

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

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**ABSTRACT.** We identify two new traveling waves of the Holling-Tanner model with weak diffusion. One connects two constant states; at one of them, the model is undefined. The other connects a constant state to a periodic wave train. We exploit the multi-scale structure of the Holling-Tanner model in the weak diffusion limit. Our analysis uses geometric singular perturbation theory, compactification and the blow-up method.

**1. Introduction.** In this paper we continue the study of traveling waves of the Holling-Tanner prey-predator model with weak diffusion, which was begun in [7]. We identify two types of traveling waves that were not considered in that paper. One connects two constant states; the novelty is that at one of the constant states, the origin, the model is undefined. The other connects a constant state to a periodic wave train.

**1.1. The model.** The diffusive Holling-Tanner prey-predator model is the reaction diffusion system

$$\begin{aligned}u_t &= D_u u_{xx} + u(1-u) - \frac{uv}{u+\alpha}, \\v_t &= D_v v_{xx} + \delta v \left(1 - \frac{\beta v}{u}\right),\end{aligned}\tag{1.1}$$

In these equations,  $t > 0$  is the time variable;  $x \in \mathbb{R}$  is the spatial variable;  $D_u$ ,  $D_v$ ,  $\alpha$ ,  $\delta$  and  $\beta$  are positive parameters. The quantity  $u(x, t)$  is related to the prey population, and  $v(x, t)$  is related to the predator population. Since physically meaningful solutions have  $u$  and  $v$  nonnegative, but the system (1.1) is undefined for  $u = 0$ , we consider (1.1) on the region  $u > 0$ ,  $v \geq 0$ .

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The spatially homogeneous system

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

associated with (1.1) is the Holling-Tanner model [8, 15, 16, 22, 17, 19]. In this model a predator captures prey at the rate  $\frac{uv}{u+\alpha}$ , so there is a maximum rate which has been normalized to 1. The predator carrying capacity of the environment is  $\frac{u}{\beta}$ , i.e., it is proportional to the prey population  $u$ .

The bifurcation diagram of the ODE (1.2) has been elucidated in a series of papers [6, 9, 10, 11, 20]. We shall recall some of this work in the course of the paper (Proposition 2.2 and Sec. 3.1). Turing bifurcations of the PDE (1.1) are studied in [14]. Existence of traveling front solutions that connect constant states of the PDE (1.1) has been established in [1, 2, 7], and existence of a family of wave train solutions was established in [7]. The importance of wave train solutions in ecological models is emphasized in [21].

**1.2. Equilibria.** Spatially homogeneous equilibria of the system (1.1) correspond to equilibria of (1.2). The system (1.2) has the three equilibria  $(1, 0)$ ,  $(u_+, v_+)$ ,  $(u_-, v_-)$ , where

$$u_{\pm} = \frac{\beta(1-\alpha) - 1 \pm \sqrt{(\beta(1-\alpha) - 1)^2 + 4\alpha\beta^2}}{2\beta} \quad \text{and} \quad v_{\pm} = \frac{1}{\beta}u_{\pm}. \quad (1.3)$$

Since  $u_+$  and  $v_+$  are positive, but  $u_-$  and  $v_-$  are negative, we shall consider the equilibrium  $(u_+, v_+)$  but ignore  $(u_-, v_-)$ . We let  $A = (u_+, v_+)$  and  $B = (1, 0)$ .

The equilibrium  $A$  is the rightmost intersection of the parabola  $v = (1-u)(u+\alpha)$  and the line  $v = (1/\beta)u$ . The parabola opens downward and has vertex  $V = ((1-\alpha)/2, (1+\alpha)^2/4)$ .

We define two regions of  $\alpha\beta$ -parameter space,

$$\mathcal{R}_1 = \{(\alpha, \beta) : 0 < \alpha < 1 \text{ and } \beta > \frac{2(1-\alpha)}{(\alpha+1)^2}\} \cup \{(\alpha, \beta) : \alpha \geq 1 \text{ and } \beta > 0\},$$

and

$$\mathcal{R}_2 = \{(\alpha, \beta) : 0 < \alpha < 1 \text{ and } 0 < \beta < \frac{2(1-\alpha)}{(\alpha+1)^2}\}.$$

In  $\mathcal{R}_1$ ,  $A$  lies to the right of  $V$ . In  $\mathcal{R}_2$ ,  $V$  is in the first quadrant, and  $A$  lies to the left of  $V$ .

The second equation of (1.2) is not defined at  $u = 0$ ; however, if we multiply the system (1.2) by  $u$ , another equilibrium appears, at  $O = (0, 0)$ . Although the systems (1.1) and (1.2) are undefined at  $O$ , this point is nevertheless of interest, since it represents the state at which both populations are zero.

**1.3. Traveling waves.** To find traveling waves with velocity  $c$ , we rewrite the system (1.1) in a frame that is moving with velocity  $c$ , i.e., we make the change of variables  $\zeta = x - ct$ . In addition we introduce the ratio  $\mu = D_v/D_u$ . We obtain

$$\begin{aligned} u_t &= D_u u_{\zeta\zeta} + cu_{\zeta} + u(1-u) - \frac{uv}{u+\alpha}, \\ v_t &= \mu D_u v_{\zeta\zeta} + cv_{\zeta} + \delta v \left(1 - \frac{\beta v}{u}\right). \end{aligned} \quad (1.4)$$

Traveling waves of (1.1) with velocity  $c$  correspond to stationary solutions of (1.4). We consider only traveling waves with nonzero velocity.

It turns out that traveling waves exist for any  $c \neq 0$ . It is therefore convenient to introduce the scaling  $z = \zeta/c$ , so (1.4) becomes

$$\begin{aligned} u_t &= \frac{D_u}{c^2} u_{zz} + u_z + u(1-u) - \frac{uv}{u+\alpha}, \\ v_t &= \frac{D_u}{c^2} \mu v_{zz} + v_z + \delta v \left(1 - \frac{\beta v}{u}\right). \end{aligned} \quad (1.5)$$

Finally we set  $\epsilon = D_u/c^2$  to obtain

$$\begin{aligned} u_t &= \epsilon u_{zz} + u_z + u(1-u) - \frac{uv}{u+\alpha}, \\ v_t &= \epsilon \mu v_{zz} + v_z + \delta v \left(1 - \frac{\beta v}{u}\right). \end{aligned} \quad (1.6)$$

A stationary solution of (1.6) corresponds, for a given  $D_u > 0$  and  $c \neq 0$  with  $\epsilon = D_u/c^2$ , to a stationary solution of (1.4), and hence to a traveling wave of (1.1) with  $D_v = \mu D_u$  and velocity  $c$ .

We assume  $\epsilon \ll 1$ , i.e.,  $D_u \ll c^2$ . Thus diffusion is very slow compared to the speed of the wave.

