**EXISTENCE OF TRAVELLING WAVE SOLUTIONS
FOR A BISTABLE EVOLUTIONARY ECOLOGY MODEL**

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1. Introduction. Consider the equation

$$(1) \quad u_t = u_{xx} + h(u) \quad \text{in } \mathbf{R} \times [0, \infty)$$

where $h \in C^1[0,1]$, $h(0)=0$ and $h(1)=0$. In 1937, Fisher used this equation with $h(u)=u(1-u)$ to model the spatial spread of an advantageous gene in a population living in a homogeneous one-dimensional habitat [10]. Fisher assumed that the individuals in the population carry a gene that occurs in two forms, A and a. Then there are three genotypes: the homozygotes AA, aa and the heterozygote Aa. Individuals in this population are classified according to which genotype they belong and the fitness of an individual depends entirely on its genotype. Fisher also assumed that the fitness of the heterozygote is between those of the homozygotes which resulted in h having the above form.

In 1975, Aronson and Weinberger studied (1) allowing h to have an intermediate zero, say α , between 0 and 1 [1]. Under such an assumption, there are two additional cases to consider: when $h > 0$ on $(0, \alpha)$, $h < 0$ on $(\alpha, 1)$ and when $h < 0$ on $(0, \alpha)$, $h > 0$ on $(\alpha, 1)$. Aronson and Weinberger called Fisher's model the heterozygote intermediate case, and the above two cases the heterozygote superior and heterozygote inferior case, respectively. These last two cases correspond to the situations when the heterozygotes are more fit and less fit to survive than the homozygotes.

Fisher's model is based on assumption of a highly idealized situation. The authors of this paper are interested in extending the results of Fisher's model to the case when the fitnesses of the individuals also depend on the population size. Equation (1) then becomes a system of reaction-diffusion equations:

$$(2) \quad \begin{aligned} p_t &= p_{xx} + f(p, n)p(1-p), \\ n_t &= n_{xx} + g(p, n)n, \end{aligned}$$

where $0 \leq p \leq 1$ is the frequency of allele A and $n \geq 0$ is the population size. The function $f(p, n) = \eta_A(p, n) - \eta_a(p, n)$ where η_A , η_a represent the average fitnesses of allele A and allele a, respectively. If we denote the fitness of genotypes AA, Aa and aa by $\eta_1(n)$, $\eta_2(n)$ and $\eta_3(n)$, then $\eta_A = p\eta_1 + (1-p)\eta_2$ and $\eta_a = p\eta_2 + (1-p)\eta_3$. The second equation in (2) models the growth and spread of the population. The function g is the specific growth rate and may be thought of as the average fitness of the entire population. Thus $g(p, n) = p\eta_A + (1-p)\eta_a = p^2\eta_1 + 2p(1-p)\eta_2 + (1-p)^2\eta_3$. We have the following important relation:

$$(3) \quad \frac{\partial g}{\partial p}(p, n) = 2f(p, n).$$

For more details of the model, the reader is referred to [11].

The mathematical theory of (1) is very rich and well understood. One of the most intriguing properties of (1) is the existence of travelling waves. A travelling wave solution

of (1) with speed θ is a non-constant function $\tilde{u}(z)$ such that $\tilde{u}(x + \theta t)$ satisfies (1) for all x and $t > 0$. In the heterozygote intermediate case, it is known that there exists $\theta^* > 0$ such that increasing travelling wave $\tilde{u}$ exists with the properties that $\tilde{u}(-\infty) = 0$, $\tilde{u}(\infty) = 1$ if and only if $\theta \geq \theta^*$. For the heterozygote inferior case, if $\int_0^1 h > 0$, then there exists $\theta^* > 0$ such that increasing travelling wave solutions connecting 0 and 1 exist if and only if $\theta = \theta^*$. For the heterozygote superior case, since 0 and 1 are unstable solutions of the o.d.e. $u' = h(u)$, there does not exist any travelling wave connecting 0 to 1.

For the system (2), it turns out that under appropriate assumptions on f and g , the model may be classified into four cases: the first and second heterozygote intermediate cases, the heterozygote superior case and the heterozygote inferior case [11]. The existence and stability of travelling wave solutions for the second intermediate case has been proved in [12].

In this paper, we consider the heterozygote inferior case. In [13], the existence and stability of travelling wave solutions in the special case when $\eta_1 - \eta_2$ and $\eta_3 - \eta_2$ each equals a positive constant was studied. In this paper, we use a continuation argument to prove the existence of travelling wave solutions for the general case.

An outline of the paper is as follows: The assumptions on f and g as well as the existence result are given in the next section. Our method of proof is based on the connection index from the Conley index theory. For the sake of completeness, we have provided a brief description of this index in section 3. The computation of the connection index as well as the proof of our theorem are given in section 4. To compute the connection index, we continue the original problem to a problem where the computation is much easier. In the last section, we provide a specific example and show that one can easily follow the above mentioned continuation method numerically.

2. Hypotheses and Result. We assume the following about f and g :

(A1) f and g are C^1 in p and n with $\partial f / \partial n > 0$, $\partial f / \partial p > 0$, $\partial g / \partial n < 0$ and relation (3) holds.

(A2) The curves $f = 0$ and $g = 0$ intersect only at (p^*, n^*) in the region $Q \equiv \{(p, n) | 0 < p < 1 \text{ and } n > 0\}$ with $p^* \in (0, 1/2)$, $n^* > 0$ and

$$(4) \quad \int_0^1 f(p, n^*) p(1 - p) dp > 0.$$

(A3) The curve $g = 0$ intersects the line $p = 0$ at K_3 and the line $p = 1$ at K_1 with $0 < K_3 < K_1$. We also assume that

$$\int_0^{p^*} f(p, K_3) p(1 - p) dp < 0.$$

The form of the nullclines, $f(p, n) = g(p, n) = 0$, are shown in Figure 1.

It is obvious that the constant solutions of (2) in $cl(Q)$ are $(0, 0)$, $(1, 0)$, (p^*, n^*) , $(0, K_3)$ and $(1, K_1)$. One easily checks that assumption (A1) implies that the first three solutions are unstable and the last two solutions are stable for the system (2) without diffusion.

