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# EXISTENCE AND STABILITY OF TRAVELING WAVE SOLUTIONS FOR A POPULATION GENETIC MODEL VIA SINGULAR PERTURBATIONS*

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**Abstract.** Using singular perturbation methods, the existence and stability of traveling wave solutions for a density-dependent selection migration model in population genetics is proved. Single locus and two alleles are assumed, and it is also assumed that the fitnesses of the heterozygotes in the population are close to but below those of the homozygotes. Unlike previous models, this paper does not assume that the population is in Hardy–Weinberg equilibrium.

**Key words.** population genetics, traveling waves, stability, singular perturbations

**AMS subject classifications.** 35K57, 35B25, 92D10

## 1. Introduction.

In 1975, Aronson and Weinberger [2] proposed the following population genetic model based on the work of Fisher [11]. Consider a population of diploid individuals living in a one-dimensional homogeneous habitat, which we assume to be the entire real line. Suppose that a particular pair of chromosomes carries at one of its locus a particular gene that occurs in two forms, called alleles, which we denote by A and a. Then the population may be divided into three classes or genotypes: AA, aa, and Aa. Individuals with the first two genotypes are called the homozygotes, while individuals with the last genotype are called the heterozygotes.

Let $\rho_1(x,t)$, $\rho_2(x,t)$, $\rho_3(x,t)$ be the densities of genotypes AA, Aa, and aa at point $x$ and time $t$, respectively. We assume that the population mates randomly, producing offspring with a birthrate $r$, and that the population diffuses with a constant rate 1. Let $\tau_1, \tau_2, \tau_3$ denote the deathrates of the individuals with genotypes AA, Aa, and aa, respectively, and let $n(x,t)$ denote the total population density. Then, under the above assumptions, $\rho_1, \rho_2, \rho_3$ satisfy the following system of partial differential equations:

$$
\begin{aligned}
\rho_{1,t} &= \rho_{1,xx} - \tau_1\rho_1 + \frac{r}{n}\left(\rho_1 + \frac{1}{2}\rho_2\right)^2,\\
\rho_{2,t} &= \rho_{2,xx} - \tau_2\rho_2 + \frac{2r}{n}\left(\rho_1 + \frac{1}{2}\rho_2\right)\left(\rho_3 + \frac{1}{2}\rho_2\right),\\
\rho_{3,t} &= \rho_{3,xx} - \tau_3\rho_3 + \frac{r}{n}\left(\rho_3 + \frac{1}{2}\rho_2\right)^2.
\end{aligned}
\tag{1.1}
$$

These equations hold without any assumptions on the birthrates and deathrates. For example, $r$ and $\tau_i$ may depend on $x, t$, or $\rho_i$, for $i = 1, 2, 3$.

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In population genetics, we are more interested in the frequency of an allele than in the densities of the genotypes. Let $p(x,t) = (\rho_1 + \frac{1}{2}\rho_2)/n$ be the frequency of allele $A$ in the population and let $\sigma = (\rho_2^2 - 4\rho_1\rho_3)/n^2$. Then a straightforward but tedious calculation yields the following equations for $p$ and $n$:

$$\begin{aligned} p_t &= \frac{1}{n^2}(n^2 p_x)_x + f(p,n)p(1-p) + \frac{1}{4}\{(\eta_3 - \eta_2)p - (\eta_1 - \eta_2)(1-p)\}\sigma, \\ n_t &= n_{xx} + g(p,n)n - (\eta_1 - 2\eta_2 + \eta_3)\frac{\sigma n}{4}, \\ \sigma_t &= \frac{1}{n^2}(n^2\sigma_x)_x + h(p,n,\sigma)\sigma - 4(\eta_1 - 2\eta_2 + \eta_3)p^2(1-p)^2 - 8(p_x)^2, \end{aligned} \tag{1.2}$$

where

$$\begin{aligned} f(p,n) &= p(\eta_1 - \eta_2) + (1-p)(\eta_2 - \eta_3), \\ g(p,n) &= p^2\eta_1 + 2p(1-p)\eta_2 + (1-p)^2\eta_3, \\ h(p,n,\sigma) &= -r + (\eta_3 - \eta_1)(1-2p) - \tfrac{1}{4}(\eta_1 - 2\eta_2 + \eta_3)\sigma, \end{aligned} \tag{1.3}$$

and

$$\eta_i(n) = r(n) - \tau_i(n) \quad \text{for } i = 1,2,3. \tag{1.4}$$

Note that the function $\eta_i$, being the difference between the birthrate and deathrate, represents the fitness of the corresponding genotype. We also assume that $r$ and $\tau_i$ depend only on the population density $n$, as indicated in (1.4).

The quantity $\sigma$ measures the deviation of the population from Hardy–Weinberg equilibrium. Most of the papers we have seen on this model with the exception of [4] assumed that $\sigma \equiv 0$, meaning that the population is always in Hardy–Weinberg equilibrium. Using a scaling argument, Fife [9] showed that, if the fitnesses of the genotypes are close to each other, then, as a first approximation, we can assume that the population is a constant, so that (1.2) reduces to a single equation in $p$. Many mathematical theories were developed for such an equation; see, for example, [2] and [10]. However, in this paper, we do not assume that $\sigma \equiv 0$, nor that $n$ is a constant.

We consider the heterozygote inferior case of (1.2) with weak selection; that is, $\eta_2(n)$ lies below $\eta_i(n)$ for $i = 1,3$ and $|\eta_i - \eta_2|, i = 1,3$ are sufficiently small. Under some additional assumptions on $\eta_i$, we prove the existence and stability of traveling wave solutions for (1.2). In [5] we proved the existence of traveling wave solutions for (1.2) under quite general assumptions on $f$ and $g$, but assuming that $\sigma \equiv 0$. The proof was based on the connection index from the Conley index theory. For a similar proof in the case where $\sigma \neq 0$, see [4]. These papers give an existence result but no uniqueness or stability of the traveling waves.

In this paper, the existence result is proved via singular perturbation methods. The linear stability analysis given here is also based on geometric singular perturbation theory. We closely follow the development of the stability index [1]. This recently developed theory equates the winding number of an analytic function, the Evans function, whose zeros correspond to eigenvalues of the linearized differential operator to the first Chern number of a complex vector bundle. The Chern number approach is very powerful, especially in cases where the underlying waves pass near more than one slow manifold. For the problem under consideration, we do not need this generality; we use the geometric singular perturbation theory developed by Fenichel [8] to compute approximate solutions for the linear equations so as to allow us to estimate the location of the zeros of the Evans function.

The organization of the paper is as follows. A statement of the assumptions and results are given in §2. Section 3 contains a proof of our existence result, while the remaining sections are devoted to proving the stability result.

**2. Hypotheses and results.** We begin by listing the hypotheses of the fitness functions.

(A1) We assume that the birthrates and deathrates depend on $n$ only and are $C^2$ in their arguments.

(A2) We assume that

$$\begin{aligned} \eta_1(n) &= \eta_2(n) + \varepsilon^2 \hat{\eta}_1(n,\varepsilon), \\ \eta_3(n) &= \eta_2(n) + \varepsilon^2 \hat{\eta}_3(n,\varepsilon), \end{aligned} \tag{2.1}$$

where $\hat{\eta}_1(n)$ and $\hat{\eta}_3(n) > 0$ for $n \geq 0$ and $\varepsilon$ is a small constant. Since $\eta_1, \eta_2, \eta_3$ measure the fitness of the genotypes AA, Aa, aa, respectively, the fact that $\hat{\eta}_1(n)$ and $\hat{\eta}_3(n) > 0$ means that the heterozygotes are less fit than the homozygotes. Thus we are considering the heterozygote inferior case.

(A3) In ecological models, it is frequently assumed that resources are scarce, so that the growth rate of the population decreases with an increase in population size. Thus, it is reasonable to assume that $\eta_i, i = 1,2,3$ are decreasing functions of $n$, positive near 0 and negative for large $n$. We define $n^*$ by $\eta_2(n^*) = 0$.

(A4) We assume that $d\eta_2(n)/dn|_{n=n^*} < 0$. This is a reasonable assumption, in light of assumption (A2). We also assume that the birthrate satisfies $r(n^*) > 0$. We will use these assumptions to show that certain invariant manifold is normally hyperbolic.

