

# TRAVELING WAVES IN THE HOLLING-TANNER MODEL WITH WEAK DIFFUSION

ABSTRACT. For wide range of parameters, we study traveling waves in a diffusive version of the Holling-Tanner predator-prey model from population dynamics. Fronts are constructed using geometric singular perturbation theory and the theory of rotated vector fields. We focus on the appearance of the fronts in various singular limits. In addition, periodic traveling waves of relaxation oscillation type are constructed using a recent generalization of the entry-exit function.

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## 1. INTRODUCTION

The Holling-Tanner predator-prey model is the ODE system

$$(1.1) \quad \begin{aligned} u_t &= u(1-u) - \frac{uv}{\alpha+u}, \\ v_t &= \delta v \left(1 - \frac{\beta v}{u}\right), \end{aligned}$$

where  $t$  is time and  $\alpha$ ,  $\delta$  and  $\beta$  are positive parameters; see [1, 2, 3, 4, 5, 6]. The quantities  $u$  and  $v$  are related to prey and predator populations respectively. The rate at which the predator captures the prey is a normalized type II functional response  $\frac{u}{\alpha+u}$  according to the classification of Holling [7].

We will add diffusive terms to the system (1.1), with non-negative diffusion coefficients  $D_u$  and  $D_v$ :

$$(1.2) \quad \begin{aligned} u_t &= D_u u_{xx} + u(1-u) - \frac{uv}{\alpha+u}, \\ v_t &= D_v v_{xx} + \delta v \left(1 - \frac{\beta v}{u}\right). \end{aligned}$$

Now  $t > 0$  and  $x \in \mathbb{R}$ .

The ODE Holling-Tanner model has a unique equilibrium  $A$  with positive predator and prey concentrations. It corresponds to a spatially homogeneous equilibrium of the diffusive Holling-Tanner model (1.2). Previous work on (1.2) focuses on this equilibrium. For example, in [8, 9] Turing patterns that bifurcate from  $A$  are observed in numerical simulations. In [10], conditions for Turing and Hopf bifurcations are derived, and the stability of the bifurcating periodic solutions is studied.

In [11] the spreading speed of a perturbation to  $A$  in the PDE system (1.2) posed on  $N$ -dimensional space is studied using its relation to the spreading speed in the Fisher-KPP equation. To guarantee that the dynamics of the scalar Fisher-KPP equation is dominant, initial conditions of a special type are considered: the predator is introduced in a compactly supported manner, while the prey is initially uniformly well distributed.

For the ODE Holling-Tanner model (1.1), a parameter regime is found in [6] where the equilibrium  $A$  is globally stable. On the other hand, in [12] the ODE Holling-Tanner model is transformed to a generalized Liénard equation and the existence of limit cycles is investigated.

In this paper we investigate the existence of traveling waves for the system (1.2). We use the result of [6] to show the existence of traveling fronts in several parameter regimes. We complement this existence result by providing geometric constructions of the fronts that exhibit how their appearance depends on the parameters in the system. In addition, we show the existence of periodic traveling waves in one parameter regime. This result is based on a construction of relaxation oscillations for the ODE Holling-Tanner model. The construction uses a recent generalization [13] of the entry-exit function of geometric singular perturbation theory [14, 15]. Finally, we discuss the possible disappearance of these periodic traveling waves in a Hopf bifurcation.

## 2. BACKGROUND AND RESULTS

Physically relevant solutions of (1.2) are non-negative. Since the system is not defined on the line  $u = 0$  (and the line  $u = -\alpha$ ), we shall consider (1.2) on the domain  $P = \{(u, v) : u > 0, v \geq 0\}$ .

**2.1. Equilibria.** Equilibria of the ODE (1.1), and spatially homogeneous equilibria of the PDE (1.2), are given by the solutions of the algebraic system

$$u(1-u) - \frac{uv}{\alpha+u} = 0, \quad \delta v \left(1 - \frac{\beta v}{u}\right) = 0.$$

Algebraic manipulation yields  $v = (1-u)(\alpha+u)$ , and  $v = 0$  or  $v = \frac{1}{\beta}u$ . The solutions are  $(u, v) = (1, 0)$ ,  $(u, v) = (-\alpha, 0)$ , and two points  $(u_{\pm}, v_{\pm})$ , where

$$(2.1) \quad u_{\pm} = \frac{\beta(1-\alpha) - 1 \pm \sqrt{(\beta(1-\alpha) - 1)^2 + 4\alpha\beta^2}}{2\beta}, \quad v_{\pm} = \frac{1}{\beta}u_{\pm}.$$

Of these four points, the only ones in  $P$  are  $A = (u_+, v_+)$  and  $B = (1, 0)$ . They are independent of  $\delta$  and the diffusion coefficients.

In [6] the following result about the equilibrium  $A$  is proved.

**Theorem 2.1.** *Let*

$$\alpha_{\pm} = \frac{1}{4}(1 - \alpha - \delta \pm \sqrt{(1 - \alpha - \delta)^2 - 8\alpha\delta}), \quad \beta_{\pm} = \frac{\alpha_{\pm}}{(1 - \alpha_{\pm})(\alpha + \alpha_{\pm})}.$$

*Then  $0 < \alpha_- < \alpha_+ < 1$ . For the system (1.1), the equilibrium  $A$  is globally asymptotically stable in the open first quadrant if one of the following holds*

- (i)  $\alpha \geq 1$ ;
- (ii)  $\alpha < 1$  and  $\alpha + \delta \geq 1$ ;
- (iii)  $\alpha + \delta < 1$ ,  $(1 - \alpha - \delta)^2 - 8\alpha\delta > 0$ , and  $\beta > \beta_+$ ;
- (iv)  $\alpha + \delta < 1$  and  $(1 - \alpha - \delta)^2 - 8\alpha\delta > 0$ ,  $\beta$  sufficiently small and  $\beta < \beta_-$ ;
- (v)  $\alpha + \delta < 1$  and  $(1 - \alpha - \delta)^2 - 8\alpha\delta \leq 0$ .

**2.2. Traveling waves.** Replacing  $x$  in (1.2) by the moving coordinate  $\zeta = x - ct$ , we obtain

$$\begin{aligned} u_t &= D_u u_{\zeta\zeta} + cu_{\zeta} + u(1 - u) - \frac{uv}{\alpha + u}, \\ v_t &= D_v v_{\zeta\zeta} + cv_{\zeta} + \delta v \left(1 - \frac{\beta v}{u}\right). \end{aligned} \tag{2.2}$$

Traveling waves with velocity  $c$  are stationary solutions of (2.2). We consider only truly traveling waves by assuming  $c \neq 0$ . Because (2.2) is invariant under the transformation  $(\xi, c) \rightarrow (-\xi, -c)$ , it is enough consider  $c > 0$ .

To reduce the number of parameters, we let  $z = \zeta/c$ , so (2.2) becomes

$$\begin{aligned} u_t &= \frac{D_u}{c^2} u_{zz} + u_z + u(1 - u) - \frac{uv}{\alpha + u}, \\ v_t &= \frac{D_v}{c^2} v_{zz} + v_z + \delta v \left(1 - \frac{\beta v}{u}\right). \end{aligned} \tag{2.3}$$

We assume  $D_u$  and  $D_v$  are positive and set  $\epsilon = \frac{D_u}{c^2}$ ,  $\mu = \frac{D_v}{D_u}$ , so that  $\epsilon$  and  $\mu$  are positive. The system (2.3) becomes

$$\begin{aligned} u_t &= \epsilon u_{zz} + u_z + u(1 - u) - \frac{uv}{\alpha + u}, \\ v_t &= \epsilon \mu v_{zz} + v_z + \delta v \left(1 - \frac{\beta v}{u}\right). \end{aligned} \tag{2.4}$$

We assume that  $0 < \epsilon \ll 1$ , or, in other words, that the diffusion coefficient  $D_u$  is small relative to the wave velocity  $c$ . For any fixed  $c$ , this assumption is satisfied if  $D_u$  is sufficiently small. It is also satisfied for any fixed  $D_u$  if  $c$  is sufficiently large.