By a travelling wave solution of (2) with speed θ , we mean a nonconstant, bounded solution $(\tilde{p}, \tilde{n})$ such that $(\tilde{p}, \tilde{n})(x + \theta t)$ satisfies (2) for all x and $t > 0$. Equivalently, $(\tilde{p}, \tilde{n})$ satisfies the system of ordinary differential equations,

$$(5) \quad \begin{aligned} p'' - \theta p' + f(p, n)p(1 - p) &= 0, \\ n'' - \theta n' + g(p, n)n &= 0, \end{aligned}$$

on $\mathbf{R}$ where $' = d/dz$. As in the case of a single equation, we look for a travelling wave solution of (2) which connects the two stable equilibria $(0, K_3)$ and $(1, K_1)$, i.e., $(\tilde{p}, \tilde{n})$ satisfies the boundary conditions:

$$(6) \quad \begin{aligned} \lim_{z \rightarrow -\infty} (p(z), n(z)) &= (0, K_3), \\ \lim_{z \rightarrow \infty} (p(z), n(z)) &= (1, K_1). \end{aligned}$$

Under the hypotheses (A1-A3) we can prove:

THEOREM 2.1. *There exists a positive wave speed θ such that (5) has a solution $(\tilde{p}, \tilde{n})$ which satisfies (6). Furthermore, $\tilde{p}' > 0$ while $\tilde{n}$ has at most one local minimum on $\mathbf{R}$.*

The proof of Theorem 2.1 is based on the connection index theory. For the sake of completeness, we give a brief description of this theory in the next section.

3. The connection index. The connection index was developed in [3] to study connection problems for one-parameter families of flows where it is not expected that connecting orbits exist for values of the parameter belonging to an entire interval. Our problem of finding travelling wave solutions is such a problem; we need to find the wave speed parameter θ so that (5) has a solution connecting the two stable equilibria $Y_3 = (0, K_3)$ and $Y_1 = (1, K_1)$. If we write (5) as a first order system, then a connection from Y_3 to Y_1 means that the stable manifold at the rest point $(p, p', n, n') = (0, 0, K_3, 0)$ and the unstable manifold at the rest point $(1, 0, K_1, 0)$ intersect. One easily checks that the dimension of both manifolds are two. In $\mathbf{R}^4$, these manifolds do not intersect transversely, implying that connection cannot exist for θ belonging to an interval. It follows that a homotopy invariant index cannot be used to detect such an intersection since if so, all near by flows would also have such an intersection.

The idea behind the connection index is to add the equation $\theta' = 0$ to the original system. This increases the dimensions of the stable and unstable manifolds, now center-stable and center-unstable manifolds, by one. Since the flow is now on $\mathbf{R}^5$ and since two

three-manifolds intersect transversely in this space, there is a chance that a homotopy index theory could detect such an intersection. The connection index was developed for this purpose.

In this section we will provide a cursory description of this index and refer the reader to [3, 4, 8] for the details as well as applications to similar problems. Before we describe the connection index, we recall some of the basic ingredients from the Conley index theory [2].

3.1. The Conley index. Consider a flow that is defined by an autonomous system of differential equations on $\mathbf{R}^n$. Suppose $N \subset \mathbf{R}^n$ is compact. Let $I(N)$ denote the set of all orbits of this flow that remain in N for all time. If $S = I(N)$ is interior to N , then S is said to be an isolated invariant set and N an isolating neighborhood. It is clear that a compact set N is an isolating neighborhood for S if every orbit which hits the boundary of N eventually leaves N in either forward or backward time and if no orbits in S get arbitrarily close to the boundary of N .

DEFINITION 1. *Let S be an isolated invariant set with isolating neighborhood N . An index pair for S is a pair of compact sets (N_1, N_0) with $N_0 \subset N_1 \subset N$ such that:*

- (i) *$cl(N_1 \setminus N_0)$ is an isolating neighborhood for S .*
- (ii) *N_i is positively invariant relative to N for $i=0,1$, i.e., given $x \in N_i$ and $x \cdot [0, t] \subset N$, then $x \cdot [0, t] \subset N_i$.*
- (iii) *N_0 is an exit set for N_1 , i.e. if $x \in N_1$, $x \cdot [0, \infty) \not\subset N_1$, then there is a $T \geq 0$ such that $x \cdot [0, T] \subset N_1$ and $x \cdot T \in N_0$.*

Given an index pair, the Conley (homotopy) index of S is defined to be the homotopy type of the pointed space N_1/N_0 obtained by collapsing N_0 to a point. This homotopy index is well defined (see, e.g. [2]) and depends only on the invariant set S . We shall denote the Conley index of S by $h(S)$.

The easiest example is when $S = \emptyset$, the empty set. Then one can take $(\emptyset, \emptyset)$ to be the index pair. On collapsing the empty set to a point, one obtains a pointed one-point space. The homotopy type of this space, hence $h(\emptyset)$, is denoted by $\bar{0}$. If S is a hyperbolic rest point for the flow with a k -dimensional unstable manifold, then $h(S) = \Sigma^k$, the homotopy type of a pointed k -sphere.

An important property of the index is the sum formula. The sum of two pointed spaces (A, a) and (B, b) is defined as $A \cup B / \{a, b\}$, the pointed space obtained by taking the union of A and B and identifying the distinguished points a and b . This sum is denoted by $(A, a) \vee (B, b)$. If S_1 and S_2 are two isolated invariant sets with $S_1 \cap S_2 = \emptyset$, then it can be shown [2] that $h(S_1 \cup S_2) = h(S_1) \vee h(S_2)$. Furthermore, $\bar{0}$ acts as the additive identity, i.e., $\bar{0} \vee h(S) = h(S)$ for any isolated invariant set S .

One can also define the product of two pointed spaces (see, e.g. [2]). If S_1 and S_2 are isolated invariant sets for the two flows $x' = f(x)$ and $y' = g(y)$, respectively, then $S_1 \times S_2$ is an isolated invariant set for the product flow. The index of $S_1 \times S_2$ is given by $h(S_1 \times S_2) = h(S_1) \wedge h(S_2)$ where $\wedge$ is the smash product. For pointed spheres, one

has $\Sigma^m \wedge \Sigma^n = \Sigma^{m+n}$ for all m and $n \geq 0$. Furthermore, $\bar{0} \wedge h(S) = \bar{0}$.

