

RELAXATION OSCILLATION PROFILE OF LIMIT CYCLE IN PREDATOR-PREY SYSTEM

SZE-BI HSU

Department of Mathematics, National Tsing Hua University
Hsinchu 300, Taiwan

JUNPING SHI

Department of Mathematics, College of William and Mary
Williamsburg, Virginia 23187, USA
and

Department of Mathematics, Harbin Normal University
Harbin, Heilongjiang 150025, China

(Communicated by Yang Kuang)

ABSTRACT. It is known that some predator-prey system can possess a unique limit cycle which is globally asymptotically stable. For a prototypical predator-prey system, we show that the solution curve of the limit cycle exhibits temporal patterns of a relaxation oscillator, or a Heaviside function, when certain parameter is small.

1. Introduction. For a class of conventional predator-prey interaction models, it is known that a stable limit cycle exists for a range of parameters [19]. A typical model is

$$\frac{dU}{ds} = \gamma U \left(1 - \frac{U}{K}\right) - C\phi(U)V, \quad \frac{dV}{ds} = -DV + \phi(U)V, \quad (1)$$

where the prey U satisfies a logistic growth pattern; $\gamma > 0$ represents the intrinsic growth rate of the prey; $K > 0$ is the carrying capacity of the prey; $D > 0$ is the death rate of the predator; $C > 0$ measures the relative loss of the prey; the function $\phi(U)$ is the functional response of the predator, which corresponds to saturation of their appetites and reproductive capacity, and like effects [7, 19]. A functional response (of Type II [7]) usually satisfies $\phi(0) = 0$, $\phi(U)$ is increasing and concave, and $\phi(U) \rightarrow M > 0$ for some $M > 0$ as $U \rightarrow \infty$. Examples include $\phi(U) = MU/(A + U)$ (Holling) and $\phi(U) = 1 - e^{-AU}$ (Ivlev).

In this paper, we consider the Holling type II functional response. The system considered is

$$\frac{dU}{ds} = \gamma U \left(1 - \frac{U}{K}\right) - \frac{CMUV}{A + U}, \quad \frac{dV}{ds} = -DV + \frac{MUV}{A + U}. \quad (2)$$

2000 *Mathematics Subject Classification.* Primary: 34C26, Secondary: 34C15, 34C07, 92D25.

Key words and phrases. Relaxation oscillator, limit cycle, predator-prey model.

S.B. Hsu is partially supported by National Science Council of Taiwan; and J.P. Shi is Partially supported by NSF grant DMS-0314736, DMS-0703532, NSFC grant 10671049, Longjiang Scholarship of Heilongjiang Province, and Summer Research Grant of College of William and Mary.

We introduce a change of variables:

$$t = \gamma s, \quad u = \frac{U}{K}, \quad \text{and} \quad v = \frac{C}{K} V, \quad (3)$$

then we obtain a dimensionless equation:

$$\frac{du}{dt} = u(1-u) - \frac{muv}{a+u}, \quad \frac{dv}{dt} = -dv + \frac{muv}{a+u}, \quad (4)$$

where

$$m = \frac{M}{\gamma}, \quad d = \frac{D}{\gamma}, \quad \text{and} \quad a = \frac{A}{K}. \quad (5)$$

Here $a, m, d > 0$ are dimensionless parameters. Phase portrait analysis can show for certain parameters, a prey-only or coexistence equilibrium is globally stable (see Section 2 or [8]); and for other parameters, a periodic solution exists. It has been shown that for a class of systems including (4), the periodic solution is unique thus a globally stable *limit cycle*. The first such uniqueness result was proved by Cheng [2], and more general uniqueness results for limit cycle in predator-prey systems have been proved later in [13, 14, 16, 27, 30, 31]. A main idea of later result is to transform (4) or a more general predator-prey system into a Liénard equation.

Our interest in this article is on the asymptotic behavior of the limit cycle of (4) when the predator death rate d tends to zero. A bifurcation point of view could ease the understanding of our result. If we fix other parameters in the system (4) so that $0 < a < 1$, and take d as a bifurcation parameter, then the behavior of the system changes as the v -isocline $\frac{mu}{a+u} = d$ slides when d changes. It is more convenient

to solve this v -isocline as $u = \lambda \equiv \frac{ad}{m-d}$. When $\lambda \geq 1$, the semi-trivial steady state $(1, 0)$ is globally stable; when $(1-a)/2 < \lambda < 1$ ($u = \lambda$ intersects with the falling part of u -isocline), then the coexistence steady state is globally stable; and when $0 < \lambda < (1-a)/2$ ($u = \lambda$ intersects with the rising part of u -isocline), then the limit cycle is globally stable. Notice that $\lambda = (1-a)/2$ is the Hopf bifurcation point, where a subcritical Hopf bifurcation occurs, and a small amplitude periodic solutions emerges for $\lambda < (1-a)/2$.

Our main result in the article is on the limiting behavior of the unique limit cycle Σ_λ when the death rate of predator d tends to zero (or equivalently λ tends to zero). When d is not very small, the periodic functions $u(t)$ and $v(t)$ are still sinusoidal-like (see Figure 1). Some sharp patterns emerge as $d \rightarrow 0$ (or $\lambda \rightarrow 0$). For small λ , we show that the period of Σ_λ is in an order of $O(\lambda^{-1})$; the prey population $u(t)$ is low in order of $O(\lambda)$ for a time scale of $O(\lambda^{-1})$, then it has a spike to reach the maximum but only for a time scale of $O(|\ln \lambda|)$, hence the graph of $u(t)$ is a periodic pulse; the predator population $v(t)$ reaches the maximum value from the minimum value in a time scale of $O(|\ln \lambda|)$, then it slowly decays to the minimum value in a time scale of $O(\lambda^{-1})$ and the decay is exponentially slow (see Figure 2). See Theorem 3.5 for a more mathematical description.

The phenomenon which we describe above makes the limit cycle of predator-prey system (4) behave similar to a nonlinear relaxation oscillator. Well-known examples of nonlinear relaxation oscillators are Van der Pol oscillator in electrical circuits employing vacuum tubes, Fitzhugh-Nagumo oscillator in action potentials of neurons (see [6, 10, 26, 28, 29].) The existence of relaxation dynamics in predator-prey model (4) seems to be first discovered in this article. For a two competing predators and one prey model considered in [11, 12], it is known that stable relaxation oscillations

exist for some parameter ranges by using singular perturbation methods [18, 21]. In these work, it is assumed that the prey population has fast dynamics, *i.e.* the prey population grows much faster than those of the predators. In the current article, we assume that the predator has small death rate, and our method is totally different. Notice that from (5), fast prey growth rate (large γ) implies small m and d , and we only assume small d and fix m . Yet another example of singular perturbation in predator-prey system can be found in Deng et. al. [4].

In comparison we also consider the case as the parameter a tends to zero (λ also tends to zero in this case). The total period of the limit cycle also tends to infinity as $a \rightarrow 0^+$. But the asymptotic profile of the limit cycle is quite different. In this limit, the predator population $v(t)$ shows a spiky pulse shape, and the temporal length of the pulse is in a scale of $O(|\ln \lambda|)$; on the other hand, the prey population $u(t)$ shows a profile of Heaviside function, with slow time scales $O(\lambda^{-1})$ when $u(t) \approx 0$ or $u(t) \approx 1$ (the carrying capacity), connected by fast time scales of $O(|\ln \lambda|)$ between them (see Figure 3). See Theorem 4.2 for a more mathematical description.

The latter result provides further answer to an old question in ecological studies. In [24], Rosenzweig argues that enrichment of the environment (larger carrying capacity K in (2)) leads to destabilizing of the coexistence equilibrium, which is so-called paradox of enrichment. From (5), when other parameters are fixed, increasing K is necessarily equivalent to decreasing a . Our result shows that the time interval when the prey is population near zero is extremely long when the carrying capacity K is extremely large. That could make the prey population even more vulnerable to catastrophe perturbation with long time with very low population density.

Our result is rigorously proved by using basic differential and integral calculus, a Lyapunov function, and phase plane analysis. It is noteworthy that the orbit of the limit cycle in (4) does not follow the slow manifold as other nonlinear relaxation oscillators. It is well known that (4) can be converted to a generalized Liénard equation with a nontrivial transformation (see [16]), but the relaxation oscillation found here does not follow from known results for Liénard equations or Van der Pol equations. In fact, by using the change of variables:

$$u = \frac{ad}{m-d}x, \quad v = \frac{m-d}{m}y, \quad t = \frac{a+u}{ad}\tau,$$

we can convert (4) to

$$\frac{dx}{d\tau} = x(a_1 + a_2x - a_3x^2) - xy, \quad \frac{dy}{d\tau} = -y + xy, \quad (6)$$

where a_i ($i = 1, 2, 3$) are positive constants defined by

$$a_1 = \frac{1}{d}, \quad a_2 = \frac{1-a}{m-d}, \quad a_3 = \frac{ad}{(m-d)^2}.$$

The system (6) has a unique coexistence equilibrium point $(x, y) = (1, y_0 \equiv a_1 + a_2 - a_3)$ and

$$y_0 = \frac{1}{d} + \frac{1-a}{m-d} - \frac{ad}{(m-d)^2}.$$

A further change of variables

$$x = e^u, \quad y = y_0 e^{v/y_0}, \quad (7)$$

transform (6) into a generalized Liénard equation:

$$\frac{du}{d\tau} = -[\phi(v) + F(u)], \quad \frac{dv}{d\tau} = h(u), \quad (8)$$

where $\phi(v) = y_0(e^{v/y_0} - 1)$, $F(u) = a_2 - a_3 - a_2e^u + a_3e^{2u}$, and $h(u) = y_0(e^u - 1)$. Using this form and a uniqueness result of limit cycle of Liénard equation by Zhang [31], one can prove the uniqueness of limit cycle of (4) (see [16]). But when $d \rightarrow 0$, we have $y_0 \rightarrow \infty$ and the profile of the limit cycle does not follow from any existing results. We point out that the relaxation oscillation property of Van der Pol system

$$\varepsilon \frac{dx}{dt} = y - F(x), \quad \frac{dy}{dt} = h(x),$$

when $\varepsilon \rightarrow 0$ has been studied by Liénard [17], Ponzo and Wax [22, 23], Grasman [6]. More delicate limiting behavior of the limit cycle of the special system

$$\frac{dx}{dt} = y - \frac{x^2}{2} - \frac{x^3}{3}, \quad \frac{dy}{dt} = \varepsilon(a - x),$$

has been recently obtained by Dumortier and Roussarie [5], Krupa and Szmolyan [15] and others.