Stationary solutions of (1.6) correspond to solutions of the traveling wave ODE system

$$\begin{aligned} 0 &= \epsilon u_{zz} + u_z + u(1-u) - \frac{uv}{u+\alpha}, \\ 0 &= \epsilon \mu v_{zz} + v_z + \delta v \left(1 - \frac{\beta v}{u}\right), \end{aligned} \quad (1.7)$$

**1.4. Results.** In [7] the following results are shown.

**Theorem 1.1.** *Assume (1)  $(\alpha, \beta)$  is in  $\mathcal{R}_1$ ,  $\mu > 0$ , and  $\delta > 0$ , or (2)  $(\alpha, \beta)$  is in  $\mathcal{R}_2$ ,  $\mu > 0$ , and  $\delta > 1 - \alpha$ . Then for sufficiently small  $\epsilon > 0$ , there is a positive solution  $(u(z), v(z))$  of (1.7) that satisfies the boundary conditions*

$$\lim_{z \rightarrow -\infty} (u(z), v(z)) = A, \quad (1.8)$$

$$\lim_{z \rightarrow +\infty} (u(z), v(z)) = B, \quad (1.9)$$

*The solution is unique up to a shift in  $z$ .*

The solution of Theorem 1.1 corresponds to a traveling front of (1.1) that connects the equilibria  $A$  and  $B$ . The state  $A$ , in which predator and prey coexist, gradually expands in space to replace the state  $B$ , in which only the prey is present.

**Theorem 1.2.** *Assume  $(\alpha, \beta)$  is in  $\mathcal{R}_2$ ,  $\mu > 0$ , and  $\delta > 0$  is sufficiently small. Then for sufficiently small  $\epsilon > 0$ , there is a positive periodic solution  $(u(z), v(z))$  of (1.7).*

The periodic solution of Theorem 1.2 corresponds to a wave train of (1.1).

In this paper we shall prove the following results, which extend the above theorems.

**Theorem 1.3.** *Assume  $(\alpha, \beta)$  is in  $\mathcal{R}_1$  or  $\mathcal{R}_2$ ,  $\mu > 0$ , and  $\delta > 1$ . Then for sufficiently small  $\epsilon > 0$ , there is a 2-parameter family of positive solutions  $(u(z), v(z))$  of (1.7), defined for all  $z$ , that satisfy the boundary conditions*

$$\lim_{z \rightarrow -\infty} (u(z), v(z)) = A, \quad (1.10)$$

$$\lim_{z \rightarrow +\infty} (u(z), v(z)) = O, \quad (1.11)$$

One of the parameters in Theorem 1.3 of course represents shifts in the traveling waves. We specify that the solutions are defined for all  $z$  since *a priori* solutions that approach  $O$ , where the system is undefined, could do so in finite time.

The solutions of Theorem 1.3 correspond to traveling fronts of (1.1) that connect the equilibrium  $A$  to the point  $O$ . The state  $A$ , in which predator and prey coexist, gradually expands in space to replace the state  $O$ , in which both predator and prey are absent.

**Theorem 1.4.** *Assume  $(\alpha, \beta)$  is in  $\mathcal{R}_2$ ,  $\delta > 0$ , and there exists a hyperbolic positive closed orbit of the spatially homogeneous system (1.2). Let  $\mu > 0$ . Then for sufficiently small  $\epsilon > 0$ , there is a positive solution  $(u(z), v(z))$  of (1.7) that connects a periodic solution at  $z = -\infty$  to the constant state  $B$  at  $z = \infty$ .*

Positive closed orbits of (1.2) must surround  $A$ . By [7], such orbits exist at least for small  $\delta$ , and cannot exist for  $\delta > 1 - \alpha$ . We discuss the interval of existence further in Sec 3.

The solutions of Theorem 1.4 correspond to traveling waves of (1.1) that connect a wave train to the point  $B$ . The wave train, in which predator and prey populations oscillate, gradually expands in space to replace the state  $B$ , in which only the prey is present.

The remainder of the paper is devoted to the proofs of Theorems 1.3 and 1.4. We shall always assume that the parameters  $\alpha$ ,  $\beta$ ,  $\mu$  and  $\delta$  are positive, and shall indicate where further assumptions on  $(\alpha, \beta)$  and  $\delta$  are required. The paper ends with a brief discussion of other traveling waves in the model and another approach.

## 2. First-order system, rescaling, blow-up, and proof of Theorem 1.3.

2.1. **First-order system.** We set

$$(u, u_1, v, v_1) = \left( u, \frac{du}{dz}, v, \frac{dv}{dz} \right)$$

and rewrite (1.7) as the first-order system

$$\begin{aligned} \frac{du}{dz} &= u_1, \\ \epsilon \frac{du_1}{dz} &= -u_1 - u(1-u) + \frac{uv}{u+\alpha}, \\ \frac{dv}{dz} &= v_1, \\ \epsilon \frac{dv_1}{dz} &= -\frac{1}{\mu}v_1 - \frac{\delta}{\mu}v \left( 1 - \frac{\beta v}{u} \right). \end{aligned} \quad (2.1)$$

System (2.1) is known as the slow system in geometric singular perturbation theory. The corresponding fast system is obtained by setting  $z = \epsilon\xi$ :

$$\frac{du}{d\xi} = \epsilon u_1,$$

$$\begin{aligned}
 \frac{du_1}{d\xi} &= -u_1 - u(1-u) + \frac{uv}{u+\alpha}, \\
 \frac{dv}{d\xi} &= \epsilon v_1, \\
 \frac{dv_1}{d\xi} &= -\frac{1}{\mu}v_1 - \frac{\delta}{\mu}v \left(1 - \frac{\beta v}{u}\right).
 \end{aligned} \tag{2.2}$$

**2.2. Blow-up at the origin.** We will work with the fast system (2.2). In order to see solutions of (2.2) near the origin more clearly, we use the blow-up coordinates

$$u_1 = Pu, \quad v = Qu, \quad v_1 = Ru \tag{2.3}$$

in (2.2). Note that this will convert the term  $\frac{v}{u}$  in the fourth equation of (2.2) to  $Q$ . In order to have a polynomial system, which will be convenient in Sec. 3, we multiply the resulting vector field by  $u + \alpha$ . Equivalently, we make the change of independent variable

$$\eta = \int_0^\xi \frac{1}{u(s) + \alpha} ds,$$

which makes sense as long as  $u(s) > -\alpha$ . We obtain

$$\begin{aligned}
 \frac{du}{d\eta} &= \epsilon Pu(u + \alpha), \\
 \frac{dP}{d\eta} &= -\epsilon P^2(u + \alpha) - P(u + \alpha) + u^2 + (Q + \alpha - 1)u - \alpha, \\
 \frac{dQ}{d\eta} &= \epsilon(R - PQ)(u + \alpha), \\
 \frac{dR}{d\eta} &= -\frac{1}{\mu}(u + \alpha)(\epsilon\mu PR - \beta\delta Q^2 + \delta Q + R).
 \end{aligned} \tag{2.4}$$

