{x_1}^{x_0} \frac{g(q(x,0))}{xf(q(x,0))}dx. \end{aligned}$$

Since $z = q(x, 0)$ satisfies

$$1 - z - \frac{m_1 x}{\beta_1 + z} = 0,$$

we have $x = q^{-1}(z) = (1-z)(\beta_1+z)/m_1$. For the last integral in the expression of I_1, we make the change of variable $z = q(x, 0)$. If we denote $z_0^1 = q(x_0, 0) = (1-\beta_1)/2$, $z_1^1 = q(x_1, 0)$, then

$$\begin{aligned} I_1 &= \frac{d_2}{d_1}\frac{m_1}{\beta_1}(x_1 - x_0) + \int_{z_1^1}^{z_0^1} \frac{g(z)}{q^{-1}(z)f(z)q'(q^{-1}(z))}\, dz \\ &= \frac{d_2}{d_1}\frac{m_1}{\beta_1}(x_1 - x_0) + \int_{z_1^1}^{z_0^1} \frac{(m_2 z - d_2 z - \beta_2 d_2)(1 - \beta_1 - 2z)}{(1-z)(m_1 z - d_1 z - \beta_1 d_1)(\beta_2 + z)}\, dz \\ &= \frac{d_2}{d_1}\frac{m_1}{\beta_1}(x_1 - x_0) + \int_{z_0^1}^{z_1^1} \frac{(m_2 z - d_2 z - \beta_2 d_2)(2z - 1 + \beta_1)}{(1-z)(m_1 z - d_1 z - \beta_1 d_1)(\beta_2 + z)}\, dz \\ &= \frac{d_2}{d_1}\frac{m_1}{\beta_1}(x_1 - x_0) + \frac{2(m_2 - d_2)}{m_1 - d_1}\int_{z_0^1}^{z_1^1} \frac{(z - \lambda_2)(z - z_0^1)}{(1-z)(z - \lambda_1)(z + \beta_2)}\, dz. \end{aligned}$$

The first term in the final expression of I_1 is negative since $0 < x_1 < x_0$ and the second term is positive since $z_0^1 > \max\{\lambda_1, \lambda_2\}$ by **(H2)**. We remark that the last integral can be evaluated to yield

$$I_1 = \frac{d_2}{d_1}\frac{m_1}{\beta_1}(x_1 - x_0) + \frac{m_2 - d_2}{m_1 - d_1}\left(A\ln\frac{1 - z_0^1}{1 - z_1^1} + B\ln\frac{z_0^1 + \beta_2}{z_1^1 + \beta_2} + C\ln\frac{z_0^1 - \lambda_1}{z_1^1 - \lambda_1}\right),$$

where

$$A = \frac{(1+\beta_1)(1-\lambda_2)}{(1+\beta_2)(1-\lambda_1)}, \quad B = \frac{(1 - \beta_1 + 2\beta_2)(\beta_2 + \lambda_2)}{(1+\beta_2)(\beta_2 + \lambda_1)}$$

and

$$C = \frac{(2\lambda_1 - 1 + \beta_1)(\lambda_2 - \lambda_1)}{(\beta_2 + \lambda_1)(1 - \beta_1)}.$$

Similarly, we have

$$I_2 = \frac{d_1}{d_2}\frac{m_1}{\beta_1}(y_1 - y_0) + \frac{2(m_1 - d_1)}{m_2 - d_2}\int_{z_0^2}^{z_1^2} \frac{(z-\lambda_1)(z-z_0^2)}{(1-z)(z-\lambda_2)(z+\beta_1)}\,dz,$$

where $z_0^2 = (1-\beta_2)/2$, $y_0 = (1+\beta_2)^2/(4m_2)$, $y_1 = y_0 e^{-d_2 t_1(y_0)}$, $z_1^2 = q(0, y_1)$ with $t_1 = t_1(y_0)$ satisfying

$$\int_0^{t_1} h(0, y_0 e^{-d_2 s}, 0)\,ds = 0 \quad \text{or} \quad t_1 + \frac{m_2 y_0}{\beta_2 d_2}\left(e^{-d_2 t_1} - 1\right) = 0.$$

Theoretically, one can determine the precise range of parameter values of m_i, d_i and β_i so that both integrals I_1 and I_2 are positive. We only discuss one scenario in the following.