Finally, the Conley index also has the continuation property which allows one to compute the index easily in many situations. If S_0 is an isolated invariant set with isolating neighborhood N and we continuously deform the flow so that N remains an isolating neighborhood throughout. Then the index of $I(N)$ after the deformation and the index of S_0 are the same.

The Conley index can often be used to find heteroclinic orbits, that is, orbits that connect distinct rest points of the flow. (A rest point is a point where the flow is invariant.) Suppose S_1 and S_2 are distinct rest points and N is an isolating neighborhood containing both. If it can be shown that $h(S_1) \vee h(S_2) \neq h(I(N))$, then by the sum formula, there must be another orbit in N besides the two rest points. Often, by proper choice of the isolating neighborhood, one can conclude that this orbit is a heteroclinic orbit connecting the two rest points. If one proves the existence of heteroclinic orbit by this method, then since the index is homotopy invariant, it would follow that there is a heteroclinic connection for all near-by flows since they are homotopic to each other. For our travelling wave problem, this is not expected. This brings us to a modification of the Conley index which can be used in this case, namely the connection index.

3.2. The connection index. Suppose that a one-parameter family of flows on $\mathbf{R}^n$ is given by

$$(7) \quad x' = f(x, \theta),$$

where f depends continuously on $\theta \in [\theta_1, \theta_2]$. By appending the equation

$$(8) \quad \theta' = 0,$$

to this, we obtain a flow on $X = \mathbf{R}^n \times [\theta_1, \theta_2]$. Let S , S' and S'' be isolated invariant sets for this product flow on X . We let S_{θ_0} etc. denote the $\theta \equiv \theta_0$ slice of S .

DEFINITION 2. *The triple (S, S', S'') is called a connection triple if:*

- (i) $S' \cup S'' \subset S$,
- (ii) $S' \cap S'' = \emptyset$,
- (iii) $S_{\theta} = S'_{\theta} \cup S''_{\theta}$ for $\theta = \theta_1$ and θ_2 .

A homotopy invariant index can be defined for connection triples [4]. We will denote the connection index by $\bar{h}(S, S', S'')$ as it only depends on the connection triple (S, S', S'') . It is defined by modifying the trivial flow $\theta' = 0$ in the neighborhoods of S'_{θ_i} and S''_{θ_i} for $i = 1, 2$. If N is an isolating neighborhood for S in the original flow, then N remains an isolating neighborhood for the modified flow. The connection index $\bar{h}$ is then defined to be $h(I(N))$ where $I(N)$ is the maximal invariant set in N for the modified flow. Since $\bar{h}$ is the Conley index for the modified flow, it has similar properties; in particular $\bar{h}$ is invariant under continuation and there is a corresponding product formula for $\bar{h}$.

Our proof of Theorem 2.1 relies on the following result in [4]:

THEOREM 3.1. *Suppose (S, S', S'') is a connection triple and $S = S' \cup S''$. Then $\bar{h}(S, S', S'') = (\Sigma^1 \wedge h(S')) \vee h(S'')$ where $h(S')$ and $h(S'')$ are the Conley indices for the flow generated by (7-8) on X .*

The way we shall use this result is as follows: If $\bar{h}$ can be shown to be different from $(\Sigma^1 \wedge h(S')) \vee h(S'')$, then $S \neq S' \cup S''$. Thus there is a $\theta \in (\theta_1, \theta_2)$ for which $S_\theta \not\subset S'_\theta \cup S''_\theta$. For us, S'_θ and S''_θ will be the rest points and so this would imply that there is another orbit in N_θ besides the two rest points. By our construction of the isolating neighborhood, it will follow that the only other orbit in N_θ is a heteroclinic connection.

The way we show that $\bar{h}$ is different from $(\Sigma^1 \wedge h(S')) \vee h(S'')$ is to compute $\bar{h}$, $h(S')$ and $h(S'')$ via a continuation argument. Suppose the above flow on X is parametrized by another parameter $\lambda \in [0, 1]$. When $\lambda = 0$, the flow is easy to analyze and when $\lambda = 1$, we recover our original flow. Let $Y = X \times [0, 1]$ with the obvious flow defined on Y and let S_0 and S_1 be isolated invariant sets for the flows on X corresponding to $\lambda = 0$ and $\lambda = 1$, respectively. Then S_0 and S_1 are said to be related by continuation if there is an isolating neighborhood N for the flow on Y such that $S_0 = I(N(0))$ and $S_1 = I(N(1))$. (Note that if N is an isolating neighborhood, then so is $N(\lambda)$.) According to §3.1, $h(S_0) = h(S_1)$. Presumably, $h(S_0)$ is easier to compute than $h(S_1)$. Similarly, we can define a continuation of connection triples. Suppose S', S'', S''' are isolated invariant sets for the flow on Y and suppose for each λ , $(S'(\lambda), S''(\lambda), S'''(\lambda))$ is a connection triple. Then the connection triples at $\lambda = 0$ and at $\lambda = 1$ are related by continuation and have the same connection index. The connection index at $\lambda = 0$ is easier to compute than that at $\lambda = 1$.

We now give an intuitive idea of how to compute the connection index [8]. Let N be a compact neighborhood of S in $\mathbf{R}^{n+1}$ such that N_θ is an isolating neighborhood of S_θ for each $\theta \in [\theta_1, \theta_2]$. Let $N^2 \subset N$ be such that (N_θ, N_θ^2) is an index pair for S_θ for each θ . Finally, let $\hat{N}^2$ be N^2 unioned the closure of all orbit segments in N_{θ_i} which tend to S'_{θ_i} in backward time for $i = 1, 2$. The connection index $\bar{h}(S, S', S'')$ is defined to be the homotopy type of the pointed space $N/\hat{N}^2$. The description above is with respect to the modified flow in order that $N/\hat{N}^2$ be a true index pair. From this description we also see that the order in the triple is important.