We begin by rescaling $t$ and $x$ by letting $x \mapsto \varepsilon x$ and $t \mapsto \varepsilon^2 t$. Furthermore, we put (1.2) into traveling wave coordinates by letting $\xi = x + \theta t$. With these changes of variables and using (2.1) in (1.3), (1.2) becomes

$$\begin{aligned} p_t &= p_{\xi\xi} - \theta p_\xi + 2\frac{p_\xi n_\xi}{n} + F_1(p,n)p(1-p) + F_2(p,n)\frac{\sigma}{4}, \\ n_t &= n_{\xi\xi} - \theta n_\xi + \left[\eta_2(n) + \varepsilon^2\left\{G(p,n) - \frac{\sigma}{4}(\hat{\eta}_1 + \hat{\eta}_3)\right\}\right]\frac{n}{\varepsilon^2}, \\ \sigma_t &= \sigma_{\xi\xi} - \theta\sigma_\xi + 2\frac{\sigma_\xi n_\xi}{n} + [-r + \varepsilon^2 H(p,n,\sigma)]\frac{\sigma}{\varepsilon^2} \\ &\quad -4(\hat{\eta}_1 + \hat{\eta}_3)p^2(1-p)^2 - 8(p_\xi)^2, \end{aligned} \tag{2.2}$$

where

$$\begin{aligned} F_1(p,n) &= p[\hat{\eta}_1(n) + \hat{\eta}_3(n)] - \hat{\eta}_3(n), \\ F_2(p,n) &= p[\hat{\eta}_1(n) + \hat{\eta}_3(n)] - \hat{\eta}_1(n), \\ G(p,n) &= \hat{\eta}_1(n)p^2 + \hat{\eta}_3(n)(1-p)^2, \end{aligned}$$

and

$$H(p,n,\sigma) = [\hat{\eta}_3(n) - \hat{\eta}_1(n)](1-2p) - \tfrac{1}{4}(\hat{\eta}_1(n) + \hat{\eta}_3(n))\sigma.$$

By a traveling wave solution of (2.2) with speed $\theta$, we mean a nonconstant, bounded, $t$-independent solution of (2.2). Thus, if $(\tilde{p},\tilde{n},\tilde{\sigma})$ is a traveling wave solution, then $(\tilde{p},\tilde{n},\tilde{\sigma})$ must satisfy the following system of ordinary differential equations:

$$
\begin{aligned}
&p'' - \theta p' + 2\frac{p'n'}{n} + F_1(p,n)p(1-p) + F_2(p,n)\frac{\sigma}{4} = 0,\\
&\varepsilon^2 n'' - \varepsilon^2\theta n' + \left[\eta_2(n) + \varepsilon^2\left\{G(p,n) - \frac{\sigma}{4}(\hat{\eta}_1 + \hat{\eta}_3)\right\}\right]n = 0,\\
&\varepsilon^2\sigma'' - \varepsilon^2\theta\sigma' + \varepsilon^2 2\frac{\sigma' n'}{n} - r\sigma + \varepsilon^2 H(p,n,\sigma)\sigma\\
&\qquad -4\varepsilon^2(\hat{\eta}_1 + \hat{\eta}_3)p^2(1-p)^2 - 8\varepsilon^2(p')^2 = 0
\end{aligned}
\tag{2.3}
$$

on $\mathbb{R}$, where $' = d/d\xi$.

Formally, by setting $\varepsilon = 0$ in (2.3), we see that $\eta_2(n) = 0$ and $r\sigma = 0$. Hence $n = n^*$, and, from (A4), $\sigma = 0$. The first equation then becomes the well-studied bistable equation [9], [10]

$$
p'' - \theta p' + F_1(p,n^*)p(1-p) = 0. \tag{2.4}
$$

Since $F_1(p,n^*) = 0$ at $p = \hat{\eta}_3(n^*)/[\hat{\eta}_1(n^*) + \hat{\eta}_3(n^*)] \in (0,1)$, it follows from [10] that there is a unique value of the wavespeed $\theta$, say $\theta_0$, for which (2.4) has a unique (modulo translations) traveling wave solution connecting $p = 0$ at $\xi = -\infty$ to $p = 1$ at $\xi = \infty$. Furthermore, this solution is stable for the corresponding evolution equation. In particular, the linearization of (2.4) about the traveling wave solution has a simple eigenvalue at the origin, and the rest of the spectrum is bounded away from the imaginary axis by a parabola in the left half complex plane.

Now consider the full system (2.3). We look for traveling wave solutions for which $\sigma \to 0$, $n \to \alpha_\pm$ as $|\xi| \to \infty$ and $p \to 0$ as $\xi \to -\infty$, $p \to 1$ as $\xi \to \infty$. To find $\alpha_\pm$, we observe from (A3) that the bracket term in the second equation of (2.3), namely,

$$
\eta_2(n) + \varepsilon^2 G(p,n),
$$

has unique zeros $n = K_{3,\varepsilon}$ and $n = K_{1,\varepsilon}$ at $p = 0$ and $p = 1$, respectively, and $K_{i,\varepsilon} \to n^*$ as $\varepsilon \to 0^+$. Thus $\alpha_+ = K_{1,\varepsilon}, \alpha_- = K_{3,\varepsilon}$, and we look for traveling wave solutions that satisfy the boundary conditions

$$
\begin{aligned}
&\lim_{\xi\to-\infty}(\tilde{p}(\xi),\tilde{n}(\xi),\tilde{\sigma}(\xi)) = (0, K_{3,\varepsilon}, 0),\\
&\lim_{\xi\to\infty}(\tilde{p}(\xi),\tilde{n}(\xi),\tilde{\sigma}(\xi)) = (1, K_{1,\varepsilon}, 0).
\end{aligned}
\tag{2.5}
$$

THEOREM 2.1. *There exists $\varepsilon_0 > 0$ such that* (1.2) *has traveling wave solutions $(\tilde{p}_\varepsilon,\tilde{n}_\varepsilon,\tilde{\sigma}_\varepsilon)$ with wavespeed $\theta_\varepsilon$ satisfying the boundary conditions* (2.5) *for $0 < \varepsilon < \varepsilon_0$. The traveling wavespeed $\theta_\varepsilon$ tends to the speed $\theta_0$ of the bistable equation* (2.4) *as $\varepsilon \to 0^+$. Furthermore, if we choose $\tilde{p}_\varepsilon(0) = \frac{1}{2}$, then the curve $C_\varepsilon = \{(\tilde{p}_\varepsilon(\xi),\tilde{p}'_\varepsilon(\xi),\tilde{n}_\varepsilon(\xi),\tilde{n}'_\varepsilon(\xi),\tilde{\sigma}_\varepsilon(\xi),\tilde{\sigma}'_\varepsilon(\xi)) \mid \xi \in \mathbb{R}\}$ in $\mathbb{R}^6$ tends to the curve $C_0 = \{(\tilde{p}_0(\xi),\tilde{p}'_0(\xi),n^*,0,0,0) \mid \xi \in \mathbb{R}\}$ uniformly on $\mathbb{R}$ as $\varepsilon \to 0^+$, where $(\tilde{p}_0,\tilde{p}'_0)$ is the unique traveling wave solution of* (2.4) *satisfying $\tilde{p}_0(0) = \frac{1}{2}$.*

*Remark* 1. The sign of $\theta_0$ is the same as the sign of the integral

$$\int_0^1 F_1(s,n^*)s(1-s)\,ds.$$

*Remark* 2. The traveling wave solution is often called a heteroclinic orbit, since the limits at $\pm\infty$ of the traveling wave solution are distinct.

A proof of Theorem 2.1 based on geometric singular perturbation theory [16], [8], [14] is given in the next section. The subsequent sections are devoted to proving the following stability result.

THEOREM 2.2. *There exists $\varepsilon_1 > 0$ such that, for each $0 < \varepsilon < \varepsilon_1$, there exists $\delta > 0$ such that, if $\|(p_0,n_0,\sigma_0)-(\tilde{p}_\varepsilon,\tilde{n}_\varepsilon,\tilde{\sigma}_\varepsilon)\|_\infty \le \delta$, then there exists $\tau > 0$ (depending on $(p_0,n_0,\sigma_0)$) such that $\|(p,n,\sigma)(x,t)-(\tilde{p}_\varepsilon,\tilde{n}_\varepsilon,\tilde{\sigma}_\varepsilon)(x-\theta_\varepsilon t+\tau)\|_\infty \to 0$ as $t\to\infty$. Here, $(p,n,\sigma)$ is the solution to (1.2) with initial data $(p_0,n_0,\sigma_0)$.*

To prove the above theorem, we use a version of Theorem 4.1 in Sattinger [15], which states that, if the following hypotheses (H1)–(H3) are satisfied, then Theorem 2.2 is true. In fact, the convergence is in $C^1$ norm, and the rate is exponential. The weight function in Sattinger's theorem is chosen to be identical to the one in this case.

Let $L^\varepsilon$ be the differential operator shown on the right side of (2.2) linearized about the traveling wave solution $(\tilde{p}_\varepsilon,\tilde{n}_\varepsilon,\tilde{\sigma}_\varepsilon)$. Let

$$BU(\mathbb{R},\mathbb{R}^n) = \left\{\vec{u}:\mathbb{R}\to\mathbb{R}^n \mid \vec{u} \text{ is bounded uniformly continuous}\right\}$$

be equipped with the supremum norm. We consider $L^\varepsilon$ a closed, densely defined operator from $BU(\mathbb{R},\mathbb{R}^3)$ into $BU(\mathbb{R},\mathbb{R}^3)$.

We must verify the following conditions on $L^\varepsilon$ for each sufficiently small $\varepsilon > 0$.

(H1) $L^\varepsilon$ has an isolated simple eigenvalue at the origin, while the remainder of its spectrum lies in the region $\{\lambda \mid \mathrm{Re}(\lambda) < -\beta\}$ for some $\beta > 0$.