We remark that closed orbits of (2.2) with  $u > 0$  correspond to closed orbits of (2.4) with  $u > 0$ . Setting  $\epsilon = 0$  in (2.4), we obtain

$$\begin{aligned}
 \frac{du}{d\eta} &= 0, \\
 \frac{dP}{d\eta} &= -P(u + \alpha) + u^2 + (Q + \alpha - 1)u - \alpha, \\
 \frac{dQ}{d\eta} &= 0, \\
 \frac{dR}{d\eta} &= \frac{1}{\mu}(u + \alpha)(\beta\delta Q^2 - \delta Q - R).
 \end{aligned} \tag{2.5}$$

In  $u \geq 0$  the set of equilibria of (2.5) is the two-dimensional manifold

$$\mathcal{W}_0 = \left\{ (u, P, Q, R) : P = \frac{Qu + \alpha u + u^2 - \alpha - u}{u + \alpha}, R = \beta\delta Q^2 - \delta Q, u \geq 0 \right\}, \tag{2.6}$$

the critical manifold of (2.4) in  $u \geq 0$ . Linearizing (2.5) about each point of  $\mathcal{W}_0$ , we find two zero eigenvalues and two negative eigenvalues  $-(u + \alpha)$  and  $-(u + \alpha)/\mu$ , so  $\mathcal{W}_0$  is normally hyperbolic and attracting for the system (2.5).

Let  $\mathcal{M}_0 \subset \mathcal{W}_0$  be a compact two-dimensional manifold with boundary. By Fenichel's First Theorem [5], [12, Theorem 1], [13, Theorem 3.1.4],  $\mathcal{M}_0$  perturbs,

for small  $\epsilon > 0$ , to a manifold with boundary

$$\mathcal{M}_\epsilon = \mathcal{M}_0 + \mathcal{O}(\epsilon)$$

that is locally invariant under (2.4), normally hyperbolic, and attracting. We can use  $u$  and  $Q$  as coordinates on  $\mathcal{M}_0$ . In terms of these coordinates, we choose  $\mathcal{M}_0$  so that it includes a set of the form  $0 \leq u \leq \omega$ ,  $0 \leq Q \leq \omega$  with  $\omega$  large.

The slow system corresponding to (2.4) is obtained by setting  $w = \epsilon\eta$ :

$$\begin{aligned} \frac{du}{dw} &= u(u + \alpha)P, \\ \epsilon \frac{dP}{dw} &= -\epsilon P^2(u + \alpha) - P(u + \alpha) + u^2 + (Q + \alpha - 1)u - \alpha, \\ \frac{dQ}{dw} &= (R - PQ)(u + \alpha), \\ \epsilon \frac{dR}{dw} &= -\frac{1}{\mu}(u + \alpha)(\epsilon\mu PR - \beta\delta Q^2 + \delta Q + R). \end{aligned} \quad (2.7)$$

The reduced slow system on  $\mathcal{M}_0$  is obtained by substituting the equations for  $P$  and  $R$  in (2.6) into (2.7) and setting  $\epsilon = 0$ :

$$\begin{aligned} \frac{du}{dw} &= u(u^2 + (Q + \alpha - 1)u - \alpha), \\ \frac{dQ}{dw} &= Q((\beta\delta Q - \delta)(u + \alpha) - (u^2 + (Q + \alpha - 1)u - \alpha)). \end{aligned} \quad (2.8)$$

In the definition of  $\mathcal{M}_0$ , the number  $\omega$  is chosen large enough so that  $\mathcal{M}_0$  contains all the orbits of (2.8) that are used in the remainder of the proof.

The slow system on  $\mathcal{M}_\epsilon$  is a perturbation of (2.8):

$$\begin{aligned} \frac{du}{dw} &= u((u^2 + (Q + \alpha - 1)u - \alpha) + \mathcal{O}(\epsilon)), \\ \frac{dQ}{dw} &= Q((\beta\delta Q - \delta)(u + \alpha) - (u^2 + (Q + \alpha - 1)u - \alpha)) + \mathcal{O}(\epsilon). \end{aligned} \quad (2.9)$$

**2.3. The reduced slow system (2.8) on  $\mathcal{M}_0$ .** For the reduced slow system (2.8), both axes are invariant. There are four equilibria in  $u \geq 0$ :  $K = (0, 0)$ ,  $L = (0, \frac{\delta-1}{\beta\delta})$ ,  $\tilde{B} = (1, 0)$ , and  $\tilde{A} = (u_+, Q_+)$ , with

$$\begin{aligned} u_+ &= \frac{1}{2\beta} \left( (1 - \alpha)\beta - 1 + \sqrt{((1 - \alpha)\beta - 1)^2 + 4\alpha\beta^2} \right), \\ Q_+ &= \frac{1}{\beta}. \end{aligned}$$

The points  $\tilde{B}$  and  $\tilde{A}$  correspond to  $B$  and  $A$ , defined earlier, in  $uv$ -coordinates. The line  $u = 0$  in  $uQ$ -space, including the points  $K$  and  $L$ , corresponds to the origin  $O$  in  $uv$ -coordinates.

For the system (2.8):

- (i) The equilibrium  $K$  has the eigenvalues  $-\alpha$  and  $-\alpha(\delta - 1)$ . It is therefore a hyperbolic saddle for  $\delta < 1$  and a hyperbolic attractor for  $\delta > 1$ .
- (ii) The equilibrium  $L$  has a positive (resp. negative)  $B$ -coordinate for  $\delta > 1$  (resp. for  $\delta < 1$ ). It has the eigenvalues  $-\alpha$  and  $\alpha(\delta - 1)$ . It is therefore a hyperbolic saddle for  $\delta > 1$  (resp. a hyperbolic attractor for  $\delta < 1$ ).
- (iii) The equilibrium  $\tilde{B}$  has the eigenvalues  $1 + \alpha$  and  $-\delta(1 + \alpha)$ . It is therefore a hyperbolic saddle.

The nature of the equilibrium  $\tilde{A}$  is less evident. However, a calculation shows:

**Proposition 2.1.** *If we make the change of variables  $v = Qu$  in the spatially homogeneous system (1.2), then multiply the resulting system by  $-(u+\alpha)$ , we obtain the reduced slow system (2.8). The system (1.2) in the region  $u > 0, v \geq 0$ , with time reversed, is therefore smoothly equivalent to the system (2.8) in the region  $u > 0, Q \geq 0$ .*

Therefore the nature of the equilibrium  $\tilde{A}$  in (2.8) follows from the nature of the corresponding equilibrium  $A$  in (1.2).

More generally, using Proposition 2.1, known facts about the spatially homogeneous system (1.2) translate immediately into facts about the reduced slow system (2.8). The following Proposition gathers some facts about (2.8) that are derived this way.