By way of example, consider the following system of equations,

$$u' = v,$$

$$v' = \theta v - u(1 - u)(u - u^*)$$

where $\theta > 0$ and $u^* \in (0, 1/2)$. This is the bistable equation which has an increasing travelling wave solution connecting $(u, v) = (0, 0)$ to $(1, 0)$ for a positive wave speed $\theta = \theta^*$. The points $(0, 0)$ and $(1, 0)$ are saddles for all values of θ while $(u^*, 0)$ changes from an unstable spiral to an unstable node as θ increases, say from θ_1 near zero to

$\theta_2 > \theta^*$. The phase plane diagram for the two values of θ are shown in Figures 2 and 3 below. An isolating neighborhood is also shown where the exit set is marked. Let N denote this set cross $[\theta_1, \theta_2]$. Then N is an isolating neighborhood for the flow defined above and $\theta' = 0$. Up to homotopy, N is a ball in $\mathbf{R}^3$. Let $S = I(N)$, $S' = (0, 0) \times [\theta_1, \theta_2]$ and $S'' = (1, 0) \times [\theta_1, \theta_2]$. Then (S, S', S'') is a connection triple. To calculate its index, we must find the homotopy type of the pointed space $N/\hat{N}^2$ where $\hat{N}^2$ is defined above. Now the exit set at θ_i , $i=1,2$, consists of three disjoint parts and two of these parts are connected to the unstable manifold at S'_{θ_i} . Therefore, $\hat{N}^2$ is contractable to a point on the surface of the ball. Thus $N/\hat{N}^2$ is homotopy equivalent to the one-point space, or $\bar{0}$. The connection index is $\bar{0}$ for this example.

4. Proof of Theorem. In this section we will give a proof of Theorem 2.1. We will use the connection index to show the existence of travelling waves. It is difficult to compute this index for the original model, so we homotopy the model to a system for which the connection index is easy to compute.

4.1. The Homotopy. We will use the following homotopy:

$$(9) \quad \begin{aligned} p'' - \theta p' + f^\lambda(p, n)p(1-p) &= 0, \\ n'' - \theta n' + g^\lambda(p, n)n &= 0, \end{aligned}$$

where $f^\lambda(p, n) = \lambda f(p, n) + (1-\lambda)(p - p^*)$, $g^\lambda(p, n) = \lambda g(p, n) + (1-\lambda)(n^* - n)$, and where (p^*, n^*) is the intersection of the curves $f = 0$ and $g = 0$ (see fig. 1). For $\lambda = 1$ we recover the original model while at $\lambda = 0$, (9) decouples. The first equation is the bistable equation:

$$(10) \quad p'' - \theta p' + p(1-p)(p - p^*) = 0,$$

and the second equation is the Fisher equation:

$$(11) \quad n'' - \theta n' + n(n^* - n) = 0.$$

Since $p^* \in (0, 1/2)$, it is well known that (10) has a monotone travelling wave solution connecting $p = 0$ to $p = 1$ for some unique $\theta > 0$.

It is easy to check that except for relation (1.3) conditions (A1) to (A3) of Section 2 hold for the functions f^λ and g^λ with K_i replaced by K_i^λ for $i = 1, 3$. We define K_i^λ by $g(0, K_3^\lambda) = 0$ and $g(1, K_1^\lambda) = 0$. The nullclines $f^\lambda = 0$ and $g^\lambda = 0$ are similar in form to the nullclines $f = 0$ and $g = 0$, respectively. In fact the curve $f^\lambda = 0$ lies between $f = 0$ and the vertical line $p = p^*$ while the curve $g^\lambda = 0$ lies between $g = 0$ and the horizontal line $n = n^*$. They intersect only at (p^*, n^*) .

It is convenient to write (9) as a first order system:

$$\begin{aligned}
(12) \quad p' &= v_1, \\
v_1' &= \theta v_1 - f^\lambda(p, n)p(1-p), \\
n' &= v_2, \\
v_2' &= \theta v_2 - g^\lambda(p, n)n.
\end{aligned}$$

For each θ and λ , (12) defines a flow on $\mathbf{R}^4$. The rest points are $Y_1^\lambda = (1, 0, K_1^\lambda, 0)$, $Y^* = (p^*, 0, n^*, 0)$, $Y_3^\lambda = (0, 0, K_3^\lambda, 0)$, $(1, 0, 0, 0)$ and $(0, 0, 0, 0)$. We seek a solution of (12) which connects Y_3^λ to Y_1^λ . For the rest of this section we frequently refer to an orbit or a maximal invariant set meaning that it is so for the flow (12) where $\lambda \in [0, 1]$.

4.2. The Isolating Neighborhood. In order to use the connection index we need to find a set N , independent of θ and λ , that will be an isolating neighborhood for the flow (12) and contains the desired connecting orbit for all $\lambda \in [0, 1]$. The only rest points in this isolating neighborhood will be Y_1^λ and Y_3^λ , p will be monotone increasing along any nonconstant orbit which remains in this neighborhood.

First we choose K^+ and K^- so that $0 < K^- < K_1^\lambda, K_3^\lambda < K^+$ for all $\lambda \in [0, 1]$. We assume that K^+ and K^- are chosen so that the curve $f = 0$ intersects the line $p = 0$ above K^+ and intersects the line $p = 1$ below K^- . Let $A_0 = \{(p, n) \mid 0 \leq p \leq 1 \text{ and } K^- \leq n \leq K^+\}$ (see fig.4).

If $Y(z) = (p(z), v_1(z), n(z), v_2(z))$ is a solution of (12) with $\theta \geq \theta_0 > 0$ and $-1 \leq p(z) \leq 2$, $K^- \leq n(z) \leq K^+$ for all $z \in \mathbf{R}$, then $|v_i| \leq L$ for $i = 1, 2$. To see this, choose C such that $|f^\lambda(p, n)p(1-p)|$ and $|g^\lambda(p, n)n|$ are bounded above by C for all $\lambda \in [0, 1]$ and above values of p, n and define $L = C/\theta_0$. Suppose $v_1(z_0) > L$. Then from (12), $v_1'(z_0) > 0$ which implies that $v_1(z) > L$ for all $z \geq z_0$. This contradicts the assumption that p is bounded. The proof for the other cases are similar.

Let $N_0 = \{(p, v_1, n, v_2) \mid (p, n) \in A_0, 0 \leq v_1 \leq L \text{ and } |v_2| \leq L\}$. It is clear that N_0 cannot be an isolating neighborhood since the rest points Y_1^λ, Y_3^λ and Y^* are contained in the boundary of N_0 . We need to add to N_0 neighborhoods of Y_1^λ and Y_3^λ and remove a neighborhood of Y^* to obtain an isolating neighborhood.