Thus traveling waves with velocity  $c$  of (1.2) correspond to stationary solutions of (2.4) with  $\epsilon = \frac{D_u}{c^2}$ ,  $\epsilon\mu = \frac{D_v}{c^2}$ . These solutions satisfy the ODE system

$$\begin{aligned} 0 &= \epsilon u_{zz} + u_z + u(1 - u) - \frac{uv}{\alpha + u}, \\ 0 &= \epsilon \mu v_{zz} + v_z + \delta v \left(1 - \frac{\beta v}{u}\right). \end{aligned} \tag{2.5}$$

We are concerned with two types of traveling waves:

- Fronts: solutions of (2.5) that connect  $A$  to  $B$  or  $B$  to  $A$ .
- Periodic traveling waves (wave trains): periodic solutions of (2.5).

We consider two regions in  $\alpha\beta$ -parameter space:

- Region 1: the union of the two sets  $\{(\alpha, \beta) : 0 < \alpha < 1 \text{ and } \beta > \frac{2(1-\alpha)}{(\alpha+1)^2}\}$ , and  $\{(\alpha, \beta) : \alpha \geq 1 \text{ and } \beta > 0\}$ .
- Region 2: the set  $\{(\alpha, \beta) : 0 < \alpha < 1 \text{ and } 0 < \beta < \frac{2(1-\alpha)}{(\alpha+1)^2}\}$ .

The union of these two regions is the entire open first quadrant in  $\alpha\beta$ -space, except for the curve  $\beta = \frac{2(1-\alpha)}{(\alpha+1)^2}$ ,  $0 < \alpha < 1$ . The inequalities describing parameter regimes have a geometric meaning, which is discussed in the next section.

Based on Theorem 2.1, we shall prove the following results about existence of traveling fronts.

**Theorem 2.2.** *Assume  $(\alpha, \beta)$  is in Region 1,  $\delta > 0$ , and  $\mu > 0$ . Then there exists  $\epsilon^* = \epsilon^*(\alpha, \beta, \delta, \mu) > 0$  such that for any positive  $\epsilon < \epsilon^*$ , there is a solution  $(u(z), v(z))$  of the traveling wave system (2.5) that satisfies the boundary conditions*

$$(2.6) \quad \lim_{z \rightarrow -\infty} (u(z), v(z)) = A,$$

$$(2.7) \quad \lim_{z \rightarrow +\infty} (u(z), v(z)) = B,$$

*The solution is unique up to a shift in  $z$ . The convergence to  $B$  is always monotone. Moreover, there exist  $\delta_-$  and  $\delta_+$ ,  $0 < \delta_- < \delta_+$ , such that the following is true. For each  $\delta > 0$  with  $\delta \neq \delta_-, \delta_+$ , there exists a positive  $\epsilon^{**} \leq \epsilon^*$  such that if  $0 < \epsilon < \epsilon^{**}$ , the convergence to  $A$  is oscillatory for  $\delta \in (\delta_-, \delta_+)$  and monotone for  $\delta \in (0, \delta_-) \cup (\delta_+, \infty)$ .*

**Theorem 2.3.** *Assume  $(\alpha, \beta)$  is in Region 2,  $\delta > 0$  is sufficiently large, and  $\mu > 0$ . Then there exists  $\epsilon^* = \epsilon^*(\alpha, \beta, \delta, \mu) > 0$  such that for any positive  $\epsilon < \epsilon^*$ , there is a solution  $(u(z), v(z))$  of the traveling wave system (2.5) that satisfies the boundary conditions (2.6)–(2.7). The solution is unique up to a shift in  $z$ . The convergence to the rest state  $B$  is always monotone. Moreover, there exists  $\delta_+ > 0$  such that the following is true. For each large  $\delta > 0$  with  $\delta \neq \delta_+$ , there exists a positive  $\epsilon^{**} \leq \epsilon^*$  such that if  $0 < \epsilon < \epsilon^{**}$ , the convergence to  $A$  is oscillatory for  $\delta < \delta_+$  and monotone for  $\delta > \delta_+$ .*

The types of the fronts in Theorems 2.2 and 2.3 are shown in the first and second illustrations in Fig. 2.1. As mentioned in the Introduction, we shall complement these existence results by providing geometric constructions of the fronts.

We shall also prove:

**Theorem 2.4.** *Assume  $(\alpha, \beta)$  is in Region 2,  $\delta > 0$  is sufficiently small, and  $\mu > 0$ . Then there exists  $\epsilon^* = \epsilon^*(\alpha, \beta, \delta, \mu) > 0$  such that for any positive  $\epsilon < \epsilon^*$ , there is a periodic solution  $(u(z), v(z))$  of the traveling wave system (2.5).*

Finally we shall discuss the possible disappearance of these periodic solutions in a Hopf bifurcation as  $\delta$  increases.

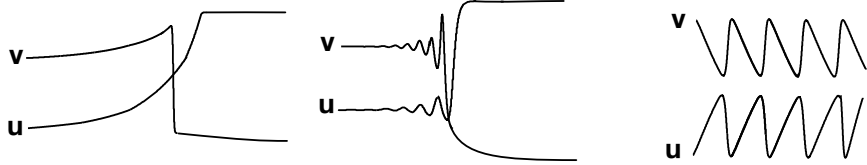


FIGURE 2.1. Different types of traveling fronts supported by the traveling wave system (2.5).

Traveling waves correspond to certain solutions of the four-dimensional dynamical system generated by the traveling wave system (2.5). To reduce the dimensionality, we use geometric singular perturbation theory to consider the limit of this four-dimensional system as  $\epsilon \rightarrow 0$ . We obtain a two-dimensional system, which is just (1.1) with time reversed. This correspondence with (1.1) allows us to apply Theorem 2.1 to show existence of fronts. To construct the fronts geometrically, we shall use geometric singular perturbation theory to investigate the singular limits  $\delta = 0$  and  $\delta = \infty$ . We then use the theory of rotated vector fields [16, 17] to extend our construction to  $\delta$  of intermediate size. We again use geometric singular perturbation theory to show that these solutions persist for small  $\epsilon > 0$ . The construction of periodic traveling waves uses the singular limit  $\delta = 0$ .

The reduction to two dimensions is carried out in Section 3. In Section 4 (resp. Section 5) we investigate the existence of fronts for  $(\alpha, \beta)$  in Region 1 (resp. Region 2). In Section 6 we investigate the existence of periodic wave trains for  $(\alpha, \beta)$  in Region 2.

### 3. REDUCTION TO TWO DIMENSIONS

We rewrite the traveling wave system (2.5) as a first order ODE system:

$$\begin{aligned}
 \frac{du}{dz} &= u_1, \\
 \epsilon \frac{du_1}{dz} &= -u_1 - u(1-u) + \frac{uv}{\alpha+u}, \\
 \frac{dv}{dz} &= v_1, \\
 \epsilon \frac{dv_1}{dz} &= -\frac{1}{\mu}v_1 - \frac{\delta}{\mu}v \left(1 - \frac{\beta v}{u}\right).
 \end{aligned}
 \tag{3.1}$$

In the terminology of geometric singular perturbation theory [18, 19, 20], (3.1) is the slow time scale formulation of a slow-fast system. To obtain the fast time scale

formulation one rescales the independent variable as  $z = \epsilon\xi$ , which yields

$$(3.2) \quad \begin{aligned} \frac{du}{d\xi} &= \epsilon u_1, \\ \frac{du_1}{d\xi} &= -u_1 - u(1-u) + \frac{uv}{\alpha+u}, \\ \frac{dv}{d\xi} &= \epsilon v_1, \\ \frac{dv_1}{d\xi} &= -\frac{1}{\mu}v_1 - \frac{\delta}{\mu}v \left(1 - \frac{\beta v}{u}\right). \end{aligned}$$

For  $\epsilon > 0$ , the slow and the fast time scale formulations are equivalent.

