

Homoclinic orbits in predator-prey systems with an Allee effect

島根大学 総合理工学部 杉江実郎 (Jitsuro Sugie)
 島根大学 総合理工学研究科 木本恭子 (Kyoko Kimoto)
Department of Mathematics
Shimane University

1 Introduction

A class of Gause-type predator-prey systems is one of the most important mathematical models in population ecology. The following is a typical form of this model:

$$u' = ur(u) - p(u)v, \quad v' = v(q(u) - D). \tag{1.1}$$

Here $u(t)$ and $v(t)$ are prey and predator densities, respectively; $' = d/dt$; $p(u)$ is the capture rate of prey per predator (the rate is called a *functional response* of predators to prey); $q(u)$ is the growth rate of the predator enhanced by an amount proportional to the prey density; $r(u)$ is the density-dependent growth rate of the prey in the absence of any predators; $D > 0$ is the death rate of the predator in the absence of any preys (for details, see [3, Chap. 4]).

System (1.1) includes various kinds of famous models (say, Lotka-Volterra type, Holling type, Ivlev type) as specific cases. It naturally has been studied by a number of authors; for example, results can be found in [1–17, 20–22] and the references cited therein. In those literature it is assumed that the rates $r(u)$, $q(u)$ and $p(u)$ are sufficiently smooth on $[0, \infty)$ and satisfy

- (i) $r(0) > 0$ and there exists a $K > 0$ such that $r(K) = 0$ and $(u - K)r(u) < 0$ for $u \neq K$;
- (ii) $q(0) = 0$, $\frac{d}{du}q(u) > 0$ for all $u > 0$ and there exists a $u^* \in (0, K)$ such that $q(u^*) = D$;
- (iii) $p(0) = 0$ and $\frac{d}{du}p(u) > 0$ for all $u > 0$,

respectively. Let $v^* = u^*r(u^*)/p(u^*)$. Then, from the assumptions above, the point $E^*(u^*, v^*)$ is a unique equilibrium in the first quadrant $Q = \{(u, v) : u > 0 \text{ and } v > 0\}$. We call E^* the *positive equilibrium* hereafter.

Main subjects of system (1.1) are the existence of a unique limit cycle which surrounds the positive equilibrium E^* (see, [1, 9–11, 13, 16, 17, 21, 22]) and the global asymptotic stability of the positive equilibrium E^* (refer to [2, 6, 12, 20]). The positive equilibrium E^* is said to be *globally asymptotically stable* if E^* is stable and if every orbit tends to E^* .

It is easy to show that all solutions of (1.1) are bounded in the future and remain in the first quadrant Q . Hence, the Poincaré-Bendixson theorem shows that if system (1.1) has a unique limit cycle, then E^* has to be unstable. Indeed, E^* is *locally repulsive*; that is, there exists some neighborhood U of E^* such that each orbit of (1.1) starting at every point in U goes away from U and each orbit of (1.1) starting at every point in $Q \setminus U$ does not enter into U . The smoothness of the rates $r(u)$, $q(u)$ and $p(u)$ in system (1.1) plays a major role in showing that E^* is locally repulsive when system (1.1) has a unique limit cycle.

In a general dynamical system, however, an equilibrium is not always locally repulsive even if it is unstable. An orbit is said to be *homoclinic* if its α - and ω -limit sets are the same equilibrium. If a homoclinic orbit exists, then the corresponding equilibrium is unstable, but it is not locally repulsive.

Sugie and Katayama [20] have shown that under the above assumptions (i)–(iii) and the smoothness condition on $r(u)$, $q(u)$ and $p(u)$, system (1.1) has no homoclinic orbits. From their result we see that there is only two possibilities: either system (1.1) has at least one limit cycle or the positive equilibrium E^* is globally asymptotically stable. It is safe to say that system (1.1) has relatively simple global phase portraits because of the smooth rates.

A question naturally arises as to what will happen in the case of non-smooth rates. Does a homoclinic orbit appear in system (1.1) for lack of smoothness of the rates? To give an answer to this question, we consider the predator-prey system with a non-smooth prey growth rate:

$$u' = u(\beta - \gamma|u - \alpha|) - uv, \quad v' = v(u^2 - \alpha^2), \quad (1.2)$$

where α , β and γ are positive constants. System (1.2) has the positive equilibrium E^* at $(u^*, v^*) = (\alpha, \beta)$. Since

$$p(u) = u, \quad q(u) = u^2, \quad r(u) = \beta - \gamma|u - \alpha| \quad \text{and} \quad D = \alpha^2$$

in system (1.2), assumption (ii) holds and assumption (iii) is satisfied with $u^* = \alpha$. Also, assumption (i) is satisfied with $K = \alpha + \beta/\gamma$ if $\beta > \alpha\gamma$. Otherwise $r(u)$ does not satisfy the assumption (i). Note that $r(u)$ is continuous for all $u \geq 0$, but is not differentiable at $u = \alpha$.