To add a neighborhood of Y_3^λ , let $A_3 = \{(p, n) \mid |p| \leq \delta, K^- \leq n \leq K^+\}$ where δ is independent of λ . By assumption (A1) we can choose $\delta > 0$ small enough so that the curve $g^\lambda(p, n) = 0$ intersects the boundary of A_3 only in the $|p| = \delta$ faces for all $\lambda \in [0, 1]$. We also assume that δ is chosen small enough so that A_3 lies below the curve $f(p, n) = 0$ (see fig. 4). Let $N_3 = \{(p, v_1, n, v_2) \mid (p, n) \in A_3 \text{ and } |v_i| \leq L \text{ for } i = 1, 2\}$. By the choice of L made above, any solution that remains in N_3 for all z can never hit the $|v_1| = L$ or $|v_2| = L$ boundaries of N_3 . The following lemma shows that the maximal invariant set in $N_0 \cup N_3$ is the same as for N_0 .

LEMMA 4.1. $I(N_0 \cup N_3) = I(N_0)$.

Proof. Since $N_0 \subset N_0 \cup N_3$, it is clear that $I(N_0) \subset I(N_0 \cup N_3)$. To see the reverse inclusion, first note that for any orbit $Y(z) \in I(N_0 \cup N_3)$, $n(z)$ must satisfy $K^- < n(z) < K^+$ for all z . To see this, suppose $n(z) = K^+$ at say $z = z_0$. Then in order for $Y(z)$ to remain in $N_0 \cup N_3$ for all z , we must have $v_2(z_0) = 0$ and $v_2'(z_0) \leq 0$. Since $g^\lambda(p, K^+) < 0$ for all $p \in [-\delta, 1]$, (12) implies that $v_2'(z_0) > 0$ which is a contradiction. Therefore $n(z) < K^+$ for all z . A similar argument shows that $n(z) > K^-$.

Next we show that $p(z) \geq 0$ along any orbit in $I(N_0 \cup N_3)$. Suppose p has a negative minimum at z_0 where $v_1(z_0) = 0$ and $v_1'(z_0) \geq 0$. Since for all $p < 0$ and $n \in [K^-, K^+]$, we have $f^\lambda(p, n) < 0$, (12) implies that $v_1'(z_0) < 0$ which is a contradiction. Therefore $p(z) \geq 0$ along orbits in $I(N_0 \cup N_3)$.

Finally we show that $v_1 \geq 0$. Suppose $v_1(z) < 0$ for some z , say $z = 0$. If $v_1(z) < 0$ for all $z < 0$, then $Y(z)$ must tend to a rest point in N_3 as $z \rightarrow -\infty$. There is only one rest point in N_3 , namely Y_3^λ . Since $p(z) \geq 0$ for all z , we must have $p(-\infty) > p(0) \geq 0$ which contradicts the fact that $p = 0$ at Y_3^λ . Therefore it must be the case that $v_1 = 0$ for some $z < 0$. Let z_0 be the first such z , i.e., assume that $v_1(z) < 0$ on $(z_0, 0]$ and $v_1(z_0) = 0$. Hence $v_1'(z_0) \leq 0$. This assumption also implies that $(p(z), n(z)) \in A_3$ for all $z \in [z_0, 0]$ and hence $f^\lambda(p, n) < 0$ at $z = z_0$. From (12), $v_1'(z_0) \geq 0$ and hence $v_1'(z_0) = 0$ and $p(z_0) = 0$. But then the orbit must lie in the invariant manifold $p \equiv 0$, $v_1 \equiv 0$ because of uniqueness which then contradicts the assumption that $v_1(0) < 0$. Therefore it must be the case that $v_1 \geq 0$ along orbit in $N_0 \cup N_3$. This completes the proof of the lemma. $\square$

We add a neighborhood of Y_1^λ in a similar manner. Let $A_1 = \{(p, n) \mid |p - 1| < \delta_1, K^- \leq n \leq K^+\}$. We choose δ_1 independent of λ and sufficiently small so that the curve $g^\lambda(p, n) = 0$ intersects the boundary of A_1 only in the $p = 1 - \delta_1$ and $p = 1 + \delta_1$ faces (see fig. 4). Let $N_1 = \{(p, v_1, n, v_2) \mid (p, n) \in A_1 \text{ and } |v_i| \leq L \text{ for } i = 1, 2\}$. The proof of the following lemma is similar to that of Lemma 4.1 and is omitted.

LEMMA 4.2. $I(N_0 \cup N_1 \cup N_3) = I(N_0)$.

Let $\hat{N} = N_0 \cup N_1 \cup N_3$. $\hat{N}$ is not an isolating neighborhood since Y^* is on its boundary. We will remove a neighborhood of Y^* to obtain an isolating neighborhood. To do this we first show that $v_1 > 0$ along any nonconstant orbit in $I(\hat{N})$.

LEMMA 4.3. *For any orbit $Y(z) \in I(\hat{N})$, $n(z) \geq n^*$ for all $z \in \mathbf{R}$.*

Proof. Suppose n has a local minimum less than n^* at say $z = 0$. Since $g^\lambda = 0$ lies above the line $n = n^*$, the point $(p(0), n(0))$ must lie below the curve $g^\lambda(p, n) = 0$ where $g^\lambda > 0$. This implies that $v_2'(0) < 0$, contradicting the assumption that n has a local minimum at $z = 0$. Therefore n is bounded below by n^* for all z . $\square$

LEMMA 4.4. *Let $\theta > 0$. Then $v_1(z) > 0$ along any orbit in $I(\hat{N})$ except when the orbit is Y^* , Y_3^λ or Y_1^λ .*

Proof. Suppose that $Y(z)$ is an orbit in $I(\hat{N}) = I(N_0)$ with $v_1(z) = 0$ at say $z = 0$. It must be the case that $v_1'(0) = 0$ for otherwise the orbit would leave N_0 in either forward or backward time. From (12), $f^\lambda(p, n)p(1-p) = 0$ at $z = 0$. If $p(0) = 0$ or 1 , then the orbit $Y(z)$ lies in the invariant manifold $p \equiv 0, v_1 \equiv 0$ or $p \equiv 1, v_1 \equiv 0$. In each case, a simple phase plane analysis reveals that the only orbit that lies between K^+ and K^- for all z is the rest point Y_3^λ or Y_1^λ , respectively. Thus we need only consider the case $f^\lambda(p(0), n(0)) = 0$. From Lemma 4.3, the point $(p(0), n(0))$ must lie on or above the curve $g^\lambda(p, n) = 0$ which implies that $p(0) \leq p^*$. If it lies on the curve $g^\lambda(p, n) = 0$ and $v_2(0) = 0$, then $Y(z) \equiv Y^*$. Otherwise, $Y(z)$ must tend to Y_3^λ as $z \rightarrow -\infty$. Clearly, $v_1(z)$ cannot vanish on an open interval in this case. Now multiply the first equation in (9) by $p' = v_1$ and integrate to obtain:

$$(13) \quad \theta \int_{-\infty}^0 (p'(z))^2 dz = \int_0^{p(0)} f^\lambda(p, n(z^{-1}(p)))p(1-p)dp$$