We shall consider (3.1) and (3.2) on the physically relevant set  $\tilde{P} = \{(u, u_1, v, v_1) : u > 0, v \geq 0\}$ . For  $\epsilon > 0$ , the equilibria of (3.1) or (3.2) in  $\tilde{P}$  are  $\tilde{A} = (u_+, 0, v_+, 0)$  and  $\tilde{B} = (1, 0, 0, 0)$ . They are independent of  $\delta$ ,  $\mu$ , and  $\epsilon$ .

For  $\epsilon = 0$  the set of equilibria of (3.2) in  $\tilde{P}$  is the two-dimensional *slow manifold*

$$(3.3) \quad M_0 = \left\{ (u, u_1, v, v_1) : u_1 = \frac{uv}{\alpha+u} - u(1-u), v_1 = \delta v \left( \frac{\beta v}{u} - 1 \right), u > 0, v \geq 0 \right\}.$$

$M_0$  can also be obtained by setting  $\epsilon = 0$  in (3.1); the first and third equations become algebraic, and  $M_0$  is their solution set.

For  $\epsilon = 0$ , the linearization of the system (3.2) at each point of  $M_0$  has two zero eigenvalues and two negative eigenvalues,  $-1$  and  $-1/\mu$ . Therefore, for the system (3.2),  $M_0$  is a normally hyperbolic and attracting manifold of equilibria. By Fenichel's First Theorem [18, 19, 20], any compact portion of  $M_0$  perturbs, for  $\epsilon > 0$  sufficiently small, to a locally invariant manifold  $M_\epsilon$  for (3.2), and  $M_\epsilon = M_0 + O(\epsilon)$ .  $M_\epsilon$  is also normally hyperbolic and attracting for the system (3.2). If a sufficiently large compact portion of  $M_0$  is perturbed to  $M_\epsilon$ , then  $M_\epsilon$  contains  $\tilde{A}$  and  $\tilde{B}$ .

The *reduced system* or *slow system* of (3.1) on  $M_0$  is given by

$$(3.4) \quad \begin{aligned} \frac{du}{dz} &= f_1(u, v) = \frac{uv}{\alpha+u} - u(1-u), \\ \frac{dv}{dz} &= \delta f_2(u, v) = \delta v \left( \frac{\beta v}{u} - 1 \right). \end{aligned}$$

Note that (3.4) is just (1.1) after time reversal. Therefore the equilibria of (3.4) in  $P$  are  $A = (u_+, v_+)$  and  $B = (1, 0)$  independent of  $\delta$ .

The restriction of (3.2) to  $M_\epsilon$ , after division by  $\epsilon$ , is given by (3.4) to lowest order, i.e., it is given by

$$(3.5) \quad \begin{aligned} \frac{du}{dz} &= \frac{uv}{\alpha+u} - u(1-u) + O(\epsilon), \\ \frac{dv}{dz} &= \delta v \left( \frac{\beta v}{u} - 1 \right) + O(\epsilon). \end{aligned}$$

The system (3.4) has a parabolic nullcline  $v = (1 - u)(\alpha + u)$  and two linear nullclines  $v = 0$  and  $v = \frac{1}{\beta}u$ . The nullclines are independent of  $\delta$ .

The equilibrium  $B = (1, 0)$  is the rightmost intersection of the parabola and  $v = 0$ . It is a saddle with eigenvalues 1 and  $-\delta$ .

The equilibrium  $A = (u_+, v_+)$  is the rightmost intersection of the parabola and  $v = \frac{1}{\beta}u$ . Let  $V = \left(\frac{1-\alpha}{2}, \frac{(1+\alpha)^2}{4}\right)$  be the vertex of the parabolic nullcline.  $V$  is in the open first quadrant when  $\alpha < 1$ ; on the positive  $v$ -axis when  $\alpha = 1$ ; and in the open second quadrant when  $\alpha > 1$ . It is not hard to see that:

- If  $(\alpha, \beta)$  is in Region 1, then  $A$  is in the open first quadrant of  $uv$ -plane and is strictly to the right of  $V$ .
- If  $(\alpha, \beta)$  is in Region 2, then  $A$  is in the open first quadrant of  $uv$ -plane and is strictly to the left of  $V$ .

The type of the equilibrium  $A$  varies with the parameters.

#### 4. REGION 1

In Subsection 4.1 we shall use Theorem 2.1 to show the existence of a heteroclinic solution of (3.4) from  $A$  to  $B$  for  $(\alpha, \beta)$  in Region 1. To exhibit the appearance of these solutions, we then investigate the singular limit  $\delta = \infty$  in Subsection 4.2, and the singular limit  $\delta = 0$  in Subsection 4.3. Finally, in Subsection 4.4 we use the theory of rotated vector fields to investigate intermediate values of  $\delta$ .

**4.1. Stability of the equilibrium  $A$  and existence of fronts.** The following result describes the stability of the equilibrium  $A$  for  $(\alpha, \beta)$  in Region 1.

**Proposition 4.1.** *For the system (3.4) with  $(\alpha, \beta)$  in Region 1 and  $\delta > 0$ , the equilibrium  $A$  is unstable. More precisely, there exist  $\delta_-$  and  $\delta_+$ ,  $0 < \delta_- < \delta_+$ , such that when  $\delta \in (\delta_-, \delta_+)$ ,  $A$  is an unstable focus; otherwise  $A$  is an unstable node.*

*Proof.* Using  $f_1$  and  $f_2$  defined by (3.4), the eigenvalues of the linearization of (3.4) at  $A$  are

$$(4.1) \quad \lambda_{1,2} = \frac{1}{2} \left( \delta f_{2v} + f_{1u} \pm \sqrt{(\delta f_{2v} + f_{1u})^2 - 4\delta(f_{1u}f_{2v} - f_{1v}f_{2u})} \right),$$

where

$$(4.2) \quad \begin{aligned} f_{1u} = f_{1u}(A) &= \frac{v_+}{\alpha + u_+} - \frac{u_+v_+}{(a + u_+)^2} - 1 + 2u_+, \\ f_{1v} = f_{1v}(A) &= \frac{u_+}{u_+ + a}, \quad f_{2u} = f_{2u}(A) = -\frac{1}{\beta}, \quad f_{2v} = f_{2v}(A) = 1. \end{aligned}$$

Since  $f_{1v}(A) > 0$ , it can be seen from the direction of the normal to the parabola depicted in Fig. 4.1 that  $f_{1u}(A) > 0$  and  $f_{1u}(A)f_{2v}(A) - f_{1v}(A)f_{2u}(A) > 0$ . Since  $f_{1u}(A) > 0$ , we see that in (4.1),  $\delta f_{2v} + f_{1u} > 0$ . Moreover, the solutions of the equation  $(\delta f_{2v} + f_{1u})^2 - 4\delta(f_{1u}f_{2v} - f_{1v}f_{2u}) = 0$  are the positive numbers

$$(4.3) \quad \delta_{\pm} = \frac{f_{1u}f_{2v} - 2f_{1v}f_{2u} \pm 2\sqrt{-f_{1v}f_{2u}(f_{1u}f_{2v} - f_{1v}f_{2u})}}{f_{2v}^2}.$$

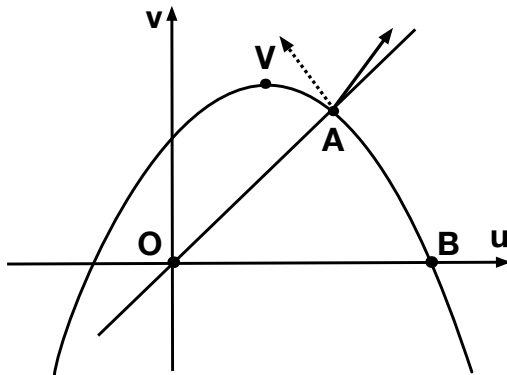


FIGURE 4.1. For the system (3.4) with  $(\alpha, \beta)$  in Region 1, so that  $A$  is to the right of  $V$ , the direction of the normal indicates that  $f_{1u} > 0$ .