Rewriting the expressions for I_1 and I_2, we have

$$I_1 = \frac{d_2}{d_1}\left(\frac{m_1}{\beta_1}(x_1 - x_0) + \int_{z_0^1}^{z_1^1} \frac{(m_2/d_2 z - z - \beta_2)(2z - 1 + \beta_1)}{(1-z)(m_1/d_1 z - z - \beta_1)(\beta_2 + z)}\,dz\right)$$

and

$$I_2 = \frac{d_1}{d_2}\left(\frac{m_1}{\beta_1}(y_1 - y_0) + \int_{z_0^2}^{z_1^2} \frac{(m_1/d_1 z - z - \beta_1)(2z - 1 + \beta_2)}{(1-z)(m_2/d_2 z - z - \beta_2)(\beta_1 + z)}\,dz\right).$$

Note that $I_1 = I_2 = 0$ if $m_2 = m_1$, $d_2 = d_1$ and $\beta_2 = \beta_1$, and in turn, one has

$$\frac{m_1}{\beta_1}(x_1 - x_0) + \int_{z_0^1}^{z_1^1} \frac{2z - 1 + \beta_1}{(1-z)(\beta_1 + z)}\,dz = 0,$$

$$\frac{m_2}{\beta_2}(y_1 - y_0) + \int_{z_0^2}^{z_1^2} \frac{2z - 1 + \beta_2}{(1-z)(\beta_2 + z)}\,dz = 0$$

for all choices of m_i, d_i and β_i satisfying the hypotheses **(H1)** and **(H2)**.

Lemma 4.4. *Choose β_1 and β_2 so that $z_1^2 < 1/2$ and $(1-\beta_1)/2 \geq z_1^2$. If*

$$\left|\frac{m_2}{d_2} - \frac{\beta_2 + z_1^2}{\beta_1 + z_1^2}\frac{m_1}{d_1}\right|$$

is sufficiently small, then $I_1 > 0$ and $I_2 > 0$.

Proof. We note that, since $z_1^2 \to 0$ as $\beta_2 \to 1$, there exist β_1 and β_2 such that $z_1^2 < 1/2$ and $(1-\beta_1)/2 \geq z_1^2$.

It is easy to see that, if

$$\frac{m_2}{d_2} = \frac{\beta_2 + z_1^2}{\beta_1 + z_1^2}\frac{m_1}{d_1},$$

then

$$\frac{(\beta_1+z)(m_2z/d_2-z-\beta_2)}{(\beta_2+z)(m_1z/d_1-z-\beta_1)}=\begin{cases}>1, & \text{for } z>z_1^2\\ \\ <1, & \text{for } z<z_1^2.\end{cases}$$

In particular, we have

$$\frac{(\beta_1+z)(m_2z/d_2-z-\beta_2)}{(\beta_2+z)(m_1z/d_1-z-\beta_1)}=\begin{cases}>1, & \text{for } z_0^1=\frac{1-\beta_1}{2}<z<z_1^1\\ \\ <1, & \text{for } z_0^2=\frac{1-\beta_2}{2}<z<z_1^2.\end{cases}$$

Hence,

$$\int_{z_0^1}^{z_1^1}\frac{(m_2/d_2z-z-\beta_2)(2z-1+\beta_1)}{(1-z)(m_1/d_1z-z-\beta_1)(\beta_2+z)}\,dz>\int_{z_0^1}^{z_1^1}\frac{2z-1+\beta_1}{(1-z)(\beta_1+z)}\,dz$$

and

$$\int_{z_0^2}^{z_1^2}\frac{(m_1/d_1z-z-\beta_1)(2z-1+\beta_2)}{(1-z)(m_2/d_2z-z-\beta_2)(\beta_1+z)}\,dz>\int_{z_0^2}^{z_1^2}\frac{2z-1+\beta_2}{(1-z)(\beta_2+z)}\,dz,$$

and thus, $I_1>0$ and $I_2>0$. We then conclude that, if

$$\left|\frac{m_2}{d_2}-\frac{\beta_2+z_1^2}{\beta_1+z_1^2}\frac{m_1}{d_1}\right|$$

is sufficiently small, one still has $I_1>0$ and $I_2>0$. □

Lemma 4.5. *If $|1-\beta_2|$ and $|d_1-d_2|$ are sufficiently small, then $q^*=z_1^2$.*