(H2) Given $\alpha \in (0,\beta)$, there is a $\delta > 0$ such that the sector

$$S_{\alpha,\delta} = \left\{\lambda = -\alpha + re^{i\gamma} \mid r>0, -(\pi/2+\delta) < \gamma < \pi/2+\delta\right\}$$

is contained in the resolvent set of $L^\varepsilon$ with the exception of the zero eigenvalue.

(H3) The resolvent operator $(\lambda - L^\varepsilon)^{-1}$ has the following asymptotic behavior. Given $\gamma \in (0,\pi/2)$, there exists a constant $c(\gamma)$ such that

$$\begin{aligned} \|(\lambda-L^\varepsilon)^{-1}\vec{g}\,\|_\infty &\le \frac{c(\gamma)}{|\lambda|}\|\vec{g}\,\|_\infty, \\ \|(\lambda-L^\varepsilon)^{-1}\vec{g}\,\|_{C^1} &\le \frac{c(\gamma)}{\sqrt{|\lambda|}}\|\vec{g}\,\|_\infty \end{aligned} \tag{2.6}$$

as $|\lambda|\to\infty$ in the sector $|\arg\lambda| \le \pi-\gamma$.

*Remark* 3. For convenience, we have stated hypotheses (H1) and (H2) slightly different from those stated in Theorem 4.1 of [15].

**3. Existence of traveling waves.** To determine the traveling wave solution, we rewrite (2.3) as a first-order system, below:

$$
\begin{aligned}
p' &= v_1,\\
\varepsilon v_1' &= \varepsilon\theta v_1 - 2\frac{v_1 v_2}{n} - \varepsilon F_1(p,n)p(1-p) - \varepsilon F_2(p,n)\frac{\sigma}{4},\\
\varepsilon n' &= v_2,\\
\varepsilon v_2' &= \varepsilon\theta v_2 - \left[\eta_2(n) + \varepsilon^2\left\{G(p,n) - \frac{\sigma}{4}(\hat\eta_1 + \hat\eta_3)\right\}\right]n,\\
\varepsilon\sigma' &= v_3,\\
\varepsilon v_3' &= \varepsilon\theta v_3 - 2\frac{v_2 v_3}{n} - [-r + \varepsilon^2 H(p,n,\sigma)]\sigma\\
&\quad + 4\varepsilon^2(\hat\eta_1 + \hat\eta_3)p^2(1-p)^2 + 8\varepsilon^2(v_1)^2.
\end{aligned} \tag{3.1}
$$

System (3.1) is clearly singular as $\varepsilon \to 0$. We resale this system to obtain a system that makes sense at $\varepsilon = 0$. Letting $\xi = \varepsilon z$, (3.1) then becomes

$$
\begin{aligned}
\dot p &= \varepsilon v_1,\\
\dot v_1 &= \varepsilon\theta v_1 - 2\frac{v_1 v_2}{n} - \varepsilon F_1(p,n)p(1-p) - \varepsilon F_2(p,n)\frac{\sigma}{4},\\
\dot n &= v_2,\\
\dot v_2 &= \varepsilon\theta v_2 - \left[\eta_2(n) + \varepsilon^2\left\{G(p,n) - \frac{\sigma}{4}(\hat\eta_1 + \hat\eta_3)\right\}\right]n,\\
\dot\sigma &= v_3,\\
\dot v_3 &= \varepsilon\theta v_3 - 2\frac{v_2 v_3}{n} - [-r + \varepsilon^2 H(p,n,\sigma)]\sigma\\
&\quad + 4\varepsilon^2(\hat\eta_1 + \hat\eta_3)p^2(1-p)^2 + 8\varepsilon^2(v_1)^2,
\end{aligned} \tag{3.2}
$$

where $\dot{} = d/dz$.

Setting $\varepsilon = 0$ in (3.2), we obtain a system that has a two-dimensional manifold of critical points that we denote by $\mathcal{M}_0$, below:

$$
\mathcal{M}_0 = \left\{(p, v_1, n, v_2, \sigma, v_3) \mid n \equiv n^*,\ \sigma = v_2 = v_3 \equiv 0, \text{ and } p, v_1 \in \mathbb{R}\right\}. \tag{3.3}
$$

Geometric singular perturbation theory proceeds by perturbing this manifold to a nearby invariant manifold and analyzing the slow equations (3.1) on the perturbed manifold. According to [8], if the manifold $\mathcal{M}_0$ is normally hyperbolic, then system (3.2) has a locally invariant manifold $\mathcal{M}_\varepsilon$ that is within $O(\varepsilon)$ of $\mathcal{M}_0$. The linearization of (3.2) at $\varepsilon = 0$ about a critical point $x \in \mathcal{M}_0$ has two zero eigenvalues, since $\mathcal{M}_0$ is two-dimensional. If the remaining four eigenvalues have nonzero real part, then $\mathcal{M}_0$ is normally hyperbolic.

LEMMA 3.1. *Under assumption* (A4), $\mathcal{M}_0$ *is normally hyperbolic.*

*Proof*. An easy calculation shows that it suffices to check the eigenvalues of the matrix

$$
\begin{pmatrix}
0 & 1 & 0 & 0\\
-\dfrac{d\eta_2(n^*)}{dn}n^* & 0 & 0 & 0\\
0 & 0 & 0 & 1\\
0 & 0 & r(n^*) & 0
\end{pmatrix},
$$

which clearly have nonzero real parts, since $d\eta_2(n^*)/dn < 0$ and $r(n^*) > 0$. $\square$

Following §10 of [8], we can write an asymptotic expansion for $\mathcal{M}_\varepsilon$. In doing so, we find that

$$\begin{aligned} \mathcal{M}_\varepsilon = \{(p, v_1, n, v_2, \sigma, v_3) \mid n = n^* + \varepsilon^2 \hat{n}(p, v_1, \varepsilon, \theta),\ v_2 = \varepsilon^3 \hat{v}_2(p, v_1, \varepsilon, \theta), \\ \sigma = \varepsilon^2 \hat{\sigma}(p, v_1, \varepsilon, \theta),\ \text{and } v_3 = \varepsilon^3 \hat{v}_3(p, v_1, \varepsilon, \theta)\}. \end{aligned} \tag{3.4}$$

It follows that the flow restricted to $\mathcal{M}_\varepsilon$ in the slow variable is given by

$$\begin{aligned} p' &= v_1, \\ v_1' &= \theta v_1 - F_1(p, n^*) p(1-p) + O(\varepsilon). \end{aligned} \tag{3.5}$$

System (3.5) at $\varepsilon = 0$ is again the bistable equation discussed earlier.

By appending the trivial flow

$$\theta' = 0 \tag{3.6}$$

to (3.5), the heteroclinic connection for (3.5) at $\varepsilon = 0$ can be realized as a transverse intersection of invariant manifolds. Let $I$ be a closed interval containing $\theta_0$. At $\varepsilon = 0$, (3.5), (3.6) have a two-dimensional center-unstable manifold, $W^{cu}(0, 0, \theta_0)$ at $(p, v_1, \theta) = (0, 0, \theta_0)$, which is the union for $\theta \in I$ of the one-dimensional unstable manifolds for the rest point $(0, 0)$ for (3.5). Similarly, the extended system has a two-dimensional center-stable manifold at $(0, 1, \theta_0)$, which we denote by $W^{cs}(0, 1, \theta_0)$. It can be shown that these two two-manifolds intersect transversely in $(p, v_1, \theta)$ space along the heteroclinic orbit at $\theta = \theta_0$ (see [12] or [16]).

*Proof of Theorem* 2.1. The equations on $\mathcal{M}_\varepsilon$ are (3.5) with $\theta' = 0$ appended. At $\varepsilon = 0$, the center-unstable manifold $W^{cu}(0, 0, \theta_0)$ intersects the center-stable manifold $W^{cs}(0, 1, \theta_0)$ transversally along $\theta \equiv \theta_0$. These manifolds perturb smoothly for $\varepsilon > 0$ and hence intersect transversely for $\varepsilon > 0$ sufficiently small. By [16, Thm. 2.2], they continue to the corresponding invariant manifolds for the critical points on $\mathcal{M}_\varepsilon$. By (A3), (A4), the relevant critical points on $\mathcal{M}_\varepsilon$ are $(p, v_1, n, v_2, \sigma, v_3) = (0, 0, K_{3,\varepsilon}, 0, 0, 0)$ and $(0, 1, K_{1,\varepsilon}, 0, 0, 0)$. Hence there is a locally unique heteroclinic orbit for (3.1). $\square$

We remark that we have been rather cavalier about the treatment of $\theta$ flow. To apply the invariant manifold theory in [8] and [16], we must modify the $\theta' = 0$ flow outside of the neighborhood of $I \ni \theta_0$ to obtain an overflowing or inflowing invariant manifold. This type of argument is standard, and we refer the reader to [8] for the details.

**4. The linearization and essential spectrum.** To study the stability of the traveling wave solution given by Theorem 2.1, we must locate the spectrum of the linear operator $L^\varepsilon$ defined near the end of §2. Since the domain of the functions in $\mathcal{D}(L^\varepsilon)$ is unbounded, $L^\varepsilon$ can have point spectrum $\sigma_p(L^\varepsilon)$ as well as essential spectrum $\sigma_e(L^\varepsilon)$.