The expression  $(\delta f_{2v} + f_{1u})^2 - 4\delta(f_{1u}f_{2v} - f_{1v}f_{2u})$  in (4.1) is negative when  $\delta \in (\delta_-, \delta_+)$ , and positive when  $\delta \in (0, \delta_-) \cup (\delta_+, \infty)$ . The result follows.  $\square$

In order to use Theorem 2.1, we note that, as is mentioned in [6], cases (i), (ii) and (iii) in the theorem cover Region 1. To see this, note that if  $A$  is to the right of  $V$ , then  $\beta > 2(1 - \alpha)/(1 + \alpha)^2$ , so  $\beta > \beta_+$ . Indeed, if we think of  $\beta_+$  as a function of  $\delta$ , then  $\beta_+(0) = 2(1 - \alpha)/(1 + \alpha)^2$ , and  $\beta'_+(0) < 0$ .

Taking into the account the time reversal, we then conclude that the following holds. See Figure 4.2 for illustration.

**Proposition 4.2.** *For the system (3.4) with  $(\alpha, \beta)$  in Region 1 and  $\delta > 0$ , there is a heteroclinic connection of (3.4) from  $A$  to  $B$ . The orbit approaches the saddle  $B$  along its stable manifold. If  $\delta \in (\delta_-, \delta_+)$  given by (4.3), then the orbit has an oscillatory tail at  $A$ . If  $\delta$  is sufficiently close to 0 or  $+\infty$ , the orbit leaves the equilibrium  $A$  along its weak unstable manifold.*

Proposition 4.2 says that for the restriction of (3.1) to the slow manifold  $M_0$ , there is a heteroclinic connection from  $\tilde{A}$  to  $\tilde{B}$ . A sufficiently large compact portion of  $M_0$  includes  $\tilde{A}$ , which is repelling within  $M_0$ ;  $\tilde{B}$ , which is a saddle within  $M_0$ ; and the heteroclinic connection. For small  $\epsilon > 0$ , this portion of  $M_0$  perturbs to a locally invariant manifold  $M_\epsilon$  that includes  $\tilde{A}$ ,  $\tilde{B}$ , and, because of the structural stability of the connection in  $M_0$ , a heteroclinic connection from  $\tilde{A}$  to  $\tilde{B}$ . Existence of the traveling wave in Theorem 2.2 follows easily from this observation. The traveling wave is unique up to a shift in  $z$  because the equilibrium  $\tilde{B}$  of (3.1) has a one-dimensional stable manifold, only one branch of which is in  $\tilde{P}$ .

In the next subsections we describe the geometric form of these orbits by relating them to singular orbits in the limits  $\delta = 0$  and  $\delta = \infty$ .



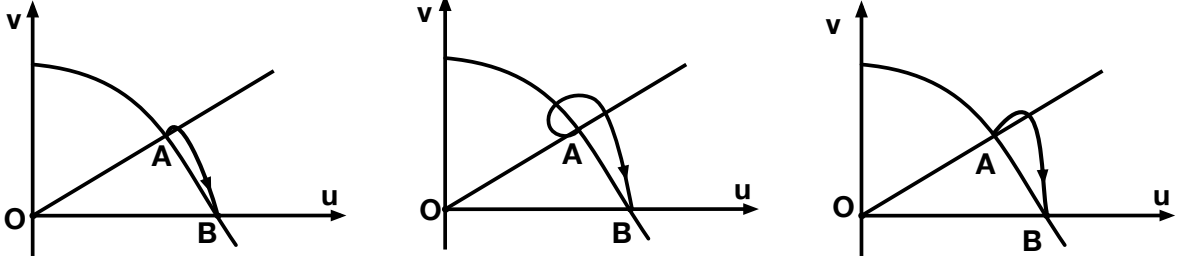


FIGURE 4.2. Schematic representation of the heteroclinic orbits on the slow manifold: (a)  $\delta \in (0, \delta_-)$ , (b)  $\delta \in (\delta_-, \delta_+)$ , (c)  $\delta \in (\delta_+, +\infty)$ .

4.2. **Singular front at  $\delta = \infty$ .** To capture the singular front at  $\delta = \infty$ , we use  $\theta = 1/\delta$  as a singular parameter and rewrite (3.4) as

$$(4.4) \quad \begin{aligned} \frac{du}{dz} &= f_1(u, v) = \frac{uv}{\alpha + u} - u(1 - u), \\ \theta \frac{dv}{dz} &= f_2(u, v) = v \left( \frac{\beta v}{u} - 1 \right). \end{aligned}$$

The system (4.4) is the slow time formulation of a slow-fast system; the small parameter is  $\theta$ . To obtain the fast time formulation, we introduce the additional scaling  $z = s\theta$ , which yields

$$(4.5) \quad \begin{aligned} \frac{du}{ds} &= \theta f_1(u, v) = \theta \left( \frac{uv}{\alpha + u} - u(1 - u) \right), \\ \frac{dv}{ds} &= f_2(u, v) = v \left( \frac{\beta v}{u} - 1 \right). \end{aligned}$$

For  $\theta = 0$ , the system (4.5) becomes

$$(4.6) \quad \begin{aligned} \frac{du}{ds} &= 0, \\ \frac{dv}{ds} &= v \left( \frac{\beta v}{u} - 1 \right). \end{aligned}$$

In  $P$ , (4.6) has two lines of equilibria,  $\mathcal{N}_0^1 = \{(u, v) : u > 0, v = 0\}$  and  $\mathcal{N}_0^2 = \{(u, v) : u > 0, v = \frac{1}{\beta}u\}$ . The first is normally attracting; the second is normally repelling.

The unstable manifold  $W^u(\mathcal{N}_0^2)$  is an open subset of  $uv$ -space. The stable manifold  $W^s(\mathcal{N}_0^1)$  is foliated by the one-dimensional stable manifolds of the points in  $\mathcal{N}_0^1$ . In particular,  $W^u(\mathcal{N}_0^2)$  intersects the one-dimensional stable manifold of  $B$ ,  $W_0^s(B)$ , in the open line segment from  $(u, v) = (1, \frac{1}{\beta})$  to  $B = (1, 0)$ .

The slow equation on  $\mathcal{N}_0^2$  is given by

$$(4.7) \quad \frac{du}{dz} = \frac{u^2}{\beta(\alpha + u)} - u(1 - u).$$

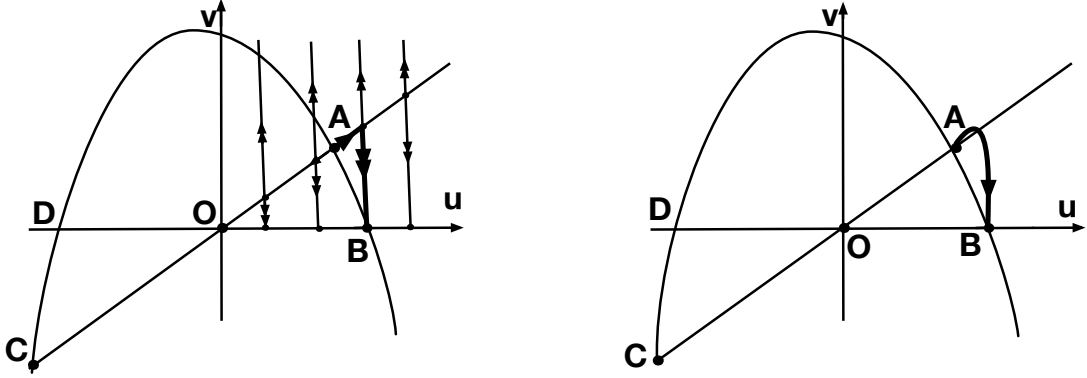


FIGURE 4.3. The dynamics of (3.4) for  $(\alpha, \beta)$  in Region 1: (a) singular solution,  $\delta = \infty$ ; (b) perturbed solution,  $\delta \gg 1$ .