We recall some well-known results regarding the dynamics of system (4) in Section 2, and we prove our main results in Section 3 and 4 for the case $d \rightarrow 0$ and $a \rightarrow 0$ respectively. We will use δ_i and C_i , ($i \in \mathbf{N}$), to denote various positive constants. These constants are independent of d in Section 3, and are independent of a in Section 4.

2. Known results. In this section we summarize known results about the predator-prey system (4). More detailed analysis can be found in [8, 10, 11]. The predator-prey system (4) has three steady state solutions: $(0, 0)$, $(1, 0)$, $(\lambda, v_\lambda) \equiv (\lambda, \frac{(1-\lambda)(a+\lambda)}{m})$, where $\lambda = \frac{ad}{m-d}$. The coexistence equilibrium (λ, v_λ) is in the first quadrant if and only if $d < \frac{m}{a+1}$ (or $0 < \lambda < 1$). When $d \geq \frac{m}{a+1}$ (or $\lambda \geq 1$), $(1, 0)$ is globally stable. Hence we always assume that $0 < d < \frac{m}{a+1}$ in the following.

Global stability of (λ, v_λ) can be established through a Lyapunov function (see [8, 9, 10]):

$$W(u, v) = \int_\lambda^u \frac{p(\xi) - d}{p(\xi)} d\xi + \int_{v_\lambda}^v \frac{\eta - v_\lambda}{\eta} d\eta, \tag{9}$$

where $p(u) = \frac{mu}{a+u}$. From straightforward calculation,

$$\dot{W}(u(t), v(t)) = [p(u) - p(\lambda)] \cdot [v_0(u) - v_0(\lambda)], \tag{10}$$

where

$$v_0(u) = \frac{u(1-u)}{p(u)} = \frac{(a+u)(1-u)}{m}. \tag{11}$$

When $a \geq 1$, $v_0'(u) < 0$ for any $u > 0$. Hence when $a \geq 1$, $\dot{W} < 0$ along an orbit $(u(t), v(t))$ of (4) and $\dot{W} = 0$ only if $(u(t), v(t)) = (\lambda, v_\lambda)$. Thus (λ, v_λ) is globally asymptotically stable when $a \geq 1$. On the other hand, if $0 < a < 1$, but $v_\lambda \leq a/m$ (which is equivalent to $v_0(\lambda) \leq v_0(0)$), then $[p(u) - p(\lambda)] \cdot [v_0(u) - v_0(\lambda)] \leq 0$ for any $u > 0$, and in this case (λ, v_λ) is also globally asymptotically stable. We notice that $v_\lambda \leq a/m$ is equivalent to

$$\lambda \geq 1 - a. \tag{12}$$

That leaves the case: for any $a, m > 0$,

$$a < 1, \quad \text{and} \quad 0 < d < m(1 - a) \quad (\text{or equivalently } 0 < \lambda < 1 - a). \tag{13}$$

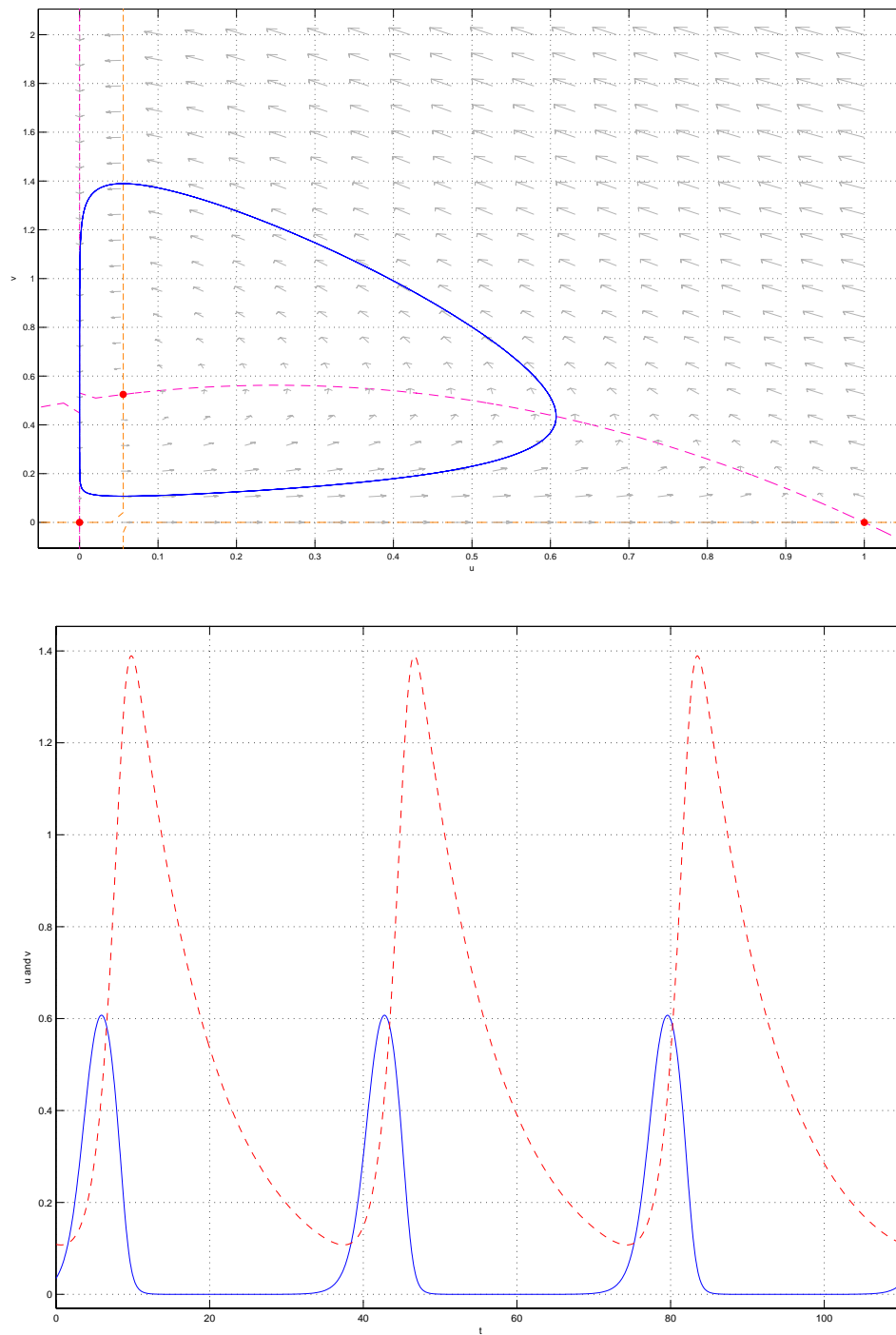


FIGURE 1. Plot of limit cycle. (left) phase portrait; (right) solution curves. Parameters: $a = 0.5$, $m = 1$, $d = 0.1$, $\lambda = 1/18 \approx 0.056$, period $T \approx 37$.