The eigenvalue problem is

$$L^\varepsilon \vec{u} = \lambda \vec{u}, \tag{4.1}$$

where the operator $L^\varepsilon$ has the form

$$L^\varepsilon \begin{pmatrix} \phi \\ \psi \\ \chi \end{pmatrix} \equiv \begin{pmatrix} \phi'' \\ \psi'' \\ \chi'' \end{pmatrix} + \mathcal{B}(\xi; \varepsilon) \begin{pmatrix} \phi' \\ \psi' \\ \chi' \end{pmatrix} + \mathcal{C}(\xi; \varepsilon) \begin{pmatrix} \phi \\ \psi \\ \chi \end{pmatrix}. \tag{4.2}$$

The $3 \times 3$ matrix $\mathcal{B}$ (respectively, $\mathcal{C}$) denotes the Jacobian of the right-hand side of (2.2) with respect to $(p', n', \sigma')$ (respectively, $(p, n, \sigma)$) evaluated along the traveling wave solution $(\tilde{p}_\varepsilon, \tilde{n}_\varepsilon, \tilde{n}_\varepsilon)$. Specifically, $\mathcal{B}$ and $\mathcal{C}$ have the form

$$\mathcal{B}(\xi;\varepsilon) = \begin{pmatrix} -\theta_\varepsilon + 2\dfrac{\tilde{n}'_\varepsilon}{\tilde{n}_\varepsilon} & 2\dfrac{\tilde{p}'_\varepsilon}{\tilde{n}_\varepsilon} & 0 \\ 0 & -\theta_\varepsilon & 0 \\ -16\tilde{p}'_\varepsilon & 2\dfrac{\tilde{\sigma}'_\varepsilon}{\tilde{n}_\varepsilon} & -\theta_\varepsilon + 2\dfrac{\tilde{n}'_\varepsilon}{\tilde{n}_\varepsilon} \end{pmatrix} \tag{4.3}$$

and

$$\mathcal{C}(\xi;\varepsilon) = \begin{pmatrix} c_{1,1}(\xi,\varepsilon) & c_{1,2}(\xi,\varepsilon) & c_{1,3}(\xi,\varepsilon) \\ c_{2,1}(\xi,\varepsilon) & \dfrac{c_{2,2}(\xi,\varepsilon)}{\varepsilon^2} & c_{2,3}(\xi,\varepsilon) \\ c_{3,1}(\xi,\varepsilon) & c_{3,2}(\xi,\varepsilon) & \dfrac{c_{3,3}(\xi,\varepsilon)}{\varepsilon^2} \end{pmatrix}. \tag{4.4}$$

There are only two terms in (4.4) that are $O(\varepsilon^{-2})$. In fact, we have the following lemma.

LEMMA 4.1. *The coefficients* $c_{i,j}(\xi;\varepsilon)$ *in* (4.4) *are uniformly bounded as* $\varepsilon \to 0^+$. *In particular,*

$$c_{2,2}(\xi;\varepsilon) \to \eta_2'(n^*)n^* \quad \textit{and} \quad c_{3,3}(\xi;\varepsilon) \to -r(n^*)$$

*uniformly on* $\mathbb{R}$ *as* $\varepsilon \to 0^+$.

*Proof*. From (2.2) and the definition of the matrix $\mathcal{C}$, we see that

$$c_{2,2}(\xi;\varepsilon) = \frac{\partial}{\partial n}\left(\left[\eta_2(n) + \varepsilon^2\left\{G(p,n) - \frac{\sigma}{4}(\hat{\eta}_1 + \hat{\eta}_3)\right\}\right]n\right),$$

evaluated at the traveling wave. By Theorem 2.1, we see that $c_{2,2}(\xi;\varepsilon) \to \eta_2'(n^*)n^*$ uniformly on $\mathbb{R}$ as $\varepsilon \to 0^+$. The argument for $c_{3,3}$ is similar. To show that $c_{3,2}(\xi;\varepsilon)$ is bounded, note that

$$c_{3,2}(\xi;\varepsilon) = \frac{\partial}{\partial n}\left[-r(n)\frac{\sigma}{\varepsilon^2} + H(p,n,\sigma)\sigma + 2\frac{\sigma' n'}{n} - 4(\hat{\eta}_1 + \hat{\eta}_3)p^2(1-p)^2\right],$$

evaluated at the traveling wave. Since the wave lies in the slow manifold $\mathcal{M}_\varepsilon$, it follows from (3.4) that $\tilde{\sigma} = O(\varepsilon^2)$, and thus $c_{3,2}(\xi;\varepsilon) = O(1)$. The boundedness of the other terms in (4.4) follow from similar arguments and are left to the reader. $\square$

Since $(\tilde{p}'_\varepsilon(\pm\infty), \tilde{n}'_\varepsilon(\pm\infty), \tilde{\sigma}'_\varepsilon(\pm\infty)) = (0,0,0)$, we can show, using the boundary conditions (2.5) and our assumptions (A1)–(A4), that $\mathcal{B}$ and $\mathcal{C}$ have the following asymptotic behavior as $\xi \to \pm\infty$:

$$\mathcal{B}(\pm\infty,\varepsilon) \equiv \mathcal{B}_\varepsilon^\pm = -\theta_\varepsilon I \tag{4.5}$$

and

$$\mathcal{C}(\pm\infty;\varepsilon) \equiv \mathcal{C}_\varepsilon^\pm = \begin{pmatrix} c_{1,1}(\pm\infty;\varepsilon) & 0 & c_{1,3}(\pm\infty;\varepsilon) \\ c_{2,1}(\pm\infty;\varepsilon) & \dfrac{c_{2,2}(\pm\infty;\varepsilon)}{\varepsilon^2} & c_{2,3}(\pm\infty;\varepsilon) \\ 0 & 0 & \dfrac{c_{3,3}(\pm\infty;\varepsilon)}{\varepsilon^2} \end{pmatrix}. \tag{4.6}$$

The following properties of the coefficients in (4.6) follow from (2.5), our assumptions (A1)–(A4), Lemma 4.1, and Theorem 2.1.

LEMMA 4.2. *For sufficiently small* $\varepsilon > 0$,

$$\lim_{\xi\to\pm\infty} c_{1,1}(\xi;\varepsilon) \equiv c_{1,1}^{\pm}(\varepsilon) < 0,$$

*where* $c_{1,1}^{+}(\varepsilon) = -\hat{\eta}_1(K_{1,\varepsilon})$ *and* $c_{1,1}^{-}(\varepsilon) = -\hat{\eta}_3(K_{3,\varepsilon})$. *Hence*

$$\lim_{\xi\to\pm\infty} c_{i,i}(\xi;\varepsilon) \equiv c_{i,i}^{\pm}(\varepsilon) < 0 \quad \text{for } i = 1,2,3$$

*for sufficiently small* $\varepsilon > 0$.

The next step is to show that the essential spectrum of $L^{\varepsilon}$ lies to the left of some parabola in the left half complex plane.

THEOREM 4.3. *There exists a parabola that lies in the left half of the complex plane and is symmetric about the real axis such that, for sufficiently small* $\varepsilon > 0$, *the essential spectrum of the operator* $L^{\varepsilon}$ *lies to the left of this parabola.*

*Proof*. To prove this result, we use [6, Thm. A.2, p. 140]. Let

$$S_{\pm}(\varepsilon) = \{\lambda \mid \det(-\tau^2 I + i\tau\mathcal{B}_{\varepsilon}^{\pm} + \mathcal{C}_{\varepsilon}^{\pm} - \lambda I) = 0 \text{ for some real } \tau,\ -\infty < \tau < \infty\}.$$

Then $S_{\pm}$ consists of a finite number of algebraic curves that are symmetric about the real axis and are asymptotically parabolas: $\lambda = -\tau^2 + O(\tau)$ as $\tau \to \pm\infty$. Let $P$ denote the union of the regions inside or on the curves $S_+, S_-$; thus $\mathbb{C}\backslash P$ is the component of $\mathbb{C}\backslash\{S_+ \cup S_-\}$ containing a right half-plane. According to [6], the essential spectrum of $L^{\varepsilon}$ is contained in $P$ and, in particular, includes $S_+ \cup S_-$. From (4.5) and (4.6), we see that the above determinant is zero if and only if

$$(-\tau^2 - i\tau\theta_{\varepsilon} + c_{1,1}^{\pm}(\varepsilon) - \lambda)\left(-\tau^2 - i\tau\theta_{\varepsilon} + \frac{c_{2,2}^{\pm}(\varepsilon)}{\varepsilon^2} - \lambda\right)\left(-\tau^2 - i\tau\theta_{\varepsilon} + \frac{c_{3,3}^{\pm}(\varepsilon)}{\varepsilon^2} - \lambda\right) = 0.$$

Letting $\lambda = \lambda_1 + i\lambda_2$, $\lambda_i \in \mathbb{R}$, it follows that $\lambda_1 = -\tau^2 + c_{1,1}^{\pm}(\varepsilon)$ or $\lambda_1 = -\tau^2 + c_{i,i}^{\pm}(\varepsilon)/\varepsilon^2$ ($i = 2,3$) and, in any case, $\lambda_2 = -\tau\theta_{\varepsilon}$. Eliminating $\tau$, we have either $\lambda_1 = -(\lambda_2/\theta_{\varepsilon})^2 + c_{1,1}^{\pm}(\varepsilon)$ or $\lambda_1 = -(\lambda_2/\theta_{\varepsilon})^2 + c_{i,i}^{\pm}(\varepsilon)/\varepsilon^2$ ($i = 2,3$). By Lemma 4.2, it follows that we can find a parabola of the form $\lambda_1 = -a\lambda_2^2 - b$ with $a, b > 0$ independent of sufficiently small $\varepsilon$, so that $\sigma_e(L^{\varepsilon})$ lies to the left of this parabola. □

We close this section with a result that puts bounds on the region in the complex plane for which we may find potentially dangerous point spectrum. This result implies that, if $\lambda$ is an eigenvalue in the right half-plane, then $|\lambda|$ must remain bounded independent of $\varepsilon > 0$. The proof of this result follows directly from the proof of Proposition 2.2 in [1] and will be omitted.