Proof. Denote $q(z)=q(x,y)$, where $(x,y)=(x_0(z)e^{-d_1t(z)},y_0(z)e^{-d_2t(z)})$, $(x_0(z),y_0(z))$ is the parameterization of J^0 for $z\in[(1-\beta_2)/2,(1-\beta_1)/2]$, and $t(z)=t_1(x_0(z),y_0(z))$ is defined as in the definition of the delay map $\mathcal{P}^0$. Since

$$1-q-\frac{m_1x}{\beta_1+q}-\frac{m_2y}{\beta_2+q}=0,$$

and $x=x_0(z)=0$ when $z=(1-\beta_2)/2$, we have

$$-\frac{dq}{dz}-\frac{m_1}{\beta_1+q}\frac{dx}{dz}-\frac{m_2}{\beta_2+q}\frac{dy}{dz}+\frac{m_2y}{(\beta_2+q)^2}\frac{dq}{dz}=0$$

at $z=(1-\beta_2)/2$. Since $m_2y=(1-q)(\beta_2+q)$ when $z=(1-\beta_2)/2$, we further have

$$\begin{aligned}\frac{1-\beta_2-2q}{\beta_2+q}\frac{dq}{dz}=&\frac{m_1}{\beta_1+q}e^{-d_1t}\frac{dx_0}{dz}+\frac{m_2}{\beta_2+q}e^{-d_2t}\frac{dy_0}{dz}-\frac{m_2}{\beta_2+q}e^{-d_2t}d_2y_0\frac{dt}{dz}\\=&C\left(\frac{1+2\beta_1-\beta_2}{\beta_1+q}e^{-d_1t}-\frac{1+\beta_2}{\beta_2+q}e^{-d_2t}\right)-\frac{m_2}{\beta_2+q}e^{-d_2t}d_2y_0\frac{dt}{dz}\end{aligned}$$

at $z = (1-\beta_2)/2$, where

$$C = \frac{1+2\beta_1-\beta_2}{2(\beta_2-\beta_1)} > 0.$$

Hence, if $d_1 = d_2 = D$, then

$$\frac{dq}{dz} = Ce^{-Dt}\frac{\beta_2-\beta_1}{\beta_1+q} - \frac{\beta_2+q}{1-\beta_2-2q}\frac{m_2}{\beta_2+q}e^{-Dt}Dy_0\frac{dt}{dz}.$$

Consider now the limiting case $\beta_2 = 1$. Since $t = 0$ when $z = (1-\beta_2)/2 = 0$ and $t > 0$ when $z \in (0, (1-\beta_1)/2]$, we have $q(z) = 0$ and $dt/dz \geq 0$ at $z = (1-\beta_2)/2 = 0$, and hence,

$$\frac{dq}{dz} \geq \lim_{\beta_2\to 1} Ce^{-Dt}\frac{\beta_2-\beta_1}{\beta_1+q} = \frac{\beta_1}{1-\beta_1}\frac{1-\beta_1}{\beta_1} = 1 > 0.$$

Thus, $q^* = q((1-\beta_2)/2) = q(0, y_0 e^{-d_2 t_1(0,y_0)}) = q(0, y_1) = z_1^2$. □

Our main result on the co-existence for the model is summarized in the following.

Theorem 4.6. *Assume* **(H1)**, **(H2)**, $(1-\beta_1)/2 \geq q^*$, *and also that*

$$\frac{m_2}{d_2} - \frac{\beta_2+q^*}{\beta_1+q^*}\frac{m_1}{d_1}, \quad 1-\beta_2, \quad |d_1-d_2|$$

are sufficiently small. Then, for $\epsilon > 0$ small, the relaxation oscillations of system (4.1) *in the xz and yz planes are unstable along the invariant cylinder, and hence there is a stable relaxation oscillation on the invariant cylinder and in the interior of the first octant of* $\mathbb{R}^3$.