Our main result is stated as follows:

Theorem 1.1. *System (1.2) has homoclinic orbits if and only if $0 < \beta \leq \gamma^2/8$.*

When any predators are absent, system (1.2) is reduced to

$$u' = u(\beta - \gamma|u - \alpha|). \quad (1.3)$$

In this model, the growth rate of the prey increases with the prey density up to the peak β and then the rate decreases as the density increases. Hence, Eq. (1.3) exhibits the so-called ‘‘Allee effect.’’ In the case that $\beta < \alpha\gamma$, a low density leads to extinction. To be precise, if the density is lower than $\alpha - \beta/\gamma$, then the prey is strictly decreasing and will die out. The Allee effect is an important phenomenon in the population dynamics.

From the above-mentioned relation between the prey growth rate and its density, we may say that system (1.2) is an ecological significant model simulating the effects of underpopulation and overpopulation of the prey. In system (1.2), the prey and the predator may coexist or they may die together. Only one side of species cannot survive. For further details, see Sec. 4.

2 Proof of the main theorem

Consider a generalized Liénard system of the form

$$\dot{x} = h(y) - F(x), \quad \dot{y} = -g(x), \quad (2.1)$$

where $\dot{} = d/ds$; $F(x)$ and $g(x)$ are continuous on an open interval I which contains 0, and $h(y)$ is continuous and strictly increasing on \mathbb{R} . The functions $F(x)$, $g(x)$ and $h(y)$ satisfy smoothness conditions for uniqueness of solutions of initial value problems. We assume that $F(0) = 0$,

$$xg(x) > 0 \quad \text{if } x \neq 0$$

and

$$yh(y) > 0 \quad \text{if } y \neq 0.$$

Then the origin is the unique critical point of (2.1). Define the nonnegative function $G(x)$ by

$$G(x) = \int_0^x g(\xi) d\xi.$$

Under the assumption that there exists an $m > 0$ such that

$$h(y) \leq my \quad (2.2)$$

for $y > 0$ sufficiently small, Sugie [18] has presented the following sufficient conditions for system (2.1) to have homoclinic orbits (see also [19]).

Theorem A. *Assume (2.2) and suppose that*

$$F(x) \geq \sqrt{m} \left\{ 2\sqrt{2G(x)} - \phi\left(\sqrt{2G(x)}\right) \right\} \quad (2.3)$$

for $|x|$ sufficiently small, where $\phi(\sigma)$ is a nonnegative continuous function satisfying

$$\frac{\phi(\sigma)}{\sigma} \text{ is nondecreasing} \quad (2.4)$$

and there exists a constant $a > 4$ such that

$$a \left(\int_0^\sigma \frac{\phi(\xi)}{\xi^2} d\xi \right)^2 \leq \frac{\phi(\sigma)}{\sigma} \quad (2.5)$$

for $\sigma > 0$ sufficiently small. Then system (2.1) has homoclinic orbits.

Remark 2.1. We can easily find a nonnegative continuous function $\phi(u)$ satisfying conditions (2.4) and (2.5). For example, we may take $\phi(\sigma) = \sigma^{1+\varepsilon}$ for some $\varepsilon > 0$; $\phi(\sigma) = b\sigma/(\log \sigma)^2$ with $0 < b < 1/4$.

Using Theorem A, we can prove 'if'-part of Theorem 1.1.