PROPOSITION 4.4. *Given any* $\delta \in (0, \pi/2)$, *there exists* $M(\delta) > 0$ *independent of* $\varepsilon > 0$ *such that, if* $|\lambda| > M(\delta)$ *and* $|arg(\lambda)| < \pi - \delta$, *then* $\lambda \notin \sigma(L^{\varepsilon})$.

**5. The point spectrum and the Evans function.** In this section, we will begin our investigation of the point spectrum for $L^{\varepsilon}$. We will define an analytic function of $\lambda$ whose zeros correspond to the point spectrum. This function is commonly referred to as the Evans function, named after J. W. Evans, who first formulated such a function for stability proofs for the nerve axon equations [7].

First, we write the eigenvalue problem $L^\varepsilon \vec{u} = \lambda \vec{u}$ as a first-order system as follows:

$$\begin{pmatrix} \phi \\ \varepsilon\psi \\ \varepsilon\chi \end{pmatrix}' = \begin{pmatrix} v_1 \\ v_2 \\ v_3 \end{pmatrix}$$

$$\varepsilon \begin{pmatrix} v_1 \\ v_2 \\ v_3 \end{pmatrix}' = -\begin{pmatrix} \varepsilon(c_{11}(\xi;\varepsilon) - \lambda) & \varepsilon c_{12}(\xi;\varepsilon) & \varepsilon c_{13}(\xi;\varepsilon) \\ \varepsilon^2 c_{21}(\xi;\varepsilon) & c_{22}(\xi;\varepsilon) - \varepsilon^2\lambda & \varepsilon^2 c_{23}(\xi;\varepsilon) \\ \varepsilon^2 c_{31}(\xi;\varepsilon) & \varepsilon^2 c_{32}(\xi;\varepsilon) & c_{33}(\xi;\varepsilon) - \varepsilon^2\lambda \end{pmatrix} \begin{pmatrix} \phi \\ \psi \\ \chi \end{pmatrix} - \begin{pmatrix} \varepsilon b_{11}(\xi;\varepsilon) & b_{12}(\xi;\varepsilon) & 0 \\ 0 & \varepsilon b_{22}(\xi;\varepsilon) & 0 \\ \varepsilon b_{31}(\xi;\varepsilon) & \varepsilon b_{32}(\xi;\varepsilon) & \varepsilon b_{3,3}(\xi;\varepsilon) \end{pmatrix} \begin{pmatrix} v_1 \\ v_2 \\ v_3 \end{pmatrix}. \tag{5.1}$$

We abbreviate this system by setting $\vec{y} = (\phi, \psi, \chi, v_1, v_2, v_3)$, so that (5.1) becomes

$$\vec{y}' = A_\varepsilon(\xi, \lambda)\vec{y}. \tag{5.2}$$

Note that the $6 \times 6$ matrix $A_\varepsilon$ contains terms that are of the order $O(1/\varepsilon)$.

The asymptotic systems associated with (5.2) will be important. Let

$$A_\varepsilon^\pm(\lambda) = \lim_{\xi \to \pm\infty} A_\varepsilon(\xi, \lambda).$$

Since the coefficients in the matrix $A_\varepsilon(\xi, \lambda)$ converge at an exponential rate as $|\xi| \to \infty$, the behavior of the solutions of (5.2) at $\pm\infty$ is the same as the behavior of the solutions of

$$\vec{y}' = A_\varepsilon^\pm(\lambda)\,\vec{y} \tag{5.3}$$

at $\pm\infty$ (see Theorem 8.1 in [3]).

The structure of (5.3) is determined by the eigenvalues of $A_\varepsilon^\pm(\lambda)$. The eigenvalues $\mu$ for the matrix $A_\varepsilon^\pm(\lambda)$ satisfy

$$\det\left(\mu^2 I + \mu B_\varepsilon^\pm + C_\varepsilon^\pm - \lambda I\right) = 0,$$

and thus, by (4.5) and (4.6),

$$\begin{aligned} \mu_{1,\pm}^\pm(\varepsilon) &= \frac{\theta_\varepsilon}{2} \pm \frac{1}{2}\left(\theta_\varepsilon^2 + 4(\lambda - c_{11}^\pm(\varepsilon))\right)^{1/2}, \\ \mu_{i,\pm}^\pm(\varepsilon) &= \frac{\theta_\varepsilon}{2} \pm \frac{1}{2}\left(\theta_\varepsilon^2 + 4\left(\lambda - \frac{c_{ii}^\pm(\varepsilon)}{\varepsilon^2}\right)\right)^{1/2} \quad \text{for } i = 2, 3. \end{aligned} \tag{5.4}$$

The $\pm$ superscripts in (5.4) refer to the $\pm$ asymptotic systems (5.3), and the subscripts refer to the $\pm$ radical term on the right-hand side of (5.4). Recall from Lemma 4.2 that, for sufficiently small $\varepsilon$, $c_{ii}^\pm(\varepsilon) < 0$ for $i = 1, 2, 3$. We let

$$\beta_0 = \max\{c_{11}^+(0), c_{11}^-(0)\}. \tag{5.5}$$

From Lemma 4.2, $\beta_0 < 0$. It follows that, if $\operatorname{Re}(\lambda) > \beta_0$, then the quantities under the radicals in (5.4) have real parts greater than $\theta_\varepsilon$, so that $\mu_{i,+}^\pm(\varepsilon)$ have positive real parts and $\mu_{i,-}^\pm(\varepsilon)$ have negative real parts for $i = 1, 2, 3$. Thus we have the following result.

LEMMA 5.1. *For sufficiently small* $\varepsilon > 0$, *each of the matrices* $A_\varepsilon^\pm(\lambda)$ *has three eigenvalues with positive real parts and three eigenvalues with negative real parts, provided that* $\mathrm{Re}(\lambda) > \beta_0$.

We will let $\Omega_{\beta_0} = \{\lambda \in \mathbb{C} \mid \mathrm{Re}\,\lambda > \beta_0\}$, where $\beta_0$ is given by (5.5). It is not hard to prove that $\lambda \in \Omega_{\beta_0}$ is an eigenvalue for $L^\varepsilon$ if and only if there exists a nontrivial solution $Y(\xi)$ of (5.2) that satisfies $\lim_{|\xi|\to\infty} Y(\xi) = \mathcal{O}$, the zero vector in $\mathbb{C}^6$. We consider the following linear subspaces of $\mathbb{C}^6$:

$$U_\lambda^- = \Big\{Y(\xi) \mid Y(\xi) \text{ is a solution of (5.8) and } \lim_{\xi\to-\infty} Y(\xi) = \mathcal{O}\Big\},$$
$$S_\lambda^+ = \big\{Y(\xi) \mid Y(\xi) \text{ is a solution of (5.8) and } \lim_{\xi\to\infty} Y(\xi) = \mathcal{O}\big\}.$$

We see that $\lambda$ is an eigenvalue if and only if $U_\lambda^-$ and $S_\lambda^+$ have nontrivial intersection. It follows from Lemma 5.1 and [3 Thm. 8.1] that, for $\lambda \in \Omega_{\beta_0}$, $\dim S_\lambda^+ = \dim U_\lambda^- = 3$.

Singular perturbation theory will be used to construct basis for $U_\lambda^-$ and $S_\lambda^+$. At each end, one basis element will be shown to depend on the slow timescale $\xi$, while the other two will depend also on the fast timescale $z = \xi/\varepsilon$. For now, let

$$\{Y_{f,1}^-(\xi,\lambda), Y_{f,2}^-(\xi,\lambda), Y_s^-(\xi,\lambda)\}$$

denote such a basis for $U_\lambda^-$ and let

$$\{Y_{f,1}^+(\xi,\lambda), Y_{f,2}^+(\xi,\lambda), Y_s^+(\xi,\lambda)\}$$

be a basis for $S_\lambda^+$. Let $\Phi_\lambda(\xi)$ denote the $6\times 6$ matrix whose column vectors are $Y_s^-(\xi,\lambda)$, $Y_s^+(\xi,\lambda)$, and $Y_{f,i}^\pm(\xi,\lambda)$ for $i = 1,2$.