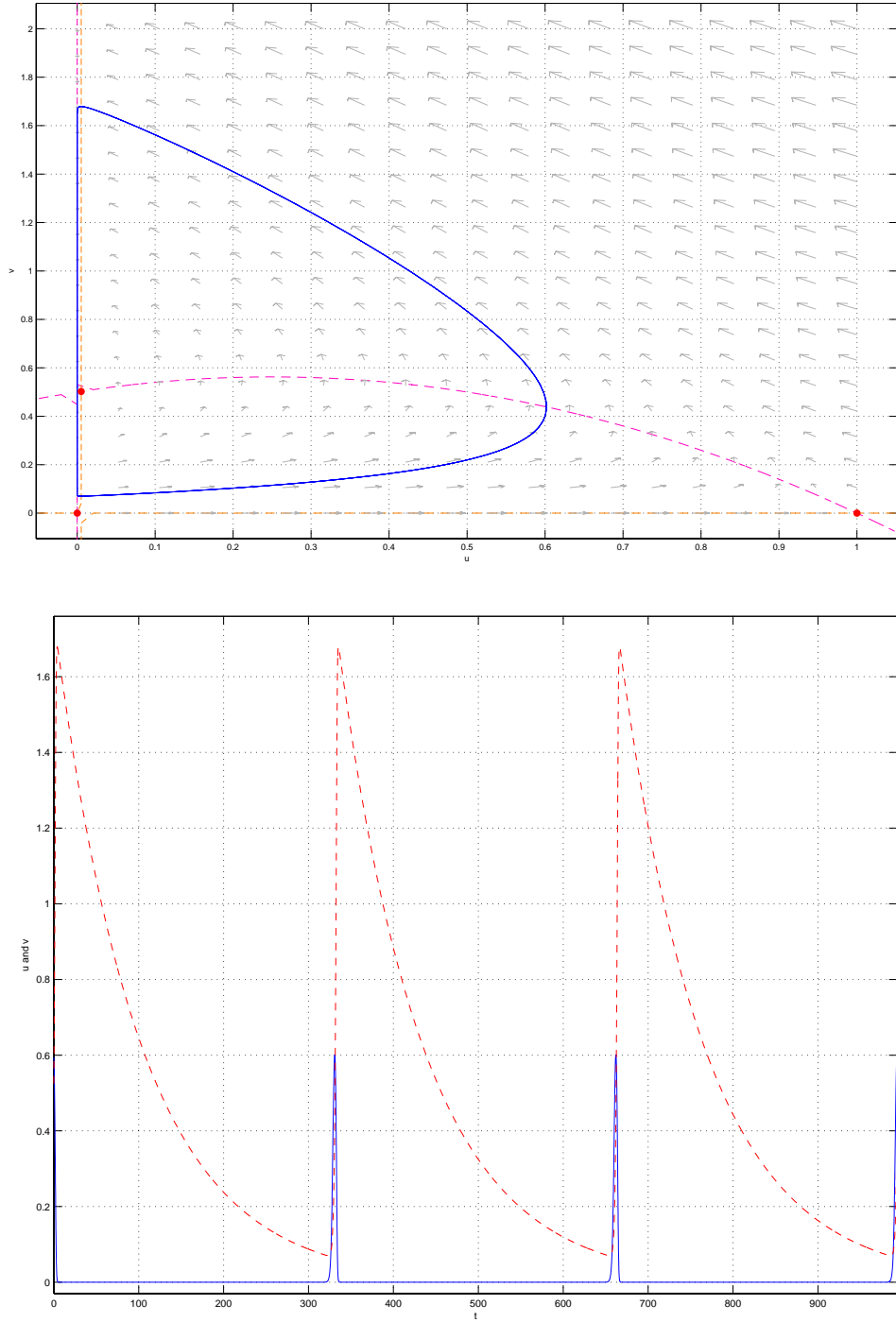


FIGURE 2. Plot of limit cycle with small d . (left) phase portrait; (right) solution curves. Parameters: $a = 0.5$, $m = 1$, $d = 0.01$, $\lambda = 1/198 \approx 0.005$, period $T \approx 336$.

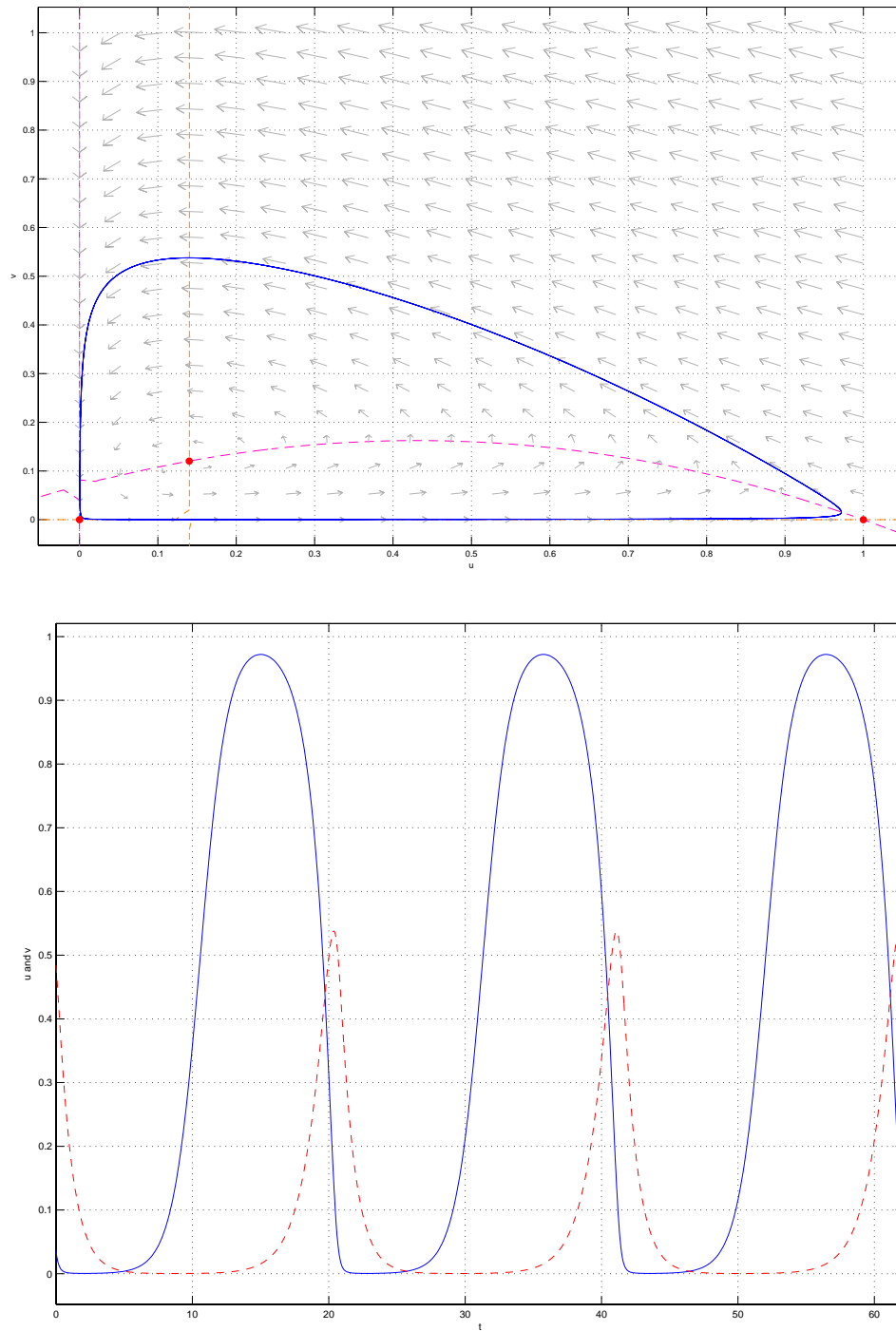


FIGURE 3. Plot of limit cycle. (left) phase portrait; (right) solution curves. Parameters: $a = 0.14$, $m = 2$, $d = 1$, $\lambda = 0.14$, period $T \approx 23$.

The dynamics of (4) under (13) is completely understood. The local stability of (λ, v_λ) can be determined from the linearization at the equilibrium. We use λ as the bifurcation parameter. The Jacobian at (λ, v_λ) is

$$J = \begin{pmatrix} \frac{\lambda(1-a-2\lambda)}{a+\lambda} & -\frac{m\lambda}{a+\lambda} \\ \frac{a(1-\lambda)}{a+\lambda} & 0 \end{pmatrix} \equiv \begin{pmatrix} \mathcal{A}(\lambda) & \mathcal{B}(\lambda) \\ \mathcal{C}(\lambda) & 0 \end{pmatrix}. \quad (14)$$

Then $\lambda_* = \frac{1-a}{2}$ is a Hopf bifurcation point. When $\frac{1-a}{2} < \lambda < 1$, (λ, v_λ) is locally asymptotically stable. Indeed the local stability indeed implies the global asymptotical stability of (λ, v_λ) from the Poincaré-Bendixon theory and Dulac Theorem [11], and the global stability of (λ, v_λ) can also be proved through a mixed type Lyapunov function (see [1, 3, 9]). Finally when $0 < \lambda < \frac{1-a}{2}$, (λ, v_λ) is locally unstable, and (4) possesses a unique limit cycle which is globally asymptotically orbital stable (see [2, 16]).

3. Asymptotic behavior of the limit cycle for d small. In the equation, we define

$$\begin{aligned} f(u, v) &= uf_1(u, v) = u \left(1 - u - \frac{mv}{a+u} \right) \\ g(u, v) &= vg_1(u, v) = v \left(-d + \frac{mu}{a+u} \right). \end{aligned} \quad (15)$$

In the first part we construct an invariant region where the limit cycle is located. For this part, we always assume that $m, d > 0$, $0 < a < 1$, and $\lambda = ad/(m-d)$ satisfies $0 < \lambda < (1-a)/2$.

We first give an estimate of the unstable manifold $U = \{(u_1(t), v_1(t)) : t \in \mathbf{R}\}$ at the saddle point $(1, 0)$. From the phase portrait, it satisfies $0 < u_1(t) < 1$ for all $t \in \mathbf{R}$; U is above the isocline $v_0(u) = \frac{(1-u)(a+u)}{m}$ when $\lambda < u < 1$. Since it is monotone for $\lambda < u < 1$, we denote this portion by $\{(u, v_1(u)) : \lambda \leq u \leq 1\}$ with $v_1(1) = 0$. We define

$$\begin{aligned} v_2(u) &= \left(1 + \frac{a+1}{m} \right) (1-u), \\ v_3(u) &= \frac{m-d}{m}(1-u) + \frac{da}{m} \ln u. \end{aligned} \quad (16)$$

Lemma 3.1. *The unstable manifold satisfies*

$$v_2(u) \geq v_1(u) \geq v_3(u), \quad \lambda \leq u \leq 1. \quad (17)$$

Proof. From the equation (4), we have

$$\frac{dv}{du} = \frac{v}{-mv + (1-u)(a+u)} \cdot \frac{(m-d)u - da}{u}.$$

Since the unstable manifold satisfies $0 < u_1(t) < 1$ for all $t \in \mathbf{R}$, then along U , we have

$$\frac{dv}{du} \leq \frac{v}{-mv} \cdot \frac{(m-d)u - da}{u} = -\frac{(m-d)u - da}{mu}.$$

Integrating along the portion of U from $u = 1$ to some $u < \lambda$, we obtain

$$v \geq \frac{m-d}{m}(1-u) + \frac{da}{m} \ln u = v_3(u),$$

if $(u, v) \in U$ and $\lambda \leq u \leq 1$.