Proof of 'if'-part of Theorem 1.1. Changing variables

$$x = u - \alpha, \quad y = \log \beta - \log v \quad \text{and} \quad ds = udt,$$

we can transform system (1.2) into system (2.1) with

$$F(x) = \gamma|x|, \quad g(x) = x + \alpha - \frac{\alpha^2}{x + \alpha} \quad \text{and} \quad h(y) = \beta(1 - e^{-y}), \quad (2.6)$$

where $F(x)$ and $g(x)$ are defined on $(-\alpha, \infty)$, and $h(y)$ is defined on \mathbb{R} . Note that $F(0) = 0$, $xg(x) > 0$ if $x \neq 0$ and $yh(y) > 0$ if $y \neq 0$. We get

$$G(x) = \frac{1}{2}x^2 + \alpha x - \alpha^2 \log \left(\frac{x + \alpha}{\alpha} \right).$$

Let $m = \beta$. Then it is easy to check that

$$h(y) \leq my,$$

namely, condition (2.2). We take $\phi(\sigma) = \sigma\sqrt{\sigma}$. Then it is clear that $\phi(\sigma)$ is nonnegative and continuous for $\sigma > 0$. Since $\phi(\sigma)/\sigma = \sqrt{\sigma}$, condition (2.4) holds. We have

$$a \left(\int_0^\sigma \frac{\phi(\xi)}{\xi^2} d\xi \right)^2 = 4a\sigma < \sqrt{\sigma} = \frac{\phi(\sigma)}{\sigma}$$

for $\sigma > 0$ sufficiently small. Thus, condition (2.5) is also satisfied with arbitrary $a > 4$.

We will show that condition (2.3) holds for $|x|$ sufficiently small. Since $\beta \leq \gamma^2/8$, it is enough to show that

$$F(x) \geq \frac{\gamma}{2} \left\{ 2\sqrt{G(x)} - \sqrt{G(x)} \sqrt[4]{2G(x)} \right\},$$

namely,

$$|x| \geq \sqrt{G(x)} \left\{ 1 - \frac{1}{2} \sqrt[4]{2G(x)} \right\} \quad (2.7)$$

in some neighborhood of $x = 0$. We first estimate that

$$\begin{aligned} g(x) &< 2x \quad \text{for } x > -\alpha \text{ and } x \neq 0; \\ g(x) &> 3x \quad \text{for } -\frac{\alpha}{2} < x < 0. \end{aligned} \quad (2.8)$$

In fact, we have

$$\frac{d}{dx}g(x) = 1 + \frac{\alpha^2}{(x + \alpha)^2} \quad \text{and} \quad \frac{d^2}{dx^2}g(x) = -\frac{2\alpha^2}{(x + \alpha)^3} < 0$$

for $x > -\alpha$, and therefore,

$$\left. \frac{d}{dx} g(x) \right|_{x=0} = 2$$

and $g(x)$ is a convex function. We also have

$$g\left(-\frac{\alpha}{2}\right) = -\frac{3}{2}\alpha = 3\left(-\frac{\alpha}{2}\right).$$

From (2.8) we see that

$$\begin{aligned} \sqrt{G(x)} &< |x| \quad \text{for } x > 0; \\ |x| &< \sqrt{G(x)} < \sqrt{\frac{3}{2}}|x| \quad \text{for } -\frac{\alpha}{2} < x < 0. \end{aligned} \tag{2.9}$$

Hence, it is clear that (2.7) holds for $x \geq 0$. Let us examine whether (2.7) is also true for $x < 0$ or not. To this end, we define

$$f_1(x) = \frac{2}{\alpha}x^2 - x + \alpha - \frac{\alpha^2}{x + \alpha}.$$

Then, from a straightforward calculation, we conclude that there exists a $\delta > 0$ such that $f_1(x) > 0$ for $-\delta < x < 0$; that is,

$$\frac{1}{\alpha}x - 1 < \frac{g(x)}{-2x} < 0 \quad \text{for } -\delta < x < 0.$$

We may assume without loss of generality that $\delta < \min\{\alpha/2, \alpha^2/4\}$. Hence, together with (2.9), we obtain

$$\frac{1}{\alpha}x - 1 < \frac{g(x)}{2\sqrt{G(x)}} < 0 \quad \text{for } -\delta < x < 0. \tag{2.10}$$

We next define

$$f_2(x) = -x - \sqrt{G(x)} + \frac{1}{2}\sqrt{G(x)}\sqrt[4]{2G(x)}.$$

Then we have

$$f_2(0) = 0 \quad \text{and} \quad \frac{d}{dx}f_2(x) = -1 - \frac{g(x)}{2\sqrt{G(x)}} + \frac{3g(x)}{8\sqrt{G(x)}}\sqrt[4]{2G(x)}.$$

From (2.8)–(2.10) and the fact that $\delta < \alpha^2/4$, we see that

$$\begin{aligned} \frac{d}{dx}f_2(x) &< -1 - \left(\frac{1}{\alpha}x - 1\right) - \frac{3}{8}\frac{2x}{\sqrt{3/2x}}\sqrt[4]{2G(x)} \\ &< \frac{1}{\alpha}|x| - \frac{\sqrt{6}\sqrt[4]{2}}{4}\sqrt{|x|} < \frac{1}{\alpha}|x| - \frac{1}{2}\sqrt{|x|} < 0 \end{aligned}$$

for $-\delta < x < 0$. Hence, (2.7) holds for $-\delta < x < 0$.