It has a single equilibrium at  $u = u_+$ , corresponding to  $A$ . This equilibrium is repelling within  $\mathcal{N}_0^2$ . Therefore, for (4.5) with small  $\theta > 0$ ,  $W^u(\mathcal{N}_0^2)$  perturbs to the two-dimensional unstable manifold  $W_\theta^u(A)$ .

The slow equation on  $\mathcal{N}_0^1$  is given by

$$(4.8) \quad \frac{du}{dz} = -u(1-u).$$

It has a single equilibrium at  $u = 1$ , corresponding to  $B = (1, 0)$ . This equilibrium is repelling within  $\mathcal{N}_0^1$ . Therefore, for (4.5) with small  $\theta > 0$ ,  $W_0^s(B)$  perturbs to the stable manifold of the saddle  $B$ ,  $W_\theta^s(B)$ .

Since the intersection of  $W^u(\mathcal{N}_0^2)$  and  $W_0^s(B)$  is transverse, for (4.5) with small  $\theta > 0$ ,  $W_\theta^u(A)$  and  $W_\theta^s(B)$  intersect. The intersection is necessarily a heteroclinic orbit from  $A$  to  $B$ .

This heteroclinic orbit can be viewed as a perturbation of a singular orbit for  $\theta = 0$ : follow the slow flow along  $\mathcal{N}_0^2$  from  $A$  to  $(1, \frac{1}{\beta})$ , then follow the fast flow along  $u = 1$  from  $(1, \frac{1}{\beta})$  to  $B = (1, 0)$ .

We next describe how the appearance of the heteroclinic orbit changes as  $\theta$  increases with  $\theta$  small. For small  $\theta > 0$ , any compact portion of  $\mathcal{N}_0^2$  perturbs to a locally invariant manifold  $\mathcal{N}_\theta^2$ . Let

$$(4.9) \quad l = (f_{2v}, -f_{2u})|_A,$$

a tangent vector to  $\mathcal{N}_0^2$ , and let

$$(4.10) \quad e_u(\theta) = \left( \frac{1}{2} \left( -\theta f_{2v} + f_{1u} + \sqrt{(\theta f_{2v} + f_{1u})^2 - 4\theta(f_{1u}f_{2v} - f_{1v}f_{2u})} \right), -f_{2u} \right) \Big|_A,$$

the eigenvector of the linearization of the right-hand side of (4.5) at  $A$  that is tangent to  $\mathcal{N}_\theta^2$ . We have  $l = e_u(0)$ . Let

$$(4.11) \quad D(\theta) = \frac{d}{d\theta}(l \wedge e_u(\theta)) \Big|_A.$$

Using (4.2) and the information about the signs of various terms that is given after that formula, we see that

$$D'(0) = -\frac{f_{2u}(f_{1u}f_{2v} - f_{1v}f_{2u})}{f_{2v}} > 0.$$

Therefore, for small  $\theta > 0$ , as  $\theta$  increases, the weak unstable eigenvector  $e_u(\theta)$  rotates counterclockwise away from  $\mathcal{N}_0^2$ , and the solution enters the equilibrium  $A$  backward in time by crossing  $\mathcal{N}_0^2$  as shown in Figure 4.3.

**4.3. Singular front at  $\delta = 0$ .** To study the limit  $\delta \rightarrow 0$  of (3.4), we regard (3.4) as the fast system for a geometric singular perturbation problem. When  $\delta = 0$ , the system becomes

$$(4.12) \quad \begin{aligned} \frac{du}{dz} &= \frac{uv}{\alpha + u} - u(1 - u), \\ \frac{dv}{dz} &= 0. \end{aligned}$$

In  $P$ , for  $0 < \alpha \leq 1$ , (4.12) has the curve of equilibria

$$\mathcal{M}_0 = \{(u, v) : u = \frac{1}{2}(1 - \alpha + \sqrt{(\alpha + 1)^2 - 4v}), 0 < v < \alpha\}.$$

See Figure 4.4.  $\mathcal{M}_0$  is part of the right branch of the parabola  $v = (1 - u)(\alpha + u)$ . If  $\alpha > 1$ , the definition of  $\mathcal{M}_0$  must be changed by replacing  $0 \leq v < \alpha$  by  $0 \leq v < \alpha < \frac{(1+\alpha)^2}{2}$ , and there is a second curve of equilibria that is part of the left branch of the parabola. We shall not discuss this case, since it is not materially different from the case  $0 < \alpha \leq 1$ .

$\mathcal{M}_0$  is normally repelling. The slow equation on it is

$$(4.13) \quad v' = -v \left( 1 - \frac{2\beta v}{(1 - \alpha + \sqrt{(\alpha + 1)^2 - 4v})} \right).$$

This scalar equation has a stable equilibrium at  $v = 0$ , which corresponds  $B = (1, 0)$ , and an unstable equilibrium at  $v = v_+$ , which corresponds to  $A = (u_+, v_+)$ . There is a heteroclinic orbit from  $v = 0$  to  $v = v_+$ .

Because of the normal hyperbolicity of  $\mathcal{M}_0$ , any compact portion that contains both  $A$  and  $B$  persists for small  $\delta > 0$  as a locally invariant manifold  $\mathcal{M}_\delta$  for (3.4).  $\mathcal{M}_\delta$  must contain both the equilibria  $A$  and  $B$ , which persist for the full system (3.4) as a repelling node and a saddle.  $\mathcal{M}_\delta$  therefore contains an orbit connecting  $A$  to  $B$ .

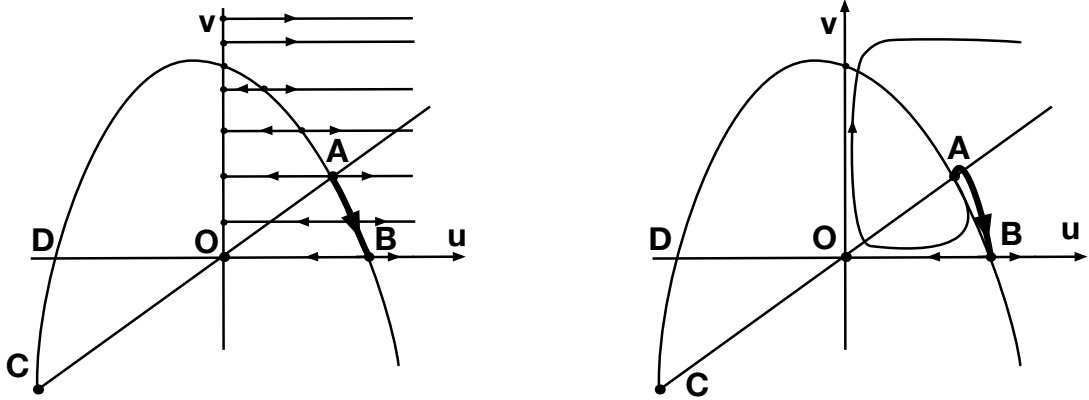


FIGURE 4.4. The dynamics of (3.4) for  $(\alpha, \beta)$  in Region 1: (a) singular solution,  $\delta = 0$ ; (b) perturbed solution,  $\delta \ll 1$ .

**4.4. Rotation of the vector field.** The geometric structure of heteroclinic orbits at intermediate values of  $\delta$  between  $\delta = 0$  and  $\delta = \infty$  can be investigated using the theory of rotated vector fields [16, 17].

We denote the angle between the  $u$ -axis and the vector given by the right hand side of (3.4) by

$$\Theta(u, v) = \tan^{-1} \frac{\delta f_2(u, v)}{f_1(u, v)}.$$

We have

$$(4.14) \quad \frac{\partial \Theta}{\partial \delta} = \frac{f_1 \frac{\partial(\delta f_2)}{\partial \delta} - \delta f_2 \frac{\partial f_1}{\partial \delta}}{f_1^2 + (\delta f_2)^2} = \frac{v}{(u + \alpha)} \frac{((1 - u)((\alpha + u) - v)(u - \beta v))}{((u(1 - u) - \frac{uv}{\alpha + u})^2 + (\delta v(1 - \frac{\beta v}{u}))^2)}.$$

Let  $\mathcal{D}$  denote the open region in the first quadrant that is bounded on the left by the parabola  $v = (1 - u)((\alpha + u))$ , above by the line  $v = (1/\beta)u$ , and on the right by the line  $u = 1$ . In other words,  $\mathcal{D}$  is bounded by the singular heteroclinic orbits at  $\delta = 0$  and  $\delta = \infty$ .