**Proposition 2.2.** *For the reduced slow system (2.8):*

- (i) *If  $(\alpha, \beta)$  is in  $\mathcal{R}_1$  and  $\delta > 0$ , the equilibrium  $\tilde{A}$  is a hyperbolic repeller.*
- (ii) *If  $(\alpha, \beta)$  is in  $\mathcal{R}_2$  there exists  $\delta_h$  with  $0 < \delta_h < 1 - \alpha$  such that the equilibrium  $\tilde{A}$  is a hyperbolic attractor for  $0 < \delta < \delta_h$ , and a hyperbolic repeller for  $\delta_h < \delta < \infty$ . A Hopf bifurcation occurs at  $\delta = \delta_h$ .*
- (iii) *If  $(\alpha, \beta)$  is in  $\mathcal{R}_2$ , a family of large closed orbits of relaxation type appears for small  $\delta > 0$  in a global bifurcation. These closed orbits are repelling and surround the attracting equilibrium at  $\tilde{A}$ .*
- (iv) *For  $(\alpha, \beta)$  in  $\mathcal{R}_1$  with  $\delta > 0$ , and for  $(\alpha, \beta)$  in  $\mathcal{R}_2$  with  $\delta > 1 - \alpha$ ,  $\tilde{A}$  is a global repeller in the region  $u > 0, Q > 0$ .*

Parts (i) and (ii) come from Propositions 4.1 and 5.1 of [7]. Part (iii) is a result of [7]. Part (iv) is stated in [7]; it is a reformulation of a result in [9].

Figure 2.1 shows equilibria of (2.8).

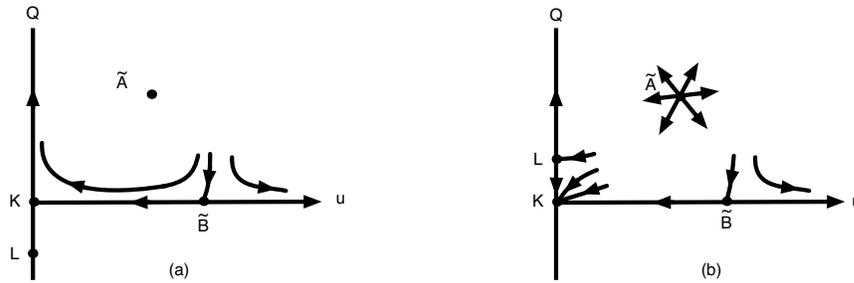


FIGURE 2.1. Equilibria of (2.8): (a)  $0 < \delta < 1$ . If  $(\alpha, \beta)$  is in  $\mathcal{R}_2$  and  $0 < \delta < \delta_h < 1 - \alpha$ , then  $\tilde{A}$  is an attractor. Otherwise  $\tilde{A}$  is a repeller. (b)  $\delta > 1$ .  $\tilde{A}$  is a repeller.

**2.4. The slow system (2.9) on  $\mathcal{M}_\epsilon$ .** Since the equilibria  $K = (0, 0)$ ,  $L = (0, \frac{\delta-1}{\beta\delta})$ ,  $\tilde{B} = (1, 0)$ , and  $\tilde{A} = (u_+, B_+)$  of the reduced slow system (2.8) are hyperbolic, the slow system (2.9) has nearby equilibria  $K_\epsilon$ ,  $L_\epsilon$ ,  $\tilde{B}_\epsilon$ , and  $\tilde{A}_\epsilon$  of the same types.

**Proposition 2.3.** *For any sufficiently small  $\epsilon > 0$ , the line  $u = 0$  is invariant under the slow system (2.9) on  $\mathcal{M}_\epsilon$ , and contains  $K_\epsilon$  and  $L_\epsilon$ .*

*Proof.* Invariance follows from the fact that for the full slow system (2.7), the 3-dimensional space  $u = 0$  is invariant for any  $\epsilon$ . Since  $K$  and  $L$  are hyperbolic within  $u = 0$  for the reduced slow system (2.8) on  $\mathcal{M}_0$ , it follows that  $K_\epsilon$  and  $L_\epsilon$  are contained in  $u = 0$ .  $\square$

**Proposition 2.4.** *For any sufficiently small  $\epsilon > 0$ ,  $K_\epsilon$  and  $\tilde{B}_\epsilon$  are contained in the line  $Q = 0$ . In addition, the portion of the line  $Q = 0$  that lies between  $K_\epsilon$  and  $\tilde{B}_\epsilon$  is invariant under the slow system (2.9) on  $\mathcal{M}_\epsilon$ .*

*Proof.* Note that for the full slow system (2.7), the 2-dimensional space  $Q = R = 0$  is invariant for any  $\epsilon$ . Within this space, for  $\epsilon = 0$  there is a curve  $\mathcal{C}_0$  of equilibria given by  $P = \frac{\alpha u + u^2 - \alpha - u}{u + \alpha}$  (compare (2.6)).  $\mathcal{C}_0$  is a normally hyperbolic curve of equilibria within  $Q = R = 0$ . It therefore perturbs to a normally hyperbolic invariant curve  $\mathcal{C}_\epsilon$  within  $Q = R = 0$ . Since  $K$  and  $L$  are hyperbolic equilibria within  $\mathcal{C}_\epsilon$  for the reduced slow system, it follows that  $\mathcal{C}_\epsilon$  includes  $K_\epsilon$  and  $\tilde{B}_\epsilon$ .

We cannot immediately conclude that  $\mathcal{C}_\epsilon$  is part of  $\mathcal{M}_\epsilon$ , due to nonuniqueness of perturbations of the normally hyperbolic invariant manifolds  $\mathcal{M}_0$ . However,  $\mathcal{M}_\epsilon$  must include all nearby bounded orbits. Therefore  $\mathcal{M}_\epsilon$  includes  $K_\epsilon$ ,  $\tilde{B}_\epsilon$ , and the portion of  $\mathcal{C}_\epsilon$  between them, which is a bounded orbit. This implies that under the slow system (2.9) on  $\mathcal{M}_\epsilon$ , the portion of the line  $Q = 0$  that lies between  $K_\epsilon$  and  $\tilde{B}_\epsilon$  is invariant.  $\square$

**Proposition 2.5.**  $K_\epsilon = K$ ,  $L_\epsilon = (0, \frac{\delta-1}{\beta\delta} + \mathcal{O}(\epsilon))$ ,  $\tilde{B}_\epsilon = \tilde{B}$ , and  $\tilde{A}_\epsilon = \tilde{A}$ .

*Proof.* By the previous propositions,  $K_\epsilon$  is contained in both  $u = 0$  and  $Q = 0$ . Therefore  $K_\epsilon = K$ .

Using (2.6),  $L$ ,  $\tilde{B}$ , and  $\tilde{A}$  correspond respectively to the following equilibria of (2.5):

$$(0, -1, \frac{\delta-1}{\beta\delta}, \frac{1-\delta}{\beta\delta}), (1, 0, 0, 0), (u_+, 0, B_+, 0).$$

The last two are equilibria of (2.4) for any  $\epsilon$ ; therefore  $\tilde{B}_\epsilon = \tilde{B}$  and  $\tilde{A}_\epsilon = \tilde{A}$ . The first is not an equilibrium of (2.4) for  $\epsilon \neq 0$ . (The problem is the term  $-\epsilon P^2(u + \alpha)$  in the second equation.) However,  $L_\epsilon$  has the given form by Proposition 2.3.  $\square$

**2.5. Proof of Theorem 1.3.** For the reduced slow system (2.8) on  $\mathcal{M}_0$  and  $\delta > 1$ , we consider in Figure 2.1 (b) the open one-parameter family  $\mathcal{F}_0$  of orbits that approach the attractor  $K$  as time increases, bounded on one side by a connection along the vertical axis from the saddle  $L$  to  $K$ , and on the other side by a connection along the horizontal axis from the saddle  $\tilde{B}$  to  $K$ .