By means of Theorem A, we conclude that system (2.1) with (2.6) has homoclinic orbits, and so has system (1.1). The proof is complete. \square

To prove ‘only if’-part of Theorem 1.1, we need the following result which is a slight modification of Theorem 2.5 in [19].

Theorem B. *Suppose that there exists an $m > 0$ such that*

$$h(y) \geq my \quad (2.11)$$

for $y > 0$ sufficiently small. Also, suppose that

$$F(x) \leq \sqrt{m} \left\{ 2\sqrt{2G(x)} - \psi\left(\sqrt{2G(x)}\right) \right\} \quad (2.12)$$

for $x > 0$ or $x < 0$, $|x|$ sufficiently small, where $\psi(\sigma)$ is a nonnegative continuous function satisfying

$$\frac{\psi(\sigma)}{\sigma} \text{ is nondecreasing and is not greater than } 2 \quad (2.13)$$

and there exists a $\sigma_0 > 0$ such that

$$\int_0^{\sigma_0} \frac{\psi(\xi)}{\xi^2} d\xi = \infty. \quad (2.14)$$

Then system (2.1) fails to have homoclinic orbits.

Remark 2.2. As simple examples satisfying conditions (2.13) and (2.14), we can cite $\psi(\sigma) = \varepsilon\sigma$ with $\varepsilon > 0$; $\psi(\sigma) = -\sigma/\log \sigma$ for $\sigma > 0$ sufficiently small.

Proof of ‘only if’-part of Theorem 1.1. As in the proof of ‘if’-part, we see that system (1.1) is equivalent to system (2.1) with (2.6). We will show that if $\beta > \gamma^2/8$, then conditions (2.11)–(2.14) in Theorem B are satisfied.

Since $\beta > \gamma^2/8$, there exists a $\rho > 0$ such that

$$\frac{\gamma}{2} + \rho = \sqrt{2\beta}.$$

Let ε be chosen so that $0 < \varepsilon < \min\{1, \gamma/2, 2\rho/(\gamma + 4)\}$. Since

$$\left. \frac{d}{dy} h(y) \right|_{y=0} = \beta,$$

condition (2.11) is satisfied with $m = \beta - \varepsilon^2/2$. Define $\psi(\sigma) = \varepsilon\sigma$. Then $\psi(\sigma)$ is nonnegative and continuous for $\sigma > 0$ and satisfies conditions (2.13) and (2.14). We have only to show that condition (2.12) also holds. From the same manner as in the proof of ‘if’-part, we can estimate that

$$|x| < \sqrt{G(x)} \quad \text{for } -\alpha < x < 0.$$

Hence, we have

$$\begin{aligned} \sqrt{m} \left\{ 2\sqrt{2G(x)} - \psi\left(\sqrt{2G(x)}\right) \right\} &= \sqrt{m}(2 - \varepsilon)\sqrt{2G(x)} = \sqrt{2\beta - \varepsilon^2}(2 - \varepsilon)\sqrt{G(x)} \\ &> \left(\sqrt{2\beta} - \varepsilon\right)(2 - \varepsilon)\sqrt{G(x)} > (\gamma/2 + \rho - \varepsilon)(2 - \varepsilon)|x| \\ &> \{(2 - \varepsilon)\rho - (\gamma/2 + 2)\varepsilon + \gamma\}|x| > (\rho - \rho + \gamma)|x| \\ &= \gamma|x| = F(x) \end{aligned}$$

for $-\alpha < x < 0$, namely, condition (2.12) is satisfied for $x < 0$, $|x|$ sufficiently small.