According to [17, Section 2], as  $\delta$  decreases from  $\infty$  to 0, the segment of the stable manifold of the saddle  $B$  that lies in  $\mathcal{D}$  rotates counterclockwise from its initial position on the vertical line  $u = 1$  to its final position on the parabola  $v = (1 - u)((\alpha + u))$ . Moreover, the segments for different  $\delta$  do not intersect each other.

In backward time these stable manifolds leave  $\mathcal{D}$  through the only way out, the line  $v = (1/\beta)u$ , with the intersection point monotonically approaching the equilibrium  $A$  as  $\delta$  decreases. The solution continues in backward time toward  $A$ .

## 5. FRONTS IN REGION 2

**5.1. Stability of the equilibrium  $A$  and existence of fronts.** The following result describes the stability of the equilibrium  $A$  for  $(\alpha, \beta)$  in Region 2.

**Proposition 5.1.** *For the system (3.4) with  $(\alpha, \beta)$  in Region 2, there exist  $\delta_-, \delta_h, \delta_+$ , with  $0 < \delta_- < \delta_h < \delta_+$ , such that the equilibrium  $A$  is*

- a stable node when  $\delta \in (0, \delta_-)$ ,
- a stable focus when  $\delta \in (\delta_-, \delta_h)$ ,
- an unstable focus when  $\delta \in (\delta_h, \delta_+)$ ,
- an unstable node when  $\delta \in (\delta_+, \infty)$ .

$\delta_h = \frac{-f_{1u}}{f_{2v}}$  is a Hopf bifurcation point.

*Proof.* Using  $f_1$  and  $f_2$  defined by (3.4), the eigenvalues of linearization of (3.4) at  $A$  are given by (4.1), (4.2).

It is clear from Fig. 5.1 that  $f_{1u} < 0$  when  $0 < \beta < \frac{2(1-\alpha)}{(\alpha+1)^2}$ , but nevertheless the vector product of the normals to the nullclines at the intersection,  $f_{1u}f_{2v} - f_{1v}f_{2u}$ , is positive. At  $\delta = \delta_h$  therefore both eigenvalues 4.1 are purely imaginary.

On the other hand, when  $\delta \in (0, \delta_h)$ , we have  $\delta f_{2v} + f_{1u} < 0$ , and when  $\delta \in (\delta_h, \infty)$ , we have  $\delta f_{2v} + f_{1u} > 0$ . Moreover, the expression  $(\delta f_{2v} + f_{1u})^2 - 4\delta(f_{1u}f_{2v} - f_{1v}f_{2u})$  is negative when  $\delta \in (\delta_-, \delta_+)$ , and positive when  $\delta \in (0, \delta_-) \cup (\delta_+, \infty)$ . Direct calculation also shows that  $\delta_h \in (\delta_-, \delta_+)$ . Therefore, when  $\delta \in (0, \delta_-)$ , both eigenvalues are real and negative; when  $\delta \in (\delta_-, \delta_h)$ , both eigenvalues are complex with negative real parts; when  $\delta \in (\delta_h, \delta_+)$ , both eigenvalues are complex with positive real parts; and, when  $\delta \in (\delta_+, \infty)$ , both eigenvalues are real and positive. □

In order to use Theorem 2.1, we note that from case (ii) of the theorem, if  $(\alpha, \beta)$  is in Region 2 and  $\delta > 1 - \alpha$ , then the equilibrium  $A$  is globally asymptotically stable for (1.1). It follows from [6] that the value of the Hopf bifurcation point  $\delta_h$  which is defined in Proposition 5.1, is such that  $\delta_h < 1 - \alpha$ . Taking into the account the time reversal, we then conclude that for  $\delta > 1 - \alpha > \delta_h$  the following holds.

**Proposition 5.2.** *For the system (3.4) with  $(\alpha, \beta)$  in Region 2 and  $\delta > 1 - \alpha$ , there is a heteroclinic connection of (3.4) from  $A$  to  $B$ . The orbit approaches the saddle  $B$  along its stable manifold. If  $\delta \in (\delta_h, \delta_+)$ , then the orbit has an oscillatory tail at  $A$ . If  $\delta$  is sufficiently close to  $\infty$ , the orbit leaves the equilibrium  $A$  along its weak unstable manifold.*

Theorem 2.3 follows from Proposition 5.2 the way Theorem 2.2 follows from Proposition 4.2; see the end of Subsection 4.1.

**5.2. Geometric construction of the fronts.** For the system (3.4) with  $(\alpha, \beta)$  in Region 2, the geometric construction of a singular heteroclinic orbit in the limit  $\delta = \infty$  is the same as the construction in Region 1; see Section 4.2 for the analysis. We schematically illustrate the singular orbit and its perturbation in Fig. 5.2.

Using the same techniques as in Section 4.4, one can show that, as  $\delta$  decreases from  $\infty$  to 0, the stable manifold of the saddle  $B$  rotates counterclockwise until it approaches the parabolic nullcline. The intersection of the stable manifold of  $B$  with the line  $v = \beta^{-1}u$  moves in a monotone way along  $v = \beta^{-1}u$  from the position defined

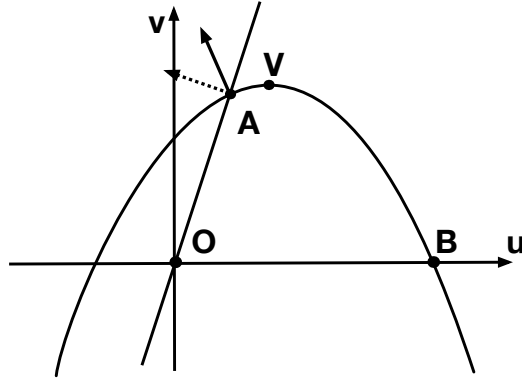


FIGURE 5.1. For the system (3.4) with  $(\alpha, \beta)$  in Region 2, so that  $A$  is to the left  $V$ , the direction of the normal indicates that  $f_{1u} < 0$ .

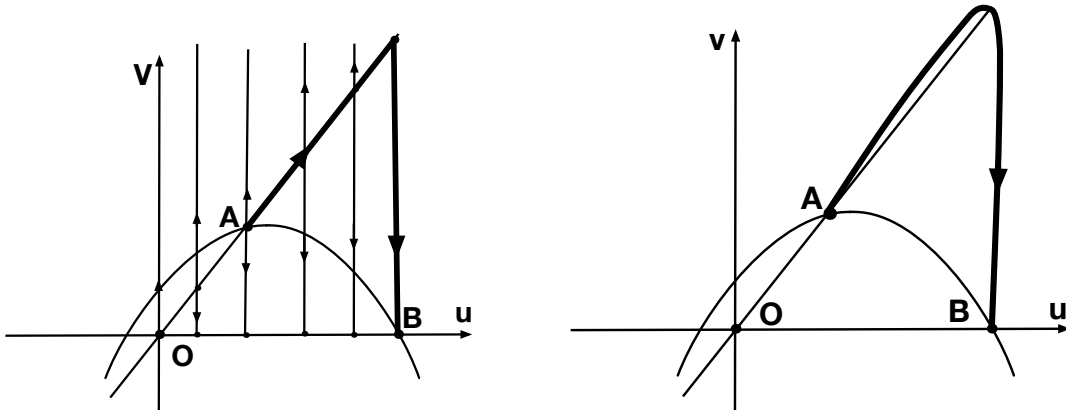


FIGURE 5.2. The dynamics of (3.4) for  $(\alpha, \beta)$  in Region 2: (a) singular solution,  $\delta = \infty$ ; (b) perturbed solution,  $\delta \gg 1$ .

by the singular orbit defined to a position strictly to the right of the equilibrium  $A$  (as opposed to Region 1 where it approaches  $A$ ).