From Proposition 2.2 (iv), the orbits in  $\mathcal{F}$ , along with the stable manifolds of  $L$  and  $\tilde{B}$ , approach  $\tilde{A}$  in backward time.

For small  $\epsilon > 0$ , we consider the slow system (2.9) on  $\mathcal{M}_\epsilon$ . The  $Q$ -axis, and the  $u$ -axis between  $K$  and  $\tilde{B}_\epsilon$ , remain invariant by Propositions 2.3 and 2.4, and the equilibria perturb as described in Proposition 2.5. There is a connection from the saddle  $L_\epsilon$  to the attractor  $K$  along the vertical axis, and a connection from the saddle  $\tilde{B}$  to  $K$  along the horizontal axis. In addition, the stable manifolds of  $L_\epsilon$  and  $\tilde{B}$  approach  $\tilde{A}$  in backward time.

We consider the open one-parameter family of orbits  $\mathcal{F}_\epsilon$  that approach  $K_\epsilon$  as time increases, bounded by the connections from  $L_\epsilon$  and  $\tilde{B}$  to  $K$ . It follows from the previous paragraph that these orbits approach  $\tilde{A}$  in backward time.

After blow-down from  $uPQR$ -coordinates to  $uu_1vv_1$  coordinates, the family  $\mathcal{F}_\epsilon$  corresponds to a one-parameter family  $\mathcal{G}_\epsilon$  of orbits of (2.2) that connect  $(u_+, 0, v_+, 0)$  to  $(0, 0, 0, 0)$ . The orbits in  $\mathcal{G}_\epsilon$  correspond to the traveling wave solutions of (1.7) described in the theorem. They are positive ( $u > 0$  and  $v > 0$ ) since for the orbits in  $\mathcal{F}_\epsilon$ ,  $u > 0$  and  $Q > 0$ . They are defined for infinite time, since the orbits in  $\mathcal{F}_\epsilon$  are defined for infinite time, and the various changes of independent variable do not affect this property.

### 3. Poincaré sphere and proof of Theorem 1.4.

**3.1. Motivation for Theorem 1.4: known facts about closed orbits of (2.8).** We recall from Proposition 2.1 that the spatially homogeneous system (1.2) and the reduced slow system (2.8) are equivalent in the open first quadrant after time reversal. The hypothesis of Theorem 1.4 is stated for closed orbits of (1.2), but closed orbits of (2.8) are more directly relevant to traveling waves. We will motivate Theorem 1.4 by discussing closed orbits of (2.8).

Positive closed orbits of (2.8) must surround  $\tilde{A}$ . From Proposition 2.2 (iv), they can only exist for  $(\alpha, \beta)$  in  $\mathcal{R}_2$  and  $0 < \delta \leq 1 - \alpha$ .

By Proposition 2.2 (iii), for  $(\alpha, \beta)$  in  $\mathcal{R}_2$ , a family of large closed orbits of relaxation type appears for small  $\delta > 0$  in a global bifurcation. These closed orbits are repelling and surround the attracting equilibrium at  $\tilde{A}$ . Assuming no other closed orbits are present, a partial phase portrait is shown in Figure 3.1(a).

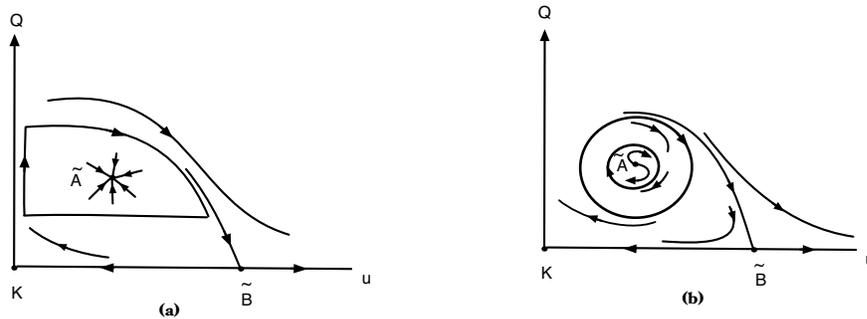


FIGURE 3.1. Equilibria and positive closed orbits of (2.8) in two cases. (a) A repelling relaxation oscillation for small  $\delta > 0$ . (b) Two closed orbits with  $\delta_h < \delta < \delta_t$  in the case of a supercritical Hopf bifurcation.

By Proposition 2.2 (ii), for fixed  $(\alpha, \beta)$  in  $\mathcal{R}_2$ , the equilibrium  $\tilde{A}$  undergoes a Hopf bifurcation at some  $\delta = \delta_h$  with  $0 < \delta_h < 1 - \alpha$ , and becomes repelling for  $\delta > \delta_h$ .

According to [20], the Hopf bifurcation may be subcritical, in which case a family of repelling closed orbits defined near and below  $\delta_h$  dies in the Hopf bifurcation.

Presumably these closed orbits are the continuation of the closed orbits of relaxation type.

On the other hand, according to [20], the Hopf bifurcation may be supercritical. In this case a family of attracting closed orbits exists near and above  $\delta_h$ , then turns at some  $\delta_t$  with  $\delta_h < \delta_t \leq 1 - \alpha$ , becoming a family of repelling closed orbits. Again the repelling closed orbits are presumably the continuation of the repelling closed orbits of relaxation type. Assuming no other closed orbits are present, the phase portrait in the region  $\delta_h < \delta < \delta_t$  is shown in Figure 3.1(b).

In both Figure 3.1(a) and Figure 3.1(b), if the stable manifold  $\gamma_0$  of the saddle  $\tilde{B}$  stays bounded in backward time, then it must approach the repelling closed orbit in backward time. Then after perturbation, the stable manifold  $\gamma_\epsilon$  of  $\tilde{B}$  must approach the perturbed repelling closed orbit in backward time. The curve  $\gamma_\epsilon$  corresponds to the traveling wave whose existence is asserted in Theorem 1.4.

Since the bifurcation diagram of closed orbits is not completely known, as far as we know, we have used a minimal hypothesis in Theorem 1.4, namely that some hyperbolic closed orbit exists.

**3.2. Sketch of proof of Theorem 1.4.** To prove Theorem 1.4, we shall first show that under the hypotheses of the theorem, for the system (2.8), the stable manifold of the saddle  $\tilde{B}$  approaches the outermost closed orbit in backward time. To do this we shall regard (2.8) as defined on the entire  $uQ$  plane, then compactify the plane by adding a circle at infinity. In other words, we look at the flow on the Poincaré sphere. This approach is also used in [20], for the system (1.2) multiplied by  $u(u + \alpha)$ , although details are not given there.