For the upper bound, we notice that the tangent line of the unstable manifold is $v = \left(1 + \frac{(a+1)(1-d)}{m}\right)(1-u)$, which is below $v = v_2(u)$. Hence we only need to show that the vector field $(f(u, v), g(u, v))$ points towards the region below the line $v = v_2(u)$ when $(u, v) = (u, v_2(u))$ and $\lambda < u < 1$. That is equivalent to

$$\left| \frac{dv}{du} \right| \leq 1 + \frac{a+1}{m}.$$

Let $l = 1 + \frac{a+1}{m}$. Indeed on $(u, v) = (u, v_2(u))$,

$$\left| \frac{dv}{du} \right| = \frac{l(1-u)[(m-d)u - da]}{|u[(1-u)(a+u) - ml(1-u)]|} \leq \frac{l(m-d)}{ml-a-u} \leq \frac{ml}{ml-a-1} = l.$$

That proves the upper bound $v_1(u) \leq v_2(u)$. \square

From Lemma 3.1, the unstable manifold reaches its maximum v -value when $u = \lambda$, and the maximum value v_* can be estimated as

$$\frac{m-d}{m}(1-\lambda) + \frac{da}{m} \ln \lambda \leq v_* \leq \left(1 + \frac{a+1}{m}\right)(1-\lambda). \quad (18)$$

From the phase portrait of the system, the limit cycle is below the unstable manifold U , then we also have the following upper bound for the location of limit cycle.

Lemma 3.2. *Define*

$$v_4(u) = \begin{cases} v_2(u), & \lambda \leq u \leq 1, \\ v_2(\lambda), & 0 \leq u \leq \lambda. \end{cases} \quad (19)$$

Then the orbit of the limit cycle $\Sigma = \{(u(t), v(t)) : 0 \leq t \leq T\}$ satisfies

$$\Sigma \subset \{(u, v) : 0 < u < 1, 0 < v < v_4(u)\} \equiv R_1.$$

In constructing a more precise region $R_2 \subset R_1$ containing Σ , we prove that for a sub-region R_3 containing (λ, v_λ) , $\Sigma \cap R_3 = \emptyset$. Define

$$R_3 = \{(u, v) \in \mathbf{R}_+^2 : W(u, v) \leq W(1-a-\lambda, v_\lambda)\}, \quad (20)$$

where $W(u, v)$ is the function defined in (9). We notice that $(1-a-\lambda, v_\lambda)$ is the reflection of (λ, v_λ) with respect to the line $u = (1-a)/2$. Such reflection technique is a key in proving the uniqueness of the limit cycle of (4) ([2]).

Lemma 3.3. *Let R_3 be defined as in (20). Then R_3 is a bounded convex subset of \mathbf{R}_+^2 containing (λ, v_λ) , and $\Sigma \cap R_3 = \emptyset$. In particular $\Sigma \subset R_2 \equiv R_1 \setminus R_3$.*

Proof. From the definition in (9), $W(u, v) = W_1(u) + W_2(v)$, where $W_1(u) = \int_\lambda^u \frac{p(\xi) - d}{p(\xi)} d\xi$ and $W_2(v) = \int_{v_\lambda}^v \frac{\eta - v_\lambda}{\eta} d\eta$. It is easy to see that $W_1(u)$ is strictly decreasing in $[0, \lambda)$ and is strictly increasing in (λ, ∞) ; and $W_2(v)$ is strictly decreasing in $[0, v_\lambda)$ and is strictly increasing in (v_λ, ∞) . Hence W achieves the global minimum at the unique critical point (λ, v_λ) , and every level curve of $W(u, v)$ is a bounded closed curve. The level curves have convex boundary since W_1 and W_2

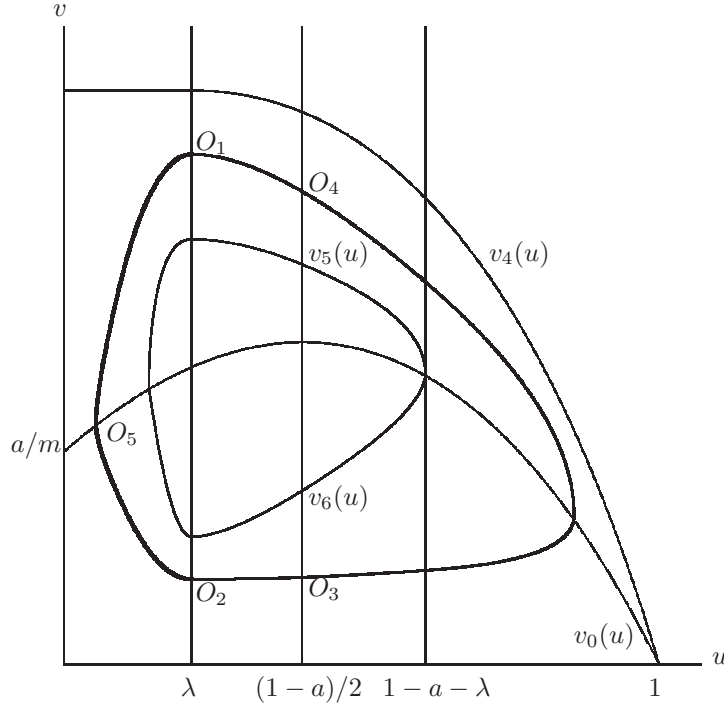


FIGURE 4. Illustration of the phase portrait (not up to scale) and the limit cycle in the proof. The isoclines are the thin solid curves: $u = 0$, $v = 0$, $u = \lambda$ and the parabola $v = v_0(u)$; the limit cycle is the thick solid curve $O_1O_2O_3O_4$; the boundary of the invariant region R_3 : $v = v_4(u)$ is the outer boundary (together with $u = 0$ and $v = 0$); $v = v_5(u)$ and $v = v_6(u)$ are the upper and lower portions of inner boundary respectively; the line $u = 1 - a - \lambda$ is the reflection of $u = \lambda$ with respect to $u = (1 - a)/2$.

are both convex one-variable functions. For R_3 defined in (20), $(1 - a - \lambda, v_\lambda)$ is the right-most point of R_3 . Thus for any solution orbit $(u(t), v(t))$ passing through $(u, v) \in R_3 \setminus \{(1 - a - \lambda, v_\lambda)\}$, $\dot{W}(u(t), v(t)) = [p(u) - p(\lambda)] \cdot [v_0(u) - v_0(\lambda)] > 0$. In particular, for $(u, v) \in \partial R_3 \setminus \{(1 - a - \lambda, v_\lambda)\}$, the vector field $(f(u, v), g(u, v))$ points outwards. Hence from the properties of periodic orbit, $\Sigma \cap R_3 = \emptyset$. \square

From Lemmas 3.2 and 3.3, we have obtained an invariant region R_2 where the limit cycle is located. Next we give some estimates for the extremal points on the orbit of limit cycle as $d \rightarrow 0^+$. The other two parameters $0 < a < 1$ and $m > 0$ are fixed, while $\lambda = ad/(m - d) \rightarrow 0$ as $d \rightarrow 0^+$. Hence d and λ are two equivalent parameters which tend to zero. Define

$$\begin{aligned} u_{\lambda,-} &= \min\{u(t) : (u(t), v(t)) \in \Sigma\}, & u_{\lambda,+} &= \max\{u(t) : (u(t), v(t)) \in \Sigma\}, \\ v_{\lambda,-} &= \min\{v(t) : (u(t), v(t)) \in \Sigma\}, & v_{\lambda,+} &= \max\{v(t) : (u(t), v(t)) \in \Sigma\}. \end{aligned} \tag{21}$$