## 6. PERIODIC TRAVELING WAVES IN REGION 2

6.1. **Relaxation oscillations for small  $\delta$ .** In the domain  $P$ , the system (3.4) has the same orbits as the system

$$(6.1) \quad \begin{aligned} u' &= -u^2((1-u)(\alpha+u)-v), \\ v' &= -\delta v(\alpha+u)(u-\beta v), \end{aligned}$$

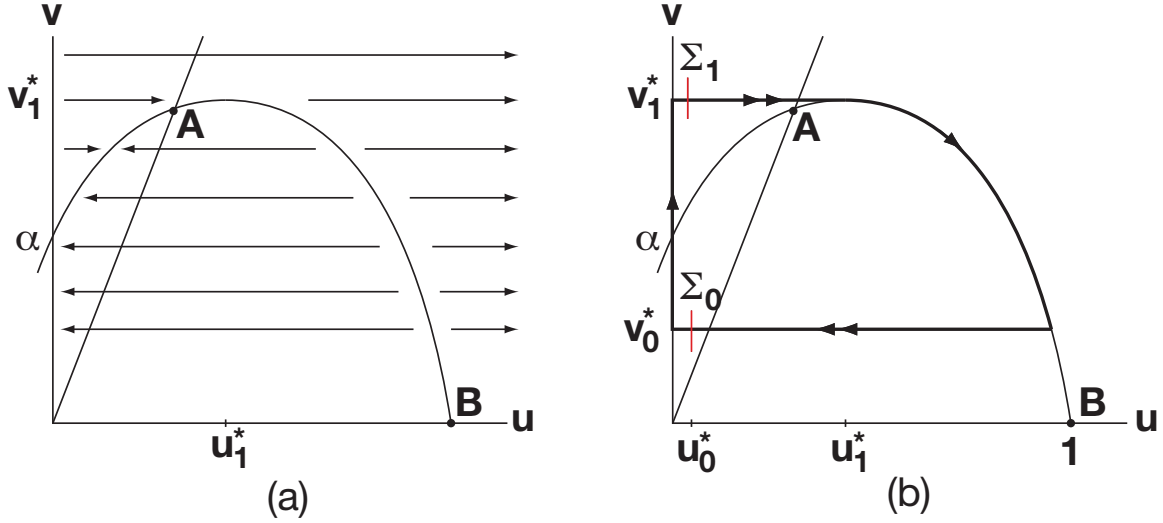


FIGURE 6.1. For  $(\alpha, \beta)$  in Region 2, a singular closed orbit of (6.1) with  $\delta = 0$ .

which is obtained from (3.4) by the change of variables

$$\zeta = \int_0^z \frac{1}{u(\alpha + u)} ds.$$

Here we use  $'$  to denote the derivative with respect the new variable  $\zeta$ . The new system (6.1) generates a polynomial vector field. It can be analyzed near the  $v$ -axis, which gives information about (3.4) near the  $v$ -axis that we will need in this section.

We regard (6.1) as the fast time formulation of a slow-fast system; the small parameter is  $\delta$ . Setting  $\delta = 0$ , we obtain the limiting system

$$(6.2) \quad \begin{aligned} u' &= -u^2((1-u)(\alpha+u)-v), \\ v' &= 0. \end{aligned}$$

Its flow for  $(\alpha, \beta)$  in Region 2 and  $\delta > 0$  is shown in Figure 6.1 (a). For the limiting system, the  $v$ -axis and the parabola  $(1-u)(\alpha+u) = v$  consist of equilibria. The vertex  $V$  of the parabola is denoted  $(u_1^*, v_1^*)$  in the figure. For small  $\delta > 0$ ,  $v' > 0$  to the left of the slanted line  $v = (1/\beta)u$ , and  $v' < 0$  to its right.

We let  $h_1(u, v) = (u-1)(\alpha+u) + v$  and  $h_2(u, v) = v(\alpha+u)(\beta v - u)$ , so that (6.1) becomes

$$(6.3) \quad u' = u^2 h_1(u, v), \quad v' = \delta h_2(u, v).$$

Note that for  $v > 0$ ,  $h_2(0, v) = \alpha\beta v^2 > 0$  (so for  $\delta > 0$ ,  $v' > 0$  on the positive  $v$ -axis), whereas  $h_1(0, v) = v - \alpha$  changes from negative to positive at  $v = \alpha$  (i.e., for the limiting system (6.2), the positive  $v$ -axis changes from attracting to repelling

when the parabola is crossed). Also note that

$$\int_{v_0}^{v_1^*} \frac{h_1(0, v)}{h_2(0, v)} dv \rightarrow -\infty \quad \text{as } v_0 \rightarrow 0.$$

From these facts it follows that there is a unique  $v_0^*$ ,  $0 < v_0^* < a$ , so that

$$\int_{v_0^*}^{v_1^*} \frac{h_1(0, v)}{h_2(0, v)} dv = 0.$$

We define a closed singular orbit  $S$  of the slow-fast system as follows; see Figure 6.1 (b). From  $(0, v_0^*)$ , follow the slow flow up the  $v$ -axis to  $(0, v_1^*)$ ; follow the fast flow to the right to the vertex  $(u_1^*, v_1^*)$  of the parabola; follow the slow flow down the right side of the parabola to the point with  $v$ -coordinate  $v_0^*$ ; finally, follow the fast flow to the left to  $(0, v_0^*)$ .

**Theorem 6.1.** *For a fixed  $(\alpha, \beta)$  in Region 2, there is a neighborhood  $U$  of  $S$  such that for small  $\delta > 0$ , (6.3) has a unique closed orbit  $S_\delta$  in  $U$ .  $S_\delta$  is hyperbolically repelling and approaches  $S$  in the Hausdorff topology as  $\delta \rightarrow 0$ .*

The theorem depends on the following result. For  $v_1$  near  $v_1^*$  we define  $p(v_1)$ , with  $0 < p(v_1) < a$ , by the formula

$$\int_{p(v_1)}^{v_1} \frac{h_1(0, v)}{h_2(0, v)} dv = 0.$$

Thus  $p(v_1^*) = v_0^*$ . The following result is a consequence of [13].

**Proposition 6.2.** *There are closed intervals  $I_j$  centered at  $v_j^*$ ,  $j = 1, 2$ , with the following property. Let  $u_0^*$  be a small positive number, and let  $\Sigma_j = \{u_0^*\} \times I_j$ . For each small  $\delta > 0$  and for each  $v_1 \in I_1$ , the solution of (6.3) through  $(u_0^*, v_1) \in \Sigma_1$ , followed in backward time, first meets  $\Sigma_0$  in a point  $(u_0^*, p_\delta(v_1))$ . As  $\delta \rightarrow 0$ ,  $p_\delta : I_0 \rightarrow I_1$  approaches  $p|_{I_0}$  in the  $C^1$ -topology.*

We note that if  $u^2$  is replaced by  $u$  in (6.3), the proposition is well-known [14, 15]; the function  $p$  is called the entry-exit or way in-way out function. The  $u^2$  case appears to be new. Interestingly, the  $u^2$  case can be proved using geometric singular perturbation theory, but the  $u$  case apparently cannot be. However, the  $u$  case can be reduced to the  $u^2$  case. See [13] for details.

Given Proposition 6.2, Theorem 6.1 is proved as follows. Using Fenichel theory to describe the flow near the repelling part of the parabola, and the analysis in [21] of the flow near the vertex of the parabola, for small  $\delta > 0$  we can define a map  $Q_\delta : \Sigma_0 \rightarrow \Sigma_1$  by following solutions of (6.3) backward; see [22], Sec. 2. As in [22], there is a constant  $C > 0$  such that the  $C^1$ -norm of  $Q_\delta$  is of order  $e^{-\frac{C}{\delta}}$ .