The flow of the extended system on the quadrant  $\mathcal{Q}_+$  of the Poincaré sphere that corresponds to the first quadrant of (2.8) is shown in Figure 3.2. Since  $\mathcal{Q}_+$  is compact, by the Generalized Poincaré-Bendixson Theorem [18, Sec. 3.7], the stable manifold  $\gamma_0$  of the saddle  $\tilde{B}$  approaches, in backward time, either an equilibrium, a closed orbit, a separatrix cycle (a closed curve consisting of unstable and stable manifolds of saddles, or their analogues at degenerate equilibria), or a graphic (a connected union of separatrix cycles). The flow shown in Figure 3.2 has no separatrix cycles. The curve  $\gamma_0$  cannot approach  $\tilde{A}$  because of the existence of a closed orbit, and the other equilibria are not approached by any interior orbits in backward time. We conclude that  $\gamma_0$  approaches a closed orbit, which is necessarily bounded away from the circle at infinity.

Consider the stable manifold  $\gamma_\epsilon$  of  $\tilde{B}$  for the perturbed system (2.9) on the Poincaré sphere. (For simplicity we will often speak of (2.8) and (2.9) as if they were defined on the Poincaré sphere.) By Lemma 1.1, proved in Appendix A, there is a compact neighborhood  $\mathcal{K}$  of  $\gamma_0$  that is bounded away from the circle of infinity and that contains  $\gamma_\epsilon$  for  $\epsilon > 0$  sufficiently small.

The compact manifold with boundary  $\mathcal{M}_0$  corresponds to a subset of  $\mathcal{Q}_+$  that is bounded away from the circle at infinity.  $\mathcal{M}_0$  can be chosen large enough to contain  $\mathcal{K}$ .

The only equilibria in  $\mathcal{M}_0$  are the hyperbolic equilibria at the origin,  $\tilde{A}$ , and  $\tilde{B}$ . Hence the only equilibria in  $\mathcal{M}_\epsilon$  are the same three. (By Proposition 2.5, the equilibria are unchanged under perturbation.) In  $\mathcal{M}_\epsilon$  the unstable manifold of  $\tilde{B}$ , and the stable and unstable manifolds of the origin, are unchanged after perturbation. Since  $\mathcal{M}_0$  contains at least one hyperbolic closed orbit surrounding  $\tilde{A}$ , so does  $\mathcal{M}_\epsilon$ .  $\mathcal{M}_\epsilon$  also contains the stable manifold  $\gamma_\epsilon$  of  $\tilde{B}$ . Again the Generalized

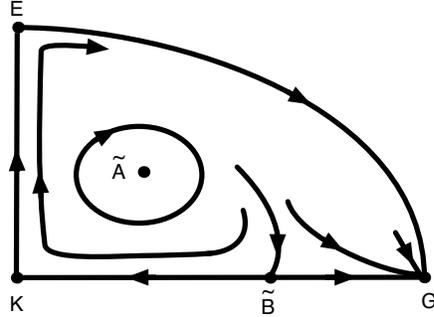


FIGURE 3.2. The flow in the quadrant  $X \geq 0, Y \geq 0$  of the Poincaré sphere when positive closed orbits are present, in which case we must have  $\beta\delta < 2$ . The flow inside the outermost closed orbit is not shown since it can vary.

Poincaré-Bendixson Theorem implies that  $\gamma_\epsilon$  approaches a closed orbit in backward time. This proves Theorem 1.4.

The remainder of this section is devoted to justifying Figure 3.2.

**3.3. Poincaré sphere.** For the analysis in this section we find it more convenient and aesthetically pleasing to rewrite (2.8) as

$$\begin{aligned} u' &= u^3 + (v + \alpha - 1)u^2 - \alpha u, \\ v' &= v((\beta\delta v - \delta)(u + \alpha) - (u^2 + (v + \alpha - 1)u - \alpha)). \end{aligned} \quad (3.1)$$

The upper hemisphere  $Z > 0$  of the Poincaré sphere  $X^2 + Y^2 + Z^2 = 1$  can be mapped onto the  $uv$ -plane by the coordinate transformation  $u = X/Z, v = Y/Z$ . Its inverse is

$$X = \frac{u}{\sqrt{1 + u^2 + v^2}}, \quad Y = \frac{v}{\sqrt{1 + u^2 + v^2}}, \quad Z = \frac{1}{\sqrt{1 + u^2 + v^2}}. \quad (3.2)$$

Since the system (3.1) is polynomial in  $u$  and  $v$ , its pullback to the upper hemisphere of the Poincaré sphere can be rescaled so that it extends smoothly to the equator  $X^2 + Y^2 = 1, Z = 0$ . The equator of the Poincaré sphere correspond to the circle at infinity of the  $uv$ -plane [18, Sec. 3.10].

In computations, typically two sets of affine coordinates are used:

- (1)  $x = 1/u, y = v/u$  on  $u \neq 0$ , and (2)  $x = u/v, y = 1/v$  on  $v \neq 0$ .

Using the rescaled flow in these coordinates, together with the flow of the original vector field (3.1), one can reconstruct the flow on the Poincaré sphere [3].

Figure 3.2 shows the flow of the pullback of (3.1) in the quadrant  $X \geq 0, Y \geq 0$  of the Poincaré sphere, which we call  $\mathcal{Q}_+$ , after rescaling. This quadrant of the Poincaré sphere corresponds to the quadrant  $u \geq 0, v \geq 0$  for (3.1). The equilibria on the circle at infinity are labeled  $E$  and  $G$ .  $G$  is a hyperbolic attractor, and  $E$  is a nonhyperbolic equilibrium for which the displayed region in the first quadrant

is a hyperbolic sector. The remainder of this section is devoted to justifying this description of the equilibria on the circle at infinity.

**3.4. The coordinate system**  $x = 1/u$ ,  $y = v/u$ . We make the change of variables  $x = 1/u$ ,  $y = v/u$  in (3.1), and multiply the resulting vector field by  $x^2$ . The result is

$$\begin{aligned} x' &= -x - xy + (1 - \alpha)x^2 + \alpha x^3, \\ y' &= (\beta\delta - 2)y^2 - 2y + (2 - 2\alpha - \delta)xy + \alpha\beta\delta xy^2 + (2\alpha - \delta)x^2y. \end{aligned} \quad (3.3)$$

On the line  $x = 0$  (which corresponds to the “line”  $u = \infty$ ) there are equilibria at  $y = 0$  and  $y = 2/(\beta\delta - 2)$ . The eigenvalues of the linearization of (3.3) at  $(0, 0)$  are  $-1$  and  $-2$ . In Figure 3.2,  $(0, 0)$  corresponds to  $G$ .