A numerical simulation using Matlab was performed on system (4.1) with the parameter values: $m_1 = 2,\ d_1 = 0.4,\ \beta_1 = 0.2,\ m_2 = 5,\ d_2 = 0.5,\ \beta_2 = 0.7,\ \epsilon = 0.1$. The numerical solution with the initial value $(x_0, y_0, z_0) = (0.28, 0.001, 0.2)$ near the relaxation oscillation in the xz-plane is plotted in Figures 4.1. Figure 4.2 is the plot of the numerical solution with the initial value $(x_0, y_0, z_0) = (0.001, 0.2, 0.2)$ near the relaxation oscillation in the yz-plane. They demonstrate that solutions with positive initial conditions near the two end relaxation circles move away from them and approach to a region of relaxation oscillations in the interior of the invariant cylinder.

5. Discussions.

In [4, 5], a set of necessary conditions for the co-existence of the model problem (1.1) is identified as the following:

$$0 < a_1 < a_2 < K,\ 1 < b_1 < b_2,\ 0 < \lambda_1 < \lambda_2,$$

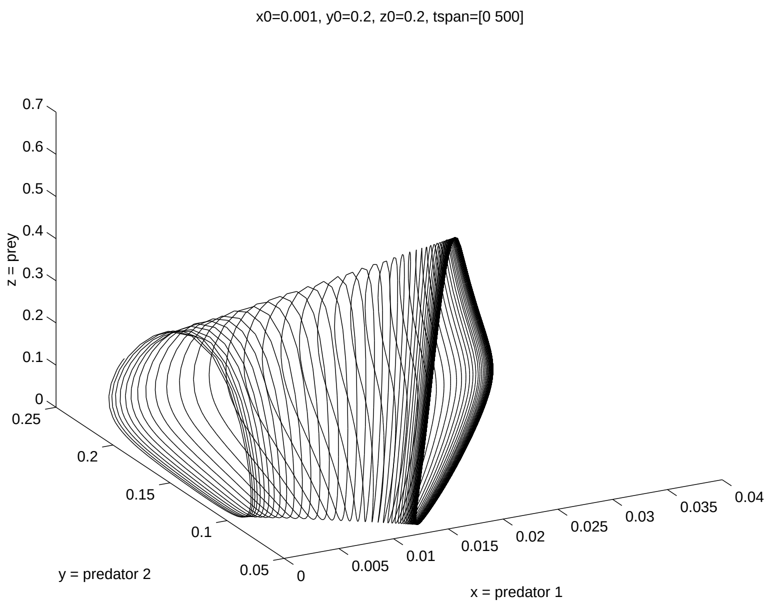

FIGURE 4.1. *An solution starting near the relaxation in the xz-plane.*

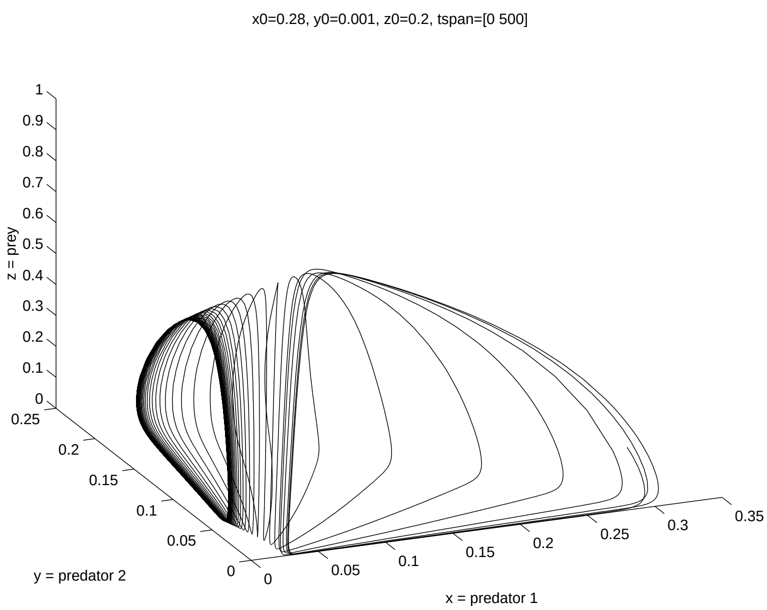

FIGURE 4.2. *An solution starting near the relaxation in the yz-plane.*

$$K > \max\left\{a_1 + 2\tilde{\lambda}_1, a_2 + 2\tilde{\lambda}_2, \frac{a_2 b_1 - a_1 b_2}{b_2 - b_1}\right\},$$