There are two cases to consider: when $n(0) \leq K_3^\lambda$ and when $n(0) > K_3^\lambda$. In the first case, since $n(z)$ cannot have a local maximum at a point above the curve $g^\lambda = 0$, $n(z) \leq K_3^\lambda$ on $(-\infty, 0]$. Therefore, (13) is less than $\int_0^{p^*} f^\lambda(p, K_3^\lambda)p(1-p)dp < 0$ because of assumption (A3) and the discussion in §4.1. This contradicts the assumption that $\theta > 0$. In the second case when $n(0) > K_3^\lambda$, we have $n(z) \leq n(0)$ and $p(z) \leq p(0)$ so that $f^\lambda(p, n) < 0$ for $z < 0$. The right side of (13) is negative, again a contradiction. Therefore it must be the case that $v_1(z) > 0$ along any nonconstant orbit in $I(\hat{N})$. $\square$

It now follows that the only orbit of (12) in $I(\hat{N})$ that hits the boundary of $\hat{N}$ is the constant solution Y^* . To see this, we may assume that the orbit $Y(z)$ lies entirely in N_0 because of Lemma 4.2. By our choice of L , $|v_i| < L$ along the orbit. By the argument given in the proof of Lemma 4.1, the n -component of the orbit cannot hit the $n = K^\pm$ faces of $\partial\hat{N}$. If $Y(z)$ hits the boundary $p = 0$ or $p = 1$ of N_0 , then $v_1 = 0$ also since $Y(z)$ lies in N_0 . According to Lemma 4.4, $Y(z) \equiv Y_3^\lambda$ or Y_1^λ which are in the interior of $\hat{N}$. Finally, if $Y(z)$ hits the boundary $v_1 = 0$ of N_0 and $p \neq 0$ or 1 , then $Y(z) \equiv Y^*$. Hence our assertion at the beginning of the paragraph is proved. We record it as a lemma.

LEMMA 4.5. *If $\theta \geq \theta_0 > 0$, then the only orbit of (12) in $I(\hat{N})$ which hits the boundary of $\hat{N}$ is $Y(z) \equiv Y^*$.*

Finally, we must remove a neighborhood of Y^* . To do this, we use a result of [4] concerning the excision of a portion of an invariant set. Let S be a compact invariant set of a flow and $S_r \subset S$ an isolated set relative to S ; that is, there is a compact relative neighborhood N_r of S_r in S such that $S_r = I(N_r)$. Let $A^+ = A^+(S, S_r)$ be the points on solutions in $S \setminus S_r$ that tend to S_r in forward time. Similarly, let $A^- = A^-(S, S_r)$ be those points which tend to S_r in backward time. A proof of the following lemma can be found in §4 D of [4].

LEMMA 4.6. Suppose $\tilde{N}$ is compact and $S = I(\tilde{N})$. Let $S_r \subset S$ be isolated relative to S and suppose that at least one of the sets A^+ and A^- is empty. Then for all sufficiently small neighborhoods W of S_r in $\tilde{N}$,

$$(14) \quad I(\tilde{N} \setminus W) \cap \partial(\tilde{N} \setminus W) = I(\tilde{N}) \cap \partial\tilde{N} \setminus (S_r \cup A^+ \cup A^-).$$

We will take $\tilde{N}$ to be $\hat{N}$ and S_r the rest point Y^* . In this case, $A^+(I(\hat{N}), Y^*)$ is the component of the stable manifold at Y^* that is contained in $I(\hat{N})$.

LEMMA 4.7. For all $\lambda \in [0, 1]$ and $\theta > 0$, $A^+(I(\hat{N}), Y^*) = \emptyset$.

Proof. First note that if $Y(z)$ is a nonconstant orbit in $I(\hat{N})$, then by Lemma 4.2, $p \in [0, 1]$ and by Lemma 4.4, $v_1(z) > 0$ for all z . Thus the only orbit in A^+ must be a heteroclinic connection from Y_3^λ to Y^* . For $\theta > 0$, there can be no such connection. The proof of this fact uses the same argument as in the second half of the proof of Lemma 4.4 and is omitted. Thus $A^+ = \emptyset$. $\square$

The set $A^-(I(\hat{N}), Y^*)$ is non-empty since it is possible to find a connecting orbit, as for example when $\lambda = 0$, from Y^* to K_1^λ for sufficiently large θ . The unstable manifold at Y^* has dimension three and connecting orbits may be found using a shooting argument (see [12]).

By Lemmas 4.6 and 4.7, for all sufficiently small neighborhoods W of Y^* , we have (14) holding. Since the λ -interval is compact, we can choose a neighborhood W so that (14) holds for all $\lambda \in [0, 1]$. Finally, let $N = \hat{N} \setminus W$.

PROPOSITION 4.8. N is an isolating neighborhood for the flow (12) for each $\lambda \in [0, 1]$ and $\theta \geq \theta_0 > 0$.