We assume that  $(\alpha, \beta)$  is in  $\mathcal{R}_2$  and  $0 < \delta \leq 1 - \alpha$ , since we noted in Sec. 3.1 that these conditions are required for the existence of positive closed orbits of (2.8). We recall that

$$\mathcal{R}_2 = \{(\alpha, \beta) : 0 < \alpha < 1 \text{ and } 0 < \beta < \frac{2(1 - \alpha)}{(\alpha + 1)^2}\}.$$

The boundary curve  $\beta = \frac{2(1 - \alpha)}{(\alpha + 1)^2}$ ,  $0 \leq \alpha \leq 1$ , attains its maximum at  $\alpha = 0$ , where  $\beta = 2$ . Therefore in  $\mathcal{R}_2$  we have  $0 < \beta < 2$ . We also note that  $0 < \delta < 1 - \alpha$  and  $0 < \alpha < 1$ , so  $0 < \delta < 1$ . We conclude that  $\beta\delta < 2$ . Therefore the equilibrium at  $y = 2/(\beta\delta - 2)$  has  $y < 0$ , so it does not lie in the first quadrant of the Poincaré sphere. We can ignore it.

For completeness we give the flow on the first quadrant of the Poincaré sphere for  $\beta\delta > 2$  in Appendix B.

**3.5. The coordinate system**  $x = u/v$ ,  $y = 1/v$ . We make the change of variables  $x = u/v$ ,  $y = 1/v$  in (3.1), and multiply the resulting vector field by  $y^2$ . The result is

$$\begin{aligned} x' &= (2 - \beta\delta)x^2 + 2x^3 + (2\alpha + \delta - 2)x^2y - \alpha\beta\delta xy + (\delta - 2\alpha)xy^2, \\ y' &= (1 - \beta\delta)xy + x^2y - \alpha\beta\delta y^2 + (\alpha + \delta - 1)xy^2 + \alpha(\delta - 1)y^3. \end{aligned} \quad (3.4)$$

On the line  $y = 0$  (which corresponds to the “line”  $v = \infty$ ) there are equilibria at  $x = 0$  and  $x = (\beta\delta - 2)/2$ .

The second of these equilibria does not lie in the first quadrant of the Poincaré sphere since, as we have seen,  $\beta\delta < 2$ . The equilibrium at  $(0, 0)$  is degenerate: all partial derivatives of (3.4) there are 0. It corresponds to  $E$  in Figure 3.2.

**3.6. Analysis of the degenerate equilibrium.** We analyze the degenerate equilibrium  $(0, 0)$  of (3.4) using the polar coordinate map

$$\Phi : \mathbb{S}^1 \times \mathbb{R} \rightarrow \mathbb{R}^2, \quad ((\bar{x}, \bar{y}), r) \mapsto (x, y),$$

where  $\bar{x}^2 + \bar{y}^2 = 1$  and

$$x = r\bar{x}, \quad y = r\bar{y}.$$

In computations, as in the previous subsections, typically two sets of affine coordinates are used:

$$(1) \ x = r, \ y = ry_1 \text{ on } x \neq 0, \text{ and } (2) \ x = rx_1, \ y = r \text{ on } y \neq 0.$$

Using the rescaled flow in these coordinates for small  $r$ , one can reconstruct the rescaled flow on  $\mathbb{S}^1 \times \mathbb{R}$  for small  $r$ , and hence the flow of (3.4) near  $(0, 0)$ .

In the coordinates  $x = r$ ,  $y = ry_1$ , the system (3.4) becomes, after division by  $r$ :

$$\begin{aligned} \dot{r} &= (2 - \beta\delta)r + 2r^2 + (2\alpha + \delta - 2)r^2y_1 - \alpha\beta\delta ry_1 + (\delta - 2\alpha)r^2y_1^2, \\ \dot{y}_1 &= -y_1 - ry_1 + ry_1^2 + (\alpha - \delta + \alpha\delta)ry_1^3. \end{aligned} \quad (3.5)$$

On the invariant line  $r = 0$ , (3.5) has the unique equilibrium  $E_1 = (0, 0)$  with eigenvalues  $2 - \beta\delta$  and  $-1$ . Since  $\beta\delta < 2$  it is a saddle.

In the coordinates  $x = rx_1$ ,  $y = r$ , the system (3.4) becomes, after division by  $r$ :

$$\begin{aligned} \dot{x}_1 &= x_1^2 + rx_1^3 + (\alpha - 1)rx_1^2 + (\delta - \alpha - \alpha\delta)x_1r, \\ \dot{r} &= (1 - \beta\delta)rx_1 + r^2x_1^2 - \alpha\beta\delta r + (\alpha + \delta - 1)r^2x_1 + \alpha(\delta - 1)r^2. \end{aligned} \quad (3.6)$$

On the invariant line  $r = 0$ , (3.6) has the unique equilibrium  $E_2 = (0, 0)$  with eigenvalues  $0$  and  $-\alpha\beta\delta$ . A center manifold is the  $x_1$ -axis, on which the system reduces to  $\dot{x}_1 = x_1^2$ .

Combining the results from the two coordinate systems, we obtain Figure 3.3, which shows the flow near the degenerate equilibrium  $(0, 0)$  of (3.4) coordinates. After blow-down we obtain a hyperbolic sector.

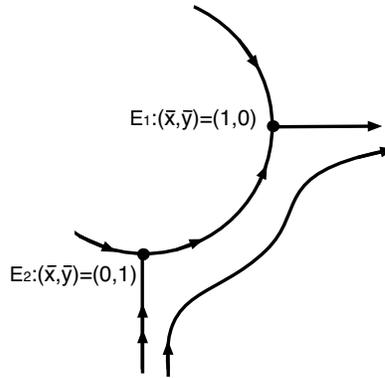


FIGURE 3.3. The flow near the degenerate equilibrium  $(0, 0)$  of (3.4) in polar coordinates when  $\beta\delta < 2$ . So that the reader can more easily compare this figure with Figure 3.2, the circle  $r = 0$  is shown upside down, with the point  $(\bar{x}, \bar{y}) = (0, 1)$  at the bottom of the circle. With some abuse of notation, the equilibria are labeled  $E_1$  and  $E_2$  to correspond to the equilibria in the two affine coordinate systems.

**4. Discussion.** We mention two other types of traveling waves that exist in the Holling-Tanner model with weak diffusion.

- (i) When closed orbits are present in the spatially homogeneous system (1.2), there is a one-parameter family of orbits of (1.2) that connect the equilibrium  $A$  to the innermost closed orbit. If we assume that (1.2) has at least one hyperbolic closed orbit, then for small  $\epsilon > 0$  there will be traveling waves that connect the constant state  $A$  to a periodic solution. If  $A$  is an attracting (resp. repelling) equilibrium of (1.2), then  $A$  is the state at  $z = -\infty$  (resp.  $z = \infty$ ) of the traveling wave.

- (ii) When two adjacent hyperbolic closed orbits are present in the spatially homogeneous system (1.2), there is a one-parameter family of orbits that connect them. For small  $\epsilon > 0$  there will be a one-parameter family of traveling waves that connect two periodic solutions.

The existence of these traveling waves is easily proved. For the slow-fast system (2.2), one constructs the critical manifold and the slow system on the critical manifold, which is just (1.2) with time reversed. It is not necessary to use the blow-up coordinates (2.3). The perturbed system for  $\epsilon > 0$  will have orbits that correspond to the traveling waves.

We also mention that the recent paper [4] takes a different approach to the problem of identifying traveling waves in a predator-prey model with diffusion. The analysis in this paper is based on global attractor theory.