Finally, for small  $\delta > 0$  we define  $P_\delta : \Sigma_1 \rightarrow \Sigma_0$  by

$$P_\delta(u_0^*, v_1) = (u_0^*, p_\delta(v_1)),$$

and we define a Poincaré map  $\Pi_\delta : \Sigma_0 \rightarrow \Sigma_0$  by  $\Pi_\delta = P_\delta \circ Q_\delta$ . From the conclusion of the previous paragraph and Proposition 6.2,  $\Pi_\delta$  is a contraction. The theorem follows.



To prove Theorem 2.4, we note that for the system (3.2) with  $(\alpha, \beta)$  in Region 2 and  $\delta > 0$  sufficiently small, Theorem 6.1 implies that a sufficiently large compact portion of the slow manifold  $M_0$  contains a hyperbolic closed orbit. For  $\epsilon > 0$  sufficiently small, this orbit persists on the nearby locally invariant manifold  $M_\epsilon$ .

**6.2. Hopf bifurcation.** Proposition 5.1 implies that, for fixed  $(\alpha, \beta)$  in Region 2, as  $\delta$  increases, a Hopf bifurcation for (6.3) at the equilibrium  $A$  occurs at  $\delta = \delta_h(\alpha, \beta)$ , with the equilibrium changing from stable to unstable. Denote the Lyapunov number [17] at the equilibrium  $A$  at the Hopf bifurcation value by  $\sigma(\alpha, \beta)$ . The sign of  $\sigma(\alpha, \beta)$  determines whether, at the Hopf bifurcation, the equilibrium  $A$  is weakly attracting ( $\sigma < 0$ ) or weakly repelling ( $\sigma > 0$ ). Hence it determines whether the Hopf bifurcation is subcritical or supercritical. For  $(\alpha, \beta)$  near the top of Region 2, we can determine the sign of  $\sigma(\alpha, \beta)$ . Recalling that Region 2 is  $\{(\alpha, \beta) : 0 < \alpha < 1 \text{ and } 0 < \beta < \frac{2(1-\alpha)}{(\alpha+1)^2}\}$ , we write

$$\beta_\alpha = \frac{2(1-\alpha)}{(\alpha+1)^2}, \quad \beta = \beta_\alpha - z.$$

Then one can calculate that

$$\sigma(\alpha, \beta_\alpha - z) = \frac{3}{64\Delta^{\frac{3}{2}}}\pi\alpha(\alpha-1)^4(\alpha+3)(\alpha+1)^2(z + O(z^2)),$$

where  $\Delta = \delta_h(f_{1u}(A)f_{2v}(A) - f_{1v}(A)f_{2u}(A)) > 0$ .

Therefore, for fixed  $\alpha$  with  $0 < \alpha < 1$ , if  $z > 0$  is sufficiently small, then

$$\sigma(\alpha, \beta_\alpha - z) > 0.$$

For such  $(\alpha, \beta)$ , the Hopf bifurcation that occurs at  $\delta = \delta_h(\alpha, \beta)$  is subcritical: the closed orbits exist for  $\delta < \delta_h$ , and, like the relaxation oscillations of the previous section, they are repelling. This is consistent with the conjecture that for such  $(\alpha, \beta)$ , the relaxation oscillations shrink as  $\delta$  grows and disappear in a Hopf bifurcation at  $\delta = \delta_h$ .

In fact, for small  $z > 0$ ,  $\delta_h$  is small:

$$\delta_h = \frac{1}{2}(1-\alpha^2)z + \mathcal{O}(z^2).$$

Thus for small  $z > 0$ , the transition from large relaxation oscillation to Hopf bifurcation takes place rapidly.

Recall that when  $\beta = \beta_\alpha$ , the equilibrium  $A$  coincides with the vertex  $V$  of the parabolic nullcline. For small  $z > 0$ , the equilibrium  $A$  is to the left of  $V$ , but close to it.

Numerical evidence indicates that when the equilibrium  $A$  is not close to  $V$ , the Hopf bifurcation at  $A$  may be supercritical. In this case the periodic orbit created from the Hopf bifurcation exists for  $\delta > \delta_h$  and has opposite stability from the relaxation oscillation. Numerical evidence indicates that there is a saddle-node bifurcation of periodic orbits at a value  $\delta > \delta_h$ . At this point the stability of the periodic orbit becomes that of the relaxation oscillation. This observation is consistent with [12, 23],

where parameter values are found for which several periodic orbits exist.

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## REFERENCES

- [1] May RM. 1973 On relationships among various types of population models, *American Naturalist* **107**, 46-57.
- [2] May RM. 1974 *Stability and Complexity in Model Ecosystems*, Princeton University Press, Princeton, NJ.
- [3] Murray JD. 1989 *Mathematical Biology*, Springer-Verlag, Berlin, 1989.
- [4] Renshaw E. 1991 *Modelling Biological Populations in Space and Time*, Cambridge University Press, Cambridge.
- [5] Tanner JT. 1975 The stability and the intrinsic growth rates of prey and predator populations, *Ecology* **56**, 855-867.
- [6] Hsu SB, Huang T-W. 1995 Global stability for a class of predator-prey systems, *SIAM J. Appl. Math.* **31**, 53-98.
- [7] Holling CS, 1959 The characteristics of simple types of predation and parasitism, *Canadian Entomologist* **91**, 293-320.
- [8] Banerjee M, Banerjee S. 2012 Turing instabilities and spatio-temporal chaos in ratio-dependent Holling-Tanner model, *Math. Biosciences* **236**, 64-76.
- [9] Sun G, Zhang J, Song LP, Jin Z, Li B-L. 2012 Pattern formation of a spatial predator-prey system, *Appl. Math. Comput.* **218**, 11151-11162.
- [10] Li X, Jiang W, Shi J. 2013 Hopf bifurcation and Turing instability in the reaction-diffusion Holling-Tanner predator-prey model, *IMA J. Appl. Math.* **78**, 287-306.
- [11] Ducrot A. 2013 Convergence to generalized transition waves for some Holling-Tanner prey-predator reaction-diffusion system, *J. Math. Pures Appl.* **100**, 1-15.
- [12] Gasull A, Kooij RE, Torregrosa J. 1997 Limit cycles in the Holling-Tanner model, *Publicacions Matemàtiques* **41**, 149-167.
- [13] De Maesschalck P, Schechter S. 2014 The entry-exit function and geometric singular perturbation theory, *preprint*.
- [14] Mishchenko EF, Kolesov YuS, Kolesov AYu. , Rozov NKh. 1994 *Asymptotic Methods in Singularly Perturbed Systems*, translated from the Russian by Aleksanova I. Monographs in Contemporary Mathematics, Consultants Bureau, New York.
- [15] De Maesschalck P. 2008 Smoothness of transition maps in singular perturbation problems with one fast variable, *J. Differ. Equations* **244**, 1448-1466.
- [16] Duff GFD. 1953 Limit-cycles and rotated vector fields, *Analysis of Mathematics* **57**, 15-31.
- [17] Perko LM 1993 Rotated vector fields, *J. Differ. Equations* **103**, 127-145.
- [18] Fenichel N. 1979 Geometric singular perturbation theory for ordinary differential equations, *J. Differ. Equations* **55**, 763-783.
- [19] Jones CKRT. 1995 Geometric singular perturbation theory, in *Dynamical Systems (Montecatini Terme, 1994)*, *Lecture Notes in Math.* **1609**, Springer, Berlin, 44-118.
- [20] Kuehn C. 2015 *Multiple Time Scale Dynamics*, Springer, New York.

- [21] Krupa M, Szmolyan P. 2001 Extending singular perturbation theory to non-hyperbolic points — fold and canard points in two dimensions, *SIAM J. Math. Anal.* **33**, 286-314.
- [22] Krupa M, Szmolyan P. 2001 Relaxation oscillation and canard explosion, *J. Differ. Equations* **174**, 312-368.
- [23] Sáez E, González-Olivares E. 1999 Dynamics of a predator-prey model, *SIAM J. Appl. Math.* **59**, 1867-1878.