Notice that the both the upper and lower portions of the limit cycle are monotone functions, thus we define

$$\Sigma = \{(u, v_+(\lambda, u)) : u_{\lambda,-} \leq u \leq u_{\lambda,+}\} \cup \{(u, v_-(\lambda, u)) : u_{\lambda,-} \leq u \leq u_{\lambda,+}\}, \tag{22}$$

such that $v_-(\lambda, u) < v_0(u) < v_+(\lambda, u)$ for $u_{\lambda,-} < u < u_{\lambda,+}$. That is, $\{(u, v_+(\lambda, u))\}$ is the upper portion of the limit cycle Σ , and $\{(u, v_-(\lambda, u))\}$ is the lower portion. From the equations, it is easy to see that $u_{\lambda,-}$ and $u_{\lambda,+}$ are achieved when Σ intersects with the isocline $v = v_0(u)$, and $v_{\lambda,-}$ and $v_{\lambda,+}$ are achieved when Σ intersects with the line $u = \lambda$. Our estimates are mainly based on the inner boundary of the region R_2 , *i.e.* the level curve $\Sigma_1 = \{(u, v) : W(u, v) = W(1 - a - \lambda, v_\lambda)\}$. Hence we also define

$$\begin{aligned} u_{1,\lambda} &= \min\{u : (u, v) \in \Sigma_1\}, & u_{2,\lambda} &= \max\{u : (u, v) \in \Sigma_1\}, \\ v_{1,\lambda} &= \min\{v : (u, v) \in \Sigma_1\}, & v_{2,\lambda} &= \max\{v : (u, v) \in \Sigma_1\}, \end{aligned} \quad (23)$$

and

$$\Sigma_1 = \{(u, v_5(u)) : u_{1,\lambda} \leq u \leq u_{2,\lambda}\} \cup \{(u, v_6(u)) : u_{1,\lambda} \leq u \leq u_{2,\lambda}\}, \quad (24)$$

such that $v_6(u) < v_0(u) < v_5(u)$ for $u_{1,\lambda} < u < u_{2,\lambda}$. Notice that $\nabla W = \left(\frac{p(u)-d}{p(u)}, \frac{v-v_\lambda}{v}\right)$, hence $v_{1,\lambda}$ and $v_{2,\lambda}$ are the two intersects of $W(u, v) = W(1 - a - \lambda, v_\lambda)$ with the line $u = \lambda$. Also $u_{2,\lambda} = 1 - a - \lambda$, and $u_{1,\lambda}$ satisfies $W(u_{1,\lambda}, v_\lambda) = W(1 - a - \lambda, v_\lambda)$ with $u_{1,\lambda} < \lambda$. We notice that

$$W(u, v) = W_1(u) + W_2(v) = \frac{a}{a+\lambda}h(u, \lambda) + h(v, v_\lambda), \quad (25)$$

where

$$h(x, b) = x - b - b \ln\left(\frac{x}{b}\right). \quad (26)$$

The function $h(x, b)$ satisfies

$$\frac{\partial h}{\partial x}(x, b) = 1 - \frac{b}{x}, \quad \frac{\partial h}{\partial b}(x, b) = -\ln\left(\frac{x}{b}\right); \quad (27)$$

and for fixed $b > 0$, $h(\cdot, b)$ achieves its global minimum 0 at $x = b$, and $\lim_{x \rightarrow 0^+} h(x, b) = \lim_{x \rightarrow \infty} h(x, b) = \infty$. Thus for any $b > 0$, $h(x, b) = c$ has exactly two roots for any $c > 0$.

Lemma 3.4. *Assume that $0 < a < 1$ and $m > 0$ are fixed. For any $\delta_0 > 0$, there exists $\delta_1 > 0$ such that for $0 < \lambda < \delta_1$,*

1. $0 < v_{\lambda,-} < v_1 + \delta_0$ and $v_2 - \delta_0 < v_{\lambda,+}$ where v_1 and v_2 are the two roots of $h(v, a/m) = 1 - a$ such that $v_1 < a/m < v_2$;
- 2.

$$0 < u_{\lambda,-} < (1 + \delta_1) \exp\left(-\frac{1-a}{\lambda}\right). \quad (28)$$

Proof. From Lemma 3.3, $v_{\lambda,-} < v_{1,\lambda}$ and $v_{2,\lambda} < v_{\lambda,+}$. By definition $v = v_{i,\lambda}$ ($i = 1, 2$) satisfy $W(\lambda, v) = W(1 - a - \lambda, v_\lambda)$. From the form of $W(u, v)$ in (25), $v = v_{i,\lambda}$ ($i = 1, 2$) satisfy

$$h(v, v_\lambda) = \frac{a}{a+\lambda}h(1 - a - \lambda, \lambda). \quad (29)$$

Clearly $v = v_{i,\lambda}$ is continuously differentiable in λ . Differentiating (29) with respect to λ with $v = v_{i,\lambda}$, and from (27), we obtain

$$\begin{aligned} &\left(1 - \frac{v_\lambda}{v_{i,\lambda}}\right) \frac{\partial v_{i,\lambda}}{\partial \lambda} - \ln\left(\frac{v_{i,\lambda}}{v_\lambda}\right) \cdot \frac{1 - a - 2\lambda}{m} \\ &= -\frac{a}{(a+\lambda)^2} \left[\frac{1 - a - 2\lambda}{1 - a - \lambda} + a \ln\left(\frac{1 - a - \lambda}{\lambda}\right) \right]. \end{aligned} \quad (30)$$

Since $v_{1,\lambda} < v_\lambda$, then (30) implies that $\frac{\partial v_{1,\lambda}}{\partial \lambda} > 0$ for all $0 < \lambda < (1 - a)/2$. In particular, $\lim_{\lambda \rightarrow 0^+} v_{1,\lambda} = v_1$ exists. On the other hand, when $\lambda \rightarrow 0^+$, the right hand side of (30) tends to $-\infty$ while the second term on the left hand side is bounded. Since $v_{2,\lambda} > v_\lambda$, then there exists $\delta_1 > 0$ such that when $0 < \lambda < \delta_1$, $\frac{\partial v_{2,\lambda}}{\partial \lambda} < 0$, and again $\lim_{\lambda \rightarrow 0^+} v_{2,\lambda} = v_2$ exists. Taking the limit of (29) as $\lambda \rightarrow 0^+$, we obtain that v_1 and v_2 satisfy $h(v, a/m) = 1 - a$. From the definitions of v_1 and v_2 , it is clear that $v_1 < a/m < v_2$. From the monotone properties of $v_{i,\lambda}$, we can assume that when $0 < \lambda < \delta_1$, $v_{1,\lambda} < v_1 + \delta_0$, and $v_{2,\lambda} > v_2 - \delta_0$. Thus when $0 < \lambda < \delta_1$, $v_{\lambda,-} < v_{1,\lambda} < v_1 + \delta_0$, and $v_{\lambda,+} > v_{2,\lambda} > v_2 - \delta_0$.

For part 2, it is clear that $u_{\lambda,-} < \lambda$ from the phase portrait. For the more precise estimate of $u_{\lambda,-}$, we observe that $u_{\lambda,-} < u_{1,\lambda}$. So it suffices to give an estimate of $u_{1,\lambda}$. Indeed $u_{1,\lambda}$ satisfies $W(u_{1,\lambda}, v_\lambda) = W(1 - a - \lambda, v_\lambda)$, thus from (25), we have $h(u_{1,\lambda}, \lambda) = h(1 - a - \lambda, \lambda)$, which implies that

$$u_{1,\lambda} - \lambda \ln(u_{1,\lambda}) = 1 - a - \lambda - \lambda \ln(1 - a - \lambda). \tag{31}$$

Taking the limit of (31) as $\lambda \rightarrow 0^+$, we obtain that

$$\lim_{\lambda \rightarrow 0^+} [u_{1,\lambda} - \lambda \ln(u_{1,\lambda})] = 1 - a. \tag{32}$$

But $0 < u_{1,\lambda} < \lambda$, hence $\lim_{\lambda \rightarrow 0^+} [-\lambda \ln(u_{1,\lambda})] = 1 - a$. This implies that

$$u_{1,\lambda} = \exp\left(-\frac{1-a}{\lambda}\right) + \text{higher order terms}, \tag{33}$$

which in turn implies the estimate in part 2. □

To obtain the global asymptotical behavior of the limit cycle Σ , we divide the orbit with four reference points (see Figure 4):

$$\begin{aligned} O_1 &= (\lambda, v_{\lambda,+}), & O_2 &= (\lambda, v_{\lambda,-}), \\ O_3 &= \left(\frac{1-a}{2}, v_- \left(\frac{1-a}{2}\right)\right), & O_4 &= \left(\frac{1-a}{2}, v_+ \left(\frac{1-a}{2}\right)\right). \end{aligned} \tag{34}$$

Let $T = T(\lambda)$ be the period of Σ . Then $T = T_1 + T_2 + T_3 + T_4$, where T_i is the time taken from O_i to O_{i+1} (with $O_5 = O_1$). We also assume that $u(0) = \lambda$ and $v(0) = v_{\lambda,+}$, i.e. the orbit starts from the highest point of $v(t)$. Our main result in this section is

Theorem 3.5. *Let $\Sigma = \{(u(t), v(t)) : t \in \mathbf{R}\}$ be the orbit of the unique periodic solution of (4) when $0 < \lambda < (1 - a)/2$. Assume that $0 < a < 1$ and $m > 0$ are fixed, the extremal points of Σ are defined as in (21), and O_i, T_i ($i = 1, 2, 3, 4$) and the period T are defined as above. When $\lambda > 0$ is sufficiently small (or equivalently $d > 0$ is small), then there exist constants $C_4, C_5 > 0$ independent of λ , such that $C_5\lambda^{-1} \geq T \geq C_4\lambda^{-1}$. Moreover, for $\lambda > 0$ sufficiently small, there exists some $C_6 > 0$, such that*

$$C_5\lambda^{-1} \geq T_1 \geq C_6\lambda^{-1}, \quad T_2 = O(|\ln \lambda|), \quad T_3 = O(1), \quad \text{and} \quad T_4 = O(|\ln \lambda|), \tag{35}$$

as $\lambda \rightarrow 0^+$.

Proof. We prove the theorem in several steps.