Proof. We must show that $I(N)$ is in the interior of N . From (14) and Lemma 4.7, we have

$$I(N) \cap \partial N = I(\hat{N}) \cap \partial\hat{N} \setminus (Y^* \cup A^-).$$

Suppose P belongs to $I(\hat{N}) \cap \partial\hat{N}$. If an orbit in $I(\hat{N})$ hits P in finite time, then by Lemma 4.5, $P = Y^*$. If P is approached by a nonconstant orbit, then by Lemma 4.4, that orbit must connect two of the three rest points Y^* , Y_3^λ and Y_1^λ . It cannot connect Y_3^λ to Y^* because of Lemma 4.7. It cannot connect Y_3^λ and Y_1^λ since neither points are on $\partial\hat{N}$. Hence it must connect Y^* to Y_1^λ in which case $P = Y^*$. Finally, we have to consider the case when there exist orbits $Y_n(z)$ in $I(\hat{N})$ such that $Y_n(z_n) \rightarrow P$ as $n \rightarrow \infty$. By translating, we may assume that the p -component of $Y_n(z)$ satisfies $p_n(0) = \hat{p} \in (0, 1)$. By the Arzela-Ascoli theorem, $Y_n(z)$ converges to an orbit in $I(\hat{N})$. Then depending on whether z_n are bounded or diverge, the limiting orbit either hits P at finite time or approach it as $z \rightarrow \pm\infty$. Therefore, $P = Y^*$. From above, $I(N) \cap \partial N = \emptyset$ which completes the proof of the proposition. $\square$

4.3. The proof of Theorem 2.1 . To prove Theorem 2.1, we first derive aprior bounds on the wave speed θ .

LEMMA 4.9. *There exist $0 < \theta_* < \theta^*$, independent of $\lambda \in [0, 1]$, such that if $(\hat{p}, \hat{n})$ is a nonconstant solution of (9) for some θ with $\hat{p}(z) \in [0, 1]$, $\hat{n}(z) \in [n^*, K^+]$, $\limsup_{z \rightarrow -\infty} \hat{p}(z) < p^*$ and $\liminf_{z \rightarrow \infty} \hat{p}(z) > p^*$, then $\theta \in (\theta_*, \theta^*)$.*

Proof. We only prove the lower bound since the proof for θ^* is similar.

Consider the equation $w_t = w_{xx} + f^\lambda(w, n^*)w(1 - w)$. This is the single bistable equation with $\int_0^1 f^\lambda(p, n^*)p(1 - p)dp > 0$. From §1, this equation has a monotone travelling wave $W^\lambda(z)$ with wave speed θ_*^λ such that $W^\lambda(-\infty) = 0$ and $W^\lambda(\infty) = 1$. Furthermore,

$$\theta_*^\lambda \int_{\mathbf{R}} ([W^\lambda]'(z))^2 dz = \int_0^1 f^\lambda(w, n^*)w(1 - w)dw.$$

This relation implies that θ_*^λ depends continuously on λ since the derivative of W^λ depends on λ uniformly on $\mathbf{R}$.

Now let $u(x, t) = \hat{p}(x + \theta t)$ and $v(x, t) = \hat{n}(x + \theta t)$. Then u satisfies $u_t = u_{xx} + f^\lambda(u, v)u(1 - u)$. From our hypotheses and assumption (A1), $u_t \geq u_{xx} + f^\lambda(u, n^*)u(1 - u)$. Let w satisfy $w_t = w_{xx} + f^\lambda(w, n^*)w(1 - w)$ and the initial condition $w(x, 0) = \hat{p}(x)$. From the maximum principle, $u(x, t) = p(x + \hat{\theta}t) \geq w(x, t)$. From [9] and our hypotheses on $p^*(z)$, there exist positive constants C, μ , and α such that

$$w(x - \theta_*^\lambda t, t) \geq W^\lambda(x - \alpha) - Ce^{-\mu t}$$

for all x and $t \geq 0$. Letting $y = x + (\theta - \theta_*^\lambda)t$, we obtain

$$\hat{p}(y) \geq W(y + (\theta_*^\lambda - \theta)t - \alpha) - Ce^{-\mu t}.$$

If $\theta < \theta_*^\lambda$, then letting $t \rightarrow \infty$ in the above inequality, we obtain $\hat{p}(y) \geq 1$ for all $y \in \mathbf{R}$ which contradicts one of our hypotheses. Thus $\theta \geq \theta_*^\lambda$. If we choose θ_* to be a positive number less than $\min_{\lambda \in [0, 1]}(\theta_*^\lambda)$, we obtain a positive lower bound for θ for all $\lambda \in [0, 1]$. The proof of the lemma is complete. $\square$

We are now ready to apply the connection index theory discussed in §3.2 to prove Theorem 2.1. Let $X = \mathbf{R}^4 \times [\theta_*, \theta^*]$ and $Y = X \times [0, 1]$ with the obvious flow Φ defined on Y . Let N be the set defined near the end of §4.2 with $\theta_0 = \theta_*$. Then Proposition 4.8 implies that $\hat{N} = N \times [\theta_*, \theta^*] \times [0, 1]$ is an isolating neighborhood for the flow Φ . Let $S' = Y_3^\lambda \times [\theta_*, \theta^*] \times [0, 1]$, $S'' = Y_1^\lambda \times [\theta_*, \theta^*] \times [0, 1]$ and $S = I(\hat{N})$. Then S, S', S'' are isolated invariant sets for the flow Φ on Y . We claim that for each λ , $(S(\lambda), S'(\lambda), S''(\lambda))$ is a connection triple. Conditions (i) and (ii) of Definition 3 are obvious and condition (iii) follows from Lemma 4.9 above. According to §3.2, the connection index $\bar{h}(\lambda) = \bar{h}(S(\lambda), S'(\lambda), S''(\lambda))$ is independent of λ . When $\lambda = 0$, (12) uncouples and $(n, v_2) = (n^*, 0)$ is a saddle point for the two dimensional flow

obtained by writing (11) as a first-order system. From the example given in §3.2, $\bar{h}(1) = \bar{h}(0) = \Sigma^1 \wedge \bar{0} = \bar{0}$.

To compute $h(S'(1))$, it is obvious that $S'(0)$ and $S'(1)$ are related by continuation. When $\lambda = 0$, $Y_3^0 = (0, 0, n^*, 0)$ and $Y_1^0 = (1, 0, n^*, 0)$. If we write (10) as a first order system, then $(p, v_1) = (0, 0)$ and $(1, 0)$ are both saddle points. Hence the Conley index $h(S'(1)) = h(S'(0)) = \Sigma^1 \times \Sigma^1 = \Sigma^2$, according to §3.1. Similarly, $h(S''(1)) = \Sigma^2$. Since $(\Sigma^1 \wedge h(S')) \vee h(S'') = \Sigma^3 \vee \Sigma^2 \neq \bar{0} = \bar{h}$ when $\lambda = 1$, Theorem 3.1 implies that there exists θ such that $I(N_\theta)$ contains a nonconstant orbit. From Lemma 4.4, this orbit must be a travelling wave solution connecting Y_3^1 to Y_1^1 with speed θ . Furthermore, p is increasing. Using the fact that $n(z)$ cannot have a maximum above the curve $g(p, n) = 0$ or a minimum below the curve $g(p, n) = 0$, it is easy to see that $n(z)$ can have at most one minimum on $\mathbf{R}$. The proof of Theorem 2.1 is complete.