where $a_i = \beta_i K$, $b_i = m_i/d_i$, and $\tilde{\lambda}_i = \lambda_i$, $i = 1, 2$. It is not hard to show that our hypotheses **(H1)**, **(H2)** and the smallness of

$$\frac{m_2}{d_2} - \frac{\beta_2 + q^*}{\beta_1 + q^*}\frac{m_1}{d_1}$$

actually imply these necessary conditions.

In [12], a co-existence result was formally obtained. But the scenario found is different from ours. In particular, in terms of system (1.1), the conditions in [12] imply that when the predator two is absent ($x_2 = 0$), the predator one (x_1) and the prey (S) survive along a stable relaxation oscillation, and when the predator one is absent ($x_1 = 0$), the predator two and the prey survive at a stable equilibrium. In our case, when exactly one of the predators is absent, the other one and the prey always survive along a relaxation oscillation.

In view of our results (Theorems 4.3 and 4.6), not only have we proved the possibility of co-existence, but also obtained the global behavior of the model. Some of our conditions are of course not optimal but should be essential for results presented in this paper. In general, we believe that as long as $\epsilon > 0$ is small, the hypothesis **(H1)** is satisfied, and $I_1 > 0$ and $I_2 > 0$, the model should admit a stable region in the interior of the first octant consisting of relaxation oscillations.

References

[1] G. J. Butler and P. Waltman, Bifurcation from a limit cycle in a two predator-one prey ecosystem modeled on a chemostat, *J. Math. Biol.* **12** (1981), 295-449.

[2] B. Deng, Glucose-induced period-doubling cascade in the electrical activity of pancreatic β-cells, *J. Math. Biol.* **38** (1999), 21-78.

[3] B. Deng, Food chain chaos due to junction-fold point, *Chaos* **11** (2001), 514-525.

[4] S.-B. Hsu, S. P. Hubbell and P. Waltman, Competing predators, *SIAM J. Appl. Math.* **35** (1978), 617-625.

[5] S.-B. Hsu, S. P. Hubbell and P. Waltman, A contribution to the theory of Competing predators, *Ecological Monographs* **48** (1978), 337-349.

[6] J. P. Keener, Oscillatory coexistence in the chemostat: A codimension two unfolding, *SIAM J. Appl. Math* **43** (1983), 1005-1018.

[7] A. L. Koch, Competitive coexistence of two predators utilizing the same prey under constant environmental conditions, *J. Theoret. Biol.* **44** (1974), 373-386.

[8] W. Liu, Exchange Lemmas for singularly perturbed problems with certain turning points, *J. Differential Equations* **167** (2000), 134-180.

[9] A. J. Lotka, *Elements of Physical Biology* Williams and Wilkins, Baltimore, MD, 1925.

[10] R. McGehee and R. A. Armstrong, Some mathematical problems concerning the principle of competitive exclusion, *J. Differential Equations* **23** (1977), 30-52.

[11] E. F. Mishchenko, Yu. S. Kolesov, A. Yu. Kolesov and N. Kh. Rozov, *Asymptotic Methods in Singularly Perturbed Systems*, Monographs in contemporary mathematics, New York, 1994.

[12] S. Muratori and S. Rinaldi, Remarks on competitive coexistence, *SIAM J. Appl. Math.* **49** (1989), 1462-1472.

[13] S. Schecter, Persistent unstable equilibria and closed orbits of a singularly perturbed equation, *J. Differential Equations* **60** (1985), 131-141.

[14] H. L. Smith, Competitive coexistence in an oscillating chemostat, *SIAM J. Appl. Math.* **40** (1981), 498-522.

[15] H. L. Smith, The interaction of steady state and Hopf bifurcation in a two-predator-one-prey competition model, *SIAM J. Appl. Math.* **42** (1982), 27-43.

[16] V. Volterra, Variazioni e fluttuaziono del numero di individui in specie animali conviventi, *Mem. Accad. Lincei,* **2** (1926), 31-113.