DEFINITION 5.2. The Evans function $D_\varepsilon(\lambda)$ is defined by

$$D_\varepsilon(\lambda) = \det[\Phi_\lambda(\xi)] \exp\left(-\int_0^\xi \mathrm{trace}\,(A_\varepsilon(s,\lambda))\,ds\right).$$

By Abel's formula for the determinant of solutions of a linear system, $D_\varepsilon(\lambda)$ is independent of $\xi$ and hence is well defined. $D_\varepsilon(\lambda)$ does, however, depend on the choices of basis for $U_\lambda^-$ and $S_\lambda^+$. Different choices of basis change $D_\varepsilon(\lambda)$ by constant multiples. However, once an orientation is fixed, the constant multiples have the same sign.

It is clear that $U_\lambda^-$ and $S_\lambda^+$ have nontrivial intersection if and only if $D_\varepsilon(\lambda) = 0$. This and other properties of the Evans function are summarized in the following proposition, whose proof may be found in [1].

PROPOSITION 5.3. *The following statements hold:*

1. $D_\varepsilon(\lambda)$ *is analytic in* $\lambda$ *for* $\lambda \in \Omega_{\beta_0}$;
2. $D_\varepsilon(\lambda_0) = 0$ *if and only if* $\lambda_0 \in \sigma_p(L^\varepsilon)$;
3. *The order of a root of* $D_\varepsilon$ *at* $\lambda = \lambda_0$ *equals the algebraic multiplicity of* $\lambda_0$ *as an eigenvalue of* $L^\varepsilon$.

In the next section, we construct, via singular perturbation theory, solutions $Y_{f,i}^\pm, Y_s^\pm$ that allow us to compute $D_\varepsilon(\lambda)$ explicitly and relate it to the corresponding Evans function for the bistable equation as $\varepsilon \to 0^+$.

**6. A basis for $S_\lambda^+$ and $U_\lambda^-$.** To evaluate the Evans function, we need a basis for $S_\lambda^+$ and $U_\lambda^-$. The idea is to use geometric singular perturbation theory to find an approximate basis. To use the geometric theory, we first write (5.2) as an autonomous system. As in [1], we introduce the independent variable $\tau$ defined by

$$\xi = \frac{1}{2\kappa} \ln \left\{ \frac{1+\tau}{1-\tau} \right\}$$

and write (5.2) as

$$\begin{aligned} \vec{y}' &= A_\varepsilon(\tau, \lambda)\vec{y}, \\ \tau' &= \kappa(1-\tau^2), \end{aligned} \tag{6.1}$$

where $A_\varepsilon(\tau, \lambda)$ is obtained from $A_\varepsilon(\xi, \lambda)$ by reparametrization by $\tau$. In particular, we define

$$A_\varepsilon(\tau, \lambda) = \begin{cases} A_\varepsilon(\xi(\tau), \lambda) & \text{for } \tau \neq \pm 1, \\ A_\varepsilon^\pm(\xi(\tau)) & \text{for } \tau = \pm 1. \end{cases}$$

Note that $\xi$ remains the independent variable; however, (6.1) is autonomous.

The planes $\tau = \pm 1$ correspond to the asymptotic limits $\xi = \pm\infty$. It can be shown [1] that, if $\kappa$ is small enough depending on the rate of decay of the traveling wave at $\xi = \pm\infty$, then the vector field (6.1) is $C^1$ on $\mathbb{C}^6 \times [-1, 1]$.

We see that (6.1) has two equilibria, namely, $Y_{\pm 1} = (\vec{0}, \pm 1)$. It follows from Lemma 5.1 that $Y_1$ has a four-dimensional stable manifold for each $\lambda \in \Omega_{\beta_0}$, which we denote by $W_1^s(\varepsilon, \lambda)$. Similarly, the rest point $Y_{-1}$ has a four-dimensional unstable manifold $W_{-1}^u(\varepsilon, \lambda)$, for each $\lambda \in \Omega_{\beta_0}$.

It follows from the linearity of the first equation in (6.1) that, for each $\tau_0 \in (-1, 1]$, $W_1^s(\varepsilon, \lambda) \cap \{\tau = \tau_0\}$ is a three-dimensional subspace of $\mathbb{C}^6$. Likewise, $W_{-1}^u(\varepsilon, \lambda) \cap \{\tau = \tau_0\}$ is a subspace of $\mathbb{C}^6$.

The idea is to find an approximation to $W_1^s(\varepsilon, \lambda)$ for small $\varepsilon$. To do this, we first note that system (6.1) is singular, due to the fact that $A_\varepsilon(\tau, \lambda)$ contains terms that are of order $O(1/\varepsilon)$. To obtain a system that makes sense when $\varepsilon = 0$, we resale using the fast variable $z = \xi/\varepsilon$. With this change of scale, (6.1) becomes

$$\begin{aligned} \dot{y} &= \varepsilon A_\varepsilon(\tau, \lambda) y, \\ \dot{\tau} &= \varepsilon\kappa(1-\tau^2), \end{aligned} \tag{6.2}$$

where $\dot{} = d/dz$. At $\varepsilon = 0$, (6.2) becomes

$$\begin{aligned} \dot{\phi} &= 0, \\ \dot{\psi} &= v_2, \\ \dot{\chi} &= v_3, \\ \dot{v_1} &= -b_{12}(\tau; 0)v_2, \\ \dot{v_2} &= -c_{22}(\tau; 0)\psi, \\ \dot{v_3} &= -c_{33}(\tau; 0)\chi, \\ \dot{\tau} &= 0. \end{aligned} \tag{6.3}$$

We see that (6.3) has a three-dimensional (two complex, one real) manifold of equilibrium, namely,

$$\mathcal{M}_0 = \{(\phi, \psi, \chi, v_1, v_2, v_3, \tau) \mid \psi = \chi = v_2 = v_3 \equiv 0,\ \phi \text{ and } v_1 \in \mathbb{C},\ \tau \in \mathbb{R}\}.$$

Since $c_{22}(\tau;0) < 0$ and $c_{33}(\tau;0) < 0$, by Lemma 4.2, it follows that this manifold is normally hyperbolic, thus, by the results [8], any compact subset of $\mathcal{M}_0$ perturbs to a locally invariant manifold $\mathcal{M}_\varepsilon$ for (6.2) (or, equivalently, (6.1)).

If we let $Y_S = (\phi, v_1)$ denote the slow variables and $Y_F = (\psi, v_2, \chi, v_3)$ the fast variables, then, following [8] and using the linearity of the first equation in (6.1), we can show that $\mathcal{M}_\varepsilon$ is given by

$$\mathcal{M}_\varepsilon = \{(Y_S, Y_F, \tau) \mid Y_F = \Gamma(\tau, \varepsilon, \lambda) Y_S\},$$

where $\Gamma$ is a $4 \times 2$ matrix. Following §10 of [8], we can show that

$$\Gamma(\tau, \varepsilon, \lambda) = \varepsilon^2 \Gamma_0(\tau) + \varepsilon^2 \Gamma_1(\tau, \varepsilon, \lambda),$$

where

$$\Gamma_0(\tau) = \begin{bmatrix} -\dfrac{c_{21}(\tau;0)}{c_{22}(\tau;0)} & 0 \\ 0 & 0 \\ -\dfrac{c_{31}(\tau;0)}{c_{33}(\tau;0)} & 0 \\ 0 & 0 \end{bmatrix} \tag{6.4}$$

and $\Gamma_1 = O(\varepsilon)$.

The flow on $\mathcal{M}_\varepsilon$ in terms of slow variable $\xi$ is given by

$$\begin{aligned} \phi' &= v_1, \\ v_1' &= (\lambda - c_{11}(\tau;0))\phi + \theta_0 v_1 + O(\varepsilon), \\ \tau' &= \kappa(1 - \tau^2). \end{aligned} \tag{6.5}$$

At $\varepsilon = 0$, (6.5) becomes

$$\begin{aligned} \phi' &= v_1, \\ v_1' &= (\lambda - c_{11}(\tau;0))\phi + \theta_0 v_1, \\ \tau' &= \kappa(1 - \tau^2), \end{aligned} \tag{6.6}$$

which is equivalent to the linearized eigenvalue problem for the well-understood bistable equation (2.4).

We see that (6.6) has two equilibria $(0, 0, \pm 1)$. To simplify the discussion, we will only be concerned with the linear space $S_\lambda^+$, the argument for $U_\lambda^-$ is similar. To this end, we will only be concerned with the equilibrium $(0, 0, 1)$. It is easy to check that the rest point $(0, 0, 1)$ for (6.6) has a two-dimensional stable manifold (one stable direction for the asymptotic system and one from the $\tau$ flow). We let $S_r(\lambda)$ denote the stable manifold. We can embed this manifold in $\mathbb{C}^6 \times \mathbb{R}$ by considering $S_r(\lambda)$ as a two-manifold in the $Y_F \equiv \vec{0}$ subspace of $\mathbb{C}^6 \times \mathbb{R}$. Without confusion, we will denote this manifold by $S_r(\lambda)$, also.