Thus, by Theorem B we see that system (2.1) with (2.6) has no homoclinic orbits, and neither has system (1.1). This completes the proof. \square

3 Discussion

Let us return to the Gause model (1.1). Recall that system (1.1) has three density-dependent rates $p(u)$, $q(u)$ and $r(u)$. We here suppose that $p(u)$ and $q(u)$ satisfy the assumptions (iii) and (ii) in Sec. 1, respectively; and $r(u)$ is continuous on $[0, \infty)$ with $r(u^*) > 0$, where u^* is a constant given in the assumption (ii). Note that this condition of $r(u)$ is easier than the assumption (i) in Sec. 1. Let $v^* = u^*r(u^*)/p(u^*)$. Then system (1.1) has a unique positive equilibrium $E^*(u^*, v^*)$.

By putting

$$x = u - u^*, \quad y = \log v^* - \log v \quad \text{and} \quad ds = p(u)dt,$$

system (1.1) is transformed into the system

$$\dot{x} = \frac{(x + u^*)r(x + u^*)}{p(x + u^*)} - v^*e^{-y}, \quad \dot{y} = -\frac{q(x + u^*) - D}{p(x + u^*)}. \quad (3.1)$$

Let

$$F(x) = v^* - \frac{(x + u^*)r(x + u^*)}{p(x + u^*)} \quad \text{and} \quad g(x) = \frac{q(x + u^*) - D}{p(x + u^*)}$$

for $x > -u^*$ and let

$$h(y) = v^*(1 - e^{-y})$$

for $y \in \mathbb{R}$. It is clear that $F(0) = 0$ and $yh(y) > 0$ if $y \neq 0$. From the assumption (ii) we also see that $xg(x) > 0$ for $x > -u^*$ and $x \neq 0$. Hence, system (3.1) is of Liénard type.

For the sake of simplicity, we denote

$$\Gamma(x) = \frac{(x + u^*)r(x + u^*)}{\sqrt{v^*p(x + u^*)}}$$

and

$$\Delta(x) = \sqrt{2 \int_0^x \frac{q(\xi + u^*) - D}{p(\xi + u^*)} d\xi}$$

for $x > -u^*$. Then, from Theorems A and B, we obtain the following results.

Theorem 3.1. *Suppose that*

$$\Gamma(0) - \Gamma(x) \geq 2\Delta(x) - \phi(\Delta(x)) \quad (3.2)$$

for $|x|$ sufficiently small, where $\phi(\sigma)$ is a nonnegative continuous function satisfying conditions (2.4) and (2.5). Then system (3.1) has homoclinic orbits, and so has system (1.1).

Theorem 3.2. *Suppose that there exists a constant c with $0 < c < 1$ such that*

$$\Gamma(0) - \Gamma(x) \leq c\{2\Delta(x) - \psi(\Delta(x))\} \quad (3.3)$$

for $x > 0$ or $x < 0$, $|x|$ sufficiently small, where $\psi(\sigma)$ is a nonnegative continuous function satisfying conditions (2.13) and (2.14). Then system (3.1) does not have homoclinic orbits, and neither has system (1.1).

In single-species population dynamics, the equation

$$u' = \lambda u \left(1 - \frac{u}{K}\right) \quad (3.4)$$

is very famous as the logistic growth model. The parameters λ and K are positive, and they are called the intrinsic rate of increase and the carrying capacity for the prey density, respectively. The Allee effect is taken no account in Eq. (3.4).

As mentioned in Sec. 1, we can reduce system (1.2) to Eq. (1.3) in case of absence of any predators. To contrast with system (1.2) and Eq. (1.3), we consider the system

$$u' = u(\beta - \gamma(u - \alpha)) - uv, \quad v' = v(u^2 - \alpha^2) \quad (3.5)$$

and the equation

$$u' = u(\beta - \gamma(u - \alpha)). \quad (3.6)$$

Arranging the right-hand side of (3.6), we see that this equation becomes the logistic-type equation (3.4) with $\lambda = \beta + \alpha\gamma$ and $K = \alpha + \beta/\gamma$. System (3.5) naturally belongs to the Gause model (1.1). In case of (3.5),

$$\Gamma(x) = \sqrt{\beta} - \frac{\gamma}{\sqrt{\beta}}x \quad \text{and} \quad \Delta(x) = \sqrt{x^2 + 2\alpha x - 2\alpha^2 \log\left(\frac{x + \alpha}{\alpha}\right)} \geq 0$$