Step 1: We show that

$$T_1 \geq d^{-1} \left(1 - \frac{u_{\lambda,-}}{\lambda}\right)^{-1} \ln \left(\frac{v_{\lambda,+}}{v_{\lambda,-}}\right). \quad (36)$$

We define $u_{\lambda,-} = \lambda(1 - \delta_2)$ for some $0 < \delta_2 < 1$. Then for $0 < t < T_1$, $\lambda(1 - \delta_2) \leq u(t) < \lambda$, and from the equation of $v(t)$,

$$v' = v \left(-d + \frac{mu}{a+u}\right) \geq v \left(-d + \frac{m\lambda(1-\delta_2)}{a+\lambda(1-\delta_2)}\right) = -v \left(\frac{d\delta_2(m-d)}{m-d\delta_2}\right) \geq -d\delta_2 v.$$

Hence $v(t) \geq v(0) \exp(-d\delta_2 t)$, which leads to

$$T_1 \geq \delta_2^{-1} d^{-1} \ln \left(\frac{v_{\lambda,+}}{v_{\lambda,-}}\right) = d^{-1} \left(1 - \frac{u_{\lambda,-}}{\lambda}\right)^{-1} \ln \left(\frac{v_{\lambda,+}}{v_{\lambda,-}}\right). \quad (37)$$

Step 2: We show there exist constants $\delta_3, \delta_4, C_1 > 0$ such that when $0 < \lambda < \delta_4$,

$$0 < T_2 \leq (\delta_3 m)^{-1} (-a \ln \lambda - \lambda + C_1). \quad (38)$$

For $T_1 \leq t \leq T_1 + T_2$, we have $\lambda \leq u(t) \leq (1-a)/2$. From the equation of $u(t)$,

$$u' = p(u)[v_0(u) - v] \geq p(u)[v_0(u) - v_6(u)], \quad (39)$$

which follows from Lemma 3.3 that the limit cycle is below the level curve $(u, v_6(u))$ in this portion. Since $v_0(u)$ is concave while $v_6(u)$ is convex, then the minimum of $v_7(u) = v_0(u) - v_6(u)$ on the interval $[\lambda, (1-a)/2]$ must achieve at either $u = \lambda$ or $u = (1-a)/2$. From the proof of Lemma 3.4, $v_6(\lambda) \rightarrow v_1$, the smaller root of $h(v, a/m) = 1 - a$, and $v_0(\lambda) = v_\lambda \rightarrow a/m$ as $\lambda \rightarrow 0^+$. Thus $v_7(\lambda) \rightarrow a/m - v_1 > 0$ as $\lambda \rightarrow 0^+$. Similarly as $\lambda \rightarrow 0^+$, $v_0((1-a)/2) \rightarrow (1+a)^2/(4m)$, and $v_6((1-a)/2) \rightarrow$ the smaller root of $h(v, a/m) = (1-a)/2$ as we take the limit of $\lambda \rightarrow 0^+$ in

$$\begin{aligned} W \left(\frac{1-a}{2}, v_6 \left(\frac{1-a}{2} \right) \right) &= \frac{a}{a+\lambda} h \left(\frac{1-a}{2}, \lambda \right) + h \left(v_6 \left(\frac{1-a}{2} \right), v_\lambda \right) \\ &= \frac{a}{a+\lambda} h(1-a-\lambda, \lambda). \end{aligned}$$

Thus there exist $\delta_3, \delta_4 > 0$ such that when $0 < \lambda < \delta_4$, then

$$v_0(u) - v_6(u) \geq \min \left\{ v_0(\lambda) - v_6(\lambda), v_0 \left(\frac{1-a}{2} \right) - v_6 \left(\frac{1-a}{2} \right) \right\} \geq \delta_3 > 0. \quad (40)$$

Now from (39) and (40), we have

$$\frac{a+u}{u} \frac{du}{dt} \geq \delta_3 m, \quad \text{and} \quad a \ln \left(\frac{1-a}{2\lambda} \right) + \frac{1-a}{2} - \lambda \geq \delta_3 m T_2, \quad (41)$$

which implies (38) with $C_1 = a \ln((1-a)/2) + (1-a)/2$.

Step 3: We show that

$$0 < T_3 \leq \left(\frac{m(1-a)}{1+a} - d \right)^{-1} \ln \left(\frac{v_+((1-a)/2)}{v_-((1-a)/2)} \right). \quad (42)$$

For this portion, $u(t) \geq (1-a)/2$. From the equation of v , we have

$$v' = v(-d + p(u)) \geq v(-d + p((1-a)/2)) = v \left(\frac{m(1-a)}{1+a} - d \right).$$

Hence $v(t) \geq v(T_1 + T_2) \exp\left(\left(\frac{m(1-a)}{1+a} - d\right)t\right)$, and in particular

$$v_+ \left(\frac{1-a}{2}\right) \geq v_- \left(\frac{1-a}{2}\right) \exp\left(\left(\frac{m(1-a)}{1+a} - d\right)T_3\right),$$

which implies (42).

Step 4: We show there exist constants $\delta_5, \delta_6, C_2 > 0$ such that when $0 < \lambda < \delta_6$,

$$0 < T_4 \leq (\delta_5 m)^{-1}(-a \ln \lambda - \lambda + C_2). \tag{43}$$

This is similar to Step 2. Now we have

$$u' = p(u)[v_0(u) - v] \leq p(u)[v_0(u) - v_5(u)] \leq p(u) \left[v_0\left(\frac{1-a}{2}\right) - v_5\left(\frac{1-a}{2}\right) \right]. \tag{44}$$

Here the first inequality is from Lemma 3.4, and the second inequality is from that fact that $v_0(u)$ is increasing while $v_5(u)$ is decreasing in $[\lambda, (1-a)/2)$, and $v_0(u) < v_5(u)$. Similar to Step 2, we obtain that when $0 < \lambda < \delta_6$,

$$|u'| \geq \delta_5 p(u).$$

The remaining part is same as Step 2.

Step 5: We show that for any $0 < \delta_7 < 1$, when $\lambda > 0$ is sufficiently small, there exists constant $C_3 > 0$ such that

$$T_1 \leq \frac{1}{\delta_7} d^{-1} \ln\left(\frac{v_{\lambda,+}}{v_{\lambda,-}}\right) + C_3. \tag{45}$$

We reconsider the portion of Σ in $(0, T_1)$ again. From Lemma 3.4 part 2, when $\lambda > 0$ is small enough, the orbit does reach $u = \lambda(1 - \delta_7)$. We write $T_1 = T_{11} + T_{12} + T_{13}$ so that $u(T_{11}) = \lambda(1 - \delta_7)$, and $u(T_{12}) = \lambda(1 - \delta_7)$. That is, T_{11} and $T_{11} + T_{12}$ are the times that Σ reaches $u = \lambda(1 - \delta_7)$. We also define $v_{11} = v(T_{11})$ and $v_{12} = v(T_{11} + T_{12})$.

For $t \in (T_{11}, T_{11} + T_{12})$, when $\lambda > 0$ is sufficiently small, similar to Step 1,

$$v' = v\left(-d + \frac{mu}{a+u}\right) \leq v\left(-d + \frac{m\lambda(1-\delta_7)}{a+\lambda(1-\delta_7)}\right) = -v\left(\frac{d\delta_7(m-d)}{m-d\delta_7}\right) \leq -\frac{d\delta_7}{1+\varepsilon}v,$$

for any small $\varepsilon > 0$ if d is small enough. Since we can choose δ_7 arbitrarily, without loss of generality we can take $\varepsilon = 0$. Hence we obtain $v_{12} \leq v_{11} \exp(-d\delta_7 T_{12})$, and

$$T_{12} \leq \frac{1}{d\delta_7} \ln\left(\frac{v_{11}}{v_{12}}\right) \leq \frac{1}{d\delta_7} \ln\left(\frac{v_{\lambda,+}}{v_{\lambda,-}}\right) \tag{46}$$

Next we estimate T_{11} . Similar to Step 4, for $\lambda > 0$ small, $|u'| \geq \delta_8 p(u)$ for some $\delta_8 > 0$, if $0 < \lambda < \delta_9$. Here the estimate of $v_0(u) - v_5(u)$ can be obtained using the same proof of Lemma 3.4 part 1. Indeed we can replace (29) by

$$\frac{a}{a+\lambda} h((1-\delta)\lambda, \lambda) + h(v_5((1-\delta)\lambda), v_\lambda) = \frac{a}{a+\lambda} h(1-a-\lambda, \lambda), \tag{47}$$

for $0 < \delta \leq \delta_7$. Then the same arguments yields $|u'| \geq \delta_8 p(u)$. Integration gives

$$a \ln\left(\frac{\lambda}{(1-\delta_7)\lambda}\right) + \delta_7 \lambda \geq \delta_8 m T_{11}.$$

Hence T_{11} is bounded by a constant independent of λ . Similarly we can prove T_{13} is bounded.

Step 6: We show that there exist constants $v_3, v_4 > 0$ such that $v_{\lambda,+} < v_3$ and $v_4 < v_{\lambda,-}$ for all small $\lambda > 0$.