As noted above, $\mathcal{M}_0$ is a manifold of equilibrium for (6.3). For each fixed $p \in \mathcal{M}_0$, the linearization of the right-hand side of (6.3) about $p$ has a zero eigenvalue of multiplicity 3, since $\mathcal{M}_0$ is three-dimensional, two with positive real parts and two with negative real parts. It follows that, each $p \in \mathcal{M}_0$ has a well-defined, two-dimensional, stable manifold that we denote by $F_0^s(p)$. If we let $p = (\phi_0, 0, 0, v_{1_0}, 0, 0, \tau_0)$ denote a point in $\mathcal{M}_0$, then, from (6.3) and an easy calculation, we find that a trajectory in the stable manifold is given by

$$\Phi(t) = (\phi_0, \psi_0 e^{-\alpha_2 t}, \chi_0 e^{-\alpha_3 t}, v_{1_0} - b_{12}(\tau_0; 0)\psi_0 e^{-\alpha_2 t}, -\alpha_2 \psi_0 e^{-\alpha_2 t}, -\alpha_3 \chi_0 e^{-\alpha_3 t}, \tau_0),$$

where we have set $\alpha_2 = (-c_{22}(0;0))^{1/2}$ and $\alpha_3 = (-c_{33}(0;0))^{1/2}$. It follows that

$$\begin{aligned} F_0^s(p) = \{(Y_s, Y_f, \tau_0) \mid Y_s &= (\phi_0, v_1),\ Y_f = (\psi_0, \chi_0, -\alpha_2\psi_0, -\alpha_3\chi_0),\ \tau \equiv \tau_0, \\ &\text{where } v_1 = v_{1_0} - b_{12}(\tau_0;0)\psi_0 \text{ for } \psi_0, \chi_0 \in \mathbb{C}\ \}. \end{aligned} \tag{6.7}$$

The manifolds $F_0^s(p)$ for $p \in S_r(\lambda)$ are often referred to as stable fibers, since they provide a foliation of the stable manifold $S_r(\lambda)$ for the slow subsystem (6.5).

We are now in a position to define a manifold that approximates stable manifold of the rest point $Y_1 = (\vec{0}, 1)$ for the full system (6.1). We let

$$W_0^s(\lambda) = \{F_0^s(p) \mid p \in S_r(\lambda)\}.$$

We need to restrict $\lambda$ to a compact subset of the complex plane. We use Proposition 4.4 for this. Given any $\delta \in (0, \pi/2)$, let $M(\delta)$ be as in Proposition 4.4. Let $\mathcal{L}_0$ denote the linearization of the bistable equation (2.4) about the heteroclinic orbit for (2.4) and choose $\beta_1 > 0$ so that the spectrum of $\mathcal{L}_0$ satisfies $\sigma(\mathcal{L}_0)\backslash\{0\} \subset \{\lambda \mid \mathrm{Re}(\lambda) \leq -\beta_1\}$. Finally, let $\Omega_{M,\beta} = \{\lambda \in \mathbb{C} \mid \mathrm{Re}(\lambda) \geq -\beta \text{ and } |\lambda| \leq M(\delta)\}$, where $\beta = \min(\beta_0, \beta_1)$ (recall that $\beta_0$ is defined by (5.5)). We then have the following proposition.

PROPOSITION 6.1. *For any $\nu > 0$, there exists an $\varepsilon_0(\nu) > 0$ such that, for all $\lambda \in \Omega_{M,\beta}$ and $0 < \varepsilon < \varepsilon_0(\nu)$, $W_0^s(\lambda)$ is $C^0$ close to $W_1^s(\varepsilon, \lambda)$ outside of a $\nu$-neighborhood of the rest point $Y_0^- = (\vec{0}, -1)$. Furthermore, $W_\varepsilon^s(\lambda)$ depends continuously on $\lambda$.*

*Proof.* The proof of the proposition follows directly from Theorem 12.2 in [8] (also see [16, Thm. 2.2]). The continuity with respect to $\lambda$ follows from a standard argument; system (6.1) is augmented with the trivial flow $\lambda' = 0$; then, for $\lambda \notin \Omega_{M,\beta}$ this flow is modified to obtain an inflowing invariant manifold. For details, we refer the reader to [8]. □

For each $\lambda \in \Omega_{M,\beta}$, we choose a solution $(\phi_0^+, \phi_0^{+'}, \tau)$ of (6.6) satisfying $\tau(0) = 0$, $\lim_{\xi \to \infty}(\phi_0^+(\xi, \lambda), \phi_0^{+'}(\xi, \lambda), \tau(\xi)) = (0, 0, 1)$, with, say, $\phi_0^+(0) = 1$. It then follows from [8] and [16] that there is a solution $Y_s^+(\xi, \lambda)$ in $S_\lambda^+$ with the form

$$Y_s^+(\xi, \lambda) = \begin{bmatrix} \phi_0^+(\xi, \lambda) + O(\varepsilon) \\ O(\varepsilon^2) \\ O(\varepsilon^2) \\ \phi_0^{+'}(\xi, \lambda) + O(\varepsilon) \\ O(\varepsilon^2) \\ O(\varepsilon^2) \end{bmatrix}$$

where the $O$ terms hold uniformly on $\mathbb{R}^+$.

It follows from Proposition 6.1 and the form of the stable fibers (6.7) that there are solutions in $S_\lambda^+$ that at $\xi = 0$ have the form

$$Y_{f,1}^+(0;\lambda) = \begin{bmatrix} \phi_0^+(0,\lambda) + O(\varepsilon) \\ 1 + O(\varepsilon) \\ O(\varepsilon) \\ \phi_0^{+\prime}(0;\lambda) - b_{12}(0;0) + O(\varepsilon) \\ -\alpha_2 + O(\varepsilon) \\ O(\varepsilon) \end{bmatrix}$$

and

$$Y_{f,2}^+(0;\lambda) = \begin{bmatrix} \phi_0^+(0,\lambda) + O(\varepsilon) \\ O(\varepsilon) \\ 1 + O(\varepsilon) \\ \phi_0^{+\prime}(0;\lambda) + O(\varepsilon) \\ O(\varepsilon) \\ -\alpha_3 + O(\varepsilon) \end{bmatrix}.$$

It is clear that the solutions $Y_s^+(\xi;\lambda)$ and $Y_{f,i}^+(\xi,\lambda)$, $i = 1, 2$ are linearly independent.

A similar argument shows that there is a vector-valued function $Y_s^- \in U_\lambda^-$ such that

$$Y_s^-(\xi,\lambda) = \begin{bmatrix} \phi_0^-(\xi,\lambda) + O(\varepsilon) \\ O(\varepsilon^2) \\ O(\varepsilon^2) \\ \phi_0^{-\prime}(\xi,\lambda) + O(\varepsilon) \\ O(\varepsilon^2) \\ O(\varepsilon^2) \end{bmatrix},$$

where $\phi_0^-(\xi,\lambda)$ is the unique solution of

$$\phi'' - \theta_0\phi' + a_0(\xi)\phi = \lambda\phi$$

on $\mathbb{R}^-$ satisfying $\lim_{\xi\to-\infty}(\phi,\phi') = (0,0)$ and $\phi(0) = 1$. Again, the $O$ terms hold uniformly on $\mathbb{R}_-$. Similarly, we can show that there are solutions in $U_\lambda^-$ that at $\xi = 0$ have the form

$$Y_{f,1}^-(0;\lambda) = \begin{bmatrix} \phi_0^-(0,\lambda) + O(\varepsilon) \\ 1 + O(\varepsilon) \\ O(\varepsilon) \\ \phi_0^{-\prime}(0;\lambda) - b_{12}(0;0) + O(\varepsilon) \\ \alpha_2 + O(\varepsilon) \\ O(\varepsilon) \end{bmatrix}$$

and

$$Y_{f,2}^{-}(0;\lambda) = \begin{bmatrix} \phi_0^-(0,\lambda) + O(\varepsilon) \\ O(\varepsilon) \\ 1 + O(\varepsilon) \\ \phi_0^{-\prime}(0;\lambda) + O(\varepsilon) \\ O(\varepsilon) \\ \alpha_3 + O(\varepsilon) \end{bmatrix}.$$

At $\varepsilon = 0$, an easy calculation shows that the Evans function is given by

$$D_0(\lambda) = \det(\Phi_\lambda(0)) = 4 \det \begin{pmatrix} \phi_0^-(0;\lambda) & \phi_0^+(0;\lambda) \\ \phi_0^{-\prime}(0;\lambda) & \phi_0^{+\prime}(0;\lambda) \end{pmatrix} \alpha_2\alpha_3. \tag{6.8}$$

We see that (6.8) only depends on $\lambda$ through the slow solutions; in fact, since

$$\det \begin{pmatrix} \phi_0^-(0;\lambda) & \phi_0^+(0;\lambda) \\ \phi_0^{-\prime}(0;\lambda) & \phi_0^{+\prime}(0;\lambda) \end{pmatrix}$$

is the Evans function for the bistable equation, we see that, up to $O(\varepsilon)$, the Evans function for the full system is just a scalar multiple, independent of $\lambda$ of the corresponding function for the bistable equation. Thus, from an application of the implicit function theorem, we obtain the following result.