for $x > -\alpha$, because $p(u) = u$, $q(u) = u^2$, $r(u) = \beta + \alpha\gamma - \gamma u$, $D = \alpha^2$ and $(u^*, v^*) = (\alpha, \beta)$. Since $\Gamma(0) - \Gamma(x) = \gamma x/\sqrt{\beta}$ for $x > -\alpha$, it turns out that for $-\alpha < x < 0$, conditions (2.13), (2.14) and (3.3) are satisfied with $c = 1/2$ and $\psi(\sigma) = \sigma$, but condition (3.2) fails to hold for an arbitrary function $\phi(\sigma)$ satisfying conditions (2.4) and (2.5). Thus, by virtue of Theorem 3.2, we conclude that system (3.5) does not have homoclinic orbits. As a matter of fact, it is easy to prove that there exist no limit cycles in system (3.5). Hence, the positive equilibrium $E^*(\alpha, \beta)$ is always globally asymptotically stable for any parameters α , β and γ . But, to argue this point would carry us too far away from the purpose of this paper, and so we omit the details.

4 Numerical Example

To illustrate our results, we give an example and a series of figures. System (1.2) has three parameters. We fix the value of γ at 2 and consider the system

$$u' = u(\beta - 2|u - \alpha|) - uv, \quad v' = v(u^2 - \alpha^2), \quad (4.1)$$

whose positive equilibrium E^* is the point (α, β) . The origin $E_0(0, 0)$ and the point $E_1(\alpha + \beta/2, 0)$ are also equilibria of (4.1). We say that an equilibrium is a *boundary equilibrium* if it is on the u -axis.

In Figures 1–4 below, we classify some orbits in five types according to the properties as follows:

- (i) an orbit starting at a point P_i ($i = 1, 2, \dots, 6$) rotates in a counterclockwise direction about E^* infinitely many times and approaches E^* ;
- (ii) an orbit starting at a point Q_i ($i = 1, 2, 3$) tends to the origin as t increases;
- (iii) an orbit starting at a point R_i ($i = 1, 2, \dots, 6$) approaches E^* without rotating about E^* perpetually;
- (iv) an orbit passing through a point S_i ($i = 1, 2, \dots, 6$) makes a loop together with E^* , namely, a homoclinic orbit;
- (v) an orbit passing through a point T_i ($i = 1, 2, 3$) connects E^* and the origin, in other words, its α -limit set is E^* and its ω -limit set is the origin.

An orbit of type (v) is said to be *heteroclinic*. The broken line in each figure indicates the graph of $v = \beta - 2|u - \alpha|$. For this reason, if an orbit meets the broken line, then it passes across the line in the vertical direction.

From Theorem 1.1 we see that system (4.1) has homoclinic orbits if and only if $0 < \beta \leq 1/2$. In Figures 1–4, we describe global phase portraits of (4.1) in the cases that $(\alpha, \beta) = (1/8, 3/4), (1/2, 3/4), (1/8, 1/3), (1/2, 1/3)$, respectively. Hence, homoclinic orbits exist only in Figures 3 and 4.

The first case: In Figure 1, we draw orbits of type (i). Each of them starts from one of the points $P_1(0.6, 0.12), P_2(0.6, 0.27), P_3(0.6, 0.42), P_4(0.6, 0.57), P_5(0.6, 0.72)$ and $P_6(0.6, 0.87)$. This figure shows that two boundary equilibria E_0 and E_1 are unstable and the positive equilibrium E^* is globally asymptotically stable. This means that the prey and the predator always exist together.

The second case: As sketched in Figure 2, another boundary equilibrium appears at the point $E_2(\alpha - \beta/2, 0)$. The boundary equilibria E_1 and E_2 are unstable, and the origin E_0 and the positive equilibrium E^* are locally asymptotically stable. There are orbits of two types (i) and (ii); each orbit starting at the point $P_1(1.2, 0.08), P_2(1.2, 0.18)$ or $P_3(1.2, 0.28)$ approaches E^* and each orbit starting at the point $Q_1(1.2, 0.32), Q_2(1.2, 0.42)$ or $Q_3(1.2, 0.52)$ tends to E_0 . Hence, E^* is not globally asymptotically stable. Both species may become extinct.

The third case: There are nine orbits in Figure 3. Each orbit passing through the point $S_1(0.125, 0.05), S_2(0.125, 0.14)$ or $S_3(0.125, 0.23)$ is homoclinic. The other orbits are not homoclinic, but they also tend to the positive equilibrium E^* . Each of them starts at the point $R_1(0.5, 0.02), R_2(0.5, 0.1), R_3(0.5, 0.18), R_4(0.5, 0.26), R_5(0.5, 0.34)$ or $R_6(0.5, 0.42)$. The boundary equilibria E_0 and E_1 are unstable. Since homoclinic orbits exist, needless to say, the

positive equilibrium E^* is not even stable. Although E^* is unstable, it is globally attractive because every orbit approaches it. Hence, the prey coexists with the predator.