From Lemma 3.1 and (18), we obtain the estimate of upper bound of $v_{\lambda,+}$ by letting $v_3 = (m + a + 1)/m$. For the estimate of v_4 , we notice that any solution orbit satisfies

$$\frac{du}{dv} = \frac{p(u)}{p(u) - d} \cdot \frac{v_0(u) - v}{v}. \tag{48}$$

Recall that $O_1 = (\lambda, v_{\lambda,+})$ and $O_2 = (\lambda, v_{\lambda,-})$ are the highest and lowest points on the orbit of the limit cycle Σ . Let the leftmost point on Σ be $O_5 = (u_{\lambda,-}, v_*)$. Then from (48), we obtain that

$$\int_{v_{\lambda,-}}^{v_*} \frac{v_0(u_2(v)) - v}{v} dv = \int_{\lambda}^{u_{\lambda,-}} \frac{p(u) - d}{p(u)} du = \int_{v_{\lambda,+}}^{v_*} \frac{v_0(u_1(v)) - v}{v} dv, \tag{49}$$

where $(u_1(v), v)$, $v_* \leq v \leq v_{\lambda,+}$, represents the orbit O_1O_5 , and $(u_2(v), v)$, $v_{\lambda,-} \leq v \leq v_*$, represents the orbit O_5O_2 . For the last integral in (49),

$$\begin{aligned} & \int_{v_{\lambda,+}}^{v_*} \frac{v_0(u) - v}{v} dv = \int_{v_*}^{v_{\lambda,+}} \frac{v - v_0(u)}{v} dv \\ & \leq \int_{v_*}^{v_{\lambda,+}} \frac{v - v_*}{v} dv = v_{\lambda,+} - v_* - v_* \ln v_{\lambda,+} + v_* \ln v_*. \end{aligned} \tag{50}$$

Since $v_2 - \delta_0 < v_{\lambda,+} < v_3$ for small λ , then the right hand side of (50) is bounded. On the other hand, for the first integral in (49),

$$\int_{v_{\lambda,-}}^{v_*} \frac{v_0(u) - v}{v} dv \geq \int_{v_{\lambda,-}}^{v_*} \frac{v_* - v}{v} dv = v_{\lambda,-} - v_* - v_* \ln v_{\lambda,-} + v_* \ln v_*. \tag{51}$$

Thus $-\ln v_{\lambda,-}$ is bounded from above from (49), (50) and (51), and consequently $v_{\lambda,-}$ is bounded from below by some $v_4 > 0$ for all small $\lambda > 0$.

Step 7: The completion of the proof.

From Lemma 3.4 and Step 6, when $\lambda > 0$ is small, $v_4 < v_{\lambda,-} < v_1 + \delta_0$ and $v_2 - \delta_0 < v_{\lambda,+} < v_3$ where v_1 and v_2 are the two roots of $h(v, a/m) = 1 - a$ such that $v_1 < a/m < v_2$, and also $\lim_{\lambda \rightarrow 0^+} \lambda^{-1} u_{\lambda,-} = 0$. Also from the definition of λ , $d^{-1} = \frac{a + \lambda}{\lambda m} > \frac{a}{m} \lambda^{-1}$, and $d^{-1} < \frac{a}{m} (1 + \delta_{10}) \lambda^{-1}$ for any small $\delta_{10} > 0$ and we assume λ small. Thus from Step 1 and Step 5, for any $0 < \delta_{11} < 1$, as long as $\lambda > 0$ is sufficiently small,

$$\frac{(1 + \delta_{10})a}{\delta_7 m} \lambda^{-1} \ln \left(\frac{v_3}{v_4} \right) + C_3 \geq T_1 \geq (1 - \delta_{11}) \frac{a}{m} \lambda^{-1} \ln \left(\frac{v_2 - \delta_0}{v_1 + \delta_0} \right). \tag{52}$$

Hence we obtain the estimate for T_1 in the theorem, since all constants except λ are independent of λ . The estimate for T_3 can also be obtained from Step 3 and Step 6 since $v_+((1 - a)/2) < v_{\lambda,+} < v_3$ and $v_-((1 - a)/2) > v_{\lambda,-} > v_4$. The estimates of T_i for $i = 2, 4$ are clear from Steps 2 and 4, and $T = \sum T_i = O(\lambda^{-1})$. This completes the proof. \square

Remark.

1. Our construction of an invariant region in Lemma 3.3 does not require the smallness of λ —it holds as long as $0 < \lambda < (1 - a)/2$. This gives a direct proof of the existence of periodic orbit.
2. When defining O_3 and O_4 , the choice of $u = (1 - a)/2$ can be replaced by any fixed $u = \beta \in (0, (1 - a)/2]$, and the results of Theorem 3.5 still hold with this change.

4. Asymptotic behavior of the limit cycle for a small. In this section, we assume that d and m are fixed so that $m > d > 0$, and $a > 0$ is small (thus $a < 1$). We will use a lot of estimates established in Section 3, and we will also use the same notations in Section 3 as well.

Lemma 4.1. *Assume that $m > d > 0$ are fixed. There exist constants $\delta_0, \delta_1, \delta_2, \delta_3, \delta_4, v_5, v_6 > 0$ such that for $0 < \lambda < \delta_0$,*

1. $\delta_1 < -a \ln v_{\lambda,-} < \delta_2$ and $v_5 < v_{\lambda,+} < v_6$,
2. $\delta_4 < -a \ln u_{\lambda,-} < \delta_3$.

Proof. We use the notations in the proof of Lemma 3.4. Recall that $v_{\lambda,-} < v_{1,\lambda}$ and $v_{2,\lambda} < v_{\lambda,+}$, and $v = v_{i,\lambda}$ satisfy (29), which can be rewritten into

$$v - v_{\lambda} - v_{\lambda} \ln \left(\frac{v}{v_{\lambda}} \right) = \frac{m-d}{m} (1 - a - 2\lambda - \lambda \ln(1 - a - \lambda) + \lambda \ln \lambda). \quad (53)$$

Then when $\lambda \rightarrow 0$ (and $a \rightarrow 0$), one can see that $v_{2,\lambda} \rightarrow (m-d)/m$, $v_{1,\lambda} \rightarrow 0$ and $\lim_{\lambda \rightarrow 0} (-v_{\lambda} \ln v_{1,\lambda}) = (m-d)/m$. On the other hand, from (18), $v_{\lambda,+} < (m+a+1)/m$. Thus $v_5 < v_{\lambda,+} < v_6$ for some constants $v_5, v_6 > 0$ independent of λ . From the estimate of $v_{1,\lambda}$, we have obtained that $-a \ln(v_{\lambda,-}) \geq \delta_1 > 0$. For the upper bound of $\ln v_{\lambda,-}$, we use the equation (48). From (49), (50) and (51), we obtain that

$$v_{\lambda,+} - v_* \ln v_{\lambda,+} \geq v_{\lambda,-} - v_* \ln v_{\lambda,-}. \quad (54)$$

Since $v_{\lambda} > v_* > a/m$, $v_*, v_{\lambda,-} \rightarrow 0$ as $a \rightarrow 0$ and $v_{\lambda,+}$ is bounded, then $-a \ln(v_{\lambda,-}) \leq \delta_2$ for some $\delta_2 > 0$. On the other hand, for the second integral in (49), we have

$$\int_{\lambda}^{u_{\lambda,-}} \frac{p(u) - d}{p(u)} du = \frac{m-d}{m} (u_{\lambda,-} - \lambda) - \frac{da}{m} \ln \left(\frac{u_{\lambda,-}}{\lambda} \right). \quad (55)$$

From (50), (51) and (55), we obtain that

$$\begin{aligned} v_{\lambda,-} - v_* - v_* \ln v_{\lambda,-} + v_* \ln v_* &\leq \frac{m-d}{m} (u_{\lambda,-} - \lambda) - \frac{da}{m} \ln \left(\frac{u_{\lambda,-}}{\lambda} \right) \\ &\leq v_{\lambda,+} - v_* - v_* \ln v_{\lambda,+} + v_* \ln v_*. \end{aligned} \quad (56)$$

Then the estimates for $-a \ln u_{\lambda,-}$ follow from those of $v_{\lambda,-}$ and $v_{\lambda,+}$. \square

Theorem 4.2. *Let $\Sigma = \{(u(t), v(t)) : t \in \mathbf{R}\}$ be the orbit of the unique periodic solution of (4) when $0 < \lambda < (1-a)/2$. Assume that $m > d > 0$ are fixed, the extremal points of Σ are defined as in (21), and O_i, T_i ($i = 1, 2, 3, 4$) and the period T are defined as in Section 3. When $\lambda > 0$ (or equivalently $a > 0$ is small) is sufficiently small, then there exist constants $C_8, C_9 > 0$ independent of λ , such that $C_8 \lambda^{-1} \geq T \geq C_9 \lambda^{-1}$. Moreover, for $\lambda > 0$ sufficiently small, there exists some $C_6 > 0$, such that*

$$C_2 \lambda^{-1} \geq T_1 \geq C_7 \lambda^{-1}, \quad T_2 = O(|\ln \lambda|), \quad C_5 \lambda^{-1} \geq T_3 \geq C_6 \lambda^{-1}, \quad \text{and} \quad T_4 = O(1), \quad (57)$$

as $\lambda \rightarrow 0^+$.