PROPOSITION 6.2. *For all sufficiently small* $\varepsilon > 0$, $D_\varepsilon(\lambda) \neq 0$ *for* $\lambda \in \Omega_{M,\beta}\backslash\{0\}$. *Furthermore,* $dD_\varepsilon(\lambda)/d\lambda \neq 0$ *at* $\lambda = 0$.

*Proof of Theorem* 2.2. In light of Propositions 4.4, 5.3, 6.2, and Theorem 4.3, we see that hypotheses (H1) and (H2) hold. The verification of (H3) is given in the Appendix, which then completes the proof of Theorem 2.2. □

**Appendix.** In this section, we verify hypothesis (H3) of Sattinger's theorem. Note that we must only verify estimates (2.6) as $|\lambda| \to \infty$. We base our proof on a regular perturbation argument, the perturbation parameter being $\delta = 1/\sqrt{|\lambda|}$, where we take the negative real axis for the branch cut for the square root function.

Consider

$$(L^\varepsilon - \lambda I)\vec{y} = \vec{g}, \tag{A.1}$$

where $\vec{g} \in BU(\mathbb{R}, \mathbb{C}^3)$. Since we must only prove (2.6) for $|\lambda| \to \infty$, we make the change of scale $x = \sqrt{|\lambda|}\xi$ in (A.1). With this change of scale, (A.1) becomes

$$\ddot{Y} + \mathcal{D}Y = \delta M(x;\varepsilon)\dot{Y} + \delta^2 N(x;\varepsilon)Y + \delta^2\vec{g}, \tag{A.2}$$

where $\dot{} = d/dx$ and $M$, $N$ are related to the matrices $B$, $C$ defined in §4 in an obvious way. Also, $\mathcal{D}$ is a diagonal matrix given by

$$\mathcal{D} = \operatorname{diag}\left\{-\exp[i\arg(\lambda)], -\left(\exp[i\arg(\lambda)] + a_2\frac{\delta^2}{\varepsilon^2}\right), -\left(\exp[i\arg(\lambda)] + a_3\frac{\delta^2}{\varepsilon^2}\right)\right\},$$

where we have set $a_2 = -\eta_2'(n^*)n^*$ and $a_3 = r(n^*)$. From Lemma 4.1 and Theorem 2.1, the matrices $M(x;\varepsilon)$ and $N(x;\varepsilon)$ are $O(1)$ uniformly on $\mathbb{R}$. By assumption (A4) in §2, we see that $a_i > 0$ for $i = 2, 3$.

We will obtain the estimates for (H3) by formulating (A.2) as a fixed-point problem on $BC^1 = \{Y : \mathbb{R} \to \mathbb{C}^3 \mid Y \in C^1$, bounded with bounded first derivatives on $\mathbb{R}\}$. To this end, we need the following lemma, whose proof is left to the reader.

LEMMA A.3. *Let* $\arg(\lambda) \in (-\pi+\gamma, \pi-\gamma)$ *with* $0 < \gamma < \pi/2$ *and* $a \geq 0$. *Consider the scalar equation*

$$\ddot{y} - (e^{i \arg \lambda} + a)y = g \quad \text{on } \mathbb{R}, \tag{A.3}$$

*where* $g \in C(\mathbb{R}, \mathbb{C})$ *is bounded. There is a unique solution of* (A.3) *given by*

$$y(x) = \frac{-1}{2\sqrt{\beta}} \int_{\mathbb{R}} e^{-\sqrt{\beta}|x-y|} g(y) dy, \tag{A.4}$$

*where* $\beta = e^{i \arg \lambda} + a$. *If we denote the linear operator on the right-hand side of* (A.4) *by* $T_\beta$, *then*

$$\|T_\beta g\|_{C^1} \leq \frac{2\|g\|_\infty}{\sin^2(\gamma/2)}.$$

To show that (A.2) has a unique solution, we use the contraction mapping principle. Define the mapping $\mathcal{T} : [BC^1]^3 \to [BC^1]^3$ by

$$\mathcal{T}(\vec{f})(x) = \begin{pmatrix} T_{d_{11}} f_1(x) \\ T_{d_{22}} f_2(x) \\ T_{d_{33}} f_3(x) \end{pmatrix},$$

where $T_{d_{ii}}$ is the operator given in Lemma A.1 with $\beta$ replaced by the $i$th diagonal element of $\mathcal{D}$, $d_{ii}$. Now, for fixed $\vec{g} \in [BC^0]^3$, let $\mathcal{R} : [BC^1]^3 \to [BC^1]^3$ be the operator

$$\mathcal{R}(Y; \vec{g}) = \mathcal{T}\big(\delta M(\,\cdot\,; \varepsilon)\dot{Y} + \delta^2 N(\,\cdot\,; \varepsilon)Y + \delta^2 \vec{g}\big).$$

It is easy to see that $Y$ is a solution of (A.2) if $Y$ is a fixed point for the map $\mathcal{R}$. Furthermore, it follows from Lemma A.1 and the fact that the matrices $M$ and $N$ are uniformly $O(1)$, that $\mathcal{R}$ is a uniform contraction mapping on $[BC^1]^3$ for sufficiently small $\delta$ and thus has a unique fixed point by the contraction mapping principle. If $Y$ denotes this fixed point, then we can show that

$$\|Y\|_{C^1} \leq K_1 \frac{\delta^2}{\sin^2(\gamma/2)} \|\,\vec{g}\,\|_\infty, \tag{A.5}$$

where $K_1$ is independent of $\delta$ and $\varepsilon$, provided that $\delta$ is sufficiently small.

Note that the sup-norms in (A.5) are with respect to the independent variable $x$, thus, in terms of the variable $\xi$, we see that

$$\|Y\|_\infty \leq K_1 \frac{\delta^2}{\sin^2(\gamma/2)} \|\,\vec{g}\,\|_\infty \tag{A.6}$$

and

$$\|Y\|_{C^1} \leq K_1 \frac{\delta}{\sin^2(\gamma/2)} \|\,\vec{g}\,\|_\infty. \tag{A.7}$$

Recalling that $\delta = 1/\sqrt{|\lambda|}$, we see that estimates (2.6) follow.

## REFERENCES


[1] J. Alexander, R. Gardner, and C. Jones, *A topological invariant arising in the stability analysis of travelling waves*, J. Reine Angew. Math., 410 (1990), pp. 167–212.

[2] D. G. Aronson and H. F. Weinberger, *Nonlinear diffusion in population genetics, combustion and nerve propagation*, in Partial Differential Equations and Related Topics, J. Goldstein, ed., Lecture Notes in Math., 446, Springer-Verlag, Berlin, New York, 1975, pp. 5–49.

[3] E. Coddington and N. Levinson, *Theory of Ordinary Differential Equations*, McGraw–Hill, New York, 1955.

[4] C. Conley and P. Fife, *Critical manifolds, travelling waves and an example from population genetics*, J. Math. Biol., 14 (1982), pp. 159–176.

[5] J. Dockery and R. Lui, *Existence of travelling wave solutions for a bistable evolutionary ecology model*, SIAM J. Math. Anal., 23 (1992), pp. 870–888.

[6] D. Henry, *Geometric Theory of Semilinear Parabolic Equations*, Lecture Notes in Math., 840, Springer-Verlag, Berlin, New York, 1981.

[7] J. W. Evans, *Nerve axon equations* IV: *The stable and unstable impulse*, Indiana Univ. Math. J., 24 (1975), pp. 1169–1190.

[8] N. Fenichel, *Geometric singular perturbation theory for ordinary differential equations*, J. Differential Equations, 31 (1979), pp. 53–89.

[9] P. C. Fife, *Mathematical Aspects of Reacting and Diffusing Systems*, Lecture Notes in Biomath., 28, Springer-Verlag, Berlin, New York, 1979.

[10] P. C. Fife and J. B. McLeod, *The approach of solutions of nonlinear diffusion equations to travelling front solutions*, Arch. Rational Mech. Anal., 65 (1977), pp. 335–361.

[11] R. A. Fisher, *The advance of advantageous genes*, Ann. Eugenics, 7 (1937), pp. 355–369.

[12] C. Jones, N. Kopell, and R. Langer, *Construction of the FitzHugh–Nagumo pulse using differential forms*, in Patterns and Dynamics in Reactive Media, IMA Volumes in Mathematics and Its Applications, H. Swinney, G. Aris, and D. Aronson, eds., Springer-Verlag, Berlin, New York, 1991, pp. 101–111.

[13] R. Lui, *Stability of travelling wave solutions for a bistable evolutionary ecology model*, Nonlinear Anal., 20 (1993), pp. 11–25.

[14] K. Sakamoto, *Invariant manifolds in singular perturbation problems for ordinary differential equations*, Proc. Roy. Soc. Edinburgh Sect. A, 116 (1990), pp. 45–78.

[15] D. Sattinger, *On the stability of waves of nonlinear parabolic systems*, Adv. Math., 22 (1976), pp. 312–355.

[16] P. Szmolyan, *Transversal heteroclinic and homoclinic orbits in singularly perturbation problems*, J. Differential Equations, 92 (1991), pp. 252–281.