The fourth case: Figure 4 is more complicated than Figures 1–3. A remarkable feature of this case is the appearance of heteroclinic orbits joining the positive equilibrium E^* and the boundary equilibrium E_0 . Such heteroclinic orbit passes through one of the points $T_1(0.2, 0.03)$, $T_2(0.2, 0.09)$ and $T_3(0.2, 0.15)$. Each orbit passing through the point $S_1(0.5, 0.05)$, $S_2(0.5, 0.15)$ or $S_3(0.5, 0.25)$ is homoclinic. There are orbits of two types (ii) and (iii) besides heteroclinic orbits and homoclinic orbits; each orbit starting at the point $Q_1(1, 0.21)$, $Q_2(1, 0.27)$ or $Q_3(1, 0.33)$ tends to E_0 and each orbit starting at the point $R_1(1, 0.02)$, $R_2(1, 0.08)$ or $R_3(1, 0.14)$ approaches E^* . As in the second case, the boundary equilibria E_1 and E_2 are unstable. Since orbits of type (ii) or (v) appear, there is a high risk of extinction of the prey and the predator.

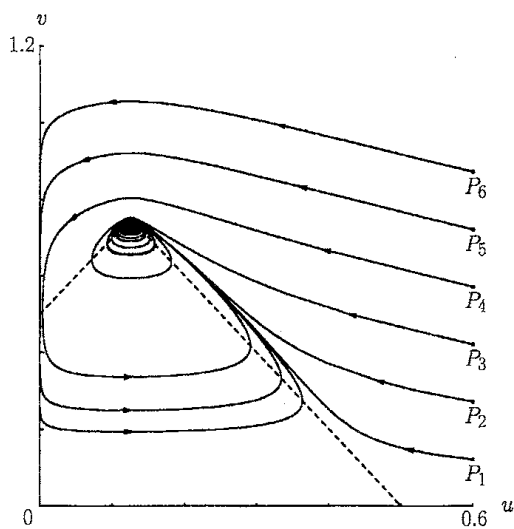


Fig. 1. Phase portrait for system (4.1) with $\alpha = 1/8$ and $\beta = 3/4$.

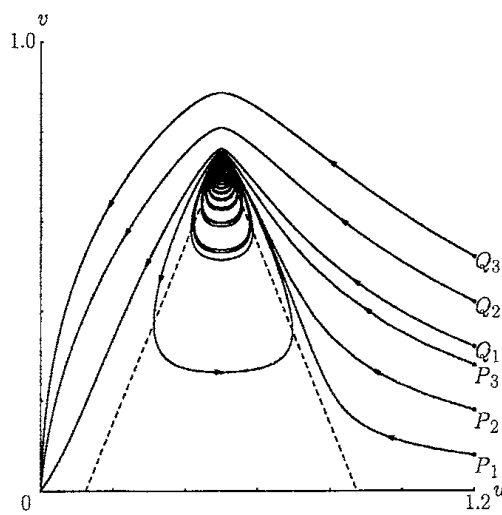


Fig. 2. Phase portrait for system (4.1) with $\alpha = 1/2$ and $\beta = 3/4$.

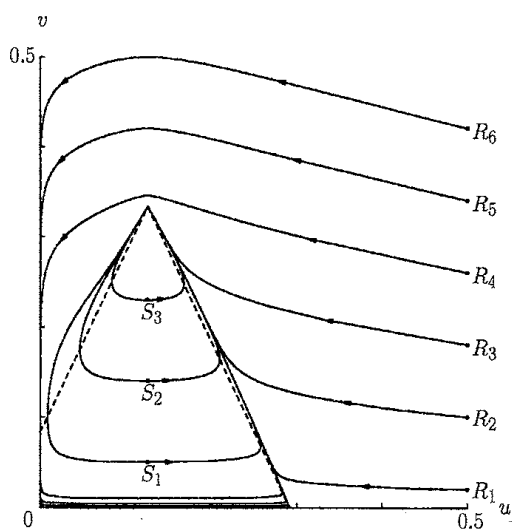


Fig. 3. Phase portrait for system (4.1) with $\alpha = 1/8$ and $\beta = 1/3$.