Proof. The proof follows and modifies the one for Theorem 3.5, and we still use the notations in the proof of Theorem 3.5 unless specified otherwise. Step 1 still holds here. Indeed we define T_{14} to be the time spent from $O_1 = (\lambda, v_{\lambda,+})$ to $O_5 = (u_{\lambda,-}, v_*)$, and T_{15} to be the time spent from O_5 to $O_2 = (\lambda, v_{\lambda,-})$. Then the same proof in Step 1 gives

$$T_{14} \geq d^{-1} \left(1 - \frac{u_{\lambda,-}}{\lambda} \right)^{-1} \ln \left(\frac{v_{\lambda,+}}{v_*} \right), \quad T_{15} \geq d^{-1} \left(1 - \frac{u_{\lambda,-}}{\lambda} \right)^{-1} \ln \left(\frac{v_*}{v_{\lambda,-}} \right). \quad (58)$$

Then from Lemma 4.1, as $\lambda \rightarrow 0^+$,

$$T_{14} \geq C_1 |\ln \lambda|, \quad \text{and} \quad T_{15} \geq C_2 \lambda^{-1}. \quad (59)$$

For Step 2, from the equation of $u(t)$, we obtain

$$u' = p(u)[v_0(u) - v] \leq u(1 - u). \quad (60)$$

then an integration of (60) gives

$$\ln \frac{1-a}{1+a} - \ln \frac{\lambda}{1-\lambda} \leq T_2, \quad (61)$$

hence $T_2 \geq -\ln \lambda$. On the other hand, from the same argument in Step 2 and Lemma 4.1, we can show that $\delta_5 < -a \ln v_6((1-a)/2) < \delta_6$ for some $\delta_5, \delta_6 > 0$. For any small $\delta_7 > 0$, we choose λ (or a) small enough so that

$$\frac{m \exp(-\delta_6/a)}{a + \lambda} = \frac{(m-d) \exp(-\delta_6/a)}{a} < \delta_7, \quad (62)$$

then

$$\begin{aligned} u' &= p(u)[v_0(u) - v] \geq p(u) \left[\frac{(a+u)(1-u)}{m} - v_- \left(\frac{1-a}{2} \right) \right] \\ &\geq p(u) \left[\frac{(a+u)(1-u)}{m} - v_6 \left(\frac{1-a}{2} \right) \right] \\ &\geq p(u) \left[\frac{(a+u)(1-u)}{m} - \exp(-\delta_6/a) \right] \\ &\geq p(u) \frac{(a+u)(1-\delta_7-u)}{m} = u(1-\delta_7-u). \end{aligned} \quad (63)$$

Then the integration of (63) yields

$$\frac{1}{1-\delta_7} \left[\ln \frac{1-a}{1+a-2\delta_7} - \ln \frac{\lambda}{1-\lambda-\delta_7} \right] \geq T_2, \quad (64)$$

Therefore if a and δ_7 are small, then $T_2 \leq -(1-\delta_7)^{-1} \ln \lambda$. We have proved

$$C_3 |\ln \lambda| \leq T_2 \leq C_4 |\ln \lambda|. \quad (65)$$

For Step 4, the proof is similar to that in Theorem 3.5 since both $v_0((1-a)/2)$ and $v_5((1-a)/2)$ are bounded and tend to limits when $a \rightarrow 0^+$, and $\lim_{a \rightarrow 0} [v_0((1-a)/2) - v_5((1-a)/2)] < 0$. Hence we still obtain that $T_4 = O(1)$.

For Step 3, the estimate (42) still holds, which gives $T_3 \leq C_5 |\ln v_-((1-a)/2)| \leq C_5 |\ln v_{\lambda,-}| \leq C_5 \lambda^{-1}$. On the other hand, from the equation of v , when $u > \lambda$, we have

$$v' = v(-d + p(u)) \leq v(-d + p(1)) = v \left(\frac{m}{1+a} - d \right). \quad (66)$$

We integrate the equation (66) from $t = T_1$ (when $(u(T_1), v(T_1)) = O_2$) to $t = T = \sum_{i=1}^4 T_i$ (when $(u(T), v(T)) = O_1$, that is, the right half of the orbit), then

$$T_2 + T_3 + T_4 \geq \left(\frac{m}{1+a} - d \right)^{-1} \ln \left(\frac{v_{\lambda,+}}{v_{\lambda,-}} \right) \geq C_6 \lambda^{-1}. \quad (67)$$

However $T_2 = O(|\ln \lambda|)$ and $T_4 = O(1)$, then

$$C_6 \lambda^{-1} < T_3 \leq C_5 \lambda^{-1}. \quad (68)$$

Finally the arguments in Step 5 are also valid, then $T_1 \leq C_7 \lambda^{-1}$. \square

Remark.

1. Theorem 4.2 can be interpreted as that the orbit is very slow when it is near the two saddle equilibrium points $(0, 0)$ and $(1, 0)$. From our proof, the orbit is exponentially close to $(0, 0)$ and $(1, 0)$, and from numerical simulation, the orbit is also fairly close to the unstable manifolds at $(0, 0)$ and $(1, 0)$.
2. From the proof of Theorem 4.2, we can also see that the time when $v(t) < O(a)$ is in order of $O(\lambda^{-1})$, and the time when $v(t) > O(a)$ is in order of $O(|\ln \lambda|)$.

Acknowledgements. JS thanks the hospitality of Center of Mathematical Science in National Tsing-Hua University when this work was done. We would like to thank the reviewer for helpful comments.

REFERENCES

- [1] A. Ardito and P. Ricciardi, *Lyapunov functions for a generalized Gause-type model*, J. Math. Biol., **33** (1995), 816–828.
- [2] Kuo Shung Cheng, *Uniqueness of a limit cycle for a predator-prey system*, SIAM J. Math. Anal., **12** (1981), 541–548.
- [3] Chuang-Hsiung Chiu and Sze-Bi Hsu, *Extinction of top-predator in a three-level food-chain model*, J. Math. Biol., **37** (1998), 372–380.
- [4] Bo Deng, Shannon Jessie, Glenn Ledder, Alex Rand and Sarah Srodulski, *Biological control does not imply paradox*, Math. Biosci., **208** (2007), 26–32.
- [5] Freddy Dumortier and Robert Roussarie, *Canard cycles and center manifolds*, Mem. Amer. Math. Soc., **121** (1996), 100 pp.
- [6] Johan Grasman, “Asymptotic Methods for Relaxation Oscillations and Applications,” Applied Mathematical Sciences, **63**, Springer-Verlag, New York, 1987.
- [7] C. S. Holling, *The components of predation as revealed by a study of small mammal predation of the European Pine Sawfly*, Canadian Entomologist, **91** (1959), 293–320.
- [8] S. B. Hsu, *On global stability of a predator-prey system*, Math. Biosci., **39** (1978), 1–10.
- [9] Sze-Bi Hsu, *A survey of constructing Lyapunov functions for mathematical models in population biology*, Taiwanese J. Math., **9** (2005), 151–173.
- [10] Sze-Bi Hsu, “Ordinary Differential Equations with Applications,” Series on Applied Mathematics, **16**. World Scientific Publishing Co. Pte. Ltd., Hackensack, NJ, 2006.
- [11] S. B. Hsu, S. P. Hubbell and Paul Waltman, *Competing predators*, SIAM J. Appl. Math., **35** (1978), 617–625.
- [12] S.-B. Hsu, S. P. Hubbell and P. Waltman, *A contribution to the theory of competing predators*, Ecological Monographs, **48** (1978), 337–349.
- [13] Sze-Bi Hsu, Tzy-Wei Hwang and Yang Kuang, *Global analysis of the Michaelis-Menten-type ratio-dependent predator-prey system*, J. Math. Biol., **42** (2001), 489–506.
- [14] Tzy-Wei Hwang, *Uniqueness of limit cycles of the predator-prey system with Beddington-DeAngelis functional response*, J. Math. Anal. Appl., **290** (2004), 113–122.
- [15] M. Krupa and P. Szmolyan, *Relaxation oscillation and canard explosion*, J. Differential Equations, **174** (2001), 312–368.
- [16] Yang Kuang and H. I. Freedman, *Uniqueness of limit cycles in Gause-type models of predator-prey systems*, Math. Biosci., **88** (1988), 67–84.
- [17] A. Liénard, *Etude des oscillations entretenues*, Revue Générale de L’électricité, **23** (1928), 901–912, 946–954.
- [18] Weishi Liu, Dongmei Xiao and Yingfei Yi, *Relaxation oscillations in a class of predator-prey systems*, J. Differential Equations, **188** (2003), 306–331.
- [19] R. M. May, *Limit cycles in predator-prey communities*, Science, **177** (1972), 900–902.
- [20] C. D. McAllister, R. J. LeBrasseur, T. R. Parsons and M. L. Rosenzweig, *Stability of enriched aquatic ecosystems*, Science, **175** (1971), 562–565.
- [21] Simona Muratori and Sergio Rinaldi, *Remarks on competitive coexistence.*, SIAM J. Appl. Math., **49** (1989), 1462–1472.
- [22] Peter J. Poincaré and Nelson Wax, *On certain relaxation oscillations: Confining regions*, Quart. Appl. Math., **23** (1965), 215–234.

- [23] Peter J. Poincaré and Nelson Wax, *On certain relaxation oscillations: Asymptotic solutions*, SIAM Jour. Appl. Math., **13** (1965), 740–766.
- [24] Michael L. Rosenzweig, *Paradox of enrichment: destabilization of exploitation ecosystems in ecological time*, Science, **171** (1971), 385–387.
- [25] M. L. Rosenzweig and R. MacArthur, *Graphical representation and stability conditions of predator-prey interactions*, Amer. Natur., **97** (1963), 209–223.
- [26] Steven Strogatz, “Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry, and Engineering,” Perseus Publishing, 2000.
- [27] Jitsuro Sugie, Rie Kohno and Rinko Miyazaki, *On a predator-prey system of Holling type*, Proc. Amer. Math. Soc., **125** (1997), 2041–2050.
- [28] B. Van der Pol, *On relaxation oscillations*, Phil. Maga., **2** (1926), 978–992.
- [29] B. Van der Pol, *Biological rhythms considered as relaxation oscillations*, Acta Med. Scand. Suppl., **108** (1940), 76–87.
- [30] Dongmei Xiao and Zhifeng Zhang, *On the uniqueness and nonexistence of limit cycles for predator-prey systems*, Nonlinearity, **16** (2003), 1185–1201.
- [31] Zhi Fen Zhang, *Proof of the uniqueness theorem of limit cycles of generalized Liénard equations*, Appl. Anal., **23** (1986), 63–76.

Received June 2008; revised December 2008.

E-mail address: sbhsu@math.nthu.edu.tw

E-mail address: shij@math.wm.edu