5. A numerical example. In the previous section we showed how the homotopy invariance of the connection index allowed us to ascertain the existence of a travelling wave solution for the model (2). In this section we show that one can follow this heteroclinic connection for a specific example using numerical continuation techniques.

Recall from the introduction that

$$f(p, n) = p\eta_1 + (1 - 2p)\eta_2 - (1 - p)\eta_3$$

and

$$g(p, n) = p^2\eta_1 + 2p(1 - p)\eta_2 + (1 - p)^2\eta_3.$$

Following [14] we assume that the fitness functions have the form:

$$\eta_i(n) = r_i(1 - n/K_i) \quad \text{for } i = 1, 2, \text{ and } 3.$$

To obtain an example of the heterozygote inferior case we use the values of parameters given in [14]:

i	1	2	3
r_i	0.6	0.7	0.8
K_i	12000	5000	8000

For the numerical computations we have found it convenient to scale n by 10^3 . One easily checks that this corresponds to scaling the K_i 's by 10^{-3} in table given above. Since g is linear in n and quadratic in p one can write down explicit formula for p^* and n^* , further, it is easy to check that the assumptions (A1)–(A3) hold for this model with the parameters given above.

We seek a heteroclinic orbit for (12) connecting Y_3^λ at $z = -\infty$ to Y_1^λ at $z = +\infty$. Here one finds that $K_3^\lambda = (0, 0, n_3^\lambda, 0)$ and $K_1^\lambda = (1, 0, n_1^\lambda, 0)$ where

$$n_i^\lambda = K_i \frac{(1 - \lambda)n^* - \lambda r_i}{(1 - \lambda)K_i - \lambda r_i} \quad \text{for } i = 1 \text{ and } 3.$$

It is easy to show that for each $\theta > 0$, (12) has a 2-dimensional unstable manifold and a 2-dimensional stable manifold at Y_i^λ for $i = 1$ and 3. For this model one can write down explicit expressions for the eigenvalues as well as formula for a set of orthonormal eigenvectors. We will let $\{\phi_3^\lambda, \psi_3^\lambda\}$ denote an orthonormal bases for the unstable tangent space at Y_3^λ and $\{\phi_1^\lambda, \psi_1^\lambda\}$ an orthonormal bases for the stable tangent space at Y_1^λ .

The numerical method used here is similar to the method given in [6]. The approximation is based on the following equations:

$$(15) \quad Y' = TF^\lambda(Y, \theta), \quad \text{for } 0 < z < 1,$$

with the boundary conditions:

$$(16) \quad Y(0) = Y_3^\lambda + \epsilon_3(m_{11}\phi_3^\lambda + m_{12}\psi_3^\lambda), \quad \text{with } m_{11}^2 + m_{12}^2 = 1,$$

and

$$(17) \quad Y(1) = Y_1^\lambda + \epsilon_1(m_{21}\phi_1^\lambda + m_{22}\psi_1^\lambda), \quad \text{with } m_{21}^2 + m_{22}^2 = 1.$$

Here, $F^\lambda(Y, \theta)$ is the vector field on the right hand side of (12) and T is a large positive constant.

Equation (15) is just the differential equation (12) with z scaled by T . The boundary condition (16) is the requirement that the initial value $Y(0)$ lies on the sphere of radius ϵ_3 intersect the linear approximation to the unstable manifold at Y_3^λ . Likewise, (17) implies that $Y(1)$ lies on the sphere of radius ϵ_1 intersect the linear approximation to the stable manifold of Y_1^λ . Here T is the time of travel between these two points for the original unscaled independent variable z . The m_{ij} 's are the projections onto the unstable and stable directions. For T large and ϵ_i 's small, each solution of (15)-(17) represents an approximate heteroclinic connection.

In [6], the parameter T is fixed and the ϵ_i 's are allowed to vary. Since translate of a travelling wave is also a travelling wave, another constraint is needed to fix the phase of the solution. In [6], it was required that the L^2 - norm of the difference between the derivatives of two successive approximations be at a minimum. This requirement takes the form of an integral condition. In the presence of sharp fronts this condition is derived so as to economize the numerical calculations. We have found that for this model it is more economical to simply set $\epsilon_1 = \epsilon_3 \equiv \epsilon$, a fixed positive number, forego the integral constraint and allow T to be a free parameter. Along the solution branch we need to compute for each λ the solution vector Y , the wave speed θ , T and the m_{ij} 's so that the boundary conditions (16)-(17) hold.

To find a starting solution of (15) at $\lambda = 0$ we use $Y(z) = (u(z), u'(z), n^*, 0)$ where

$$u(z) = \frac{\exp(T\sqrt{2}/2(z - 1/2))}{1 + \exp(T\sqrt{2}/2(z - 1/2))},$$

with $\theta = \sqrt{2}(1/2 - p^*)$. It is easy to check that this is a solution of (12) at $\lambda = 0$ connecting Y_3^0 to Y_1^0 . At $\lambda = 0$ we fix $T = 30$ and compute ϵ from the exact solution,

thereafter holding ϵ fixed and allow T to vary. The numerical continuation is computed using the continuation program AUTO [7]. The results of this computation are shown below.

In Figure 5 we have plotted the wave speed θ versus the homotopy parameter λ . In Figure 6 we have plotted the n - component of the solution as a function of z for $\lambda = 0, 1/2$, and 1. We see that n is clearly not monotone at $\lambda = 1$. In the last figure we have plotted the projection of the solutions for $\lambda = 0, 1/2$ and 1 onto the $p - n$ phase plane.

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FIG 1

$$\theta = \theta^1$$

$$\theta = \theta^*$$

$$\theta = \theta^2$$

Fig. 3.

Fig. 4.

FIG. 5. The wave speed θ versus the homotopy parameter λ .

FIG. 6. The n -component of the solution for $\lambda = 0.0, 0.5$ and 1.0 .

FIG. 7. The projection onto the p - n plane of the solution for $\lambda = 0.0, 0.5$ and 1.0 .

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