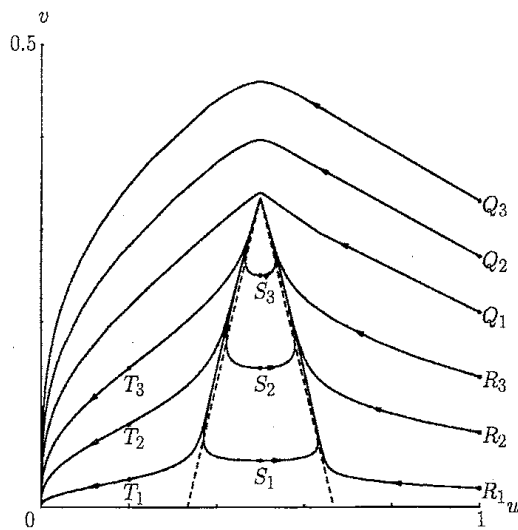


Fig. 4. Phase portrait for system (4.1) with $\alpha = 1/2$ and $\beta = 1/3$.

References

- [1] K.-S. Cheng, Uniqueness of a limit cycle for a predator-prey system, *SIAM J. Math. Anal.* **12** (1981) 541–548.
- [2] K.-S. Cheng, S.-B. Hsu and S.-S. Lin, Some results on global stability of a predator-prey system. *J. Math. Biol.* **12** (1981) 115–126.
- [3] H. I. Freedman, *Deterministic Mathematical Models in Population Ecology* (Marcel Dekker, 1980).
- [4] G. F. Gause, *The Struggle for Existence* (Williams and Wilkins, 1934).
- [5] C. S. Holling, The components of predation as revealed by a study of small-mammal predation of the European pine sawfly, *Canad. Entomol.* **91** (1959) 293–320.
- [6] S.-B. Hsu, On global stability of a predator-prey system, *Math. Biosci.* **39** (1978) 1–10.
- [7] V. S. Ivlev, *Experimental Ecology of the Feeding of Fishes* (Yale University Press, 1961).
- [8] N. D. Kazarinoff and P. van der Driessche, A model predator-prey system with functional response, *Math. Biosci.* **39** (1978) 125–134.
- [9] R. E. Kooij and A. Zegeling, A predator-prey model with Ivlev's functional response, *J. Math. Anal. Appl.* **198** (1996) 473–489.
- [10] R. E. Kooij and A. Zegeling, Qualitative properties of two-dimensional predator-prey systems, *Nonlinear Anal.* **29** (1997) 693–715.
- [11] Y. Kuang, Nonuniqueness of limit cycles of Guase-type predator-prey systems, *Appl. Anal.* **29** (1988) 269–287.
- [12] Y. Kuang, Global stability of Guase-type predator-prey systems, *J. Math. Biol.* **28** (1990) 463–474.
- [13] Y. Kuang and H. I. Freedman, Uniqueness of limit cycles of Guase-type models of predator-prey systems, *Math. Biosci.* **88** (1988) 67–84.
- [14] R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton University Press, 1974).
- [15] M. L. Rosenzweig and R. H. MacArthur, Graphical representation and stability conditions of predator-prey interactions, *Am. Naturalist.* **97** (1963) 209–223.
- [16] J. Sugie, Two-parameter bifurcation in a predator-prey system of Ivlev type, *J. Math. Anal. Appl.* **217** (1998) 349–371.
- [17] J. Sugie, Uniqueness of limit cycles in a predator-prey system with Holling-type functional response, *Quart. Appl. Math.* **58** (2000) 577–590.
- [18] J. Sugie, Homoclinic orbits in generalized Liénard systems, *J. Math. Anal. Appl.* (2005), in press.
- [19] J. Sugie and T. Hara, Existence and non-existence of homoclinic trajectories of the Liénard system, *Discrete Contin. Dynam. Systems* **2** (1996) 237–254.
- [20] J. Sugie and M. Katayama, Global asymptotic stability of a predator-prey system of Holling type, *Nonlinear Anal.* **38** (1999) 105–121.
- [21] J. Sugie, R. Kohno and R. Miyazaki, On a predator-prey system of Holling type, *Proc. Amer. Math. Soc.* **125** (1997) 2041–2050.
- [22] J. Sugie, K. Miyamoto and K. Morino, Absence of limit cycles of a predator-prey system with a sigmoid functional response, *Appl. Math. Lett.* **9** (1996) 85–90.