**Appendix A. Perturbed stable manifold of  $\tilde{B}$ .** We saw in Sec. 3.2 that under the assumption of Theorem 1.4, for the system (2.8) on the Poincaré sphere, the stable manifold  $\gamma_0$  of  $\tilde{B}$  approaches a closed orbit  $\Gamma$  in backward time.

**Lemma 1.1.** *There is a compact neighborhood  $\mathcal{K}$  of  $\gamma_0$ , bounded away from the circle at infinity, such that for small  $\epsilon > 0$ , the stable manifold of  $\tilde{B}$  is contained in  $\mathcal{K}$ .*

*Proof.* . The proof is based on the proof of the Poincaré-Bendixson Theorem; see [3, Sec. 1.9]. Let  $\Sigma$  be a compact line segment that is transversal to  $\Gamma$  such that the vector field for (2.4) is transverse to  $\Sigma$ ; see Figure A.1(a). Let  $p_1$  be the first intersection of  $\gamma_0$  with  $\Sigma$ , and let  $p_2$  be the second intersection of  $\gamma_0$  with  $\Sigma$ . The portion of  $\gamma_0$  from  $p_1$  to  $p_2$ , together with the portion of  $\Sigma$  from  $p_2$  to  $p_1$ , forms a closed curve. This closed curve bounds a closed disk  $\mathcal{D}$ .  $\mathcal{D}$  is backward invariant under the flow of (2.8). Therefore  $\mathcal{D}$  contains all of  $\gamma_0$  after  $p_1$ .

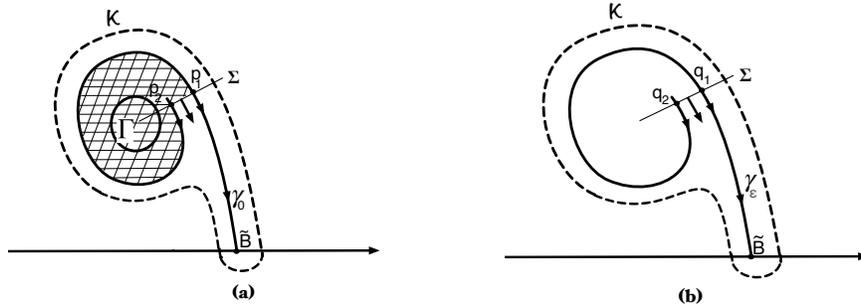


FIGURE A.1. (a)  $\gamma_0$  and  $\mathcal{K}$ . The disk  $\mathcal{D}$  is shaded. (b)  $\gamma_\epsilon$  and  $\mathcal{K}$ .

Consider the set  $\mathcal{S}$  consisting of  $\tilde{B}$ , the portion of  $\gamma_0$  from  $\tilde{B}$  to  $p_1$ , and the disk  $\mathcal{D}$ . Let  $\mathcal{K}$  be a compact neighborhood of  $\mathcal{S}$ . Then  $\mathcal{K}$  contains  $\gamma_0$ ; see Figure A.1(a).

For small  $\epsilon > 0$ , the vector field for (2.9) is transverse to  $\Sigma$ , we can define  $q_1$  and  $q_2$  to be the first and second intersections of  $\gamma_\epsilon$  with  $\Sigma$ , and the portion of  $\gamma_\epsilon$  from  $\tilde{B}$  to  $q_2$  will lie in the interior of  $\mathcal{K}$ . See Figure A.1(b).

The portion of  $\gamma_\epsilon$  from  $q_1$  to  $q_2$ , together with the portion of  $\Sigma$  from  $q_2$  to  $q_1$ , form a closed curve that bounds a closed disk. This disk is contained in  $\mathcal{K}$  and is backward invariant under the flow of (2.9). Therefore the entire curve  $\gamma_\epsilon$  is contained in  $\mathcal{K}$ .  $\square$

**Appendix B. Poincaré sphere when  $\beta\delta > 2$ .** In Sec. 3 we described the flow of (2.8) in the first quadrant of the Poincaré sphere when  $\beta\delta < 2$ . For completeness we shall describe the flow of (2.8) in the first quadrant of the Poincaré sphere when  $\beta\delta > 2$ . In this case there are no closed orbits. It is still true that the equilibria on the circle at infinity do not attract any orbits in the finite plane in backwards time. The equilibrium  $\tilde{A}$  is a global repeller. See Figure B.1.

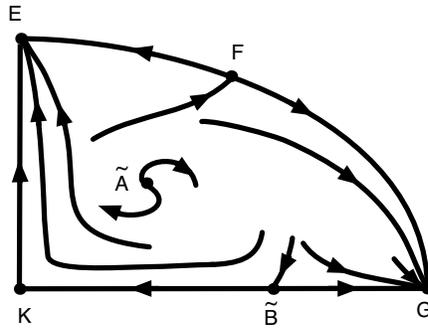


FIGURE B.1. The flow in the quadrant  $X \geq 0, Y \geq 0$  of the Poincaré sphere when  $\beta\delta > 2$ .

Comparing to Figure 3.2, there is a new equilibrium on the circle at infinity, labeled  $F$ .  $F$  is a hyperbolic saddle. In addition, the nonhyperbolic equilibrium  $E$  has changed. It now has an attracting parabolic sector in the first quadrant.

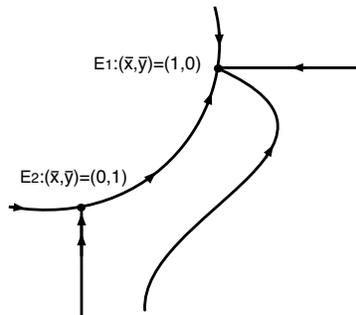


FIGURE B.2. The flow near the degenerate equilibrium  $(0,0)$  of (3.4) in polar coordinates when  $\beta\delta > 2$ . Compare Figure 3.3.

Comparing to Figure 3.2, there is a new equilibrium on the circle at infinity, labeled  $F$ .  $F$  is a hyperbolic saddle. In addition, the nonhyperbolic equilibrium  $E$  has changed. It now has an attracting parabolic sector in the first quadrant.

To justify these changes, note that in Sec. 3.4, when  $\beta\delta > 2$ , the equilibrium at  $y = 2/(\beta\delta - 2)$  is in the first quadrant. It is the equilibrium labeled  $F$  in Figure B.1. The eigenvalues of the linearization of (3.3) at  $(0, 2/(\beta\delta - 2))$  are  $\beta\delta/(2 - \beta\delta)$  and 2, so it is a hyperbolic saddle.

In Sec. 3.5 the equilibrium at  $x = (\beta\delta - 2)/2$  corresponds to  $F$  in Figure 3.2 and has already been analyzed in the other coordinate system.

In the blow-up of the degenerate equilibrium  $E$  in Sec. 3.6, the equilibrium  $E_1$  has eigenvalues  $2 - \beta\delta$  and  $-1$ . Since  $\beta\delta > 2$  it is a hyperbolic attractor. After blow-down we obtain an attracting parabolic sector. See Figure B.2.

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